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

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\textbf{A B S T R A C T}

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.

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1. Introduction

When neurologically healthy individuals are asked to distribute their attention equally across the left and right hemisfields, 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...
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 (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 contralateral 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). Posterio 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
tasks (Kelly, Gomez-Ramirez, & Foxe, 2009; Thut et al., 2006). The small number of studies that have looked at the relationship between interhemispheric distribution of prestimulus alpha and target detection in uncued tasks have not yet found a significant link (Newman et al., 2013; Perez et al., 2009) but both studies used dual-task paradigms which may have complicated or obscured any relationship between alpha asymmetry and behavior. Most importantly in the context of the present study, it is not known if alpha power is equally sensitive to attentional deployment in the upper and lower fields. Here, we analyzed the hemispheric distribution of alpha power in the pre-target window to establish if any observed behavioral asymmetries reflect a pre-existing bias in the endogenous allocation of spatial attention.

Given that the alpha analysis is restricted to an overall comparison of left versus right hemisphere activity we also sought to isolate a neural marker of attention resource allocation for each sector of the visual field. For this we exploited the Multifocal Visual Evoked Potential (MVEP) technique which makes it possible to isolate primary visual responses for each checkerboard patch despite their simultaneous presentation (Baseler & Sutter, 1997; Baseler, Sutter, Klein, & Carney, 1994; Sutter, 2000). Previous work has demonstrated that the amplitude of MVEPs is increased by attention (Seiple, Clemens, Greenstein, Holopigian, & Zhang, 2002), in line with classic studies of the standard VEP (Clark & Hillyard, 1996; Hillyard, Vogel, & Luck, 1998). Thus, in theory, MVEPs have the unique potential to index the allocation of attentional resources to specific regions of space without the requirement of discrete stimulus presentations or overt behavioral responses. We predicted that, following the behavioral results, the lower field leftward bias would be supported by larger MVEP responses to the lower left versus lower right checkerboard patches.

Together with measurement of alpha asymmetry, these neural signals provide a rich objective measurement of the endogenous distribution of attention across the entire visual field.

2. Materials and methods

2.1. Participants

Data were collected from 25 right-handed volunteers with normal or corrected-to-normal vision and no history of neurological disorder or head injury. One subject was excluded from further analysis due to unusable EEG data (>50% of trials rejected for artifacts) leaving a final sample size of 24 (13 males), aged 18–40 years ($M = 23.1$). All participants provided written informed consent and all procedures were approved by the ethical review board of the School of Psychology, Trinity College Dublin, in accordance with the Declaration of Helsinki.

Fig. 1 – Time-course of events on each trial of the Diffuse Spatial Attention Task (running from top left to bottom right). Participants initiate each trial with a button click which leads to the presentation of the checkerboard array accompanied by an uninformative warning cue. Participants monitor the array for a target stimulus (four adjacent gray squares) that can appear at any location with equal probability. Checkerboard stimuli are flickered in independent sequences throughout the pre-target interval in order to generate a spatially-specific primary visual response in the EEG. Checkerboard stimuli continued to flicker after target onset. A 2000 msec deadline was imposed on responses to targets, after which participants received feedback. Trials were interrupted and re-started if participants broke fixation (movement outside region shaded in blue in panel at bottom left of figure).
2.2. Diffuse Spatial Attention Task

