STUDIES OF VISUOSPATIAL ATTENTION

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

Pseudoneglect (PN) reveals a contralateral bias in the deployment of visuospatial attention by the dominant (right) hemisphere. The magnitude of PN is phasically modulated by transient exogenous visual cues which automatically recruit attention to cued locations. Optimal cue-line onset asynchrony (SOA), cue-contrast of this cueing effect and the relative effectiveness of cue locations relative to line endpoints are unknown. Similarly, the direction of line scanning modulates the tonic bias, although the origin of this modulation is unknown. The present experiments aim at informing theories about visuospatial attention as well as some neurological conditions such as hemispatial neglect. Four experiments were conducted where observers performed a tachistoscopic visual line bisection task. In experiments 1-3, pretransected lines were preceded by peripheral cues delivered to the left and right line ends at a variety of (1) stimulus onset asynchronies (SOAs), (2) contrasts and (3) horizontal positions relative to the line endpoints. Experiment 4 used a tachistoscopic line bisection protocol to manipulate the type (saccadic, smooth pursuit) and direction (leftward, rightward) of attentional scanning, executed with or without eye movements (overt, covert) while performing eye-tracking. Experiment 1 demonstrated early attentional capture with optimal cue-line SOA of 60 ms. Experiment 2 demonstrated that cue contrasts below 12% were ineffective in modulating perceived midpoint and the maximal effect occurred for cues of 100% contrast. Experiment 3 demonstrated modulation of the spatial error resulting from cues at all locations except the one lying completely beyond the line endpoints. Experiment 4 showed that leftward scanning resulted in leftward error and rightward scanning resulted in rightward error. Smooth pursuit scanning was more potent than saccadic scanning. Overt scanning was more potent than covert scanning and overall the strongest effects were found in leftward overt smooth pursuit scanning. Results from the cueing experiments suggest that the mechanisms subserving exogenous attentional capture in line bisection are fast, predominantly parvocellular-mediated and exert their effects at least partially in an object-referenced coordinate system. Experiment 4 suggests attentional magnification of the left line halve where visuospatial attention is deployed asymmetrically ahead of a scanned target.

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CHAPTER I. INTRODUCTION

A. Visuospatial attention

The estimation of the midpoint of visual stimuli by healthy observers is usually characterized by attentional asymmetry, an example of which is the consistent leftward error when judging the midpoint of horizontal lines (Bowers & Heilman, 1980; Caramazza & Hillis, 1990; Di Pellegrino, 1995; Hausmann, Waldie, & Corballis, 2003; Jewel & McCourt, 2000; Kinsbourne, 1970; McCourt, 2001; McCourt, Garlinghouse, & Slater, 2000; McCourt & Olafson, 1997; Mesulam, 1999; Ptak, Schnider, Golay, & Müri, 2007; Sheppard, Bradshaw, Mattingley, & Lee, 2007; Tamietto, et al., 2005; Wolfe, 1923). This asymmetry is not unique to humans; for example, the domestic chick and pigeon are known to display leftward spatial biases when localizing and pecking at food (Diekamp, Regolin, Güntürkün, & Vallortigara, 2005). Similar biases have been described in reptiles (Deckel 1995; Dharmaretnam & Rogers 2005), insects (Kight, Steelman, Coffey, Lucente, & Castillo, 2008) and fish (Dadda, Koolhaas, & Domenici, 2010; Dadda, Zandona, Agrillo, & Bisazza, 2009) performing various spatial tasks. A typical paradigm for exploring behavioral asymmetries consists of a detour task, where observers face an obstacle while the experimenter observes if left or right space is systematically preferred to avoid the obstacle in order to reach a reward. Observers' response choice is usually associated with their lateralization.

In primates, including humans, there is a strong preference for cradling infants on the left side (Bourne & Todd, 2004; Harris, 2010; Harris, Cardenas, Spradlin, & Almerigi 2009; Sieratzki & Woll, 1996). This bias is selective for infant holding and is not consistently found when random objects such as books or bags are held (Harris et al., 2009).

Some theories propose that lateralized behaviors in higher vertebrates are the result of homology, i.e. behavior inherited from a common ancestor (Diekamp et al., 2005). Others link observed lateralization to subtle anatomical asymmetries found in many body organs. Asymmetries in the brain have been linked to adaptive mechanisms like parallel processing (Hopkins & Cantalupo, 2008). Hemispheric separation of the brain allows information to be processed by the two hemispheres in parallel rather than serially which doubles processing capacity. The interhemispheric differences theory is the most widely accepted explanation for the asymmetry observed in spatial behaviors such as the deployment of visual attention. This account states that each hemisphere has specific and complementary functions. Dramatic examples of hemispheric specialization include the nearly universal association of left hemisphere damage with aphasia, and the equally strong specialization of the right hemisphere for the deployment of visuospatial attention.

Generally, attention is difficult to conceptualize. At the neural level, it manifests as series of reversible modulations in the magnitude of neuronal responses to certain events, spaces or objects (Mesulam, 1999). Behavioral manifestations of this neuronal activity include the ability to selectively filter incoming sensory signals, thereby enhancing the processing of some information while excluding other information (Broadbent, 1970; Cherry, 1953; Kahneman, 1973). While this is a manifestation of selective spatial attention, the concept of attention is rather broad. For example, selective attention can be allocated covertly or overtly depending on whether eye movements are executed. Overt attention includes foveation while covert attention is allocated in the absence of eye movements.

Attention can also be endogenous or exogenous (Corbetta, 1998; Nobre, Gitelman, Dias, & Mesulam, 1999; Okubo, Laeng, Saneyoshi, & Michimata, 2010; Posner & Cohen, 1984). Endogenous attentional allocation is voluntary and relatively slow while exogenous attention capture is automatic and relatively fast. Endogenous and exogenous orienting involve the activation of overlapping brain regions (Hunt & Kingstone, 2003; Nobre et al., 2000). However the magnitude of these activations is larger in endogenous compared to exogenous orienting (Nobre et al., 2000). The main brain areas involved with endogenous and exogenous attention are located within parietal and frontal regions (Corbetta, 1998).

Different metaphors have been employed to explain the cognitive mechanisms of spatial attention. For example, space-based attention has been compared to a spotlight that selects areas of space without minding the boundaries between objects. In this account, the spotlight can move around shifting between locations (or objects) but possessing non-flexible edges (LaBerge & Brown, 1989). On the other hand, attention can act as an "intelligent" spotlight with a zoom-lens that adapts its shape, size and focus every time the spotlight illuminates a space or object within the lens' borders (Eriksen & St. James, 1986). Other accounts propose that attention enhances sensory signals by improving spatial resolution. This idea is illustrated by the finding that attention allocated to peripheral stimuli improves processing within these peripheral locations while worsening processing at foveal locations (Yeshurun & Carrasco, 1998). Attention can also act by reducing noise. In conditions of low noise, exogenous attention improves performance by enhancing sensory signals, for example, by increasing contrast sensitivity. However, in high noise conditions, exogenous attention acts by reducing external noise. Endogenous attention then performs signal enhancement (Lu & Dosher, 1998, 2000). The present experiments focused on exogenous and motor factors in the asymmetric allocation of visuospatial attention. Specifically, the aim of this research was to investigate the influences that exogenous cues and oculomotor factors exert on the asymmetric deployment of spatial attention evinced in visual line bisection task.

1. Neural mechanisms of visuospatial attention

The asymmetries observed in visuospatial attention are often attributed to anatomical differentiation between left and right hemispheres. The association between hemispheric asymmetry and behavioral lateralization is not a new idea. More than a century ago, Hall and Hartwell (1884) proposed the idea of a 'dual mind', where there are 'two brains' which create 'two beings'. One brain is always superior to the other and therefore assumes control of most functions. An elaborate theory of interhemispheric competition in the processing of spatial information was later proposed by Kinsbourne (1970) and will be described in a subsequent section.

Asymmetries in visuospatial attention are commonly associated with increased activity within the right hemisphere (Amunts et al., 2007; Bradshaw & Nettleton, 1981; Foxe, McCourt, & Javitt, 2003; Geschwind & Levitsky, 1968; Heilman & Van Den Abell, 1980; Jewel & McCourt, 2000; Luck et al., 1989; Mesulam, 1999; Nicholls, Mattingley, & Bradshaw, 2005; Nicholls, Loftus, Mayer, & Mattingley, 2007; Posner et al., 1984; Rounis et al., 2007). The principal network involved in spatial attention is comprised of fronto-parietal cortical regions. Other regions include the right temporo-parietal junction (TPJ) (Behrmann et al., 2004; Foxe et al., 2003; Kincade et al., 2005; Shulman et al., 2010; Thiel et al., 2004), right posterior parietal (Corbetta, Miezin, Shulman, & Petersen, 1993; Fink, Dolan, Halligan, Marshall, & Frith, 1997; Mohanty, Gitelman, Small, & Mesulam, 2008;

Sapir, d'Avossa, McAvoy, Shulman, & Corbetta, 2005), intraparietal sulcus (Mohanty et al., 2008; Shulman et al., 2010) and other frontal and subcortical structures (Mohanty et al., 2008).

Interhemispheric asymmetries in spatial attention are also found using electroencephalographic (EEG) recordings (Foxe et al., 2003; Heilman & Van Den Abell, 1980), repetitive transcranial magnetic stimulation (rTMS) (Rounis et al., 2007), diffusion-weighted (DW) imaging (Fabiano, Horsfield, & Bakshi, 2005) and functional magnetic resonance imaging (fMRI) (Kim et al., 1999). Studies employing all of these techniques generally reveal increased activity within right hemisphere networks when observers perform tasks requiring the processing of spatial stimuli presented to bilateral visual hemifields, although increased activity is stronger when stimuli are presented within the contralateral hemifield (Heilman & Van Den Abell, 1980; Proverbio, 2004).

Normal observers undergoing rTMS of the right posterior cortex bisect lines rightward of veridical center. Stimulation of the right posterior cortex decreases the attentional capacity allocated towards the left hemispace (Bjoertomt, Cowey, & Walsh, 2002). Additional support for the right hemisphere's superiority in processing spatial stimuli has been provided by analyses of the connectivity between the two hemispheres in healthy observers. When observers judged color changes over a central fixation point while viewing faces unilaterally within the left or right hemispace, MR images demonstrated significantly stronger connections originating from the right hemisphere and crossing into the left hemisphere relative to those crossing from left to right (Siman-Tov et al., 2007). These results were found using a Bayesian framework to analyze brain activity. Another method revealing asymmetries of attentional allocation within the brain involves evaluating the behavioral consequences of attending to certain stimuli.

2. Exogenous cueing in visuospatial attention

As mentioned previously, attention can be allocated endogenously or exogenously. Exogenous cueing paradigms can be employed to study functional asymmetries in the brain. In cueing tasks, the differential processing of unilateral visual stimuli is evaluated. Specifically, stimulus processing relative to no cue conditions can be evaluated after presenting transient exogenous unilateral cues. In exogenous cueing paradigms, a target is presented either in the same or different location where a cue was previously presented. Exogenous cues usually consist of luminance changes, brief flashing letters abruptly presented in the periphery (Marzouki et al., 2007). The cue has no predictive value, in other words, exogenous cues are uninformative regarding target location. In most studies exploring covert exogenous attention using Posner-type (endogenous) cues, observers are instructed to attend to the cued location while maintaining central fixation. Posner (1980) demonstrated RT facilitation when targets were presented in the valid location (indicated by a briefly presented visuospatial cue). Exogenous attention is a bottom-up, externally (stimulus) driven process. Attentional capture resulting from exogenous cues is transient. Exogenous cues capture involuntary attention towards their location producing significant improvement in task performance i.e. improved accuracy and decreased RT. If cue and target are presented in the same location, target detection is usually improved compared to when target is presented at an uncued location (Marzouki et al., 2007). However, task facilitation after valid cueing is dependent upon several factors such as number of stimuli, number of cued locations (Mordkoff, Halterman, & Che, 2008), and whether the cue remains visible or disappears during target presentation (Chen, Moore, & Mordkoff, 2008).

Exogenous spatial attention can be captured by cues even when observers are not aware of the presence of these cues. Although these phenomena are well known, little is understood about the mechanisms underlying these attentional effects. It is hypothesized that attention allocated to the cued region (in an spatiotopic reference frame) or to the cued object (in an allocentric reference frame) increases saliency thus inducing enhanced processing of the attended region (or object).

Attentional capture resulting from valid cues has also been linked to cognitive and motor processes (Rizzolatti, Riggio, Dascola, & Umitá, 1987). In terms of cognitive processes, attentional capture has been associated with defective attentional disengagement from a previously inspected location. When comparing RT to targets in cued and uncued conditions, RT is faster to targets appearing in a validly cued location and slower when targets appear in invalidly cued locations (Posner & Petersen, 1990). An RT cost is also found when responding to invalidly cued targets compared to neutral cue conditions (Mascetti, Nicoletti, Carfagna, Cilia, & Marzi, 2001). Attentional capture by spatial cues has also been linked to specific motor responses such as eye movements. According to the "premotor theory of attention" spatial attention can be allocated only after eye movements have been programmed (Rizzolatti et al., 1987). Supporting evidence for this theory has been provided by evaluation of the deficits of observers suffering from various neurological conditions. Opthalmoplegia, for example, is defined as the congenital inability to execute eye movements in the absence of neurological lesion. When compared to normal observers, no RT facilitation occurs for observers with opthalmoplegia after valid exogenous cueing (Smith, Rorden, & Jackson, 2004). Hemineglect patients (defined in later section titled Hemispatial neglect) experience deficits in the ability to execute exploratory eye movements within the egocentric coordinate frame. Specifically these manifest as deficits in exploration of the contralesional hemispace (Karnath & Fetter, 1995).

Evidence suggesting a disconnection between eye movements and attention, however, has also been illustrated by dysfunction found in patients suffering from hemineglect. Làdavas, Zeloni, Zaccara, and Gangemi (1997) showed that observers suffering from hemineglect experience an intact ability to execute eye movements with inability to attend to contralesional stimuli. When asked to orient to peripheral objects, patients with hemineglect could shift their gaze to exogenously cued stimuli presented contralesionally without having awareness of the stimuli. The conflict posed by the contradicting data regarding eye movements and the allocation of exogenous attention has not been resolved.

a. Neural mechanisms linked to exogenous cueing

Shared bilateral neural mechanisms mediate the allocation of exogenous and endogenous covert attention. Regions within parietal and dorsal-premotor cortices including the frontal eye fields (FEF) are related to the modulation of attentional capture in covert tasks. Moreover, in attentional cueing there are connections between posterior parietal cortex (PPC) and lateral and medial regions within the frontal cortex (Goldman-Rakic, 1988). It is hypothesized that exogenous and endogenous attention are separate processes within the same system (Ries & Hopfinger, 2011). Evidence from fMRI studies has shown that the main difference between the brain activity induced by endogenous and exogenous cues is reflected in the magnitude of the activations, with greater brain activity in response to endogenous cues compared to exogenous cues (Rosen et al., 1999).

Some studies propose separate endogenous and exogenous attentional systems that partially overlap (Bavelier et al., 2002). Hopfinger and West (2006) suggested this separation manifests as differences in the time-course between endogenous and exogenous orienting. There is earlier response to exogenous cueing than for endogenous cueing. Electrophysiological evidence in favor of separate systems includes work by Ries and Hopfinger (2011) demonstrating that exogenous attention is characterized by increased amplitude of the late P1 ERP component. The P1 component in response to exogenous cues is usually generated in the extrastriate cortex with a peak around 150 ms. In contrast, voluntary controlled processes, i.e. endogenous, are characterized by enhanced peak of the N1 component.

There is a link between oculomotor behavior and subcortical structures within the superior colliculus (SC) (Mulckhuyse & Theeuwes, 2010). Specifically the SC has been associated with bottom up attentional capture resulting from exogenous cues. Attended information travels in a feedforward fashion from sensory receptors to areas such as the SC, FEF and parietal cortex. Together these areas are linked to involuntary orienting of attention.

3. Asymmetric distribution of visuospatial attention

Stimuli viewed within left hemifield are more salient than stimuli viewed within right hemifield. Differential saliency has been revealed by studies employing a variety of experimental paradigms. For example, when objects are displayed bilaterally there is better recall for objects in left hemispace compared to right hemispace (Della Sala, Darling, &

Logie, 2010). Additionally, there is left-hemifield advantage when observers select targets presented simultaneously with color-matched distracters in a rapid serial visual presentation (RSVP) task (Du & Abrams, 2010). Pseudoneglect (PN), a phenomenon which will be discussed later in further detail, is also depicted as a left hemifield bias in the estimation of brightness (Mattingley et al., 2004; Nicholls, Bradshaw, & Mattingley, 1999; Nicholls et al., 2005), facial expression (Asthana & Manual, 2001; Bradshaw & Nettleton, 1981; Butler & Harvey, 2005; Everdell, Marsh, Yurick, Munhall, & Paré, 2007; Heller & Levy, 1981; Indersmitten & Gur, 2003; Levy, Heller, Banich, & Burton, 1983; Natale, Gur, & Gur, 1983; Yovel, Levy, Grabowecky, & Paller, 2003), size (Charles, Sahraie, & McGeorge, 2007; McManus & Tomlinson, 2004; Nicholls et al., 1999;), numerosity (Nicholls et al., 1999; Pasini & Tessari, 2001; Piazza, Mechelli, Price, & Butterworth, 2006), mental-number (Fischer, 2001; Loftus et at., 2009; Nicholls, Loftus, & Gevers, 2008) and visual line midpoint (Bowers & Heilman, 1980; Caramazza & Hillis, 1990; Di Pellegrino, 1995; Hausmann, Waldie, & Corballis, 2003; Jewel & McCourt, 2000; Kinsbourne, 1970; McCourt, 2001; McCourt, Garlinghouse, & Slater, 2000; McCourt & Olafson, 1997; Mesulam, 1999; Ptak, Schnider, Golay, & Müri, 2007; Sheppard, Bradshaw, Mattingley, & Lee, 2007; Tamietto, et al., 2005; Wolfe, 1923).

a. Hemispatial neglect

Hemispatial neglect is an anomaly in the distribution of visuospatial attention. Stroke is the most common cause of hemineglect; recent studies based on United States samples demonstrate that over 20% of individuals who suffer a stroke develop hemineglect (Appelros, Karlsson, Seiger, & Nydevik, 2002). The deficits characterizing hemineglect cannot be explained by sensory or motor dysfunction, or by psychiatric conditions. Instead many individuals suffering from hemineglect have intact visual function, and yet fail to locate or even detect stimuli located within the affected visual hemifield, which is overwhelmingly the left (Heilman & Van Den Abell, 1980; Mesulam, 1999).

Hemineglect is characterized by an unawareness of sensory stimuli presented in the hemispace contralateral to the brain lesion (typically right hemisphere) or, alternatively, a hyper-awareness of the stimuli located in the ipsilesional hemispace. Patients suffering from hemineglect are generally unable to orient towards or respond to stimuli located within the affected hemifield; rather they exhibit a tendency to spontaneously orient toward the unaffected hemispace. Hemineglect can occur in multiple spatial frames of reference. It can, for example, be restricted to a particular region of space (peripersonal or extrapersonal), to the body itself, and even to visual imagery. Peripersonal neglect is a deficit of awareness of stimuli (within arm's reach). Extrapersonal neglect refers to a pathological unawareness of stimuli located in space (beyond arm's reach). The most common manifestation of hemineglect is a combination of peripersonal and extrapersonal unawareness of stimuli located contralateral to the associated brain lesion.

