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Research Report

A toggle switch of visual awareness?

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ABSTRACT

Major clues to the human brain mechanisms of spatial attention and visual awareness have come from the syndrome of neglect, where patients ignore one half of space. A longstanding puzzle, though, is that neglect almost always comes from right-hemisphere damage, which suggests that the two sides of the brain play distinct roles. But tests of attention in healthy people have revealed only slight differences between the hemispheres. Here we show that major differences emerge if we look at the timing of brain activity in a task optimized to identify attentional functions. Using EEG to map cortical activity on a millisecond timescale, we found transient (20–30 ms) periods of interhemispheric competition, followed by short phases of marked right-sided activity in the ventral attentional network. Our data are the first to show interhemispheric interactions that, much like a toggle switch, quickly allocate neural resources to one or the other hemisphere.

1. Introduction

Imagine browsing a busy store. You gaze at a shelf, then a face, and then your mind focuses on a coat's price tag, yet you never stop noticing the surrounding buzz as you continue to explore. Underlying your explorations are mechanisms of spatial attention and visual awareness, fundamental to human cognition. Key aspects of these mechanisms must be implemented in the right hemisphere because they fail in right-brain damaged patients with spatial neglect who cease to perceive and respond to the world on their left (Karnath, Fruhmann Berger, Kuker, & Rorden, 2004; Mort et al.,, 2003; Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, 2010).

But research to date has not been able to consistently isolate equivalent right-dominant mechanisms in healthy participants. Probing intact visuospatial functions in several tasks has revealed two attentional networks (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Vossel, Geng, & Fink, 2013): One dorsal attentional network (DAN) responds during goal-directed behavior, involving superior frontal and intra-parietal areas mainly in both hemispheres as early as 150 ms post-stimulus onset (Simpson et al., 2011). A ventral attentional network (VAN) responds to unexpected events, implicating the temporo-parietal junction and middle and inferior frontal cortex, starting from around 200 ms or later, coinciding in time with the N2pc, an ERP component that is sensitive to spatial attention (Hickey, Di Lollo, &

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McDonald, 2009). Furthermore, the VAN tends to be more lateralized to the right hemisphere than the left, but not always (Asplund, Todd, Snyder, & Marois, 2010).

To chart right-dominant mechanisms related to neglect, research has turned neglect tests into experimental paradigms for healthy participants. As such, perceptual judgment tasks, known to capture strong rightward attentional biases in patients (Mattingley et al., 2004; Schenkenberg, Bradford, & Ajax, 1980), have revealed small leftward biases in healthy people (Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994; McCourt & Jewell, 1999). This "pseudoneglect" complements biases in neglect; it activates areas (Çiçek et al., 2009; Fink et al., 2000; Loftus et al., 2012) similar to lesion sites in patients (Rorden, Fruhmann Berger, & Karnath, 2006), and responds to similar modulations of stimuli (McCourt & Jewell, 1999), attention (Bultitude & Aimola, 2006; McCourt, Garlinghouse, & Reuter-Lorenz, 2005), and cognitive load (Emrich, Burianova, & Ferber, 2011; O'Connell, Schneider, Hester, Mattingley, & Bellgrove, 2011). Still, the right-brain dominance is relative because activation tends to vary with task (Cavézian et al., 2012), control condition (Revill, Karnath, & Rorden, 2011), and instruction (Fink, Marshall, Weiss, Toni, & Zilles, 2002); moreover, perceptual measures tend to show inconsistent results, such as limited correlations of biases across similar tasks (Mattingley et al., 2004) and limited test-retest reliability with longer presentation times (McCourt, 2001).

Three factors could obscure right-brain dominance. (1) Mechanisms could be short-lived and missed by temporally sluggish imaging. (2) Pseudoneglect paradigms could activate unrelated functions, thus requiring better control. (3) Intact right dominance could be subtle. Asymmetries could surge when lesions push interhemispheric competition out of balance (Koch et al., 2008). However, interactions between competition and right dominance have yet to be demonstrated.

