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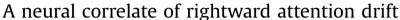
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Linking time-on-task, spatial bias and hemispheric activation asymmetry:



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ABSTRACT

Biases of spatial attention may be moderated by non-spatial factors such as attentional load and time-on-task. Although these effects are thought to arise from depletion of right hemisphere processing resources, their neurophysiological bases have yet to be confirmed. We recorded posterior α -band EEG – a marker of cortical excitability linked to spatial attention orienting – from 66 non-clinical participants who detected transient, unilateral visual targets while also monitoring stimuli at fixation. Asymmetry indices were derived for both lateral target reaction times and hemispheric differences in α -activity before and after lateral target onsets. Pre-target α became more prominent over the right, relative to left, hemisphere as the task progressed over 48-min, and this change was correlated with a significant rightward shift in spatial bias. Contrary to past studies of posterior α -asymmetry and orienting, here participants did not receive pre-target cues. Thus we show that asymmetries in the hemispheric distribution of anticipatory α are not only apparent during externally-cued attention orienting, but are also sensitive to decreasing alertness over time. These data are the first to link rightward attention drift over time with change in hemispheric activation asymmetry, providing important implications for our understanding of interacting spatial attention and non-spatial alertness networks.

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1. Introduction

Healthy subjects tend to exhibit a subtle bias of visual attention favouring left space, termed 'pseudoneglect', which occurs for a variety of stimuli (Nicholls, Bradshaw, & Mattingley, 1999; Voyer, Voyer, & Tramonte, 2012) and is thought to reflect the right hemisphere's dominance of the networks governing spatial attention (Loftus & Nicholls, 2012; Mesulam, 1981). Recent research with healthy volunteers and patient groups exhibiting pathological visuo-spatial asymmetries suggest that spatial biases are regulated by non-spatial factors, such as attentional load and time-on-task (Dodds et al., 2008; Matthias et al., 2009; Peers, Cusack, & Duncan, 2006). Despite our increasing knowledge of the cognitive factors that might modulate spatial biases, our knowledge of the physiological bases of these effects remains unclear. Here we employed electrophysiology to understand the influence of attentional load and time-on-task on neural biases of spatial attention in healthy volunteers.

A number of lines of evidence suggest that non-spatial factors modulate biases of spatial attention. First, the modulatory influence of non-spatial processes on spatial bias has been documented in unilateral spatial neglect (hereafter 'neglect'), a common outcome of right hemisphere damage that is characterised by pronounced deficits in attending to contralesional stimuli despite adequate sensory processing (Corbetta & Shulman, 2011; Husain & Nachev, 2007; Husain & Rorden, 2003). Robertson et al. (1998) found that loud tones designed to increase alertness could temporarily reduce symptoms of leftward inattention in neglect patients (see also George et al., 2008). Peers et al. (2006) also demonstrated that imposing a non-spatial dual-task during a spatial attention task caused the same general rightward shift in patients with left neglect, patients with right neglect and control participants. Furthermore, it has been shown that neglect can be temporarily ameliorated by psychostimulants but exacerbated by sedatives, suggesting a critical modulatory influence of arousal (Fleet, Valenstein, Watson, & Heilman, 1987; Geminiani, Bottini, & Sterzi, 1998; Grujic et al. 1998; Lazar et al., 2002; Malhotra, Parton, Greenwood, & Husain, 2006; Mukand et al., 2001).

Second, a number of studies have shown that even in healthy populations, spatial bias is significantly modulated by sleep deprivation (Manly, Dobler, Dodds, & George, 2005), non-spatial attentional load (Peers et al., 2006; Pérez et al., 2009), diminishing alertness with time-on-task (Dodds et al., 2008; Dufour, Touzalin, & Candas, 2007) and psychostimulants (Dodds, Müller, & Manly, 2009). The links between non-spatial attention processes and spatial bias in both

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clinical and non-clinical populations highlight a need to understand how these mechanisms are integrated in the human brain.

At a neural level, it has been proposed (Corbetta & Shulman, 2011) that the effects of alertness and attentional load on spatial bias result from increased demand on a right lateralised ventral attention network (Coull, Frackowiak, & Frith, 1998; Pardo, Fox, & Raichle, 1991; Sturm et al., 1999, 2004) that regulates interhemispheric rivalry in the bilateral dorsal orienting network (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2011; Husain & Nachev, 2007). The bilateral orienting network is activated by selectively attending to stimuli across space and linking them to appropriate responses, whilst the right lateralised ventral attention network has been linked to non-spatial attention capacity (Culham, Cavanagh, & Kanwisher, 2001; Schwartz et al., 2005; Vuilleumier et al., 2008) and vigilance/alertness (Paus et al., 1997; Sturm & Willmes, 2001). Decreased activation within the right lateralised ventral network may cause a more global decrease in right hemisphere activation, giving the left dorsal orienting network a competitive activation advantage over the right dorsal network, thus driving attention rightwards (Corbetta & Shulman, 2011).

Support for the above neuroanatomical model comes from an fMRI study of neglect patients with damage restricted to the right ventral attention network whose rightward spatial bias was associated with a functional imbalance in the structurally intact dorsal orienting network (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). A recent diffusion imaging study (De Schotten et al., 2011) provides a neuronatomical basis for the pseudoneglect of healthy individuals by demonstrating a clear right lateralisation in tracts connecting the dorsal and ventral networks which was strongly related to the degree of pseudoneglect displayed by participants. To date however, a neurophysiological marker that is sensitive to interactions between spatial and non-spatial attention systems has yet to be identified.