The lesions most commonly associated with hemineglect are cerebrovascular accidents affecting PPC. Regions near the temporo-parietal-occipital junction (TPO) as well as inferior parietal regions are also implicated in visuospatial neglect (Corbetta et al., 2005; Foxe et al., 2003; Karnath, 2001; Nobre, 2004). Other areas associated with the mechanisms of hemineglect include frontal and other cortical and subcortical structures of the right brain (Committeri et al., 2007; Corbetta et al., 2005). The finding that left hemisphere lesions rarely result in hemineglect provides supporting evidence for asymmetric spatial processing in the brain. The key differences between the asymmetries in spatial processing found in healthy observers and observers with hemineglect are the magnitude of the asymmetries and the direction of the bias.

b. Pseudoneglect

As early as 85 years ago research began to demonstrate that healthy observers consistently display small but systematic and significant leftward errors in many tasks demanding midpoint judgments (Bowers & Heilman, 1980; Kinsbourne, 1970; Wolfe, 1923). This behavioral bias, now termed Pseudoneglect (PN), has been demonstrated in veridical visual (Bultitude & Aimola Davies, 2006; Jewell & McCourt, 2000; Leone & McCourt, 2010; Loftus, Nicholls, Mattingley, Chapman, & Bradshaw, 2009; MacLeod & Turnbull, 1999; McCourt, 2001; McCourt et al., 2000; McCourt, Garlinghouse, & Reuter-Lorenz, 2005; McCourt & Jewell, 1999; McCourt & Olafson 1997; Nicholls et al., 2005; Nicholls & Loftus, 2007; Porac, Searleman, & Karagiannakis, 2006; Rueckert, Deravanesian, Baboorian, & Lacalamita, 2002; Sosa, Teder-Sälejärvi, & McCourt, 2010) and illusory visual (McGeorge, Beschin, Colnaghi, Rusconi, & Della Salla, 2007) space representation. The behavioral manifestations of PN and hemineglect are spatial biases in opposite directions; hence PN is considered the mirror phenomenon of hemineglect and to share common neural mechanisms. PN is thought to be a normal manifestation of the right hemisphere's specialization for the allocation of spatial attention (Caramazza & Hillis, 1990; Di Pellegrino, 1995; Hausmann et al., 2003; Jewel & McCourt, 2000; McCourt, 2001; McCourt & Olafson, 1997; McCourt et al., 2000; Mesulam, 1999; Ptak, Schnider, Golay, & Müri, 2007; Sheppard et al., 2007; Tamietto, et al., 2005). In human observers PN manifests as early as 10 years of age (Hausmann et al., 2003; Sheppard, Bradshaw, Mattingley, & Lee, 2007; Waldie & Hausmann, 2010) and is of greater magnitude in males compared to females (Brodie, 2010; Jewell & McCourt, 2000).

i. Pseudoneglect in the "Landmark Task"

The landmark task was developed to assess PN. Specifically, the goal of the landmark task is to characterize the differences between perceptual and motor factors in both hemineglect and PN. In this task, observers view a pretransected line and are asked to indicate which line portion is longer (or shorter) or to which line end the transector is nearest (Harvey, Milner, & Roberts, 1995; Olk & Harvey, 2002). Another version of the landmark task requires observers to judge whether or not the line is bisected at veridical midpoint (Çiçek, Deouell, & Knight, 2009). In the landmark task, two indices are calculated that account for biases. The perceptual bias index (PB) calculates constant error across conditions. The response bias index (RB) is an index of response consistency throughout the task (Bisiach, Geminiani, Berti, & Rusconi, 1990; Toraldo, McIntosh, Dijkerman, & Milner, 2004). In the landmark task, observers directly compare the two portions of the line in order to elicit a response. Olk and Harvey (2002) found different cueing effects between VLB and landmark tasks. The performance of neglect patients was compared to a group with a right hemisphere lesion without neglect, and to a group of healthy observers. The three groups performed the VLB and a landmark task when the line ends were cued with letters and when 'invisible' cues were employed. In the invisible cue condition, the experimenter pretended to mark one line end. All three groups of observers showed significant cueing effects in the visible and invisible cue VLB task. However in the landmark task only visible cues were significantly potent at influencing observers judgments suggesting different mechanisms between the two tasks.

ii. Pseudoneglect in visual line bisection task

a.a. Manual method of adjustment

The manual method-of-adjustment visual line bisection task, in which observers indicate the center of drawn lines, results in significant PN (e.g. Caramazza & Hillis, 1990; Di Pellegrino, 1995; Mesulam, 1999; Ptak et al., 2007; Tamietto, et al., 2005). However, this task introduces confounding errors in observers' behavior. Errors in manual bisection are linked to visual scanning direction when observers are allowed to perform unconstrained eye movements though the line (Jewell & McCourt, 2000). Similarly when bisection is performed with the left hand, PN magnitude increases relative to when bisection is performed with the right hand (Brodie, 2010; Brodie & Pettigrew, 1996; Jewell & McCourt, 2000). There is no doubt that visual and motor factors in line bisection tasks introduce intentional biases in observers' behavior although the precise mechanisms of these biases are unknown (MacLeod &Turnbull, 1999; Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Jewel & McCourt, 2000; Kwon et al., 2004; McCourt, 2001; McCourt & Olafson, 1997).

a.b. Tachistoscopic visual line bisection task

Forced-choice Tachistoscopic Visual Line Bisection Task (VLB) was introduced to control for scanning eye movements and other confounding variables affecting the manual visual line bisection task (McCourt & Olafson, 1997). In the forced-choice VLB task, stimuli consisting of pre-transected lines are presented for short durations. Figure 1 illustrates the common stimuli presented in the tachistoscopic visual line bisection task. The experiment involves two-alternative one-interval forced-choice midpoint judgment. Observers are asked to indicate where the line was transected by pressing the appropriate mouse button (L or R). The short line presentation prevents observers from executing saccadic eye movements to explore the line and judge perceived midpoint. In this method, a “point of subjective equality” (PSE) is calculated. The PSE refers to the transector location for which left and right responses occur with equal frequency, i.e. observers’ perceived midpoint. The sign of the obtained PSE specifies direction of bias: negative PSE indicates leftward bias whereas positive values denote rightward bias (Foxe et al., 2003; Jewell & McCourt, 1999; Jewel & McCourt, 2000; McCourt, 2001; McCourt & Olafson, 1997). Hemineglect is usually characterized by positive PSE in VLB, while PN is usually characterized by negative PSE in VLB.

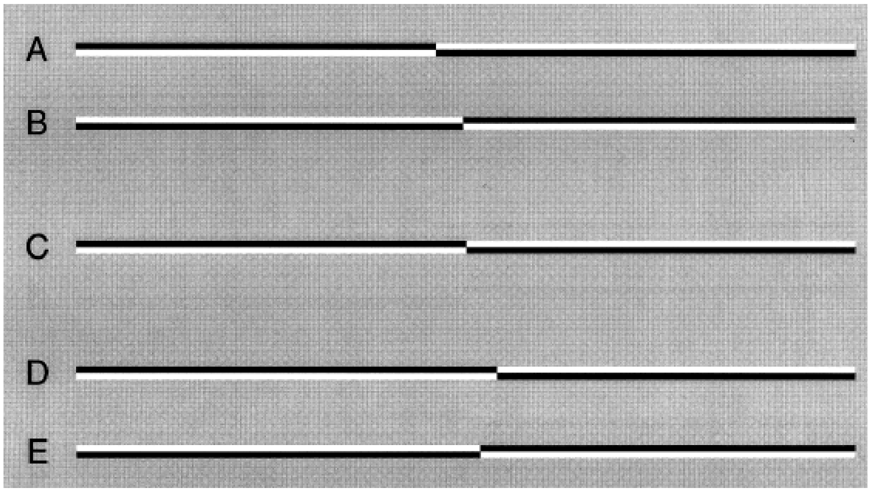

Figure 1. Sample stimuli used in visual line bisection task. Lines A and B are transected left of veridical midpoint, lines D and E are transected right of veridical midpoint and line C is veridically transected (figure reproduced from McCourt & Jewell, 1997).

iii. Asymmetric attentional capture by exogenous spatial cues

The tonic asymmetries of visuospatial attention can be modulated by spatial cues which result in reflexive attention capture to the cued location (Halligan & Marshall, 1989; Harvey, Milner & Roberts, 1995; Marzouki et al., 2007; McCourt et al., 2005;

Mennemeier, Vezey, Chatterjee, Rapcsak & Heilman, 1997; Milner, Brechmann & Pagliarini, 1992; Nichelli, Rinaldi & Cubelli, 1989; Nicholls & McIlroy, 2010; Reuter-Lorenz, Kinsbourne & Moscovitch, 1990; Riddoch & Humphreys, 1983; Singh et al., 2010; Sosa et al., 2011). Greene and Zaidel (2001) found that cues' social relevance increases their salience. These authors demonstrated asymmetric attention capture in the form of RT facilitation for left targets preceded by centrally presented gaze shifts. They found these asymmetric effects for short (150 ms) and long (950 ms) SOAs.

The notion of asymmetric cue potency is consistent with studies evaluating attentional capture by peripheral cues in horizontal visual lines (McCourt et al., 2005; Sosa, Clarke, & McCourt, 2011). Exogenous visual cues presented to the right or left line ends modulate the magnitude of hemineglect (Harvey, Milner, & Roberts, 2005; Mennemeier et al., 1997) and PN (Bultitude & Aimola Davies, 2006; McCourt et al., 2005; Mennemeier et al., 1997; Sosa et al., 2011). In patients with hemineglect and in normal observers, exogenous cues shift perceived midpoint towards the cue location. That exogenous cues capture attention asymmetrically towards their location has been demonstrated using various paradigms. For example, cue location influences outcome in mental number line bisection task. Nicholls and Mcllroy (2010) demonstrated a significant left shift from veridical midpoint when observers judge perceived midpoint of mental number lines. This error was not found for right or bilateral cues, suggesting asymmetric cue influence.

The modulation of the spatial biases in VLB resulting from exogenous cueing is commonly explained by attentional recruitment (Yantis & Jonides, 1990). Attention is automatically recruited to the cued line end and thus increases the saliency of that line portion which in turn results in the perception of a bigger line on the cued end compared to the uncued end. Consequently, perceived line midpoint is shifted in the direction of the cued line end. For example, in hemineglect patients, (who typically demonstrate a rightward bias in perceived line midpoint) cueing the left line end decreases the magnitude of the bias whereas cueing the right line end increases the magnitude of the bias (Halligan & Marshall, 1989; Harvey et al., 1995; Mennemeier, et al., 1997; Riddoch & Humphreys, 1983). In healthy observers, exogenous spatial cues also modulate perceived midpoint by modulating PN magnitude (Harvey et al., 1995; McCourt et al., 2005; Milner, Brechmann & Pagliarini, 1992; Nichelli et al., 1989; Reuter-Lorenz et al., 1990; Sosa, et al., 2011). Attentional capture by cues can also increase the weighting scheme associated with cued locations compared to non-cued locations while maintaining the perceived qualities of the processed object (Eckstein, Shimozaki, & Abbey, 2002). In some instances left cues have a greater influence in VLB than right cues increasing PN magnitude (Sosa et al., 2011). The greater potency of left visual cues is consistent with findings showing that stimuli delivered to the left hemifield possess greater saliency than those delivered to the right hemifield. For example, there is left hemifield advantage for perceived luminance, numerosity and size relative to the right hemifield (Charles et al., 2007; Nicholls et al., 1999). There is also evidence demonstrating that distracters viewed within left hemifield in visual search cause greater interference than those in the right hemifield (Burnham, Rozell, Kasper, Bianco & Delliturri, 2011; Du & Abrams, 2010). However, in other situations where unisensory visual cues precede lines, right cues influence perceived midpoint more than left cues decreasing PN magnitude (McCourt et al., 2005).

c. Theories explaining asymmetric allocation of visuospatial attention

Although the existing literature has focused primarily on the exploration of the anatomical correlates and behavioral manifestations of visuospatial asymmetries, theoretical models have been developed aimed at explaining these asymmetries.

i. Functional asymmetries

<u>There is an imbalance in spatial orienting due to unequal hemispheric functions.</u> Kinsbourne (1970) proposed the activation-orienting imbalance theory which suggests allocation of attention is biased towards the contralateral hemispace of the most active hemisphere. The lateral orienting processes of the two hemispheres are asymmetric such that left and right hemispheres compete for processing by mutual inhibition (Kinsbourne, 1970, 1977). Stimuli presented within one hemispace activate the functioning of the contralateral cerebral hemisphere which in turn inhibits the functioning of the ipsilateral hemisphere. Based on the activation-orienting imbalance theory, hemineglect resulting from right hemisphere lesions can be explained by increased approach behavior to the ipsilateral hemifield (Chen, Erdahl, & Barret, 2009; Kinsbourne, 1977).

<u>There is an imbalance between the engagement and disengagement operations of attention</u>. Posner and Peterson (1990) proposed a three stage theory of spatial attention consisting of 1. disengagement from attended location, 2. movement away from the attended location and, 3. engagement at a new location. In agreement with this theory, Di Pellgrino (1995) suggested that focal brain lesions that affect spatial attention provoking hemineglect, usually impair the engagement and/or disengagement stages of the process. In other words, hemineglect consists of the inability to disengage attention allocated to the ipsilesional visual field and/or the inability to engage attention to the contralesional visual

field. Supporting evidence for this theory comes from patients performing various behavioral tasks such as clock drawing. When copying a clock from a model, hemineglect patients usually place numbers inside the right half of the clock ignoring the clock's left side (Di Pellegrino, 1995). However during spontaneous clock-drawing, most patients are able to label the numbers on a clock from memory with few errors. Di Pellegrino (1995) theorized that a dysfunction in attentional engagement (or disengagement) operations provokes prioritization of information in the ipsilesional hemifield to the detriment of the information presented in the contralesional hemifield. This theory does not, however, account for many of the clinical signs of hemineglect, including the fact that right hemineglect rarely occurs, and left hemisphere lesions rarely result in hemineglect.

ii. Anatomical asymmetries

Spatial asymmetries are the result of structural asymmetries between the left and right hemispheres of the brain. The right hemisphere is specialized for the deployment of spatial attention (tonic difference), regardless of relative hemispheric activation (phasic differences) (Heilman & Van Den Abell, 1980; Mesulam, 1999). The right hemisphere controls for the allocation of attention in left and right hemispaces whereas the left hemisphere only controls attention allocation contralaterally. Because of this differential hemispheric function, lesions to the left hemisphere rarely result in contralateral neglect, because the right hemisphere acts over bilateral hemifields. Contralateral space is neglected after lesions to the right hemisphere while the ipsilesional space is still processed by the left hemispace. Mesulam (1999) proposed that extrapersonal spatial attention is mediated by frontal, parietal and cingulate regions where each one of these regions has specific contributions. The parietal regions contain a spatial map. The cingulate cortex contains motivational and emotional information, while the frontal cortices, especially the FEF modulate motor responses (such as those involved in scanning). These regions process space together with other subcortical structures like the thalamus (Mesulam, 1999).

Categorical and coordinate spatial processing. The mechanisms explaining the relationship between interhemispheric asymmetry and stimulus localizability have been described as a function of coordinate and categorical spatial systems mainly contained within the right and left hemispheres, respectively (Kosslyn, Chabris, Marsolek, & Koenig, 1992). Categorical spatial relationships are those marked by discrete labels such as “above,” “below,” “in,” or “out.” This categorization type allows for assignment of object to specific classes or categories. Coordinate spatial relationships, on the other hand, code spatial relationships in terms of location and distance in a way that guides action and facilitates navigation and movement. Coordinate and categorical systems are theorized to subsume location-encoding within the visual system. Based on this account, patients with focal lesions to the left hemisphere display impaired ability to perform categorical judgments, whereas patients having focal lesions to the right hemisphere display impaired performance in coordinate localization tasks (Bruce & Tsotsos, 2005; Laeng & Peters, 1994). These results suggest that parietal regions within the right hemisphere are primarily (but not exclusively) responsible for processing coordinate representations, while the left hemisphere is the primary locus for processing categorical representations. Frontal regions have also been implicated in the processing of categorical relations (Kosslyn, Thompson, Gitelman, & Alpert, 1998). Given the available data obtained from patients with focal lesions, the areas involved in processing categorical spatial relations are not as well delimited as those involved in processing coordinate spatial relations.

Current evidence suggests that coordinate and categorical spatial systems are critical for processing stimuli's location within the visual world (Kosslyn et al., 1992) and remain intact with normal aging (Meadmore, Dror, & Bucks, 2009). When observers indicate whether a test-dot is located in front of/behind or above/below a reference line where the test-dot is blurred dioptrically using eyeglasses, blur disrupts participants' categorical task performance (Cowin & Hellige, 1994). However, manipulating objects' visual blur does not disrupt observers' ability to process these objects when viewed unilaterally in the left space (Cowin & Hellige, 1994). This segregation has also been found in visual processing of stimuli of various contrasts (Du & Abrams, 2010), suggesting a possible link between categorical processing and parvocellular cells and coordinate processing and magnocellular cells. However, testing these relationships requires finer visual discrimination than observers performed in the described study (Du & Abrams, 2010).

Kosslyn et al. (1992) demonstrated that cells possessing small receptive fields (RF) are linked to categorical judgments while cells with large receptive fields are related to coordinate processing. Yeshurun and Carrasco (1998) further demonstrated that when observers performed a Posner cueing paradigm where the location of one of two figures was cued, the size of the RF was reduced by the allocation of exogenous attention such that at short SOAs (100 ms) categorical judgments were selectively affected. Exogenous cues did not affect coordinate judgments.

Global and local spatial processing. Spatial biases found in normal observers have been associated with segregation of local and global information processing (Bradshaw & Nettleton, 1981; Fagot & Deruelle, 1997; Nicholls, Mattingley, & Bradshaw, 2005). The left hemifield advantage for processing of global information was demonstrated in human and non-human primates performing matching tasks (Fagot & Deruelle, 1997). In these greyscales studies, RT differences showed that whole figures engaged more attentional resources from the right hemisphere compared to segmented figures. There was greater RT to segmented figures than to whole figures. Based on these findings it is reasonable to propose that local spatial processing is a function of the left hemisphere while global spatial processing is a function of the right hemisphere. The judgment of figure segments is suggested to be a more complex process than the judgment of whole figures (Nicholls, Mattingley, & Bradshaw, 2005). The connection of global- and local-visuospatial processing to right and left hemispheres respectively is also linked to low and high spatial frequency processing (Bruce & Tsotsos, 2005). High spatial frequency information is preferentially processed by the left hemisphere, while low spatial frequency information is preferentially processed by the right hemisphere. These dichotomies have been linked to magnocellular and parvocellular visual pathways where global and low spatial frequency information are processed within the magnocellular pathway while local and high spatial frequency information are processed within the parvocellular pathway. Cognitive and computational models have also been proposed to explain the mechanisms underlying asymmetries in visuospatial processing.

iii. Computational

<u>Each hemisphere behaves as an independent attentional system</u> (Anderson, 1996, 2008). Information processed by each hemisphere is selected based on stimulus salience, which is determined by location. Salience maps generally follow Gaussian distributions, where the left hemisphere has a smaller standard deviation than the right hemisphere. The

narrowness of the left hemisphere's salience function is associated with focused allocation of attention to local features while the width of the right hemisphere function is associated with distributed allocation of attention to global features. The asymmetries observed in patients with hemineglect, are the result of changes caused by the lesion in the mean, scaling factor and standard deviation of the original attentional function within the right hemisphere.

