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Research report

Behavioral and electrophysiological evidence of opposing lateral visuospatial asymmetries in the upper and lower visual fields

Gerard M. Loughnane [a,b,*], *John P. Shanley* [c], *Edmund C. Lalor* [a,b,c,1] *and Redmond G. O'Connell* [c,d,1]

[a] *School of Engineering, Trinity College Dublin, Dublin 2, Ireland*
[b] *Trinity Centre for Bioengineering, Trinity College Dublin, Dublin 2, Ireland*
[c] *Trinity College Institute of Neuroscience, Trinity College Dublin, Dublin 2, Ireland*
[d] *School of Psychology, Trinity College Dublin, Dublin 2, Ireland*

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ABSTRACT

Neurologically healthy individuals typically exhibit a subtle bias towards the left visual field during spatial judgments, known as “pseudoneglect”. However, it has yet to be reliably established if the direction and magnitude of this lateral bias varies along the vertical plane. Here, participants were required to distribute their attention equally across a checkerboard array spanning the entire visual field in order to detect transient targets that appeared at unpredictable locations. Reaction times (RTs) were faster to left hemifield targets in the lower visual field but the opposite trend was observed for targets in the upper field. Electroencephalogram (EEG) analyses focused on the interval prior to target onset in order to identify endogenous neural correlates of these behavioral asymmetries. The relative hemispheric distribution of pre-target oscillatory alpha power was predictive of RT bias to targets in the lower visual field but not the upper field, indicating separate attentional mechanisms for the upper and lower visual fields. Analysis of multifocal visual-evoked potentials (MVEP) in the pre-target interval also indicated that the opposing upper and lower field asymmetries may impact on the magnitude of primary visual cortical responses. These results provide new evidence of a functional segregation of upper and lower field visuospatial processing.

1. Introduction

When neurologically healthy individuals are asked to distribute their attention equally across the left and right hemifields, they typically display a subtle leftward attentional bias, a phenomenon known as “pseudoneglect” (Bowers & Heilman, 1980). Pseudoneglect has attracted a great deal of interest from researchers over several decades for the insights it offers into the functional asymmetries of the neural systems

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[*] *Corresponding author*. Trinity College Dublin, Dublin 2, Ireland.
E-mail addresses: gerontium@gmail.com, loughnag@tcd.ie (G.M. Loughnane).
[1] These authors made an equal contribution to the manuscript.

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governing directed visuospatial attention (Bowers & Heilman, 1980; Kinsbourne, 1977; Thiebaut de Schotten et al., 2011) and because it represents a stable individual trait (Bellgrove et al., 2009; Benwell, Thut, Learmonth, & Harvey, 2013; McCourt, 2001; Newman, O'Connell, Nathan, & Bellgrove, 2012; Tomer, 2008; Tomer et al., 2013) that is reliably disrupted by a number of clinical conditions such as Attention Deficit Hyperactivity Disorder (ADHD) (Bellgrove et al., 2009; Chan et al., 2009; Sheppard, Bradshaw, Mattingley, & Lee, 1999) and Alzheimer's Disease (Sorg et al., 2012). There is an emerging consensus that pseudoneglect likely arises from the dominant role played by the right hemisphere in regulating visuospatial attention e.g. (Benwell, Harvey, & Thut, 2013; Foxe, McCourt, & Javitt, 2003; O'Connell, Schneider, Hester, Mattingley, & Bellgrove, 2011; Thiebaut de Schotten et al., 2011). However, as will be discussed below, any theory of pseudoneglect will have to encompass evidence that the magnitude and direction of this lateral (left *vs* right) bias may vary as a function of the vertical (upper *vs* lower) eccentricity of the stimulus.