Participants performed a non-cued target detection task, in which they were presented with 8 black-and-white checkerboard stimuli spanning a large portion of the visual field (Fig. 1). Participants performed 20 blocks of the task, each consisting of 13 trials and were instructed to fixate on the center of the screen for the trial duration up until target onset. Each trial was initiated by the participant clicking the mouse button in response to a ‘Ready’ prompt. The trial started with the appearance of the checkerboard stimuli and a red square at fixation which acted as a non-predictive warning cue (2500 msec after trial-initiating click). The checkerboard stimuli began to flicker (see below) upon cue offset and targets (500 msec duration) were presented between 2600 msec and 9600 msec thereafter. The target consisted of 4 small gray squares superimposed within 4 adjacent squares of one of the checkerboards. Participants had 2000 msec to respond as quickly as possible to the target with a speeded right index finger button push. Previous studies have demonstrated pseudoneglect using this response method (Newman et al., 2013; Thiebaut de Schotten et al., 2011). Another advantage of using only right index finger button presses is that the topography of any motor-related activity in the EEG is held constant across trials ruling out any influence on the observed alpha asymmetry results. After this the flickering stopped and the trial ended. Four different target onset times were used (Length A = 2665 msec, B = 4797 msec, C = 6797 msec, D = 9563 msec), comprising 10%, 20%, 20% and 50% of trials respectively. A further 20 no-target catch trials (9563 msec duration) were randomly interspersed throughout the session. The relatively long trial durations were required to facilitate MVEP analysis (described below) and trial lengths were varied to ensure that participants attended to the stimuli for the full duration of each trial. Participants were informed that targets could appear at any point throughout the trial. Targets appeared with equal probability at each checkerboard and at each location within each checkerboard and were designed to be detected with close to perfect accuracy such that the primary emphasis was placed on reaction time. In order to maintain performance levels, positive and negative feedback was given at the end of each trial indicating a missed target, a slow reaction time (>500 msec) or an adequate reaction time (<500 msec).

The sizes of the checkerboard patches were selected to account for cortical magnification (Daniel & Whitteridge, 1961) in order to approximately equalize signal-to-noise ratio for MVEP measurement across patches. The inner checkerboard patches subtended 5.5° visual angle on the horizontal dimension and 8.5° on the vertical dimension while the outer patches subtended 7.5° on the horizontal dimension and 8.5° on the vertical dimension. The whole stimulus area subtended 27° (horizontal) × 17° (vertical) visual angle. During the trial period, the contrast reversal of each patch was modulated by a binary m-sequence, which can be represented as a pseudorandom series of 1s and −1s (Baseler et al., 1994). Each patch was modulated by cyclically-shifted versions of the same m-sequence. Each shifted m-sequence was assigned to a particular patch. A particular property of the m-sequence is that it is uncorrelated with cyclically-shifted versions of itself. This property of orthogonality allowed acquisition of a specific cortical response to each of several simultaneously presented contrast-reversal checkerboard patches. The resulting analyses in this paper are of the second-order kernel, first-slice, similar to the traditional contrast-reversal VEP (Baseler & Sutter, 1997; Schmid et al., 2009; Sutter, 2000). See Appendix A for a more detailed explanation of the method. Importantly for the present study, the m-sequence has a flat power spectrum, thus not preferentially activating neuronal responses to particular patches, as would happen in a spread-spectrum VEP (SSVEP) paradigm.

Stimuli were presented using Neurobehavioral Systems Presentation software on a 40 cm × 30 cm CRT monitor, using a refresh rate of 60 Hz and a screen resolution of 1024 × 768 pixels. Participants were seated comfortably with their head in a chin rest 56 cm from the screen and told to fixate on a central dot throughout the task. An SR Research Eyelink eye tracker (EyeLink version 2.04, SR Research Ltd/SMI) recorded eye movements and ensured that participants maintained fixation. If a participant blinked or moved their eyes >2.8° from fixation in the trial period before target onset, the trial was restarted. Calibration was performed before each block and a drift correction was conducted midway through each block.

Continuous EEG was acquired via the ActiveTwo Biosemi electrode system from 128 electrode positions. The data were filtered in the range of 0–134 Hz and digitized at the rate of 512 Hz.

2.3. Data analysis

2.3.1. Behavioral data

All participants had >95% detection accuracy, therefore only reaction time (RT) was considered. The trials of shortest duration (10%) provided insufficient data for both MVEP and alpha analyses and were therefore excluded from all analyses (inclusion of these trials did not affect the behavioral results reported below). RTs faster than 100 msec and slower than 1500 msec (representing >5SD above the mean for all participants) were also excluded. All behavioral and EEG analyses were restricted to trials on which targets were presented, and correctly detected. For behavioral analyses, trials with post-target fixation breaks (e.g., blinks and eye movements) were also excluded (Mean trials excluded = 2%, SD = 4%). This lead to a mean rejection of 9.87% (SD = 2%), with an effective mean trial count for behavioral analyses of 234 (SD = 5, Range = 215–239) for each participant.