Spatial asymmetries found in hemineglect have also been related to a dysfunction of the prior probability estimate (Anderson, 2008). In Bayesian probability theory, healthy observers possess an internal estimate of the likelihood that certain events will occur (prior probability estimate). According to Anderson (2008) patients suffering from HN possess a prior improbability of events occurring within left hemispace. Anderson suggested that in spatial attention tasks, RT is a reflection of the amount of time required to accumulate evidence about the occurrence of an event. Anderson demonstrated that observers suffering from hemineglect exhibit slower average RT and larger variance to stimuli in left hemispace. According to this model, the increased RT shown by hemineglect observers indicates that a dysfunction in the patient's estimate of the prior probability of target appearance occurs such that a larger amount of evidence is needed before observers can respond to stimuli presented within the left hemifield. In summary, anatomical, cognitive and computational models aim at explaining the mechanisms underlying the asymmetries commonly found in visuospatial attention. However, many of these theories rely on evidence from behavioral manifestations of brain trauma leading to hemineglect. How accurately these theories explain the complex dimensions observed in normal visuospatial processing is unclear.

B. The present studies

Overall, when observers are asked to respond to a stimulus after a cue, several factors influence effective attentional capture. For example, attentional capture by exogenous cues is influenced by the onset of the stimulus relative to the cue, i.e. SOA (Fuller & Carrasco, 2009), inter-trial interval, visual clarity of the stimulus and spatial proximity between cue and stimulus. Specifically, in VLB, the cue-line SOA and cue contrast which result in the maximal influence on perceived midpoint have not been determined.

In addition to basic visual and temporal factors influencing attentional capture by cues in VLB, the attentional asymmetry characterizing PN at baseline occurs in several reference frames, e.g., spatiotopic (space-referenced) and allocentric (object-referenced). Whether space-based or object-based mechanisms mediate attentional cue capture in VLB is unknown. To test the impact of temporal, visual and spatial factors of exogenous cues on perceived line midpoint, three experiments were performed in which exogenous cues preceded line stimuli in VLB.

There is presumably also a strong link between eye movements and the allocation of spatial attention. Despite this presumption, few studies have systematically evaluated the mechanisms underlying this effect. Experiment 4 explores motor processes modulating line midpoint judgment by measuring the effects of oculomotor and manual scanning in VLB. In all of the present experiments, shifts in perceived midpoint resulting from spatial cues (experiments 1-3) and scanning (experiment 4) differentially within left and right space will be evaluated as the manifestation of attention modulation. This study is aimed at addressing these lacunas in current knowledge about the mechanisms of normal asymmetric allocation of visuospatial attention.

CHAPTER II. EXPERIMENT 1: TIMECOURSE OF EXOGENOUS CUEING IN VLB

A. Rationale

Müller and Rabbitt (1989) proposed that attentional capture by spatial cues can be linked to two separate processes. In the first process, automatic responses are triggered by the physical properties of cues resulting in transient attentional capture. The second process is caused by a voluntary mechanism. This is slow, sustained and more analytical about the information provided by the cue than the first process. Because the second process is slow, the irrelevant elements located around uncued locations are analyzed and therefore interfere with the processing of the stimuli within the cued location. At long cue-target SOAs the first process, is eliminated, allowing only the second process to occur.

Cues exert motor and perceptual influences. In some instances cue facilitation provokes increased contrast-sensitivity and visual target detection (Bavelier et al., 2002) whereas in other instances, cues' influence on attentional capture is manifested as perceptual illusions. The line-motion illusion (LMI) consists of the perception that a line presented following a cue grows in the opposite direction from the cue, i.e. the line appears to grow from the cue (Bavelier et al., 2002; Fuller & Carrasco, 2009; Hikosaka et al., 1993; Tse, Cavanagh, & Nakayama, 1996). The LMI was first explained by increased processing speed at the attended location, i.e. the cued location. Attention allocated to the cue location results in processing acceleration where the areas in proximity to the attended cue location are processed faster than the areas far from the cue (Hikosaka et al., 1993). Increased processing speed at the attended location in the LMI is linked to accelerated neural responses triggered by stimuli located within the attended location. The LMI can be induced in paradigms using exogenous and endogenous cues because it is not affected by motor factors such as eye movements; however the specific temporal factors that influence the illusion are unknown (Bavelier et al., 2002).

Spatial cues capture attention immediately after their presentation, with a gradually decreasing effect. The temporal proximity between cue and target affects the cue's influence on target detection. Focal attention captured by cues facilitates target response if there is spatial coincidence between cue and target, where stimuli in the areas in close proximity to the cue are processed faster than stimuli in the areas far from the cue (Bavelier et al., 2002). Maximal facilitation occurs at some optimal SOA. For example, in exogenous orienting, maximal cueing effect is found when target is presented at valid cue locations at cue-target SOAs between 100 and 200 ms (Folk et al., 1992; Milliken et al., 2003; Müller, 1994). At cue-target SOAs greater than 200 ms, the cueing effect decreases. In LMI, the greatest illusion effect is usually found around 300 ms cue-line SOA (Bavelier et al., 2002). Cue influence on target facilitation depends on whether targets are presented during the optimal temporal window where observers are capable of promptly allocating attention to targets (Milliken et al., 2003).

Singh, Stojanoski, Le, and Niemeier (2010) found that only the spatial cues preceding gratingscales at an SOA of 150 were significantly potent at biasing responses when observers judged spatial frequency from a pair of grating bars. Cues preceding stimuli at 200 or 300 ms had no significant biasing effect on observers judgment. When RT is plotted against SOA, the function is characterized by monotonic RT increase with increased SOAs until facilitation gradually becomes inhibition (Milliken et al., 2003). Target facilitation at short cue-target SOA is linked to automatic allocation of attention to the cued location. In successive visits of the cued location, there is no longer facilitation and RT is greater when target is presented at the cued location compared to the uncued location. This RT increase is presumably linked to the disengagement of attention from the cued location when the target is presented (Posner & Cohen, 1984). The slowing of responses to the cued location is called inhibition of return (IOR) (Posner & Cohen, 1984; Klein, 2000). IOR is presumed to result from directing attention and eye movements away from the cue location in order to explore novel ones (Ivanoff & Klein, 2003; Langley, Fuentes, Hochhalter, Brandt, & Overmier, 2001). IOR depends on attentional set, demands (Ivanoff & Klein, 2003) and task complexity (Ivanoff & Klein, 2003; Langley et al., 2001).

The magnitude of PN is modulated by exogenous cues preceding lines, luminance gradients and other visual stimuli. Most studies evaluating attentional capture by exogenous cues find facilitation at short cue-target SOAs and increased reaction time at long cue-target SOAs where cue influence usually decreases. Experiment 1 evaluated the timecourse of attentional capture by exogenous cues in VLB by determining optimal cue-line SOA. To this end, participants performed VLB in trials where visuospatial cues preceded lines at different SOAs relative to instances where no cue was presented. In order to evaluate the differential power of cues within left and right hemispaces, cues were presented at left or right line ends. Cue efficacy will be evaluated as modulations in perceived line midpoint, i.e. PSE relative to cue-line SOA. PSE will be measured using the psychometric function relating midpoint estimations to transector location, as well as the slope of the psychometric function (related to bisection precision, or variance, σ^2). Based on previous findings, the main prediction of this study was that of a rapid attentional capture resulting from the peripheral cue. Although there is no precedent in evaluating the timecourse of cued VLB, results from studies evaluating temporal adaptation of exogenous cues suggest optimal SOA for cues preceding stimuli ranging between 100-200 ms. At longer SOAs, there should be no significant effect of cue relative to baseline. At cue-line SOAs longer than 240 ms, there should be no cueing efficacy at capturing transient attention and modulating perceived midpoint.

B. Method

1. Participants

A total of 34 (21 male) healthy right-handed naïve observers participated in Experiment 1. Observers were recruited from the Psychology Department undergraduate observers' pool and the greater Fargo-Moorhead community. Observers received compensation for their participation. Observers recruited through the 1st method received extra credit points for their participation at the rate of 1 credit/15 mins of participation while observers recruited through the 2nd method received monetary compensation at the rate of $10.00/hour of participation. Prior to participation in the experiment, laterality scores (Oldfield, 1971) were obtained from all observers. Mean handedness for males and females was 86.2 and 80.0 respectively. Mean age for males and females was 20.3 and 20.7 respectively. There was are no significant difference between age [$t_{(12)}$=.168, p=.869] and handedness [$t_{(12)}$=-.964, p=.354] between male and female observers, therefore inferential statistics are performed on data collapsed across sex.

This and all of the present experiments were conducted conforming to the 1964 Declaration of Helsinki involving the ethical treatment of human research observers. All observers provided written informed consent and the procedures were approved by the Institutional Review Board of North Dakota State University.

2. Instrumentation and calibration

Stimuli were presented by means of microcomputer and displayed on a cathode ray tube monitor (CRT) (40 x 30 cm, 38.67^o x 29.49^o). Display resolution consisted of 1024 x 768 pixels, mean luminance was 50 cd/m^2 and refresh rate was 100 Hz. A microcomputer sensed and collected observers' responses. Stimulus generation and response collection were performed using a customized Presentation script (Neurobehavioral Systems, Albany, CA).

3. Stimuli

Figure 2 depicts a sample line stimulus used in experiments 1-3. Stimuli consisted of horizontal lines presented at 50% Michelson contrast on a mid-gray background. Michelson contrast is defined as:

$$(1) \quad C = (L_{max}-L_{min})/(L_{max}+L_{min})$$

where L_{max} and L_{min} refer to maximum and minimum luminance. At a viewing distance of 57 cm, line stimuli measured 27 x 3 cm (26.65^o x 3.01^o). Line stimuli were centrally presented in the display. Each line was pre-transected at one of 15 locations ranging from -0.30^o to +0.30^o relative to veridical line midpoint. Lines of opposite contrast polarity appeared with equal frequency and the order of appearance of lines with different transector locations was randomized within trial blocks.

Figure 2 also depicts the visual cue employed in Experiments 1-3. Visual cues consisted of a radial cosine function (a bull's-eye target) with a 3 cm diameter (3.01^o), 100% contrast (experiment 1 and 3) and a radial spatial frequency of approximately 3 c/d. When present, cues preceded line stimuli.

4. Procedure

Experiment 1 was performed in a single session. Observers were seated upright in straight-backed chairs. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971) on which a combined score of -100 denotes exclusive left-handedness and +100 denotes exclusive right-handedness. Observers were instructed to ignore the cues and to make single-interval two-alternative forced-choice decisions judging transector location relative to the line's perceived midpoint by pressing either the left or right mouse button. Observers responded with their right hand and were allowed to take breaks between stimuli's blocks.

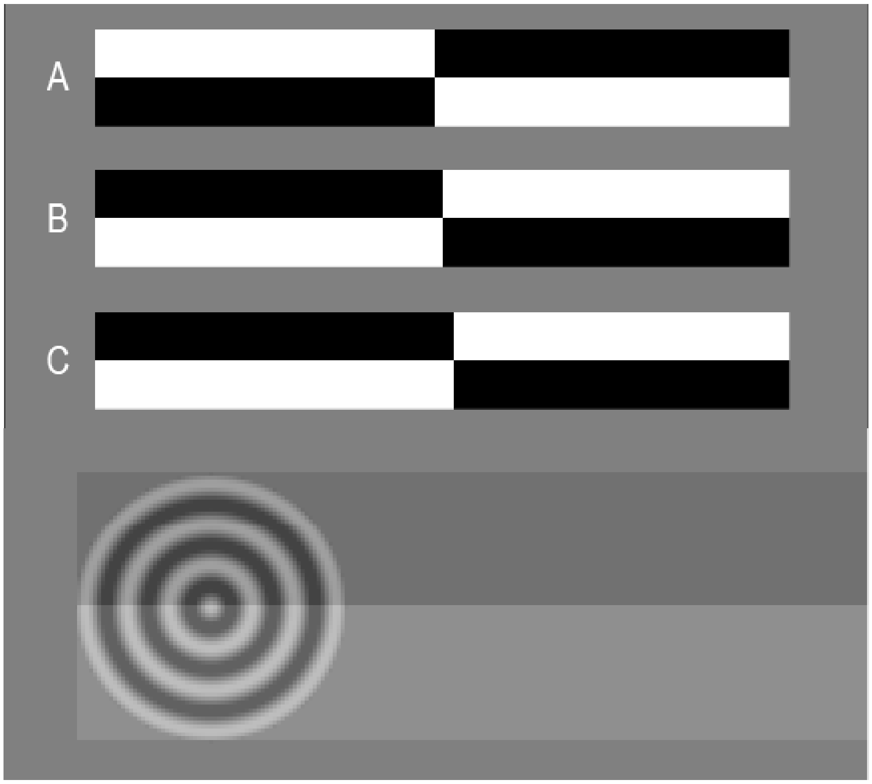

Figure 2. Schematic of cue and line stimuli used in experiment 1. At the left-most edge of the line is an example of the visual cue presented. Cue always preceded line and was located at the line's most eccentric edge within the line such that line completely occluded

previously presented cue. Line contrast was 50% while cue contrast was 100%.

Figure 3 describes the time course of the experimental procedures. Line stimuli were presented tachistoscopically (McCourt & Olafson, 1997) for 150 ms, and response prompted inter-trial interval (ITI) was 500-700 ms. Cue preceded lines at six SOAs: 40, 60, 90, 120, 240 and 500 ms. A no-cue condition was also included. As depicted in figure 2, in cue conditions, the visual cue was located such that its most eccentric edge coincided with the most eccentric edge of the line. Previous studies have proposed that cueing effects are explained by perceptual grouping where cues located lateral to the line perceptually elongates the line shifting perceived midpoint from veridical center (Fischer, 1994). In order to avoid a perceptual elongation of the line, in the present study, cues were presented to either the right or left line end for 30 ms. The cue was never presented simultaneously with the line. Observers made 10 right/left judgments at each of 15 transector locations, such that determination of perceived line midpoint was based on 90 (15 lines x 6 cueing conditions) forced-choice trials in each of 5 blocks. Each participant performed a total of 2250 trials where 150 were no-cue trials.

5. Design and data analysis

The dependent measure was the proportion of trials where observers indicated that the line was transected to the "left" of its veridical midpoint. The method of constant stimuli was used to fit psychometric functions to data. In psychophysics, the psychometric function is the graph that relates observers response to the levels of the stimuli presented (Klein, 2001). The psychometric function informs about the optimal parameters for the dataset fitted (Treutwein & Strasburger, 1999). The Weibull cumulative density function was used to fit a sigmoid to the data using a constrained maximum likelihood optimization

(Klein, 2001) using Matlab (Matlab R2007a, Mathworks). Maximum likelihood optimization was performed to estimate the slope and inflection point of the function. The weibull function is described by the equation:

$$(2) \quad \rho = \gamma + (1-\gamma) \mathrm{X} (1\text{-exp} -(x.^{\text{beta}}))$$

where beta is the slope of the psychometric function, x is transector location and gamma(γ) refers to the lower asymptote.

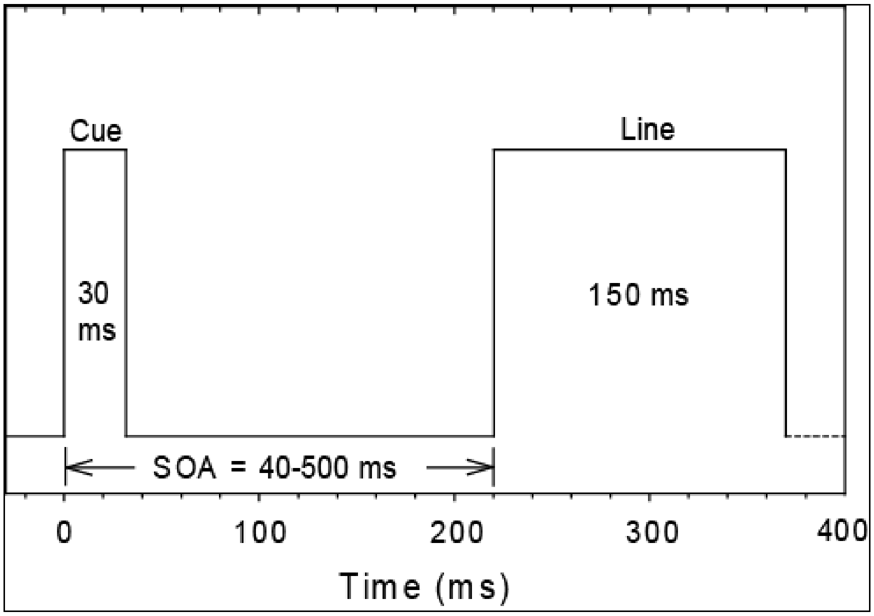

Figure 3. Time-course of procedures employed in experiment 1.

PSE in each cue-line SOA condition was determined such that the effect of cues on PSE was indexed by taking the difference in PSE between the R and L cue conditions:

$$(3) \quad \Delta\text{PSEc} = \text{PSEcR} - \text{PSEcL}$$

where ΔPSE indicates relative displacement of PSE based on spatial cues. PSEcR and PSEcL refer to PSE obtained in trials where cues were presented within right and left line ends, respectively. For stimulus presentation, PSE was displaced Δ degrees to the left or right of midpoint.

Finally, inferential statistics were performed on averaged data. This experiment consisted of a 2 (cue location: left, right) x 6 (SOA: 40, 60, 90, 120, 240, 500 ms) within-subjects design. The dependent measure was PSE. PSE was derived from fitting psychometric functions to the L/R judgments. Repeated-measures ANOVA was used to explore main effects and interactions between the explored variables. Post hoc analyses were performed accordingly.

C. Results and discussion

1. Analysis of cue effectiveness

Figure 4 plots mean PSE (± 1 SEM) in the left (black circles) and right (white circles) cue conditions as a function of cue-line SOA. Also shown is mean PSE in the no-cue condition (gray symbol). A 2 (cue locations) X 6 (cue-line SOA) repeated-measures ANOVA disclosed a significant main effect of cue location, $F(1,33)= 35.833$, $p < .001$, such that PSE is systematically displaced toward the cued line end. While there was no significant main effect of cue-line SOA, $F(6,198)= 1.410$, $p > .05$, there was a significant cue location x cue-line SOA interaction, $F(6,198)= 5.252$, $p < .001$. Paired-samples t-tests revealed that PSEs in conditions where cues preceded line at 40, 60, 90, 120 and 240 ms SOA were significantly different when presented in left compared to right space, [$t_{(33)}= -4.951$, $p< .001$], [$t_{(33)}= -5.815$, $p< .001$], [$t_{(33)}= -4.498$, $p< .001$], [$t_{(33)}= -3.483$, $p= .001$] and [$t_{(33)}= -3.582$, $p= .001$] respectively, but not when cue preceded line at 500 ms SOA [$t_{(33)}= -.345$, $p= .732$]. There is no significant PSE difference between no cueing condition and cues preceding line only at 500 ms SOA [$t_{(33)}= -1.689$, $p= .101$], in other words, at 500 ms SOA cues have no influence on perceived midpoint. Cues exert an asymmetric influence on bisection error where right cues are more potent than left cues. This finding is consistent with previous results demonstrating asymmetric cue potency in visuospatial tasks where the right space is favored over the left space (McCourt et al., 2005; Nicholls & Roberts, 2002; Singh et al., 2010). The asymmetry in cueing power of left and right cues may be explained by a difference in available 'headroom' in left cues compared to right cues. In the absence of cues, the leftward bias is powerful enough that left cues have little or no additional biasing power, the bias has reached its maximum capacity. Right cues, on the other hand, have all the capacity to 'pull' perceived midpoint rightward.