Extensive neuroimaging and clinical research indicates that visuospatial attention relies on interaction between two distinct fronto-parietal networks: a bilateral dorsal attention network that is activated by selectively attending to stimuli across space and a ventral attention network that biases the dorsal network towards novel or unexpected stimuli and is linked to non-spatial attention capacity and arousal e.g. (Corbetta & Shulman, 2011). The ventral network is strongly lateralized towards the right hemisphere, as are its connections to the dorsal network, and this natural imbalance appears to provide a neuroanatomical basis for pseudoneglect (Thiebaut de Schotten et al., 2011). This functional asymmetry may also account for the greater prevalence of unilateral neglect – the inability to attend to contralesional space – following right hemisphere damage (Husain & Rorden, 2003; Stone et al., 1991). Numerous studies have also demonstrated that the magnitude of pseudoneglect can be attenuated, or even reversed, by depleting ventral network processing resources through increases in attentional load or decreases in arousal (Benwell, Harvey, Gardner, & Thut, 2013; Newman, O'Connell, & Bellgrove, 2013; O'Connell et al., 2011; Perez et al., 2009). It is argued that de-activating the ventral network in this manner eliminates the competitive advantage afforded to right hemisphere regions of the dorsal network thus causing a rightward attentional shift (Corbetta & Shulman, 2011; Manly, Dobler, Dodds, & George, 2005).

While pseudoneglect is reliably observed across a variety of behavioral tests such as the line bisection task (Jewell & McCourt, 2000), landmark task (Milner, Harvey, Roberts, & Forster, 1993) and greyscales task (Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994), it is most commonly measured in the form of a simple left versus right hemifield comparison, without accounting for the potential influence of vertical eccentricity. This is an important consideration in light of proposals that visual attention in the upper and lower visual fields may be mediated by separate representational systems, the lower field processed as part of peripersonal or near space and the upper field processed as part of extrapersonal or far space (Previc, 1990).

A small number of behavioral studies have measured visuospatial asymmetries as a function of vertical stimulus location and these have consistently reported a leftward bias for stimuli appearing in the lower visual field. However, results for the upper field have been inconsistent, with studies reporting leftward (McCourt & Garlinghouse, 2000; Nicholls et al., 2012), rightward (Thomas & Elias, 2010, 2011), and no bias (Barrett, Crosson, Crucian, & Heilman, 2000; Drago, Crucian, Pisani, & Heilman, 2006). There are two methodological considerations that may account for these inconsistencies. First, most of these studies did not control for eye movement, leaving their findings open to individual differences in pre-and post-target fixation strategies. The one study that did measure eye position reported that the direction of upper field bias on the landmark task was partly dependent on eye movement (Thomas & Elias, 2011). Second, the perceptual and motor features of the paradigms varied across studies and it has been well established that visuospatial bias is modulated by a range of contextual factors such as line length for the landmark task (Benwell, Harvey, Gardner, et al., 2013; McCourt & Jewell, 1999), stimulus duration in the greyscales task (Thomas & Elias, 2011), object versus space-based influences in the greyscales (Orr & Nicholls, 2005; Thomas & Elias, 2012) and line bisection (Post, Caufield, & Welch, 2001) tasks, and motor considerations in manual line bisection (Barrett et al., 2000; Drago et al., 2006).

The present study had two principal goals. First, we sought to measure the direction and magnitude of behavioral biases for processing stimuli in the upper versus lower fields, while controlling for eye movements and maintaining fixation. To this end, we utilized a task that required monitoring an array that spanned the entire visual field for the onset of an embedded target whose location and time of onset was randomized, thus encouraging a diffuse spread of attention (Fig. 1). An eye tracker was used to abort any trials on which the participants moved their eyes. Based on previous research our hypothesis was that there would be a leftward reaction time bias in the lower visual field and no bias or a rightward bias in the upper field. Second, we sought to verify whether any observed behavioral biases reflect a fundamental imbalance in the allocation of attentional resources throughout space by examining endogenous electrophysiological markers of visuospatial attention prior to the onset of the critical stimulus – thus excluding the potential influence of paradigm-specific stimulus or motor features.

This paradigm is well suited for measuring two distinct neural signals whose sensitivity to spatial attention has already been established: posterior alpha-band (8–14 Hz) activity and multifocal visual-evoked potentials (MVEP). Posterior alpha power is well known to provide a sensitive index of the deployment of attention across visual locations e.g. (Capilla, Schoffelen, Paterson, Thut, & Gross, 2012; Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000) and has been primarily linked to regions of the dorsal attention network (Capotosto, Babiloni, Romani, & Corbetta, 2009; Laufs et al., 2006, 2003; Mantini, Perrucci, Del Gratta, Romani, & Corbetta, 2007; Sadaghiani et al., 2010). Previous work has demonstrated that the relative hemispheric distribution of alpha power, measured in the interval prior to a critical stimulus, predicts the accuracy and speed of target detection in cued