In addition to analyzing the effects of target location — horizontal eccentricity (left/right), vertical eccentricity (upper/lower) and distance from fixation (inner/outer) — on raw reaction times we also derived separate horizontal RT asymmetry indices (Newman et al., 2013; Thut et al., 2006) for the upper and lower fields, and inner and outer patches, separately using the following formula:

\[
\text{RT Asymmetry Index} = \frac{(\text{Mean Left Target RT} - \text{Mean Right Target RT})}{(\text{Mean Left Target RT} + \text{Mean Right Target RT})/2}
\]
This index produces a negative value when participants responded more quickly to targets appearing in the left visual field and a positive value when participants responded more quickly to targets appearing in the right visual field. Representing asymmetry as a lateralization index minimizes the influence of individual differences in mean reaction time and therefore the RT index was utilized in all analyses relating behavioral effects to the EEG markers.

2.3.2. Pre-target alpha analysis
All EEG data were analyzed in MATLAB using a combination of custom scripts and EEGLAB routines (Delorme A and S Makeig 2004). Continuous EEG data were first re-referenced to the average of all channels and low-pass filtered to 40 Hz. Noisy channels were interpolated (spherical spline) and finally the data were high-pass filtered with a .5 Hz cutoff. Data were segmented into epochs from 200 msec before cue onset to 200 msec after target onset, leading to different epoch lengths for different length trials. In addition to the rejection criteria in Section 2.3.1, epochs with an amplitude deflection greater than 100 $\mu$V (due to electromyographic and electrode artifacts) were rejected, leading to a mean rejection per participant of 15.7% of trials (SD $= 7.7\%$). This left an effective mean trial count for EEG analyses of 175 (SD $= 19$, Range $= 140–209$) for each participant.

Our alpha analysis was based on methods initially outlined by Thut et al. (2006) with the goal of first investigating the inter-hemispheric distribution of posterior alpha activity and then measuring its relationship with RT bias. Each epoch was band-pass filtered to the alpha frequency range (8–14 Hz), full-wave rectified (converted to absolute values) and trimmed to exclude the 200 msec at the beginning and end of the epoch in order to eliminate filter warm-up artifacts. Data were then smoothed by averaging inside a moving window of 100 msec, moving forward in 100 msec increments. Single trials were then averaged together for each participant. Fig. 2a shows the topographical distribution of alpha power averaged across all trials. Two symmetrical occipital regions of interest (ROIs) were chosen based on the greatest average alpha activity in the trial period, circled in Fig. 2a. These ROIs are consistent with those used in previous studies probing links between alpha and visuospatial asymmetry (Newman et al., 2013; Thut et al., 2006).

An inter-hemispheric alpha lateralization index which was calculated on a trial-by-trial basis according to the following formula:

$$\text{Alpha Asymmetry Index} = \frac{\text{Mean Right Hemi Alpha} - \text{Mean Left Hemi Alpha}}{\text{Mean Right Hemi Alpha} + \text{Mean Left Hemi Alpha}}/2$$

This produces a negative value when there is more alpha activity in the left hemisphere compared to the right and...
positive when there is more alpha activity in the right hemisphere compared to the left. As with RT, the use of a lateralization index minimizes the influence of inter-individual differences in mean alpha power. Alpha lateralization was calculated over the interval starting 800 msec after trial onset and ending at target onset, in order to exclude the influence of stimulus flicker onset on occipital alpha activity (see Fig. B1 in Appendix B).

2.3.3. MVEP analysis
The purpose of the MVEP analysis was to first investigate the amplitude of primary visual cortical responses to the checkerboard stimuli at each visual field quadrant and then investigate their relationship with behavior, as with the alpha analysis. Second-order first-slice responses were extracted individually for each patch, representing a separate cortical response to contrast change in each patch (see Appendix A). To facilitate comparison of signals across different patches, we calculated a measure of response power over the whole scalp known as global field power (GFP) (Lehmann & Skrandies, 1980) for each patch, and baseline corrected from -100 msec to 0 msec. This left 8 separate time-domain responses, one for each patch, for each participant. Visual inspection of the responses indicated two distinct components (C1 and C2) (see Fig. C1 in Appendix C) and their amplitudes was measured as root mean square amplitude in a 30 msec window centered on each component peak for each individual participant and for each checkerboard patch. All MVEP analyses were done separately for these timeframes.