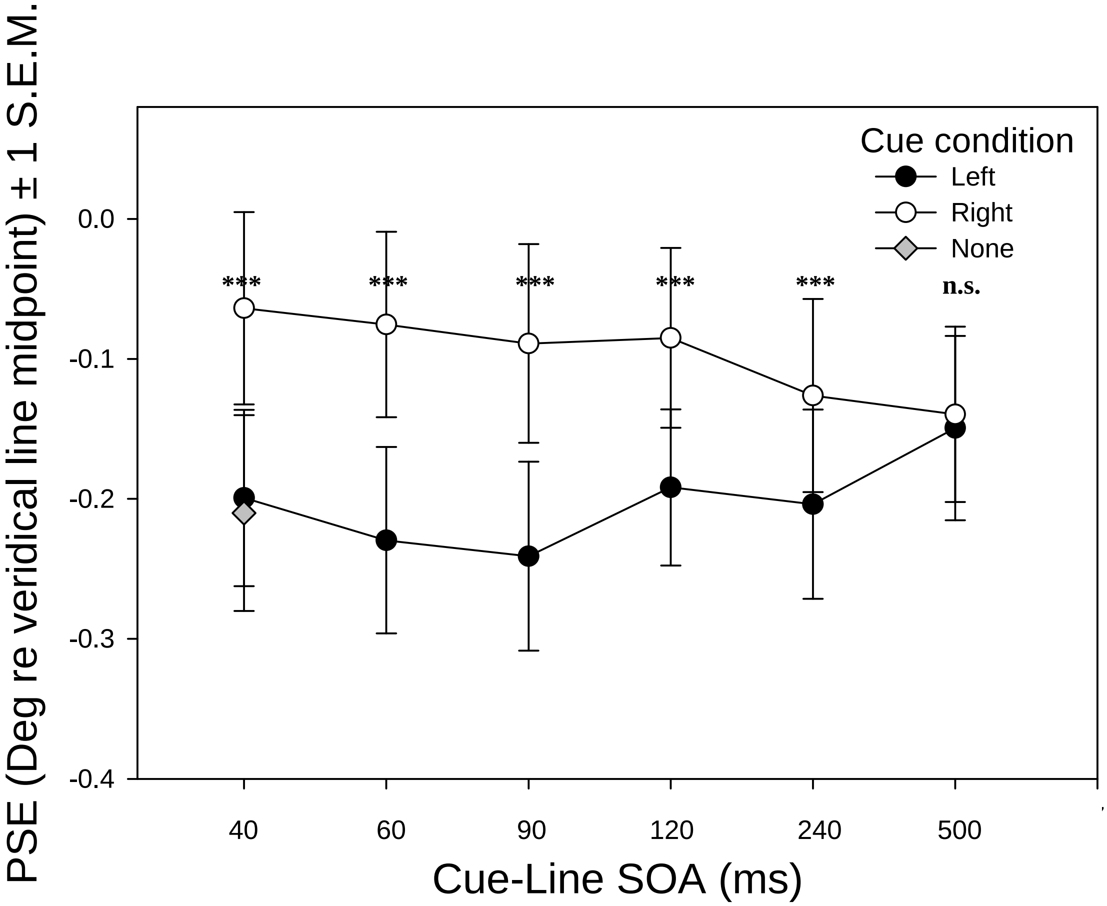

Figure 4. Mean PSEs (± 1 S.E.M.) as a function of cue-line SOAs. (*** p < .005, n.s.= not significantly different PSEs for cues in left versus right space).

In order to determine the optimal cue-line SOA for biasing PSE we plotted the difference in PSE between the R and L cue conditions as a function of cue-line SOA in

Figure 5 which shows the best fitting weibull curve to the data. We fit the time course of cueing efficacy to a three-parameter weibull curve using method of least-squares. The weibull curve has the form:

$$(4) \quad CE\ (t,\alpha,\beta,\gamma) = \alpha * (t/\beta)^{(\gamma - 1)} * \exp\left(-(t/\beta)^{\gamma}\right)$$

The parameter values are $\alpha = 0.23$; $\beta = 178.1$ and $\gamma = -0.78$ where α scales the curve along the horizontal axis, β defines the shape of the curve and γ scales the curve along the vertical axis. In order to determine the optimal cue-line SOA for biasing PSE we computed the peak of the weibull curve, t. In figure 5, abscissa depicts different SOAs while ordinate depicts average ΔPSE. The goal of fitting PSE to a weibull curve was to determine absolute biasing effect of cue. The weibull curve allowed for the determination of the manipulation of the independent variable exerting the greatest effect on the evaluated behavior (Weibull & Sweden, 1951; Sharif & Islam, 1980). Optimal cue-line SOA is 58 ms. The optimal cue-line SOA we observe is consistent with the notion that cues result in facilitation when these are presented in close temporal proximity to target stimuli (Singh et al., 2010). However, the cue-line SOA resulting in maximal cue efficacy is somewhat earlier than has been reported in previous studies using endogenous (Bavelier et al., 2002; Folk et al., 1992) and exogenous cues (Singh et al., 2010). Sustained attention takes up to 300 ms to allocate while involuntary attention is transient and takes about 100-200 ms to fully allocate (Egeth & Yantis, 1997; Ling & Carrasco, 2006; Mulckhuyse & Thewues, 2010; Singh et al., 2010). The apparent discrepancy between our findings and previous experiments may be due to methodological differences, for example in the study by Singh et al. (2010 observers made spatial frequency judgments after a location was cued; and in the study by Müller and Rabbitt (1989) as well as the study by Egeth and Yantis (1997) observers attended to a brightening of a peripheral box before target appeared. However the 95% bootstrapped confidence interval for optimal SOA (shown in fig 5) ranged from 26-90 ms which is consistent with previous findings. The efficacy of right cue preceding line at short SOAs demonstrates a rapid cue-adapting mechanism which modulates perceived midpoint in visual line bisection judgments.

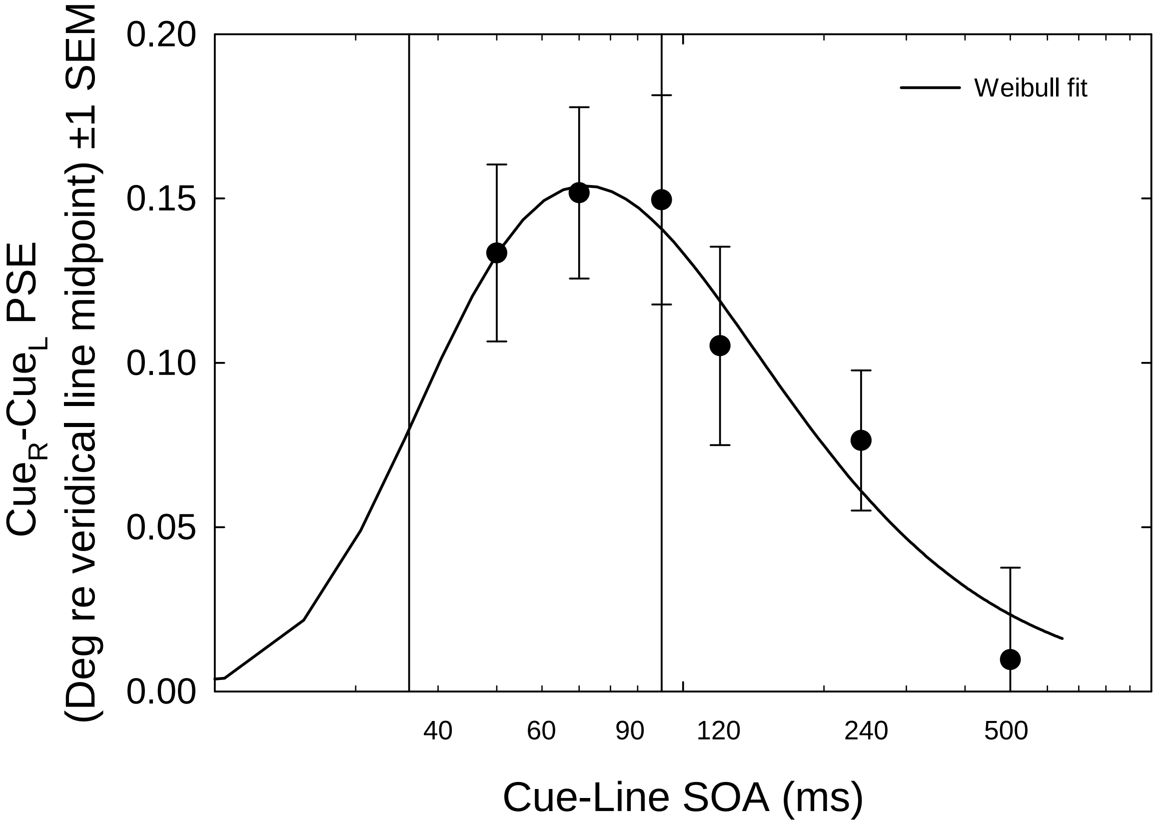

Figure 5. Difference PSE (±1 S.E.M.) at different cue-line SOAs. Abscissa plots different SOAs (in logarithmic scale) whereas ordinate plots mean ΔPSEs.

The present study found no evidence for inhibition of return (IOR) (Chica, Rafal, Klein, & Hopfinger, 2010; Klein, 2000). The withdrawal with inhibition of attention which IOR signifies would be expressed in the present study by the cue causing perceived line midpoint to change in a direction away from the cued line end. We find that PSE returns to the uncued condition at a cue-line SOA of 500 ms, but at no SOA do cues cause PSE to deviate in the uncued direction. IOR is usually found in speeded tasks, such as RT, rather than in unspeeded tasks, like the left-right transector location judgments made in the current paradigm. Future studies should evaluate longer SOAs to investigate the influence of attentional control settings in such VLB paradigms (Klein, 2000). When observers perform tasks characterized by high attentional demands, the attention allocated to the task ‘expands’ to the cue for longer time and IOR can be found with a late onset. In conditions of lower attentional demands the target captures attention earlier and IOR can be seen earlier (Klein, 2000).

PN analysis. PSE was significantly leftward of veridical (PN) at baseline [$t_{(33)}$= -3.032, p= .005]. The finding of PN in VLB (at baseline) replicates previous findings in visuospatial attention.

CHAPTER III. EXPERIMENT 2: EFFECT OF CUE CONTRAST IN VLB

A. Rationale

Exogenous attention can alter the perception of objects and their features. Attention can affect the perception of size, hue and contrast (Ling & Carrasco, 2006; Liu, Abrams, & Carrasco, 2009). Contrast sensitivity is expressed as the inverse of contrast threshold. The contrast sensitivity function (CSF) plots sensitivity to sinusoidal luminance gratings as a function of their frequency. The CSF possesses an inverted u shape, with a peak sensitivity between 500-1000 occurring at middle spatial frequencies (5-10 cycles per degree). CSF ranges from 1 to a number larger than1, and in human observers possesses a band pass filter. Band pass filter implies neuronal sensitivity to a selected range (band) of contrasts excluding others (Blakemore & Campbell, 1969; De Valois, 1977; Norton, Lakshminarayanan, & Bassi, 2002). The firing rate of neurons depends on stimulus' contrast. Neurons respond weakly to stimuli presented at low visual contrasts, possessing a monotonic response function which increases for high contrasts until neurons saturate (Pestilli, Viera, & Carrasco, 2007).

There are three parallel pathways which originate in the retina of most primates and project to the lateral geniculate nucleus (LGN) of the thalamus. The magnocellular, parvocellular and koniocellular pathways project to cortical and subcortical regions and are sensitive to different types of stimuli. The magnocellular pathway is composed of cells with large cell bodies and large receptive fields (M-cells). M cells are tuned to relatively low spatial frequencies and possess high contrast sensitivity, that is, they possess high contrast gain such that their response reaches a maximum (saturates) at relatively low stimulus contrasts. M cells have a transient response and project to layers 1 and 2 of the

LGN. The parvocellular pathway is composed of cells with small cell bodies and small receptive fields (P-cells). P cells have low contrast gain and are tuned to relatively high spatial frequencies (Casagrande, 1994). P cells have a sustained response (White et al., 2009) and project to layers 3 to 6 of the LGN. The low sensitivity of P cells is evidenced by their contrast response function which follows a monotonic trend with a shallower slope than M cells (Casagrande, 1994; Murray & Plainis, 2003). K cells project to the ventral portion of each LGN layer and receive direct connections from the superficial layers of the SC. There is some overlap between the temporal and spatial resolution of K, P and M cells. However the response of the K cells is more heterogeneous than that of P and M cells, perhaps because of its location in the LGN (Xu et al., 2001). Neuronal responses also decrease when stimulus contrast is viewed for prolonged periods of time producing adaptation (De Valois, 1977; Pestilli et al., 2007).

Spatial cues influence the allocation of attention. High contrast peripheral cues have a greater influence on the ability to discriminate stimulus orientation than low contrast peripheral cues (Pestilli et al., 2007). The allocation of exogenous attention is influenced by cue saliency. Cue saliency is influenced by visual contrast. Fuller, Park & Carrasco (2009) demonstrated that optimal cue contrast for attentional capture is about 10%, with individual variability ranging from 5 to 12%. These contrast sensitivities were found in a localization task where peripheral locations were cued with stimuli of various contrasts. Cues were randomly presented within left and right space for 50 ms at Michelson contrasts ranging from 4% to 100%. Contrast sensitivity demonstrated pre-asymptotic responses when cues were presented at contrasts of 12% and post-asymptotic responses at cue contrasts above 12%.

In VLB, it has been noted that changes in line contrast (McCourt & Jewell, 1999) and more importantly that changes in cue contrast (McCourt et al., 2005) produce asymmetric modulations on perceived midpoint. McCourt et al. (2005) demonstrated that spatial cues of 10% and 100% contrast preceding lines have influence over perceived midpoint in VLB. The aim of Experiment 2 is to measure how cue contrast modulates the efficacy of cues to influence perceived line midpoint in line bisection. Fuller et al. (2009) found that cues presented at contrasts below 10% are not effective at capturing exogenous attention. Based on these findings, the main prediction of the present experiment was that of optimal cue contrast of 12%.

B. Method

1. Participants

A total of 33 (20 male) healthy right-handed naïve observers participated in Experiment 2. Observers were recruited following the same criteria and strategy as in Experiment 1. Mean Oldfield handedness for males and females was 77.8 and 78.8, respectively. Mean age for males and females was 20.0 and 18.8 respectively. There was no significant difference in age [$t_{(12)}$= -.976, p=.349] or handedness [$t_{(12)}$= -.055, p=.957] between male and female observers, and inferential statistics are performed on data collapsed across sex.

2. Instrumentation and calibration

As in Experiment 1.

3. Stimuli

As in Experiment 1.

4. Procedure

Cue and lines were presented as in Experiment 1 at the cue-line SOA where the maximal effect was found (60 ms). In addition to a no-cue condition, observers performed the line bisection task in trials where cues of 0.4, 0.8, 1.0, 1.4, 3, 6, 12, or 100% Michelson contrast were presented to the left or right line ends. Observers performed 2550 trials.

5. Design and data analysis

The design and analyses are as in Experiment 1. This study consists of a 2 (cue location: left, right) x 8 (cue contrast: 0.4, 0.8, 1.0, 1.4, 3, 6, 12, or 100 %) within-subjects design.

C. Results and discussion

1. Cue contrast effectiveness on PSE modulation

Figure 6 plots mean PSE as a function of cue contrast for the left- and right-cue conditions, as well as in the no-cue condition. A 2 (cue location) x 8 (cue contrast) repeated-measures ANOVA revealed a significant main effect of cue location, F(1,32)= 8.16, p= .007, where perceived midpoint shifted towards cue location. There was no significant main effect of cue contrast, F(7,224)= 1.26, p= .270, but there was a significant cue location x cue contrast interaction, F(7,224)= 9.18, p< .001. In order to trace the source of the significant interaction, a series of paired-samples t-tests were conducted. Mean PSE differed significantly in the left- versus right-cue condition only at cue contrasts of 12% [t (32)= -3.103, p= .004] and 100% [t (32)= -4.484, p< .001], but not at 0.4% [t (32)= 1.243, p= .223], 0.8% [t (32)= .133, p= .895], 1.0% [t (32)= .994, p= .328], 1.4% [t (32)= .864, p= .394], 3% [t (32)= -.760, p= .453], or 6% [t (32)= -.364, p= .718].

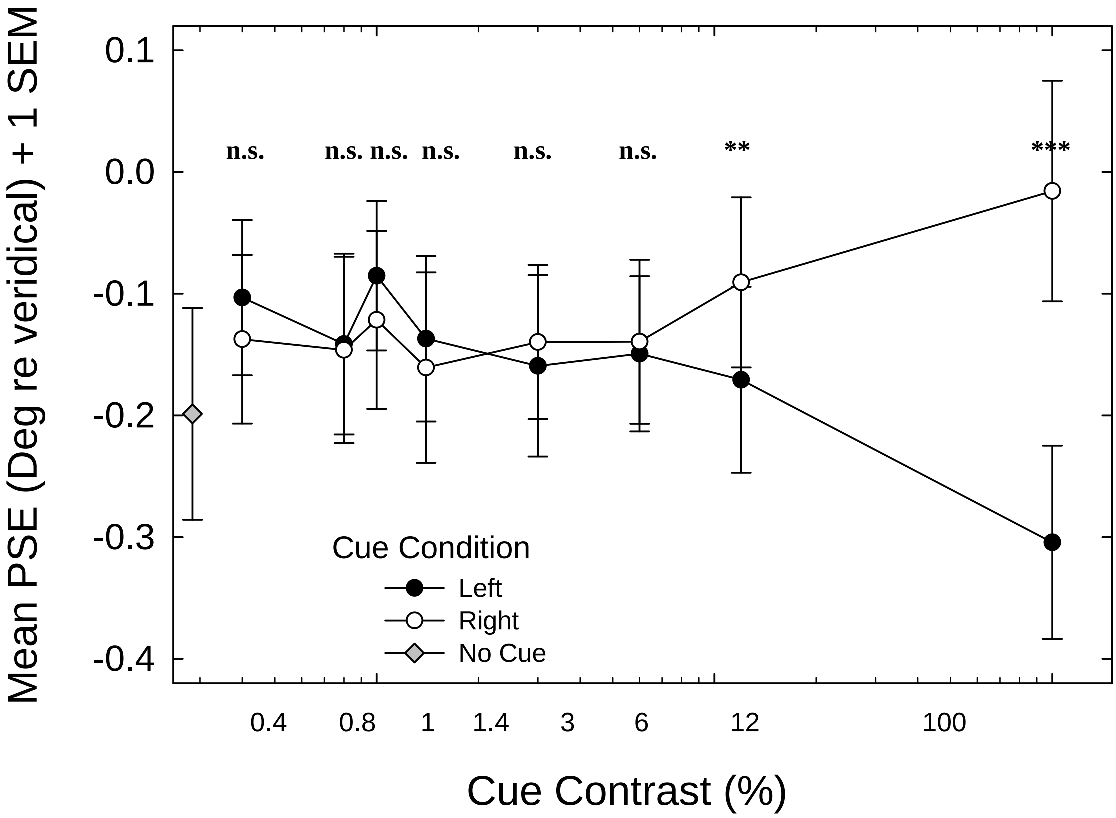

Figure 6. Mean PSE (± 1 S.E.M.) as a function of cue contrast. Abscissa plots cue contrast (in logarithmic scale) while ordinate plots mean PSE. White symbols denote PSE in trials where right cues preceded lines, while black symbols plot PSEs in trials where left cues precede lines. Grey diamond plots average PSEs at baseline. **p<.005, ***p<.001, n.s. not significant.

Figure 7 plots the difference in PSE in the right-cue versus left-cue conditions as a function of cue contrast, and represents the cue contrast response function. Cue efficacy is seen to be a monotonic function of contrast. Cues at contrasts below 12% were ineffective at biasing perceived midpoint. The maximal biasing effect occurred for cues of 100% contrast.