Here we show that all three factors are crucial to identify right-dominant visuospatial functions. We capture pseudoneglect with a sensitive grating-scales task (Niemeier, Stojanoski, & Greco, 2007; initially derived from tasks such as the "greyscales task", e.g., Nicholls, Bradshaw, & Mattingley, 1999) that asks people to compare compound gratings (Fig. 1a). Importantly, only comparing the higher spatial frequencies of the stimuli (HI condition) produces more attention-sensitive biases than lower frequencies (LO condition), due to lower stimulus salience in the latter (Singh, Stojanoski, Le, & Niemeier, 2011). Using continuous electroencephalography (EEG) to map correlates of the HI/LO contrast, we expected modulations with the right hemisphere starting at around the N2, and as expected, we observe transient interhemispheric competition followed by pronounced right dominance in the posterior and frontal VAN from 242 to 394 ms.

2. Materials and methods

2.1. Participants

Nineteen right-handed undergraduate students (8 females, median age 19, no history of neurological or vision problems) at the University of Toronto Scarborough gave their informed and written consent to participate. All procedures were approved by the Human Participants Review Subcommittee of the University of Toronto.

2.2. Procedure

Participants fixated the centre of a 19″ CRT monitor (768 by 1024 pixels, 100 Hz) at a distance of 90 cm and performed a grating-scales task (Fig. 1a; Niemeier et al., 2007), a sensitive and specific measure of pseudoneglect (Niemeier et al., 2007; Singh et al., 2011). The task presented pairs of horizontal bars (14.5° wide) filled with luminance-defined sine wave gratings (.6–2 cycles/°). Spatial frequency increased as a function of a half-cycle of a cosine within an approximately central area (dashed rectangle, not shown during experiment), and was constant outside the area. The central area was placed at 11 different positions from ± 12.5% left or right of bar center (positions −12.5%, 0%, and +12.5% are shown). Participants chose the upper or lower bar depending on which appeared to have "more of the thinner" or "thicker stripes" (HI and LO condition, respectively).

Both tasks produce biases, and these biases are positively correlated. Nevertheless, these biases exhibit some important properties, suggesting that the tasks trigger different neural mechanisms. First, only HI biases interact with attentional cues (Singh et al., 2011), as mentioned earlier. Second, HI and LO biases respond differently when distracting pixel noise is added to the stimuli such that HI biases shift exponentially to the left, whereas LO biases shift rightward (Chen & Niemeier, 2014; Niemeier, Singh, Keough, & Akbar, 2008a).

The two grating-scales bars were surrounded by one white and one black frame, respectively. During the FRAME control condition participants indicated which frame was black. Stimuli were presented for 75 ms to discourage attempts to count the stripes of the stimuli or to make exploratory eye movements. Systematic differences in fixation across conditions could be ruled out given the nil effects of the early ERP components, as will be seen in the Results (Section 3.2).

The HI, LO, and FRAME conditions were administered in 18 separate blocks (96 trials each) and the order of blocks was randomly chosen from 1 of 6 possible ones: AABBCCCCB-BAAAABBCC, where letters A, B, and C could indicate any of the three conditions. Participants were asked to delay their response by about 1 s to separate readiness potential over premotor and motor cortex from stimulus-related ERPs (Foxe, McCourt, & Javitt, 2003), and subsequent trials started 500 ms after their responses.

2.3. Data analysis

2.3.1. Behavioral measures

Based on 11 levels of (a)symmetry of the grating-scales stimuli and participant responses (Fig. 1a) we used sigmoid Weibull functions to model probabilities of choosing the grating-scales bar with the target feature (high or low spatial frequencies) on the left and to estimate the asymmetry that would produce a probability of .5. This point of subjective equality tends to be biased to the left in the HI condition (Niemeier et al., 2007). For instance, the second grating-scales stimulus in Fig. 1a consists of two mirror-symmetric bars, but most people would perceive the lower rectangle as carrying "more of the thinner stripes". In contrast, in the LO condition people tend to show