MVEP lateralization indices were calculated for the upper and lower fields (separately for inner and outer patches) to further probe the difference in MVEP response in the left and right hemifields. Calculation of inter-hemifield MVEP lateralization was done according to the following formula:

\[
\text{MVEP Asymmetry Index} = \frac{(\text{Mean Right Patch GFP} - \text{Mean Left Patch GFP})}{(\text{Mean Left Patch GFP} + \text{Mean Right Patch GFP})/2}
\]

This produces a negative value when there is more MVEP activity to left compared to right hemifield patches and positive when there is more MVEP activity to right compared to left hemifield patches.

2.3.4. Order of analyses
Analysis of data focused on three separate measures: behavioral (RTs), pre-stimulus alpha power, and the MVEP. For all three measures the same structure of analyses was followed, (i) raw left versus right hemifield/hemisphere differences were measured first, via Repeated-Measures ANOVAs or t-tests, where appropriate; (ii) lateralization indices of each measure were created, according to the equations detailed above, and tested using one-sample t-tests; (iii) to investigate the influence of lateralization of our EEG indices (pre-stimulus alpha power and the MVEP) on lateralization of our behavioral indices (RTs), a binning method was used and subjected to Repeated-Measures ANOVAs, detailed below.

Before performing parametric tests on the data, normal distribution was checked using the Shapiro–Wilks test. Since RT data was expectedly not normal, the same tests were performed on log-normalized RT data. None of the below analyses were affected by this transformation. All post hoc comparisons were corrected for multiple comparisons using the Bonferroni method and all relevant p-values are shown corrected.

3. Results

3.1. Behavioral data
Mean RTs were subjected to a 3-Way ANOVA with the target’s Horizontal Eccentricity (Left, Right), Vertical Eccentricity (Upper, Lower), and Distance From Fixation (Inner, Outer) as factors. This revealed a main effect of Vertical Eccentricity [F(1,23) = 10.23, p = .004, \(\eta_p^2 = .354\)], with responses to lower targets faster than responses to upper targets (Fig. 2b). There was also a significant Horizontal by Vertical Eccentricity interaction [F(1,23) = 38.3, p = .001, \(\eta_p^2 = .594\)], which was primarily driven by left RTs being faster than right RTs in the lower field (t[23] = -3.84, p = .002). In contrast, right RTs were faster than left RTs in the upper field (t[23] = 2.37, p = .054), although the latter result did not survive Bonferroni correction. These results were recapitulated when the RT asymmetry index was analyzed via a 2-Way ANOVA with the target’s Vertical Eccentricity (Upper, Lower), and Distance From Fixation (Inner, Outer) as factors. There was a significant main effect of Vertical Eccentricity [F(1,23) = 31.3, p = .001, \(\eta_p^2 = .576\)], with a close to significant rightward RT bias (i.e., faster responses to right sided targets) in the upper field (t[23] = 2.3, p = .062) and a significant leftward RT bias in the lower field (t[23] = -3.83, p = .002), after collapsing across Distance From Fixation (Fig. 2c). Interestingly, there was no main effect or interaction involving Distance From Fixation in the behavioral analysis (most likely due to our scaling of checkerboard patches and targets to account for cortical magnification), see (Anton-Erxleben & Carrasco, 2013; Carrasco, Evert, Chang, & Katz, 1995; Carrasco & Frieder, 1997).

3.2. Pre-target alpha results
The first analysis investigated simple lateralization of pre-target alpha, regardless of target location. Collapsing across all included trials, there was more pre-target alpha activity in the left hemisphere ROI (M = 3.11 \(\mu\)Volts, SD = 1.28) than in the right hemisphere ROI (M = 2.9, SD = .83) but this difference did not reach statistical significance (t[23] = 1.65, p = .1, Fig. 2a). The average alpha lateralization index was also observed to be negative, i.e., left-lateralized (mean alpha lateralization = -.04) but a t-test against zero did not reach significance (t[23] = -1.24, p = .23). These analyses indicate that there was no general bias in the hemispheric distribution of alpha across participants.