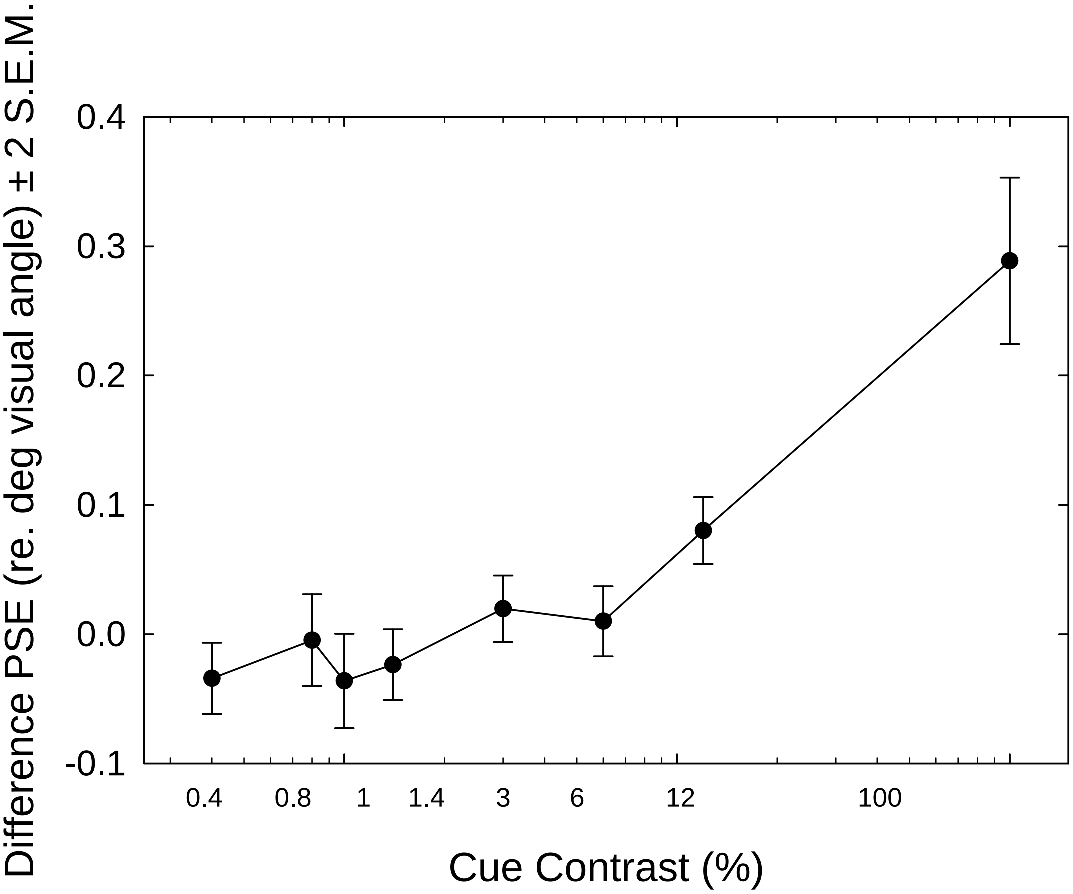

Figure 7. Difference PSE (± 1 S.E.M.) as a function of cue-contrast. Abscissa (in logarithmic scale) plots cue contrast while ordinate plots mean ΔPSE.

Experiment 2 shows that a cue contrast of at least 12% is required to significantly influence perceived line midpoint. These findings are consistent with those of previous experiments exploring the influence of exogenous cue contrasts on localization judgments. Murray and Plainis (2003) showed that the slope of the contrast-sensitivity function is steeper at high compared to low contrast demonstrating higher sensitivity for high versus low contrast. Murray and Plainis measured RT when observers responded to vertical sinusoidal gratings with abrupt onset and offset. The gratings were presented at various luminance levels. In such judgments, optimal cue contrast for attentional capture was 10-12% (Fuller et al., 2009).

At the neural level, contrast sensitive neurons have been identified in various areas. For example, there are cells with band pass filters in the retina, LGN, FEF and V1 (Norton et al., 2002). Various fMRI and neuroanatomical studies suggest the existence of connections between the M pathway and parietal regions (Tootell et al., 1995). Additional neural mechanisms projecting from the superior colliculus to parietal regions are usually related to attention allocated to low contrast spatial cues. These brain areas are active even when the information conveyed by the spatial cue is weak and doesn't reach awareness (McCormick, 1997; Mulckhuyse, 2007). Although it was usually thought that neurons in the SC do not receive input from retinal S-cones (de Monasterio, 1978), recent evidence shows that neurons in the intermediate layers of the SC are sensitive to the color signals that usually activate the geniculostriate system (White, Boehnke, Marino, Itti, & Munoz, 2009). The present findings demonstrating that at least with respect to line bisection, exogenous cues only begin to recruit attention at contrasts of 12% and above argue against a strict magnocellular involvement. Instead stimuli presented at high contrasts activate M and P cells (Casagrande, 1994; Murray & Plainis, 2003). In exogenous cues preceding VLB, the interhemispheric asymmetry in the processing of stimuli based on contrast and spatial frequency suggests hemispheric specialization of M and P pathways. At high contrast, stimuli may be preferentially processed by the left hemisphere; whereas at low contrast, stimuli may be preferentially processed by the right hemisphere.

<u>PN analysis</u>. Significant leftward bisection error, as evaluated using single-sample t-test against veridical line midpoint (no error), was found in the no-cue (baseline) condition [$t_{(32)} = -2.29$, $p = .029$]. Baseline PN was significantly modulated by cues presented in right space demonstrating asymmetric potency compared to left cues. The

relative influence of right compared to left cues is consistent with the findings of Experiment 1 as well as previous studies of cueing in VLB (McCourt et al., 2005).

CHAPTER IV. EXPERIMENT 3: OBJECT-BASED ATTENTIONAL CAPTURE IN VLB

A. Rationale

Object-centered attention. Experiment 2 showed that the magnitude of PN is modulated by changes in cue contrast (object features). PN occurs in several reference frames including spatiotopic (space-), allocentric (object-) and feature-based coordinate systems. In allocentric attention, left and right are defined in terms of the attended object and maintain constancy despite changes in object orientation and/or location. Object's perceived midpoint is preserved (Humphreys, 1998). However, there is no strong evidence demonstrating that allocentric and spatiotopic attention operate as completely separate systems. Instead visual attention could parsimoniously be explained by different but coexisting reference frames (Tipper & Behrmann, 1996; Humphreys, 1998; Soto & Blanco, 2004).

PN is demonstrated when observers judge the midpoint of objects, in visual search tasks involving individual and overlapping letters (Valsangkar-Smyth, Donovan, Sinnet, Dawson, & Kingstone, 2004) and in bisection tasks (Pia, Neppi-Modona, & Folegatti, 2010). An interesting example of object-based PN occurs when observers perform bisection of caricature dogs. The leftward error is found for different dog-orientations, i.e. head left or tail left and shifts significantly rightward when mirror images are presented suggesting that attention is allocated to the object rather than the space occupied by it (Pia et al., 2010). Additionally, PN magnitude in VLB is modulated by changes in the object (the line) or its features. For example, changes in object properties such as azimuthal position (McCourt & Jewell, 1999; McCourt et al., 2000), contrast (McCourt & Jewell, 1999), length (McCourt & Jewell, 1999), and geometry modulate leftward bias in various ways (McCourt & Jewell, 1999; McCourt & Garlinghouse, 2000; McCourt et al., 2005).

Some accounts explain object-based attention as resulting from figure-ground assignment processes (Qiu, Sugihara, & von der Heydt, 2007; Vecera, Flevaris, & Filapek, 2004). When an ambiguous figure-ground display (figure 8) is cued, the bar cue is usually grouped with the figure instead of the ground presumably because the cue influences the allocation of exogenous attention towards the figure. The spatial cue, however, does not exert any influence over figure-ground assignment when the cue is displayed outside of the figure-ground region (Vecera et al., 2004). In the brain, figure-ground assignment due to exogenous attention is usually related to visual area V2 (Qiu et al., 2007). Object-based attentional selection is usually related to the activity of various parietal, frontal (Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004) and extrastriate areas (Yantis & Serences, 2003).

Object-based attention is also hypothesized to be related to the 'what' pathway (ventral stream) of visual processing (Ungerleider & Mishkin 1982; Humphreys, 1998). For example, Foxe et al. (2003) found modulation of the N1 ERP component when observers performed VLB with lines at low visual contrasts. The N1 ERP component has been associated with the time course of object processing within the ventral stream (Foxe et al., 2003; Ho & Atchley, 2009; Martínez et al., 2006). In VLB, the ventral stream may be sending the object information to the dorsal stream before attention can be allocated to the line (Foxe et al., 2003).

It is still unknown whether space- or object-based mechanisms mediate attentional capture by exogenous cues in VLB. Experiment 3 evaluated the relative effectiveness of azimuthal cue position in modulating bisection error. Eight azimuthal cue positions were evaluated in order to explore the role of object- and space-based attention. Based on experiments 1 and 2, asymmetrical cue capture was predicted with right cues exerting greater influence on perceived midpoint than left cues. Moreover, if the cues presented within the boundaries of the line had a greater modulation effect than the cue presented outside of the boundaries of the line, it may indicate that cue and line are being grouped within the same object. In other words, cue and line grouping would be interpreted as an object-based attentional process. The differential cue influence was evaluated in terms of PSE modulations in cued relative to no cued conditions.

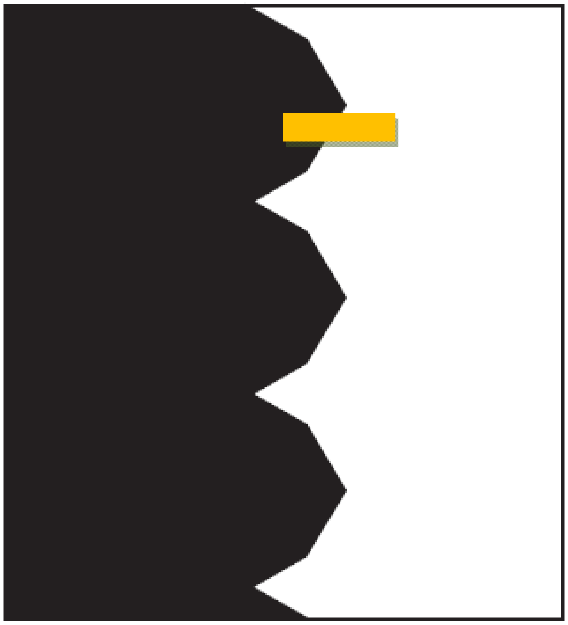

Figure 8. Figure-ground assignment. Perception sometimes segregates ambiguous images into figure and ground such that figure pops out whereas background is easily ignored. The criteria for selection figure ownership depends on different object features (Vecera et al., 2004).

B. Method

1. Participants

A total of 31 (16 male) healthy right-handed naïve observers participated in Experiment 3. Observers were recruited following the same criteria and strategy as in experiments 1 and 2. Mean handedness for males and females was 75.9 and 77.6, respectively. Mean age for males and females was 23.4 and 25.8 years, respectively. There was no significant difference in age [$t_{(15)}$= 1.321, p=.206] or handedness [$t_{(15)}$= .480, p=.638] between male and female observers, therefore inferential statistics were performed on data collapsed across sex.

2. Stimuli

As in Experiment 1.

3. Procedure

Procedure was as in Experiment 1. Additionally, cue-line SOA was 60 ms and cue contrast was 100%. Cues were randomly presented at 8 different positions within the azimuth. As depicted by Figure 9, cue locations ranged from completely beyond the line endpoint (cue position A) to within approximately 1 radius distance from veridical line midpoint (cue position H). The center point of the cues was 1 radius distance from each other. A no-cue comparison condition was also included. Observers performed 2550 trials.

4. Design and data analysis

Design and analyses are as in Experiment 1 and 2. This study consists of a 2 (hemifield: left, right) x 8 (cue azimuthal position: A-H) within-subjects design.

C. Results and discussion

1. Horizontal cue position in visual line bisection

Figure 10 plots the main results from experiment 3. White circles plot average PSE in conditions where right cues preceded lines while black circles plot average PSE in conditions where left cues preceded lines. The grey diamond plots average PSE in no cue condition. Cue effectiveness was analyzed with a 2 (hemifield) x 8 (cue position) repeated measures ANOVA demonstrating a significant main effect of hemifield where cue was presented. PSE was significantly biased in the direction of the cue, $F(1,30)= 57.008$, $p< .001$. There was a significant main effect of horizontal position, $F(7,210)= .640$, $p= .722$, and there was a significant hemifield x position interaction, $F(7,210)= 10.574$, $p< .001$. Paired-samples t-test showed that all cues except the cues presented in positions A had significant biasing effects. Left and right cues resulted in significantly different biasing effects when presented in positions B [$t_{(30)}= -3.316$, $p= .002$], C [$t_{(30)}= -7.181$, $p< .001$], D [$t_{(30)}= -6.185$, $p< .001$], E [$t_{(30)}= -6.612$, $p< .001$], F [$t_{(30)}= -5.791$, $p< .001$], G [$t_{(30)}= -5.810$, $p< .001$] and H [$t_{(30)}= -5.311$, $p< .001$]. No difference in perceived midpoint occurred in conditions where left and right cues preceded lines in position A [$t_{(30)}= .329$, $p= .745$] . These results demonstrate that only the cues that spatially physically coincide with the line are powerful at influencing perceived midpoint. Moreover, relative to no cue condition, cue had no biasing power when this was presented in positions A, B, C, D, E, F, G and H within the left [$t_{(30)}= -.529$, $p= .601$], [$t_{(30)}= .220$, $p= .828$], [$t_{(30)}= .972$, $p= .339$], [$t_{(30)}= 1.433$, $p= .162$], [$t_{(30)}= 1.387$, $p= .176$], [$t_{(30)}= 1.229$, $p= .229$], [$t_{(30)}= 1.110$, $p= .276$] and [$t_{(30)}= .888$, $p= .382$] respectively, and positions A, B, D, F, G, and H within the right [$t_{(30)}= -.376$, $p= .709$], [$t_{(30)}= -1.001$, $p=.325$], [$t_{(30)}= -1.885$, $p= .069$], [$t_{(30)}= -1.845$, p= .075], [$t_{(30)}$= -1.789, p=.84] and [$t_{(30)}$=-1.827, p= .078] line ends, respectively.

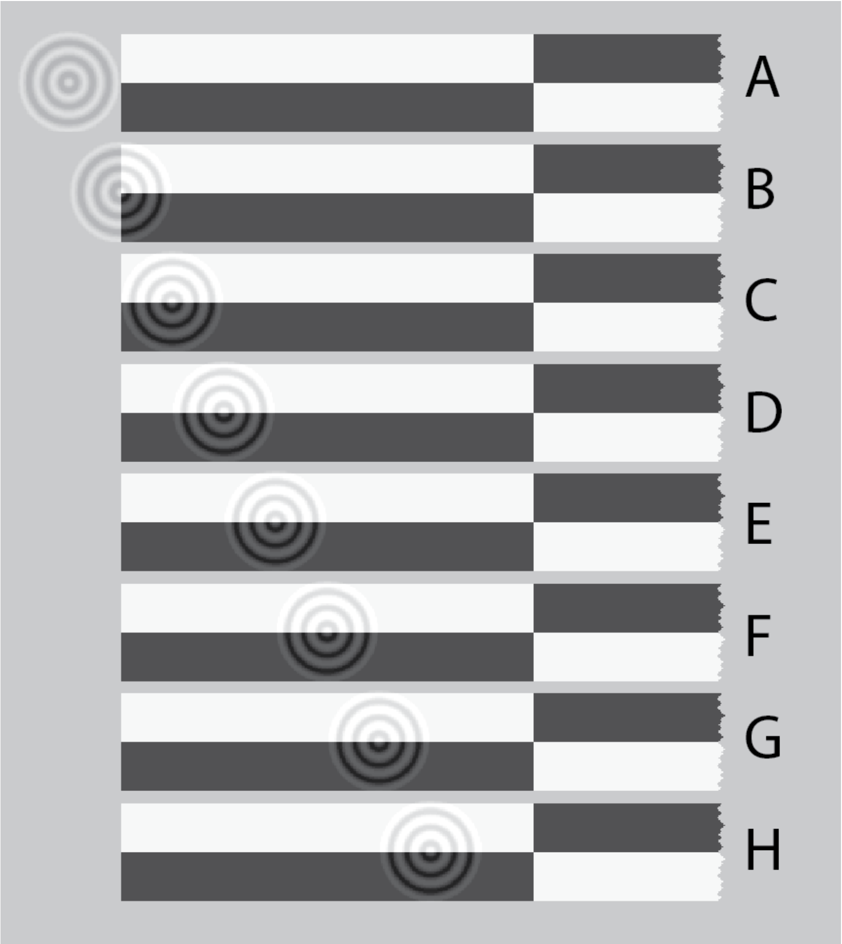

Figure 9. Stimuli displayed in experiment 3. In this experiment, cues preceded lines at the eight different horizontal locations depicted here.

Figure 10 and 11 demonstrate that cues exert no influence on perceived line midpoint when located completely outside of the boundaries of the line. The lack of cue potency observed for cue position A was not found for any other cue position. Significantly different biasing effects occur when cues partially occupy the space of the line (position B) than occur in any other cue condition. In other words, partial spatial overlap between cue and line is sufficient for the cue to significantly influence attentional capture in VLB but not to the extent that complete overlap with the line does. When cues spatially overlap with the line completely (positions C-H) there is no significant difference in their biasing power based on spatial position; instead the critical factor determining cue power is the hemifield where cues are displayed.

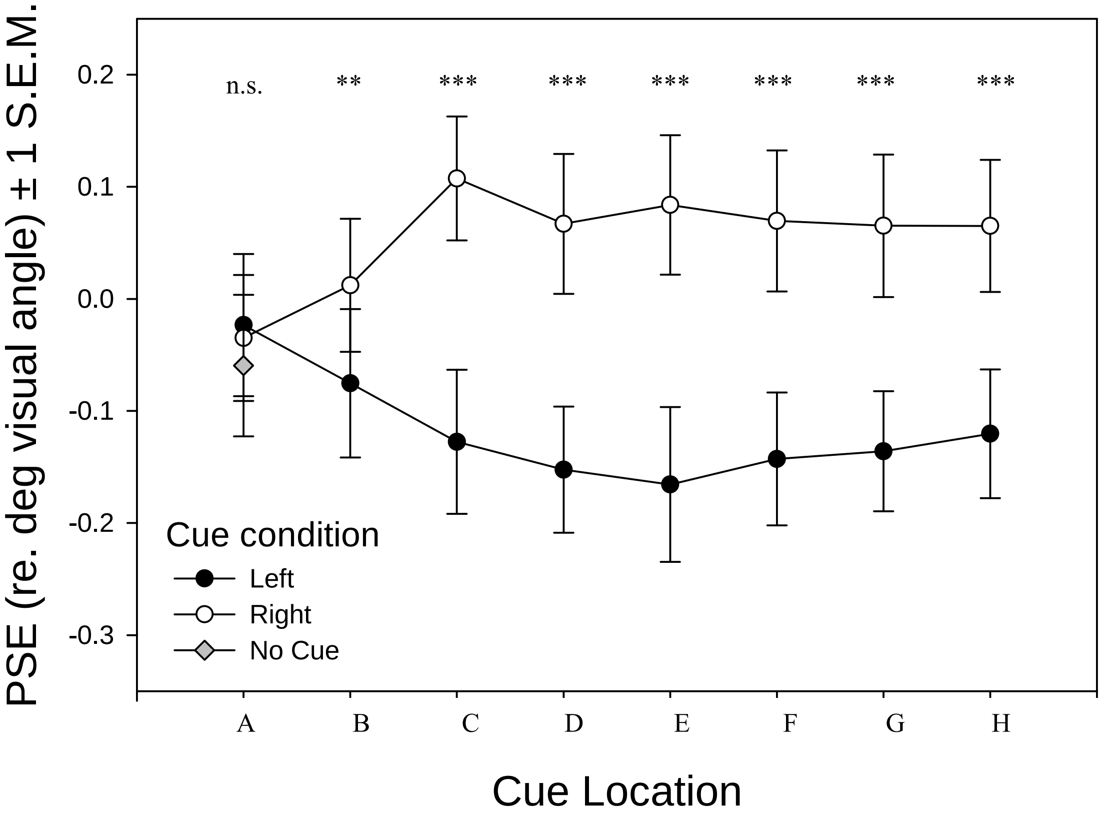

Figure 10. Mean PSE (± 1 S.E.M.) as a function of cue location within the azimuth. Abscissa depicts cue locations ranging from the most lateral (A) to the most central (H), while the ordinate depicts average PSE.