In the present study we tested the hypothesis that a rightward attentional shift with time-on-task and attentional load is linked to changing hemispheric activation asymmetry. We recorded continuous EEG from healthy participants during a fixationcontrolled spatial attention task that allowed us to separately manipulate attentional load and time-on-task. Participants detected sudden onset targets that occurred at uncued peripheral locations while performing a concurrent task at fixation. Demand on non-spatial attention was manipulated across three levels (no, low and high central load) by changing the difficulty of the task at fixation, and changes in behavioural and neurophysiological markers of spatial attention were analysed as a function of time-ontask. We capitalised on hemispheric asymmetry in α -band (8–14 Hz) as a marker of cortical activation asymmetry before and after the onset of a peripheral event. Decreased α -band activity reflects increased cortical activation or excitability, whereas increased a activity reflects cortical deactivation (Pfurtscheller, 2001; Romei et al., 2008; Romei, Rihs, Brodbeck, & Thut, 2008; Sadaghiani et al., 2010). Several recent studies employing simultaneous EEG and fMRI have demonstrated that α -band activity is negatively correlated with activity of the dorsal attention network (Laufs et al., 2003, 2006; Mantini, Perrucci, Del Gratta, Romani, & Corbetta, 2007; Sadaghiani et al., 2010; Scheeringa et al., 2009).

Thut, Nietzel, Brandt, and Pascual-Leone (2006) measured α activity over the parieto-occipital cortex during a variant of the Posner spatial cueing task (Posner, Walker, Friedrich, & Rafal, 1984) and found that preparatory hemispheric α asymmetry (expressed as a lateralisation index) during the epoch between spatial cue and target onset predicted reaction-time asymmetries for imminent peripheral targets. Spatial cueing promotes desynchronization of α (decreased α activity) at contralateral parieto-occipital sites, reflecting facilitated processing at the locus of attention (Kelly,

Gomez-Ramirez, & Foxe, 2009; Rihs, Michel, & Thut, 2009; Sauseng et al., 2005; Thut et al., 2006; Yamagishi, Goda, Callan, Anderson, & Kawato, 2005) whereas synchronization (increased α activity) over ipsilateral sites, may index suppression of unattended space (Kelly, Lalor, Reilly, & Foxe, 2006; Rihs, Michel, & Thut, 2007, 2009; Worden, Foxe, Wang, & Simpson, 2000). These cueing studies explicitly directed the attention of participants in the pre-target interval to one or the other hemifield. In the current study, by contrast, we presented targets at uncued lateral locations, eliminating any strategic top-down biasing of attention. This allowed us to investigate the impact of depleting non-spatial attention resources – either via central task load or time-on-task – on both the balance of α power between the two hemispheres and corresponding visuospatial bias. We predicted that depleting non-spatial attention resources via time-on-task and central task load would lead to a rightward shift in posterior α -asymmetry and spatial bias.

2. Method

2.1. Participants

Data were collected from 91 right-handed volunteers of Caucasian descent, reporting normal or corrected to normal vision, no history of neurological or psychiatric disorder and no head injury resulting in loss of consciousness. Event-related potential (O'Connell, Schneider, Hester, Mattingley, & Bellgrove, 2011) and molecular genetics (Newman, O'Connell, Nathan, & Bellgrove, 2012) data from a subset of these participants were previously published, however no analyses of α activity were conducted. All participants gave written informed consent, and all procedures were in accordance with the Declaration of Helsinki. Four participants responded to fewer than 75% of peripheral targets, suggesting they were insufficiently engaged in the task. These participants were excluded from further analysis. Two were excluded due to a technical error relating to response acquisition. Three participants lacked full time-on-task data within each load condition, so could not be included, and 16 participants displayed small but systematic eve movements during trials (see procedure below) and were thus excluded (Lins, Picton, Berg, & Scherg, 1993). This exclusion of participants due to systematic eye movements was necessary to ensure that peripheral stimuli were transmitted to contralateral visual cortex and that the key changes in alpha and behavioural bias could not be accounted for by systematic biases in eye movements. This left a final sample of 66 participants (40 females) aged 18–47 (M=24).

2.2. Visual attention task

Full details of the current task are presented in O'Connell et al. (2011). Briefly, the task comprised short (3600 ms) rapid serial visual presentation (RSVP) streams of eight central alphanumeric characters on which participants fixated and monitored for the appearance of a target. At the same time, participants covertly monitored left and right lateralised target locations to detect a sudden-onset unilateral peripheral stimulus (Fig. 1A). The peripheral stimulus appeared in either left or right target locations or not at all (catch trials). These three trial types occurred in a randomised order and with equal probability. Participants indicated their detection of the peripheral target with a speeded button press with their right hand, with a valid response window of up to 1000 ms. Using a similar paradigm Peers et al. (2006) found response hand had no effect on spatial bias. Peripheral stimuli appeared randomly at one of two time points in the RSVP stream: at 800 ms (simultaneous with the onset of the third character) or 2000 ms (simultaneous with the onset of the sixth character).

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