To test for a trial-to-trial relationship between hemispheric alpha lateralization and RT asymmetry, the alpha lateralization index was calculated on each single trial. Trials were then sorted as a function of alpha asymmetry and divided into two equal sized bins for each participant and separate RT asym-
metry indices were then calculated for each bin. Thus, this analysis allowed us to contrast trials on which targets were preceded by a relative leftward versus rightward alpha asymmetry. This relationship was explored via a 3-Way ANOVA, with factors of Alpha Lateralization Bin (Left Lateralized Alpha, Right Lateralized Alpha), Target Distance From Fixation (Inner, Outer) and Target Vertical Eccentricity (Upper, Lower), and RT Asymmetry as the dependent variable.

There was a significant interaction between Alpha Lateralization and Target Vertical Eccentricity \( F(1,23) = 7.5, p = .012, \eta^2_p = .246 \), with no interaction involving Target Distance From Fixation. Collapsing across Distance From Fixation, follow up t-tests indicated a significant difference in RT lateralization as a function of alpha bin in the lower visual field \( t(23) = -3.38, p = .006 \) such that a relative decrease of alpha power over one hemisphere was associated with a contralateral advantage in target detection speed. In contrast, there was no significant relationship between pre-target alpha and RT lateralization in the upper visual field \( t(23) = .93, p = .74, \) Fig. 2d).

To rule out the possibility that there may be distinct alpha foci reflecting attentional deployment to the upper and lower visual fields, the above analysis was repeated at each of 18 symmetric pairs of electrodes spanning occipital and parietal scalp sites (Fig. 2a), and included in a 4-Way ANOVA, with factors of Alpha Lateralization Bin, Target Distance From Fixation (Inner, Outer), Target Vertical Eccentricity and Electrode Pair Position. The same Alpha Lateralization \times/ Target Vertical Eccentricity interaction \( F(1,23) = 4.5, p = .045, \eta^2_p = .164 \) was observed while there was no Alpha Bin \times/ Target Vertical Eccentricity \times/ Electrode Position interaction

3.3. MVEP results

The first analysis of the MVEP investigated differences in GFP responses to each patch in the pre-target period. Separate 3-Way ANOVAs were performed with factors of Horizontal Eccentricity (Left, Right), Distance From Fixation (Inner, Outer), and Vertical Eccentricity (Upper, Lower) for the C1 and C2 timeframes. In the C1 timeframe, there was a significant main effect of Vertical Eccentricity \( F(1,23) = 28.95, p = .001, \eta^2_p = .557 \), with GFS larger to patches in the lower field than those in the upper field. There were no other significant effects for the C1. In the C2 timeframe, there was a significant main effect of vertical eccentricity \( F(1,23) = 7.93, p = .01, \eta^2_p = .256 \), with more GFP activity to patches in the lower versus upper field. There was also a significant interaction of Horizontal and Vertical Eccentricity \( F(1,23) = 15.96, p < .001, \eta^2_p = .410 \), and no interaction with Distance From Fixation. Collapsing across Distance From Fixation, post-hoc pairwise comparisons did not reach significance after correcting for multiple comparisons but did indicate a strong trend toward larger GFP to patches on the left in the upper field \( t(23) = 2.19, p = .078 \) and to the right in the lower field \( t(23) = -2.28, p = .064 \), (see Fig. 3a and b). However, the effect was confirmed by analysis of MVEP asymmetry indices, where a 2-way ANOVA with Distance From Fixation (Inner, Outer), and Vertical Eccentricity (Upper, Lower) as factors showed a main