Experiment 3 provides supporting evidence for the existence of object-based attention and for object-based attentional capture (Shomstein & Yantis, 2004). We find that when cues are located completely within the boundaries of an object (the line) they exert similar effects on PSE regardless of their spatial proximity to either the line end or its midpoint. Cues which are located partially outside the line boundary have a reduced efficacy, and cues located completely outside the borders of lines have no significant effect on perceived line midpoint. Vecera et al. (2004) found that exogenous spatial attention can influence figure-ground assignment. Observers in their experiment had to judge the figure from the background in an ambiguous image containing two regions after one region was cued. There is also a relationship between object-based attention and figure-ground assignment such that the differentiation between figure and ground determines the object that will be attended (Qiu el al., 2007; Vecera et al., 2004). In the present findings this relationship was suggested by the fact that cues B-H had effects on PSE while cue A had no effect. Cues <u>B</u>-<u>H</u> were grouped with the line and assigned to the figure whereas the cue displayed outside of the line (cue position A) was assigned to the background. The neural mechanisms determining the means by which exogenous attention is captured in the process of figure-ground assignment are usually related to areas such as LOC and populations of neurons within V2. The role of area V2 was demonstrated by performing extracellular recording in non-human primates (Qiu et al., 2007). Similarly, the deployment of object-based attention has been associated with area LOC. After bilateral lesions to this area, there is increased RT for within-object discrimination tasks but not for between-object discrimination tasks. Lesions to area LOC also result in form-perception deficits (de-Wit, Kentridge, & Milner, 2009). Our findings show exogenous attention capture where cues that are grouped with lines influence line in an allocentric reference framework. The neural mechanisms of object- and space-based biases may overlap within parietal and frontal structures (Serences et al., 2004; Yantis & Serences, 2003).

<u>PN analysis</u>. There was a mean bisection error of -.041° in no-cue condition. Despite this leftward error in the no-cue condition, it was not significantly different from

zero [t $_{(30)}$= -.944, p= .352]. The lack of PN evident may be explained by variability. Atypical observers can present a rightward error in VLB. Previous studies have also attributed the lack of significant PN to individual variability (Post, Caufield, & Welch; 2001).

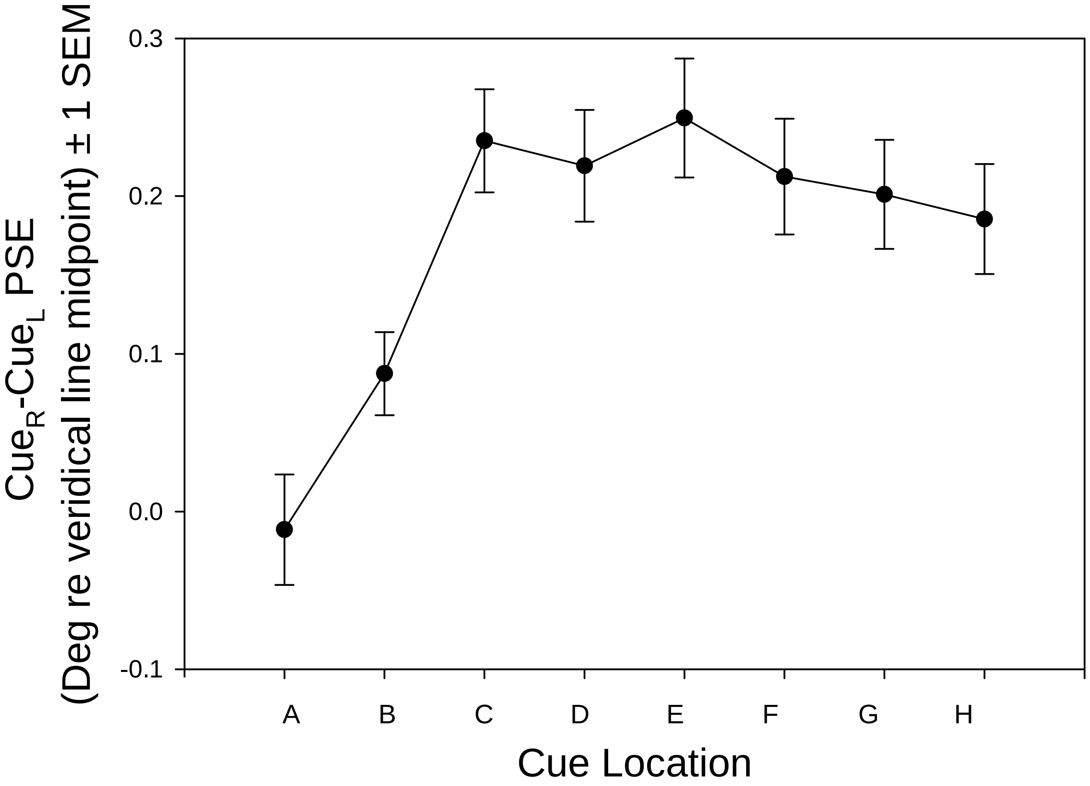

Figure 11. Difference PSE (± 1 S.E.M.) as a function of cue location within the azimuth. Abscissa (in logarithmic scale) plots cue location while ordinate plots mean ΔPSE.

CHAPTER V. EXPERIMENT 4: SCANNING EFFECTS IN VLB

A. Rationale

Experiments 1-3 evaluated how attention phasically captured by exogenous cues interacts with the tonic spatial attentional asymmetry which gives rise to the leftward error in pseudoneglect to further influence line bisection error. In addition to these attentional factors, motor factors also modulate spatial biases in manual method-of-adjustment line bisection task (Jewell & McCourt, 2000). When observers perform line bisection tasks in free viewing conditions, bisection errors are influenced by the direction of visual scanning. Dextral and sinistral observers (Brodie & Dunn, 2005; Brodie & Pettigrew, 1996) show a scanning influence where left-to-right visual scanning of the line results in leftward errors while right-to left visual scanning of the line results in rightward errors. The direction of this bias is hypothesized to be related to cultural factors such as reading direction habits. The idea that the direction of spatial errors depend on observers' reading habits is known as the 'directional hypothesis' (Chokron & Imbert, 1993). Scanning influences in VLB have also been found in hemineglect patients. Halligan and Marshall (1989) found that the magnitude of the rightward bisection error characterizing hemineglect decreases when patients move a computer cursor from left to right. The magnitude of hemineglect increases when a computer cursor is moved from right to left in free-viewing line bisection task. Despite the current evidence demonstrating the scanning influence in VLB, the mechanisms of this biasing effect are unknown. Furthermore the manner whereby oculomotor and attentional scanning jointly influence errors in VLB task has never been systematically studied.

In manual visual line bisection tasks, the execution of scanning eye movements has been reported to modulate bisection bias relative to no-scanning condition (Brodie, 2010; Brodie & Pettigrew, 1996; Chokron, Bartolomeo, Perenin, Helft, & Imbert, 1998; Chokron & DeAgostini, 1995; Chokron & Imbert, 1993). However, Hurwitz, Valadao, and Danckert (2011) have reported the opposite pattern of errors, finding that rightward error is induced by L->R scanning and leftward error is induced by R->L scanning. Differences in scanning influences may be related to different mechanisms for manual and ocular scanning, where manual scanning is influenced by the starting point of the scanning while oculomotor scanning is influenced by scanning direction (Hurwitz et al., 2011). A similar pattern of scanning-induced bisection error has also been demonstrated in a sample of 10-year old learning disabled children and in children with no history of developmental or learning disability. In free viewing LB, children with developmental dyslexia (DD) and attention-deficit and hyperactivity disorder (ADHD) exhibit rightward errors, while the control group errs leftward (Waldie & Hausmann 2010).

When shifting gaze through space, the most common eye movements executed by primates are saccades (SEM) and smooth pursuit (SPEM). SEMs consist of fast movements executed when shifting gaze between stationary targets. The trajectory followed by SEM is influenced by re-directing attention in space (Kustov & Robinson, 1996). SPEMs on the other hand are slow eye movements and are aimed at tracking moving objects. Because SPEMs track moving objects, these are characterized by ongoing and online visual feedback about object position. SPEMs are usually initiated between 90-150 ms after object's movement onset. Two main pathways projecting from high level cortical areas to low level motor areas in the brain stem have been associated with the programming and execution of eye movements. One pathway is linked to the FEF and controls the gain and velocity of the eye movements, whereas the other pathway is linked to the medial superior temporal area (MST) and controls for eye acceleration in SPEM (Nuding, Ono, Mustari, Büttner, & Glasauer, 2008). SEMs and SPEMs are often combined in order to follow moving objects (De Brouwer, Yuksel, Blohm, Missal, & Lefevre, 2002). SEMs are meant to ‘catch up’ with fast moving objects within the fovea while SPEMs are meant to compensate for stimulus’ movement by stabilizing objects in the fovea.

FMRI studies also show activation of parietal, frontal (FEF and SEF) and temporal cortical regions during overt execution of SEMs. These regions are activated bilaterally during overt shifts of attention and contralaterally during covert shifts of attention (Corbetta et al., 1998). In tachistoscopic visual line bisection task, lines are presented for short durations thus minimizing eye movements and scanning influences (McCourt & Olafson, 1997; Jewell & McCourt, 2000). Few studies have evaluated the differential effects of eye movements on line bisection biases. The goal of the present experiment was to measure how scanning influences LB error. Specifically, using eye-tracking in conjunction with a tachistoscopic visual line bisection protocol, this experiment evaluated whether the tonic leftward bias of visuospatial attention is modulated by the type and direction of attentional scanning, executed with or without eye movements. The influence of scanning in VLB was evaluated in conditions where SEMs and SPEMs were executed overtly or covertly to track an object moving leftward or rightward. If attention is allocated after eye movements are programmed, optimal attention allocation may be combined with eye movements (Rizzolatti et al., 1987). The main prediction of this experiment is that line scanning influences perceived midpoint such that overt scanning is more powerful than covert scanning. In other words, the effects of attentional scanning are larger when it is allocated in combination with eye movements.

B. Method

1. Participants

Recruitment criteria and strategy is described in Experiment 1. The initial sample consisted of 36 healthy right-handed naïve observers. After excluding individual datasets whose means were ±3 SD from the group mean, 32 observers remained. Mean handedness as measured by the Edinburgh Handedness Inventory (Oldfield, 1971) for males and females was 68.8 and 82.2, respectively; mean age for males and females was 23.8 and 24.4, respectively. Paired-samples t-test demonstrated no significant difference in age [$t_{(30)}$= -.295, p= .390] between male and female observers. There are significant differences in handedness [$t_{(29)}$= -2.067, p= .048] between male and female observers. However because sex is not our dependent variable, inferential statistics were performed on data collapsed across sex.

2. Instrumentation and calibration

Stimuli were displayed as in Experiments 1-3. Mean display luminance was 25 cd/m^2. Eye movements were tracked using an Eyelink 1000 (Tower-mounted) video-based eye tracker (SR Research Ltd., Ontario, Canada) at a sampling rate of 500 Hz.

3. Stimuli

Figure 12 illustrates the stimulus arrangement used in Experiment 4. Stimuli were horizontal lines of 100% Michelson contrast presented on a mid-gray background. At a viewing distance of 57 cm, line stimuli measured 26.5º x .50° (26 cm x .5 cm). Lines were pre-transected at one of 15 locations ranging from -0.30° to +0.30° around line midpoint.

4. Procedure

Trials began with the onset of a black target dot peripherally located with its center at 6.53° (6.50 cm) from the edge of the line. After onset, the target moved at a constant velocity (10°/sec) toward the center of the screen and observers were instructed to track the moving target. Target movement was contingent upon observer's gaze being within 26 pixels (.67°) distance of the target.

Figure 12. Example of the line stimulus used in experiment 4.

In the experiment, the target dot:

(1) Moved smoothly from its lateral location until landing on the display's midpoint (SPEM condition).

(2) Suddenly disappeared from its initial lateral location and rapidly re-appeared at the display's midpoint (SEM).

In the first eye-movement condition, SPEM, the dot stimulus moved at a speed of 10°/sec. Under conditions of overt attention and in both eye-movement conditions, observers visually followed the dot until it disappeared and the line appeared. After the dot was located in the center of the display, it disappeared and the line was tachistoscopically presented for 150 ms. To ensure fixation in the SPEM condition, the line location was jittered around the location of the last fixation. Jittering the line around the location of the last fixation ensured that the line was presented centered around the location of the observers' eyes. In the SEM condition, where observers' fixation had to be centered in order for line to appear, line position jittered around the center of the display.

Smooth pursuit and saccadic scanning were also performed under conditions of covert attention. In covert-attention conditions the dot was presented in the same way as in conditions 1 and 2 and observers attended to the peripherally moving dot while maintaining central fixation, i.e. without executing eye movements. To ensure compliance with these instructions a tolerance value was defined within a given central radius. The tolerance region was the area in the screen where the eye position had to be located for the trial to be successful. If the last fixation was located outside of the tolerance region, the line was also presented outside of this region and the trial was eliminated from the final analysis. In the smooth covert scanning condition, the line to be bisected was randomly centered at various locations within a 20 pixels (.52°) radius inside a centrally established tolerance region of 200 pix (5.17°) radius. In the saccadic covert scanning condition, the line was randomly centered at various locations within 20 pixels (.52°) inside a centrally established 26 pixel (.67°) radius region. Lines of opposite contrast polarity appeared with equal frequency and the order of appearance of lines with different transector locations was randomized within trial blocks.

A placeholder line of similar dimensions as the line stimulus to be bisected was centrally presented in the display to ensure the presence of a line in the display during visual scanning. The placeholder line had a checkerboard pattern and was used to reproduce the effect of observers manually bisecting free-viewed lines which are always visible in the display. The line stimulus to be bisected appeared 60 ms after the placeholder-line (and target) disappeared. The dot was always presented simultaneously with the placeholder-line but the dot and line stimulus were never presented simultaneously.

Nine-point eye tracker calibration was performed at the beginning of the experiment and recalibration was done before each block of trials. Observers made single-interval two-alternative forced-choice decisions judging transector location relative to each line's perceived midpoint by pressing either the left or right mouse button. Additionally, observers performed the VLB where no dot target was tracked (no scanning) and adjusted a cursor by moving the computer's mouse and cursor to 'manually' bisect the line. PSEs were obtained from conditions where the dot was tracked in overt or covert fashion with SPEM or SEM executed in leftward or rightward direction. These PSEs were combined to yield the following conditions: left smooth pursuit overt (L-SPEM-O), right smooth pursuit overt (R-SPEM-O), left saccadic overt (L-SEM-O), right saccadic overt (R-SEM-O), left smooth pursuit covert (L-SPEM-C), right smooth pursuit covert (R-SPEM-C), left saccadic covert (L-SEM-C), right saccadic covert (R-SEM-C). Figure 13 plots pursuit as a function of dot position in the display. This is an example of individual performance in the SPEM-O condition throughout a trial. The dot and eye position are plotted as a function of the point in space. The eye position (ordinate) varies with variations of the dot. Observers performed a total of 1560 trials.

5. Design and data analysis

Design and data analyses were performed as in Experiment 1, using a 2 (scan direction: leftward, rightward) x 2 (scan type: SPEM, SEM) x 2 (attention type: covert, overt) within-subjects design.

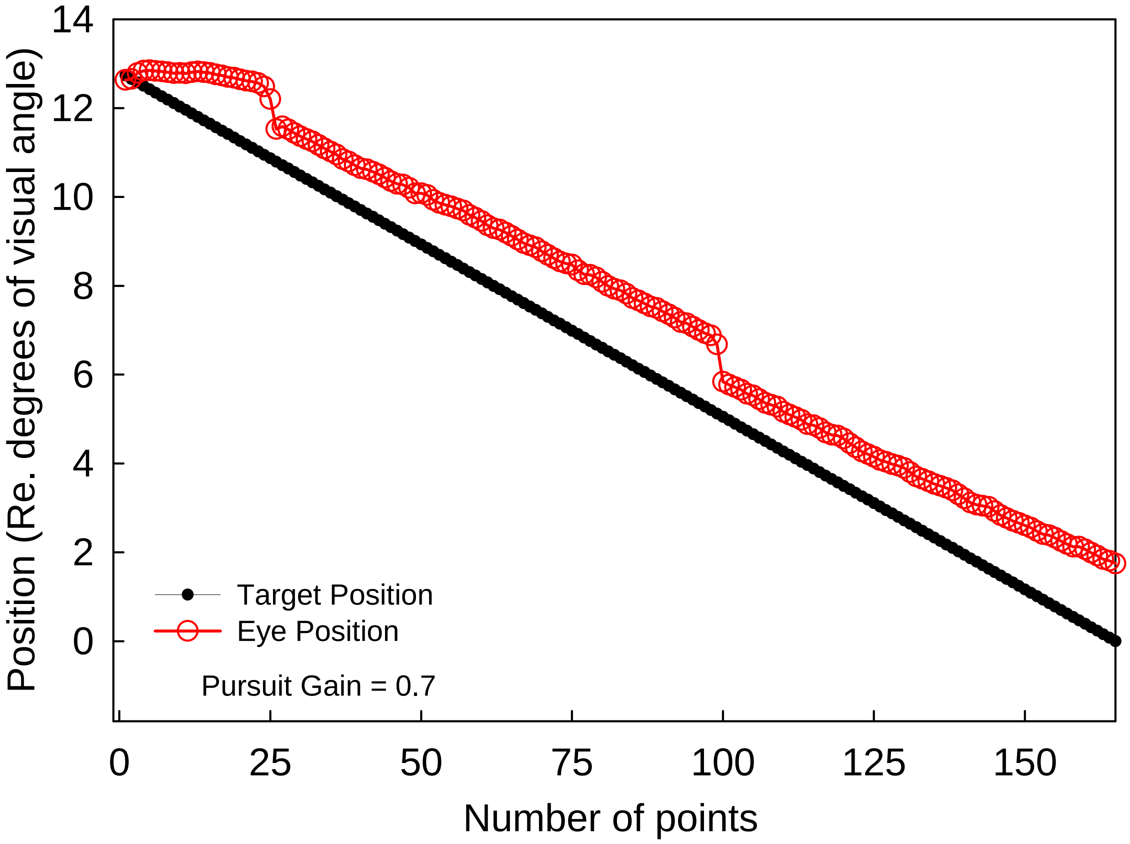

Figure 13. Smooth pursuit of target dot by one observer.

C. Results and discussion

1. Scanning effects in visual line bisection

Figure 14 illustrates the main results of experiment 4 evaluating the potency of attentional and visual scanning to bias perceived line midpoint. A 2 (scan direction) x 2 (scan type) x 2 (attention type) repeated measures ANOVA revealed a significant main effect of scanning direction, F(1,31)= 27.198, p < .001, where perceived line midpoint was significantly biased in the scanned direction. A significant main effect of scanning type, F(1,31)= 4.292, p = .047, where perceived line midpoint was significantly more influence by smooth pursuit compared to saccadic eye movements. This main effect was moderated by significant 2-way interactions. The first is a scan direction x scan type interaction where the effect of scan direction is larger for SPEM than for SEM, F(1,31)= 14.469, p = .001. The second is a scan direction x attention type interaction where the effect of scanning direction is larger for overt versus covert attention, F(1,31)= 37.031, p < .001. There was also a significant scan type x attention type interaction, where the effect of scanning type is larger for overt versus covert attention, F(1,31)= 15.059, p = .001. Finally, there was a significant scan direction x scan type x attention type 3-way interaction, F(1,31)= 10.454, p= .003. The source of the three way interaction was explored by conducting a 2 x 2 ANOVA between different conditions of the independent variables. A 2 (scan direction) x 2 (scan type) repeated measures ANOVA conducted for overt scanning conditions revealed a significant 2-way interaction where the effect of scanning direction in overt attention is larger for smooth pursuit than saccadic scanning, F(1,31)= 44.420, p< .001.

Compared to no-scanning, SEM executed leftward did not influence perceived midpoint in overt [$t_{(35)}$= -1.896, p= .066] or covert [$t_{(35)}$= -1.484, p= .147] conditions. Compared to no-scanning, SPEM executed leftward did not influence perceived midpoint in covert condition [$t_{(35)}$= -1.183, p= .245].

Figure 15 plots mean smooth pursuit gain in the leftward and rightward scanning conditions. There is a significant difference in mean gain for leftward (.671) versus rightward (.720) smooth pursuit eye movements, where rightward eye movements have the higher gain, [$t_{(35)}$= -3.209, p= .003]. The higher gain of rightward smooth pursuit eye movements indicates a greater tracking accuracy for rightward versus leftward scanning. However, the mean rightward gain was significantly different from 1, [$t_{(35)}$= -10.655, p< .001].

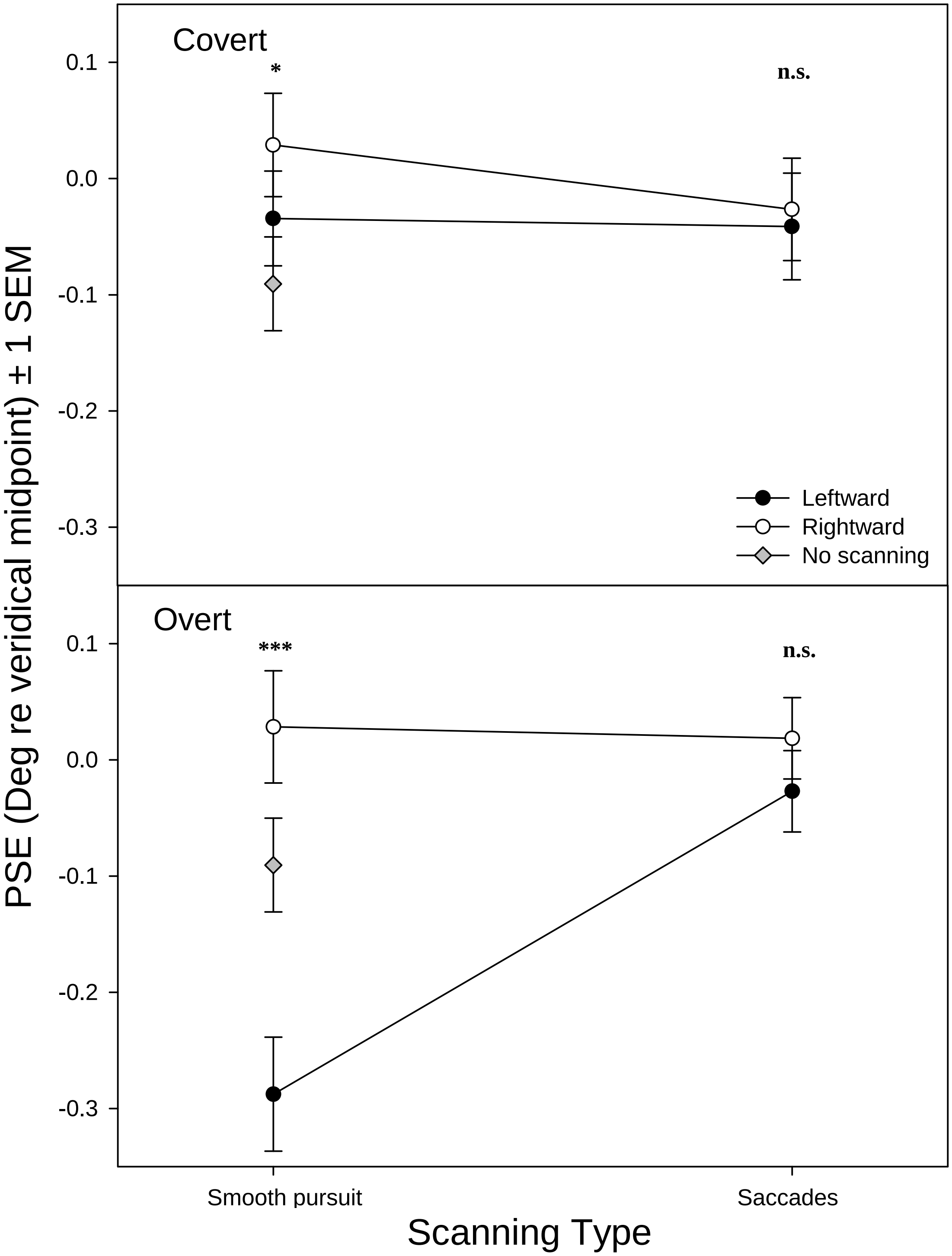

Figure 14. Mean PSE (± 1 S.E.M.) as a function of eye movement type plotted for covert (top) and overt (bottom) scanning. White symbols plot PSE in trials where observers

tracked object rightward, while black circles plot PSEs in trials where observers tracked object leftward. Grey diamond plots average PSEs in the no-scanning condition.

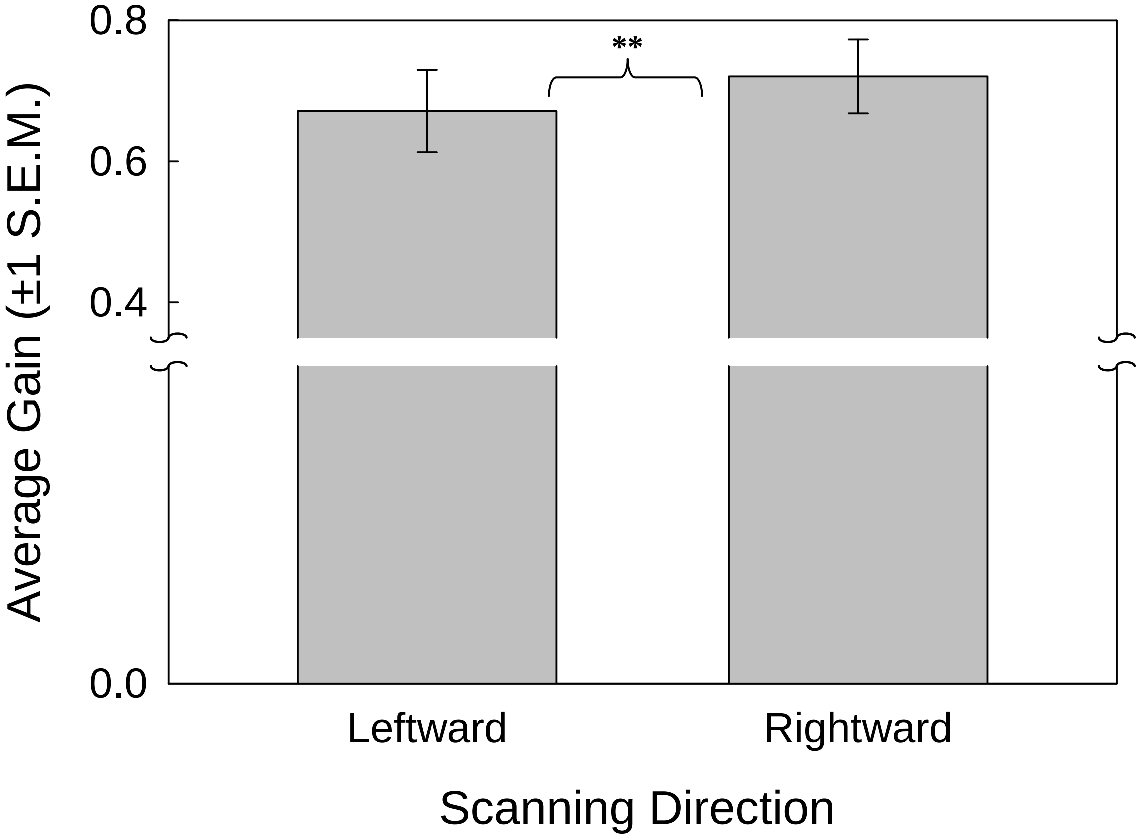

Figure 15. Average pursuit gain (±1 S.E.M.) for leftward and rightward scanning.

Figure 16 plots the effects of scanning in the manual-bisection condition. In this figure, the black bar plots average perceived midpoint in leftward manual scanning whereas the grey bar plots average perceived midpoint in rightward manual scanning. The main outcome of the manual VLB was similar to that found in oculomotor scanning VLB: leftward scanning led to significantly larger leftward bisection error than rightward scanning, [$t_{(31)}$= -5.633, p< .001].

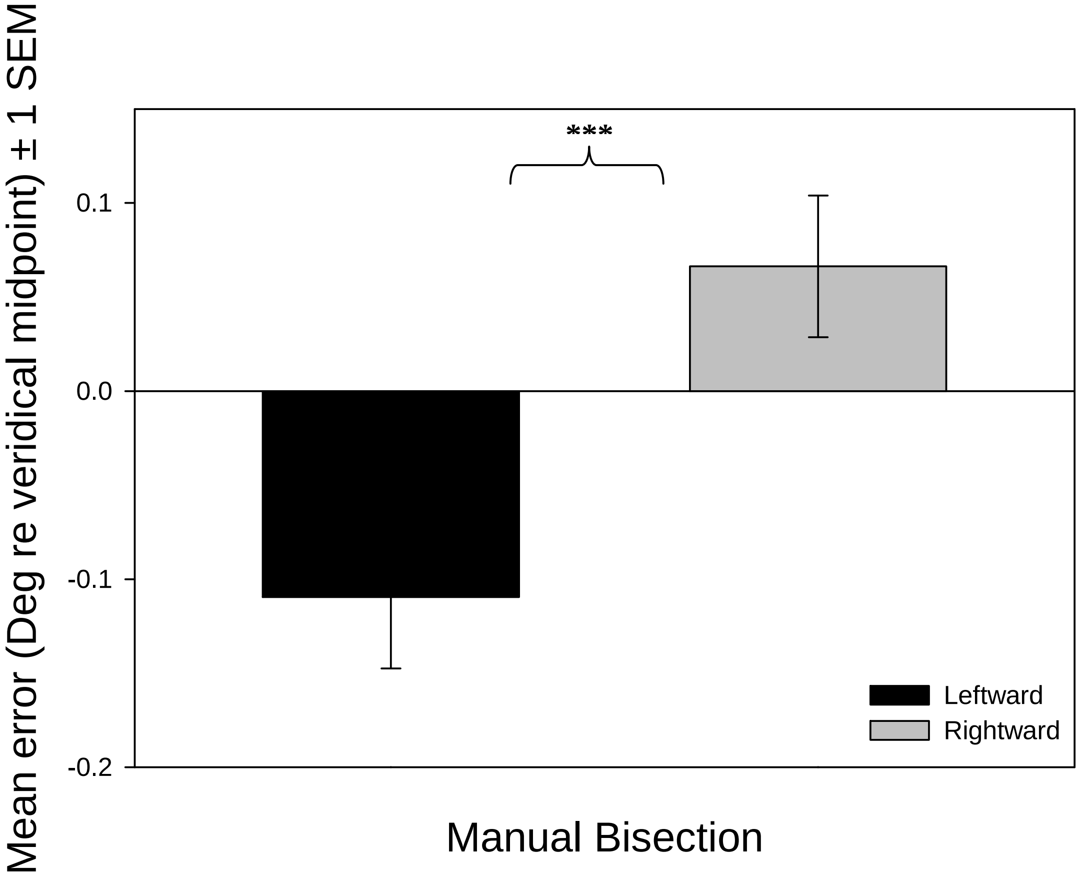

Figure 16. Mean PSE (± 2 S.E.M.) as a function of manual scanning direction in VLB.

Experiment 4 demonstrates that rightward scanning results in rightward bisection error and leftward scanning results in leftward bisection error. These findings are consistently found for ocular and manual scanning and are opposite to the majority of the literature evaluating scanning influences in VLB. While these previous experiments evaluate biases in manual-method of adjustment (Brodie, 2010; Brodie & Pettigrew, 1996; Chokron et al., 1998), few have systematically evaluated the role of eye movements on this bias. PN has been associated to the directional hypothesis, which establishes that reading direction habits determine the error direction in VLB (Chokron & DeAgostini, 1995; Chokron & Imbert, 1993). However, the present findings do not support the notion that PN is related to the direction of reading habits. First, leftward scanning resulted in heightened leftward error. Second, the influence of leftward scanning on perceived line midpoint was greater than the influence of rightward scanning. Because the present observers were English readers with left-to-right reading habits, the directional hypothesis would have predicted a bias in the opposite direction to what was found.

However, our findings are consistent with those of more recent studies indicating that L-R scanning results in rightward error and R-L scanning results in leftward error. This pattern of biases is found in children (Waldie & Hausmann, 2010) and young adults (Hurwitz et al., 2011) performing oculomotor (Hurwitz et al., 2011) and manual (Waldie & Hausmann, 2010) scanning. Additionally, this biasing pattern resulting from scanning lines has been shown in normal (Hurwitz et al., 2011) and special (Waldie & Hausmann, 2010) populations.

Smooth pursuit scanning was significantly more potent at biasing perceived midpoint than saccadic scanning. On their own, SEMs were not effective at biasing perceived midpoint. One possibility of the weak influence of SEMs may be related to an ‘oculomotor distractor effect’. Responses can be slowed by asking observers to execute SEMs to targets presented simultaneously with irrelevant stimuli. Irrelevant stimuli can interfere with the programming of SEMs by capturing attention automatically, and thus interrupting the neural signal from the SC (Walker, Mannan, Maurer, Pambakian, & Kennard, 2000). In the present experiment, a placeholder line was displayed while observers tracked the moving dot. However, there is no clear evidence demonstrating that the placeholder-line constituted a distracting stimulus during overt SEMs. Another question that remains unanswered is whether the SEMs and the SPEMs conditions impose similar attentional demands on the observers.

The biasing effect of overt scanning is significantly greater than that of covert scanning. In both instances observers were instructed to ‘attend’ to the moving dot and hence the only difference between the two conditions was the execution of the eye movements in the overt compared to the covert condition. In the present experiment, the finding that the allocation of covert attention is not sufficient to significantly modulate perceived midpoint, argues against the notion that there is a functional overlap between spatial attention and eye movements (Corbetta et al., 1998; Rizzolatti, 1987). Attention and eye movements are believed to share some neural mechanisms within prefrontal, parietal and subcortical regions where attentional scans are subthreshold versions of eye movements. The pre-motor theory of attention establishes that covert attention results from eye movement preparation within the motor system (Rizzolatti et al., 1987). Alternatively, it may be merely a quantitative difference where eye movements are caused by a larger activation than covert attentional shifts. The larger activation characterizing the eye movements is needed to bias VLB, or maybe the corollary discharge that accompanies eye movements (but not covert scans) is involved in VLB.

PN analysis. PN analysis (performed as in Experiment 1-3) demonstrates no significant leftward error in no scanning condition [$t_{(35)}$= -1.576, p= .124] demonstrating variability between the observers evaluated in this experiment relative to Experiments 1-2.

CHAPTER VI. GENERAL CONCLUSIONS

Attention is a multidimensional theoretical construct and is typically broken down and analyzed in terms of its various subcomponents (Mather, 1990; Barnett, 2005). The experiments described in this dissertation address how phasically recruited exogenous attention interacts with the tonic attentional asymmetries which give rise to PN. Experiments 1 and 2 analyzed in detail the temporal and intensive properties of cues (cue-line SOA, contrast) that make them effective in recruiting spatial attention, whereas experiment 3 focused on their spatial properties (location). Finally, Experiment 4 evaluated the influence of scanning in the tonic attentional asymmetries of VLB.

A. Exogenous attention capture in VLB

The present study shows asymmetric attentional capture by exogenous cues with right cues exerting greater influence than left cues. Our finding that exogenous cues modulate PN such that right cues are more potent than left cues is consistent with previous findings (McCourt et al., 2005; Nicholls & Roberts, 2002). However there is no unified pattern of findings addressing asymmetric cueing effects. For example, the right cue preference characterizing the present findings is not consistent with other reports (Michel et al., 2007; Michel, Bidot, Bonnetblanc, & Quercia, 2011), who find no difference in the potency of right and left cues. The apparent discrepancy between these patterns of results, however, might be explained by the fact that these studies employ different stimuli, methodology, and populations. Folk, Remington, and Johnston (1992) proposed that exogenous capture is dependent upon the relationship between stimuli characteristics and task demands. In other words, there is an interaction between exogenous and endogenous systems. Exogenous stimuli will capture attention if the cue shares some properties with the task at hand (contingent involuntary orienting).

The present study demonstrates that transient cues produce fast exogenous attentional capture in VLB. Experiment 1 shows that optimal exogenous attentional capture is found at a short cue-line SOA. In the present experiment maximal cue influence was found at SOA of around 60 ms, with a 95% bootstrapped confidence interval of 26-90 ms. These findings are consistent with previous findings evaluating the effect of cue-target SOA in exogenous attentional capture (Folk et al., 1992) and cue-line SOA in line motion illusion (Bavalier et al., 2002). Folk et al., (1992) and Folk, Remington, and Johnston (1992) cued one of five boxes with small circles and asked observers to respond to characters successively flashed inside one box. The outcome was decreased RT with increased SOAs, and a maximal effect at 150 ms. Remington, Johnston, and Yantis (1992) employed a similar cueing paradigm and found an optimal exogenous cueing effect at cue-target SOA of 200 ms. In line motion illusion, Bavelier et al. (2002) cued a line with an abrupt central gaze and found an optimal SOAs of 300 ms where the illusion was the strongest. As has been previously discussed, that IOR was not found may be explained by factors such as nature of the present experiment, the attentional demands of the task or the range of the SOAs evaluated.

Thiebaut (2011) proposed that there is imbalanced conduction speed between the two hemispheres along the middle superior longitudinal fasciculus (SLF). The imbalance favors the right hemisphere. The authors interpret increased speed in the right compared to the left hemisphere from diffusion tractography revealing the right middle SLF to be larger than the left. Larger tracts in the right middle-SLF may result from greater myelination, greater number of axons, or large axonal diameter in right than the left hemisphere. Brain asymmetry is significantly correlated with PN in VLB and left target facilitation in a Posner-type cueing paradigm. In the brain, the fronto-parietal connections are organized in dorsal superior, middle and ventral SLF longitudinal tracts. The authors suggest that the middle-SLF mediates the activity of the dorsal and ventral SLF (Thiebaut et al., 2011). A future experiment should expand the range of the SOAs tested in order to evaluate if cueing effects occur at shorter cue-line SOAs.