Fig. 3 – (a) Grand-average MVEP GFP responses elicited by the background checkerboard stimuli as a function of horizontal and vertical eccentricity. Green lines denote the C1 and C2 time-frames (b) Root mean square of the GFP responses in the C2 timeframe as a function of horizontal and vertical eccentricity. (c) MVEP GFP responses binned as a function of RT.
effect of Vertical Eccentricity $F(1, 23) = 19.88, p = .001, \eta^2_p = .464$, with a significantly negative index in the upper field [Mean = −1.19, $t(23) = −2.84, p = .018$] and a significantly positive index in the lower field [Mean = .138, $t(23) = 2.72, p = .024$] after collapsing across Distance From Fixation. Thus, MVEPs exhibited distinct upper and lower field asymmetries but in the opposite direction to expectations, based on the RT trends. To investigate this unexpected result a further post-hoc analysis of the relationship between MVEP amplitude and absolute RT was performed. Trials were sorted by RT and divided into equal-sized slow and fast bins. A 3-Way ANOVA containing factors of RT Bin, Target Horizontal Eccentricity, and Target Vertical Eccentricity was performed on the GPF in the C2 timeframe. This revealed a significant main effect of RT bin $F(1, 23) = 4.84, p = .038, \eta^2_p = .174$, with faster RTs reliably associated with smaller C2 signals (Fig. 3c).

Similarly to the alpha analysis, the effect of MVEP lateralization on RT lateralization was investigated at the single-trial level. On a trial-by-trial basis, RTs were divided into left and right-lateralized MVEP bins, separately for the upper and lower visual fields, and inner and outer patches. For each participant, RT lateralization was calculated for each bin. This led to a 3-Way Repeated-Measures ANOVA, with MVEP Lateralization Bin (Left and Right-lateralized), Distance From Fixation (Inner, Outer), and Vertical Eccentricity (Upper and Lower field) as factors and RT Lateralization as the dependent variable. This was done separately for the C1 and C2 timeframes. This revealed a close-to-significant interaction of MVEP Lateralization Bin and Vertical Eccentricity in the C1 timeframe $F(1, 23) = 4.3, p = .050, \eta^2_p = .160$. However, post-hoc pairwise comparisons revealed no significant effects. There were no significant main effects or interactions in the C2 timeframe.

4. Discussion

The present experiment demonstrates a dissociation of visuospatial biases between the upper and lower visual fields that has important implications for existing models of pseudoneglect. Participants were asked to evenly distribute their attention across a large region of visual space while maintaining central fixation. We observed opposing RT asymmetries for the upper versus lower visual fields with RTs biased to the left when critical stimuli appeared in the lower field and to the right when the stimuli appeared in the upper field, although the latter was just outside significance after correction for multiple comparisons. The acquisition of neurophysiological recordings allowed us to gain an important insight regarding the origins of these behavioral effects. We found that the relative hemispheric distribution of occipitoparietal alpha power predicted the degree of RT bias for the lower visual field but not for the upper field providing new evidence for a functional dissociation of the upper and lower visual fields (Previc, 1990). These alpha effects were observed in the pre-target period confirming that the observed behavioral trends arise from asymmetries in the endogenous allocation of attentional resources and cannot be solely attributed to object-related, stimulus-specific influences. While the findings in relation to the MVEP signals were not clear-cut, once again we found opposing asymmetries in signal amplitudes for the upper and lower fields. Thus our data indicate that, in the context of diffuse spatial attention, the leftward attentional bias associated with pseudoneglect is in fact absent in the upper portion of the visual field, where there is instead a subtle rightward bias. These findings will require a re-evaluation of pseudoneglect models and have important implications for the design of clinical and non-clinical assessment tools geared towards the measurement of visuospatial asymmetry.