<u>Results from experiment 2 demonstrate that only cues presented at high visual contrast efficiently capture exogenous attention</u>. Cues presented at contrasts below 12% did not exert any influence on perceived midpoint, and the greatest influence was found at the maximum contrast (100%). These results are consistent with previous studies on evaluating awake-behaving monkeys (Thiele, Pooresmaeilli, Delicato, Herrero, & Roelfsema, 2009) and human observers (Fuller et al., 2009) which showed that only cues stimuli of 10% contrasts or greater result in response facilitation. Thiele et al. (2009) trained macaque monkeys to detect luminance changes in a target presented at a cued location while ignoring luminance changes at the uncued locations. Neuronal firing revealed attentional facilitation for all stimulus contrasts above 10%. In human samples, Fuller et al. (2009) cued peripheral locations with stimuli of various contrasts while observers performed a localization task. Cue influence in VLB error is usually found despite explicit instructions to the observers to disregard any kind of stimulus besides the line. These cueing effects are consistent with automatic attentional capture by the cues.

Many previous accounts have proposed that the M stream disruption is a common factor involved in the attentional anomalies characterizing various neuropsychiatric conditions such as hemineglect (e.g. Doricchi, Angelelli, Luca, & Spinelli, 1996; Doricchi, Incoccia, & Galati, 2007; Pitzalis, Di Russo, & Spinelli, 2005) and schizophrenia (e.g. Bedwell, Brown, & Miller, 2003; Butler et al., 2001; Coleman et al., Martinez et al., 2008; Skottun & Skoyles, 2007; Szabolcs et al., 2005). The M stream is also related to visual asymmetries in healthy observers. However, experiment 2 shows that low contrast cues (which would be expected to activate only the M channel) were ineffective at influencing perceived midpoint. At high contrast cues both M and P channels could be operating.

Parvocellular involvement has also been found in previous evaluations of normal exogenous attention. There are similar behavioral and neural responses to exogenous cues in the P and M streams. Automatic attention is recruited by equiluminant and luminant cues. Chromatic cues are the ones processed by equiluminant channels while achromatic cues are the ones selectively processed by luminance channels. Chromatic stimuli are processed by P (and K) cells whereas achromatic stimuli are processed by both M and P channels (Ries & Hopfinger, 2011; Snowden, 2002).

Experiment 3 demonstrates that attention capture resulting from the lateral cues is found not only in spatiotopic but also in allocentric reference frames. Previous work investigating how spatial cue location modulates responses in VLB used a perceptual grouping explanation. According to this account, when the cue and the line are grouped together, the result is a perceptual elongation of the line by the cue that shifts perceived midpoint from veridical center. This account proposes that the perceptual grouping of the cue and the line is based on the gestalt perceptual principle that observers can make meaningful relations by decomposing objects into their primary features (primitives) (Fischer, 1994). Our findings, however, cannot be explained by perceptual grouping because although the cue and line were spatially overlapped they were never presented simultaneously. Instead, our results support recent studies showing that cue influences in visual line bisection task are explained by attentional rather than perceptual processes (Kashmere & Kirk, 1997; McCourt et al., 2005; Toba, Cavanagh, & Bartolomeo, 2011). The cue captures observer's attention, modulating line bisection judgment.

Post et al. (2001) found modulation in the magnitude of object based PN when observers bisected a line but not when observers bisected an interval. The line is an object but a blank interval is not. Nicholls, Hughes, Mattingley and Bradshaw (2004) as well as Orr and Nicholls (2005) showed that manipulations of relative stimulus position in greyscales task results in modulations of PN magnitude. Orr and Nicholls (2005) displayed greyscales bars at various positions around the observers midline and found increased leftward bias for centrally presented bars relative to other bars in the display. These findings demonstrate that changes in relative object arrangement modulate perceived luminance. Allocentric neglect is defined using stimulus relative position as reference and implies dysfunctional attentional selection for objects and shapes. In allocentric neglect, patients ignore the left side of objects. However neglect and PN can be affected by object and space based attentional errors. Kravitz and Behrman (2011) presented a target letter after a valid or invalid cue. The invalid cue locations could be contained within a bar (an object) or outside of a bar. In different conditions the bars could have similar or distinct color (feature). The main outcome of the experiment was that different forms of attention can coexist and affect each other where attention performs an organization rather than a mere selection process. According to this account there can be facilitation in instances where objects share location, category or membership. Facilitation can result from a dynamic and interactive influence between and within different types of attention (featural, object, and spatial). For example, cued objects may affect the processing of uncued objects if they share some semantic properties.

B. Scanning effects in VLB

Oculomotor and manual scanning influence perceived line midpoint. The main result of experiment 4 is that PN is modulated by visual scanning where left scanning increases leftward error and right scanning decreases leftward error or results in rightward error. As mentioned previously, these findings are inconsistent with some studies. Previous accounts showed that line scanning modulate bisection bias such that L->R scanning induces leftward error, and R->L scanning induces rightward error (Brodie, 2010; Brodie & Pettigrew, 1996; Chokron et al., 1998; Chokron & DeAgostini, 1995; Chokron & Imbert, 1993). Our findings agree with reports by Hurwitz et al., (2011) who found similar pattern of results in normal observers executing SPEM through lines. In these studies, leftward pursuit resulted in increased leftward error while rightward pursuit resulted in rightward error.

Chokron and DeAgostini (1995) and Chokron and Imbert (1993) also proposed a relationship between PN and reading habits. The present study shows no evidence of such a relationship. Instead we find a greater influence of leftward than rightward scanning in VLB. Additionally, previous studies have found PN in left-to-right readers as well as right-to-left readers performing the VLB (Ishii, Okubo, Nicholls, & Imai, 2011) and RSVP tasks (Smigasiewicz et al., 2010). Ishii et al., (2011) found a leftward error in English and Japanese readers performing a manual VLB. In the described study, the magnitude of the error was greater in Japanese compared to English readers. Similarly, there is a left hemifield advantage when German, Hebrew and Taiwanese readers perform a RSVP task (Smigasiewicz et al., 2010).

Experiment 4 demonstrates that scanning influence in VLB is asymmetric with greater bisection error when leftward overt scanning is executed compared to rightward scanning. Supporting evidenced that oculomotor programming has a direct effect on the allocation of visuospatial attention is provided by electrophysiological and behavioral studies. Moore and Fallah (2007) show FEF activation when monkeys execute SEMs to peripheral stimuli. Additionally, impaired SPEMs have been linked to executive dysfunctions in schizophrenia (Doniger, 2002; Szabolcs et al., 2005). The premotor theory of attention asserts that eye movements and attention share neural circuitry, where attentional shifts are programmed (but not yet executed) eye movements (Rizzolatti et al., 1987).

Primates possessing a fovea execute both SPEMs and SEMs. SPEMs are composed of an open-loop phase and a closed loop phase. The open loop phase is a ballistic movement where the eyes try to correct for the moving position of the tracked object (Krauzlis & Lisberger, 1994). This phase lasts around 100 ms (Krauzlis & Lisberger, 1994; Schutz, Braun, & Gegenfurtner, 2007). In the closed loop phase the eyes make constant online correction for the retinal slip of the moving object (Krauzlis & Lisberger, 1994). To follow objects accurately, the pursuit system calculates the speed of the moving object in order to make predictions about its trajectory. In some instances, the predictions can lead to anticipatory pursuit. This anticipation is more marked during non-randomized compared to random object movements (Heinen, Badler, & Ting, 2005). Königs and Bremmer (2010) found object mislocalization in the direction of the SPEM. When observers were asked to indicate the direction of moving flashes, perceived positions were shifted in direction of the pursuit. This mislocalization starts in the open-loop phase. In SPEM, gain is defined as relative velocity (Bayer, Eggert, Glasauer, & Buttner; 2008). Experiment 4 demonstrates asymmetric pursuit gain where rightward gain is greater than leftward gain suggesting that the eyes were tracking the dot more closely during rightward versus leftward scanning. However, future studies should record eye position throughout the duration of the trial to rule out the positioning of observers' center of gaze within one specific hemifield. The reason why observers center of gaze could be located in one hemifield is because the eye continues to move after the stimulus disappears.

A potential explanation for differential bisection error is that asymmetric allocation of attention magnifies the left space (or objects) relative to right space (or objects). This proposal is supported by various studies demonstrating left magnification when observers estimate the size of centrally presented objects (Nicholls et al., 1999) or the relative size of bilaterally presented stimuli (Charles et al., 2007; McManus & Tomlinson, 2004). McManus and Tomlinson (2004) asked observers to judge size of tachistoscopically presented objects and objects in free viewing conditions. When equally sized stimuli were presented tachistoscopically in left or right hemifields, observers judged the stimulus presented within the left hemifield to be larger. In free viewing conditions leftward bisection error was found when observers selected the largest stimulus from a pair of circles (McManus & Tomlinson, 2004). Moreover, RT is faster when observers select left objects as the largest relative to right objects. Fast RT suggests greater level of certainty in response to stimuli within the left visual hemifield compared to the right visual hemifield. When viewing a pair of ellipses, observers estimate the left object to be wider than the right object (Charles et al., 2007). In our experiment, the moving object was only tracked through the center. The ‘left space magnification explanation’ is a hypothesis that needs further exploration. One method for doing so would be to record eye movements while observers track a target moving across the whole display rather than half of the display. Another experiment could present a pair of objects after directional scanning of space and ask observers to judge relative size. If the leftward bisection error in line bisection (PN) at baseline is explained by attentional magnification of the left line portion, then the present results imply that visuospatial attention is deployed asymmetrically around scanned targets such that a larger portion is allocated ahead of the target compared to any other location (Khan, Lefèvre, Heinen, & Blohm, 2010).

C. Why study asymmetric attentional capture in visuospatial tasks?

Attentional capture by visuospatial stimuli is a fundamental function governing everyday tasks critical for survival. Visuospatial attention also permeates various fields of study not directly related to cognitive or brain sciences. For example, Nicholls, Orr, Okubo and Loftus (2011) demonstrated that observers judgments in likert scales are influenced by spatial biases. Observers tend to select numbers that are to the left. The outcome depends on the scale arrangement, such that satisfaction ratings in likert scales are greater in descending scales compared to ascending scales. This preference is usually related to the notion that right hemisphere structures are predominantly responsible for devoting excessive spatial attention to the contralateral hemispace and producing leftward errors in horizontal physical (Caramazza & Hillis, 1990; Di Pellegrino, 1995; Foxe et al., 2003; Jewel & McCourt, 2000; McCourt, 2001; McCourt & Jewell, 1999; McCourt & Olafson, 1997; Mesulam, 1999; Ptak et al., 2007; Tamietto, et al., 2005) and numerical (Fischer, 2001; Fischer, Castel, Dodd, & Pratt, 2003; Loftus et al., 2009; Nicholls et al., 2008) lines, luminance judgment (Mattingley et al., 2004; Nicholls et al., 1999; Nicholls et al., 2005), facial emotion judgment (Bradshaw & Nettleton, 1981; Asthana & Manual, 2001; Everdell et al., 2007; Heller & Levy, 1981; Indersmitten & Gur, 2003; Levy et al., 1983; Natale et al., 1983; Yovel et al., 2003; Butler & Harvey, 2005) numerosity judgment (Nicholls et al., 1999; Pasini & Tessari, 2001; Piazza et al., 2006), size estimation (Charles et al., 2007; McManus & Tomlinson, 2004; Nicholls et al., 1999) and visual search (Della Sala et al., 2010).

The greater activation of the right hemisphere during spatial judgments is diminished by brain lesions. The study of the normal and abnormal manifestations of visuospatial attention affects other fields of study including public health, rehabilitation, education and economics. Deficits in spatial processing have also been related to learning difficulties. There is evidence demonstrating that an appropriate development of mental number lines can predict normal learning capabilities. The ability to spatially compare numerical magnitudes within a line arrangement is a good predictor of normal development of numerical skills and subsequent dyscalculia (Laski & Siegler, 2007). It is also estimated that about 20% of people suffering from a stroke affecting the right hemisphere develop hemineglect (Appelros et al., 2002). In addition to the high incidence of hemineglect, other neurocognitive conditions are characterized by visuospatial dysfunctions. For example Hari, Renvall and Tanskanen (2001) showed that there is a deficit in automatic attention when observers with ADHD respond to stimuli presented in rapid succession. Additionally, observers with ADHD and observers suffering from dyslexia show significant rightward error in VLB. Dysfunction is also found when observers with dyslexia perform temporal order judgments and estimate motion direction in a line motion illusion paradigm (Hari, Renvall, & Tanskanen, 2001).

Abnormal allocation of visuospatial attention has also been related to dysfunctional eye movements. Observers with autism experience impaired SPEM and spatial deficits (Takarae, Minshew, Luna, Krisky, & Sweeney, 2004), and individuals with schizophrenia show atypical VLB errors (e.g. Cavézian et al., 2011; McCourt, Shpaner, Javitt, & Foxe, 2008). For example in autism, SPEM dysfunction is characterized by reduced closed-loop gain in leftward and rightward tracking and reduced open-loop gain. Results from evaluating visuospatial attention and eye movement have contributed to the development of various therapies. Some therapies for hemineglect aim at compensating for cognitive deficits by exploiting intact brain functions. One method, 'visual scanning', trains patients to scan space in complete patterns in a right-to-left direction. This strategy aims at biasing patients' attention leftward of center in order to ameliorate the left neglect (Ting et al., 2011). Interestingly, our results are consistent with current clinical practices where the bias follows the trajectory of scanning. Another strategy that has been implemented to correct for the errors characterizing hemineglect is 'training with cueing' in which spatial cues (which can be to various sensory modalities) are presented unilaterally in the neglected hemifield to aid with attentional capture. Automatic recruitment of attention towards the cue location (or object) increases saliency of cued space (or object). However, the benefits from these therapies are usually transitory. No systematic studies have explored how to optimize therapeutic effects to produce longer lasting results (Ting et al., 2011). By evaluating the optimal parameters for influencing spatial attention, customized programs could be used to train observers. The present approach provides information about the timing, visual resolution, reference frame and oculomotor mechanisms influencing visuospatial attention in VLB. The connection between spatial attention, everyday tasks and neurological symptoms establishes the need for approaching these issues from an integrated perspective where basic science, clinical practice, policy making and education work together.

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APPENDIX A. CONSENT TO PARTICIPATE IN RESEARCH

Title of Research Study: Eye Movements and Visuospatial Attention

This study is being conducted by:

Professor Mark E. McCourt, Geosciences 201 (or 119J Minard Hall), Department of Psychology; and Yamaya Sosa, 334 Minard Hall, (graduate student) from the Department of Psychology, at North Dakota State University.

Why am I being asked to take part in this research study?

You are invited to participate in a research study of eye movements and spatial attention. You have been invited to participate in this study because you are at least 18 years of age, you understand written and spoken English, and have normal or corrected-to-normal vision.

What is the reason for doing the study?

When estimating the midpoint of a horizontal line, healthy observers misjudge it systematically leftward of true center, reflecting right hemisphere dominance in the allocation of visuospatial attention. This study investigates whether this normal visuospatial bias is influenced by the type (saccadic, smooth pursuit) and direction (left-to-right, right-to-left) of eye movements. The results will inform theories of visuospatial attention and the role of eye movements.

What will I be asked to do?

If you decide to participate in this experiment we will ask you to read and sign the consent form and answer a handedness questionnaire, then we will explain you the procedures in detail.

You will then be ask to seat at a comfortable distance from a computer screen and will observe lines and dots presented on the screen. Your task is to indicate where the center of the line appears to be. You will indicate your response clicking the left or right computer mouse button. In order to investigate the exact location of your eyes during the task we will record your eye movements using a remote video-based eye tracker.

Where is the study going to take place, and how long will it take?

This study will take place in our Laboratory facility located in Minard Hall. Experiments of this kind generally take about 60-120 minutes to be completed.

What are the risks and discomforts?

There is no deception whatsoever used in this experiment. There are no known risks involved in these tasks. It is not possible to identify all potential risks in research procedures, but the researcher(s) have taken reasonable safeguards to minimize any known risks to the participant.

What are the benefits to me?

This study is designed to answer basic questions regarding the neural basis of visuospatial attention. There is no anticipated direct benefit from participating in this research study.

What are the benefits to other people?

Basic research experiments like this have no immediate and direct benefit to individual participants. It is however, hoped that through basic research of this type we will gain insight into the neural mechanisms of normal visuospatial attention which may inform treatments for neurological conditions such as hemineglect syndrome.

Do I have to take part in the study?

Your participation in this research is completely voluntary. If you decide to participate in the study, you may change your mind and stop participating at any time without penalty or loss of benefits to which you are already entitled.

What are the alternatives to being in this research study?

You have the alternative of not consenting to participate in this research study. If you do not wish to participate you may discontinue at any time. In this case, you will be given credit for your time at the rate of 1 credit point per 15 minutes completed. You can also discuss with the class Instructor other ways to earn extra credits for the course. If you are participating in this experiment for monetary compensation you will get paid for time completed at the rate of $2.50 per 15 minutes participation.

Who will see the information that I give?

All information that is obtained from your participation during this study that can be identified with you will remain strictly confidential, and will not be disclosed without your written permission. We will keep private all research records that identify you. Your information will be combined with information from other people taking part in the study. When we write about the study, we will write about the combined information that we have gathered. You will not be identified in these written documents. We may publish the results of the study, but your name and other identifying information will not be disclosed. Data and records created by this project are the property of the University and the investigator. You may have access to information collected on or about you, but not to information collected on or about others participating in the project. At the conclusion of the project the data will be archived.

Can my taking part in the study end early?

Your participation is voluntary and you may quit at any time. Your decision whether or not to participate will not affect your course grade, your present or future relationship with North Dakota State University, the Department of Psychology, or the experimenters. If you decide to participate, you are free to withdraw your consent and to discontinue participation at any time.

Will I receive any compensation for taking part in this study?

If you decide to participate you will receive extra credit in your course for your participation at the rate of 1 credit per every 15 minutes completed. Your participation in the experiments will not influence your grades or performance in classes. If instead of receiving extra credits, you choose the monetary compensation, you will be paid at a rate of $2.50 per 15 minutes completed.

What if I have questions?

Before you decide whether to accept this invitation to take part in the research study, please ask any questions that might come to mind now. Later, if you have any questions about the study, you can contact the researchers, Yamaya Sosa at Y.sosamachado@ndsu.edu or Dr. Mark McCourt at mark.mccourt@ndsu.edu.

What are my rights as a research participant?

You have rights as a participant in research. If you have questions about your rights or complaints about this research, you may talk to the researcher or contact the NDSU Human Research Protection Program by:

- Telephone: 701.231.8908
- Email: ndsu.irb@ndsu.edu

- Mail: NDSU HRPP Office, NDSU Dept. 4000, PO Box 6050, Fargo, ND 58108-6050.

The role of the IRB is to see that your rights are protected in this research; more information about your rights can be found at: www.ndsu.edu/research/irb .

Documentation of Informed Consent:

You are freely making a decision whether to be in this research study. Signing this form means that

1. you have read and understood this consent form
2. you have had the consent form explained to you
3. you have had your questions answered, and
4. you have decided to be in the study.

You will be given a copy of this consent form to keep.

____ __________________

Your signature Date

____

Your printed name

____ __________________

Signature of researcher explaining study Date

____

Printed name of researcher explaining study

APPENDIX B. OLDFIELD LATERALITY QUESTIONNAIRE

Name/Number:________________________________Sex:______Age:

Please indicate your preferences in the use of your hands/feet/eyes in the following activities by filling in the appropriate bubble.

(a) Exclusively Left
(b) Mostly Left
(c) No Preference
(d) Mostly Right
(e) Exclusively Right

Hands

1. Writing ____________

2. Drawing ____________

3. Throwing a ball ____________

4. Using a scissors ____________

5. Using a toothbrush ____________

6. Holding a knife (without fork) ____________

7. Using a spoon ____________

8. Holding a broom (upper hand) ____________

9. Striking a match (hand holding match) ____________

10. Opening a box (hand opening lid) ____________

Feet

11. Kicking a Football ____________

Eyes

12. Looking in a peephole ____________