4.1. Opposing behavioral asymmetries in the upper versus lower visual field

Of the small number of previous studies that manipulated the vertical position of the stimulus our results accord with the findings of some (Barrett et al., 2000; Drago et al., 2006; Thomas & Elias, 2010, 2011) but diverge from others (McCOURT & Garlinghouse, 2000; Nicholls et al., 2012). Our study is the first to exclude eye movements which may have been an important source of variance in previous work. Another important distinction between our paradigm and those used in previous studies is that the participant was required to continuously distribute their attention across a wide portion of the visual field. Most previous paradigms involved briefly presented stimuli appearing at one of a small number of predictable locations which is likely to place less emphasis on the competition for attentional resources across space. Finally, all of the paradigms implemented in this area (including our own) differ in terms of the perceptual features of the critical stimuli and the duration of stimulus presentation all of which may impact on the manifestation of response biases. It has been suggested that asymmetries in processing of the spatial properties of objects and asymmetries in the processing of space in general both contribute to pseudoneglect (Nicholls, Hughes, Mattingley, & Bradshaw, 2004; Orr & Nicholls, 2005; Post et al., 2001). However, as discussed in the following sections, the neurophysiological metrics analyzed here suggest that there is an endogenous bias in the spatial distribution of attention that precedes the appearance of a stimulus and that cannot be attributed to either variations in eye movement speed or differences in object-level processing.

4.2. Alpha power asymmetry dissociates upper and lower field endogenous attention

The relative hemispheric distribution of posterior alpha power, measured in the pre-target interval, was significantly predictive of RT asymmetries in the lower field only, with left-lateralized alpha indicative of left biased RTs. While previous studies have found that lateralization of alpha power is predictive of behavior in cued spatial attention tasks (Kelly et al., 2009; Thut et al., 2006), this is the first demonstration of such a relationship in a non-cued task. One possible reason for the difference in the present result compared to previous non-cued studies (Newman et al., 2013; Perez et al., 2009) is the length of epoch (between 2000 and 9000 msec) chosen for the analysis, placing a stronger emphasis on the endogenous maintenance of bilateral attention. Also, these studies used...
dual-task paradigms, and anticipatory alpha effects (Rohenkohl & Nobre, 2011) for one task could affect measurements for the other task, washing out subtle links between alpha asymmetry and behavior.

A recent study found evidence for more frequent endogenous attentional sampling for information in the left hemifield (Landau & Fries, 2012) and our significant alpha result may reflect more frequent pre-stimulus sampling of a particular hemifield over several seconds thus increasing the likelihood that the favored hemifield will be sampled at the time of target appearance. However, RT lateralization in the upper field was not explained by alpha lateralization and in fact the relationship trended in the opposite direction. This result provides new evidence of a functional dissociation in visuospatial attention mechanisms between the upper and lower visual fields (Previc, 1990). Crucially, our results could not be attributed to the choice of electrodes because the same trends were observed for symmetric electrode pairs spanning inferior occipital to superior parietal scalp sites. Aside from these single-trial brain-behavior relationships we did not find a reliable bias in the hemispheric distribution of alpha power across subjects, although there was a numerical trend favoring greater power over left hemisphere electrodes. This null result is in accordance with one previous (Newman et al., 2013) that reported behavioral pseudoneglect and likely reflects the substantial inter-subject variance that is characteristic of the alpha-band.

4.3. Opposing MVEP asymmetries in upper and lower visual fields

As a paradigm, the MVEP technique could potentially provide a useful method of objectively measuring the allocation of attentional resources to multiple discrete spatial locations in the context of diffuse attentional deployment and without the requirement of discrete stimulus presentations or overt behavioral responses. We found possible evidence that MVEPs, measured in the pre-target interval, were modulated by both the upper and lower field attentional asymmetries. However, the direction of the relationship between MVEP and RT was in the opposite direction to our initial predictions, meaning caution must be applied to the interpretation of the present results. The single study that has examined the impact of attention on MVEP amplitude (Seiple et al., 2002) found that signal amplitudes increase with attention but here analysis of pre-target MVEP lateralization indicated that greater GFP activity was associated with slower RTs. A possible explanation for this finding is that the prolonged length of our trials induced adaptation to the checkerboard stimuli. It has previously been shown that while over short periods attention to a spatial location can be beneficial, sustained attention can actually decrease contrast sensitivity over relatively long periods of stimulus presentation (2–10 sec) (Ling & Carrasco, 2006). It has been suggested that the function of adaptation in natural surroundings is to optimize perception by centering the neural response around the mean of the current stimuli (Webster, 2011), thus enabling the visual system to detect novel items (Gardner et al., 2005; Ranganath & Rainer, 2003). Here, relatively greater attention to a particular quadrant could have induced greater adaptation to the high contrast background stimuli, enabling faster segregation of the low contrast targets, while also reducing our index of the high contrast background, i.e., our MVEP.

Unlike in the case of pre-target alpha, we did not observe a significant relationship between MVEP lateralization and RT at the single-trial level. There is a high probability that this is due to the signal-to-noise ratio of the MVEP technique which may require longer periods of data recording to obtain a reliable measurement. Nevertheless, as an initial exploration of the MVEP method’s potential utility as a tool for measuring attentional asymmetry, the present study has provided a basis for future work, with potential for the refinement of clinical tools used in the diagnosis of spatial attention deficits.

4.4. Distinct representational frames for the upper and lower visual field

Where the phenomenon of pseudoneglect has typically been viewed as the manifestation of a right hemispheric dominance of spatial attention, our results appear to call for a more complicated model. In the absence of functional imaging data it was not possible to establish the precise neural origins of these opposing asymmetries but it has already been argued that the upper and lower fields are assigned to distinct attentional networks, with the lower visual field specialized for global processing in peripersonal space, and the upper visual field specialized for local processing of extrapersonal space (Previc, 1990). From an evolutionary perspective this upper versus lower field distinction may arise from the fact that objects in our upper field are likely to be beyond our grasp while objects in our lower visual field tend to be within reach.

The notion that visuospatial attention is segregated into distinct spatial reference frames and distinct cortical networks is supported by evidence that the symptoms of unilateral neglect are most prominent when stimuli are presented in peripersonal space and in the lower visual field (Aimola, Schindler, Simone, & Venneri, 2012; Rubens, 1985). Moreover, in direct correspondence to the present results, studies that have varied the representational context in which stimuli appear have observed a greater leftward bias for stimuli falling in peripersonal space (Longo & Lourenco, 2006; McCourt & Garlinghouse, 2000; McCourt & Jewell, 1999) with one study reporting a rightward bias for stimuli appearing in extrapersonal space (Nicholls et al., 2011). According to Previc (1998; 1990) evidence from lesion studies in monkeys indicates that peripersonal and extrapersonal space are mapped onto the dorsal and ventral visual streams respectively (as distinct from the dorsal and ventral attention networks) but further research using more spatially accurate neuroimaging techniques, such as fMRI, will be required to establish whether such a model could account for our results.

It has also been proposed that deficits in hemispatial neglect are primarily body centric rather than retinotopic (Driver & Vuilleumier, 2001) and the same may be true of the attentional asymmetries observed in the healthy brain. The broad spread of stimuli in the present study may mean that the upper visual field stimuli are also in the upper field of body-centric space and vice versa for the lower visual field. The two other studies known to us which investigated
pseudoneglect in terms of body-space (Barrett et al., 2000; Drago et al., 2006) also found dissociation in upper and lower field biases. This will be an important consideration for future work.

One final point is that the present data need not be only considered in terms of left versus right biases, separately in the upper and lower visual field, but may be considered in other frames also. The analytic approach adopted in this study accords with that of the general pseudoneglect literature but there are other possible interpretations. An alternative hypothesis is that the bias is more continuous in nature, i.e., that there is a bias along the diagonal axis from bottom left to upper right. Furthermore, one could flip the axes of analysis to show a lower field bias in the left visual field, and no vertical bias in the right visual field. One way for future studies to arbitrate between these possibilities is to use neuroimaging techniques such as fMRI to establish if the asymmetrical effects we report can be ascribed to distinct upper and lower field frames of reference.

4.5. Conclusion

We have shown a dissociation of upper and lower visual field biases in a novel diffuse attention paradigm, calling for a more nuanced understanding of visuospatial asymmetries and pseudoneglect. Our results provide empirical support for a functional segregation of upper and lower field processing. Theoretical models of visuospatial attention will need to accommodate this difference in upper and lower field biases, with the possible specification of separate attentional streams for upper and lower fields. The present findings also go some way towards shedding light on inconsistencies in the pseudoneglect literature. Finally, future studies of visuospatial bias in both research and clinical settings need to account for this difference in the upper and lower fields.

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Supplementary data

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