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A matter of hand: Causal links between hand dominance, structural organization of fronto-parietal attention networks, and variability in behavioural responses to transcranial magnetic stimulation

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ABSTRACT

Considerable evidence suggests that, on a group level, human visuospatial attention is asymmetrically organized, with a right-hemispheric dominance. The asymmetrical organization of the superior longitudinal fasciculus (SLF) has been shown to account for the right-hemispheric dominance in visual attention. However, such account is by no means universal, and large individual differences in asymmetrical performance on visuospatial tasks have been reported. Furthermore, the variability in the SLF lateralization has been shown to correlate with behavioural asymmetries. Continuous theta burst stimulation (cTBS) enables to temporarily interfere with cortical activity. cTBS applied over the posterior parietal cortex (PPC) has been previously used to systematically study attentional asymmetries. Interestingly, large individual differences in the effectiveness of stimulation have been reported. In accordance with earlier both animal and human studies, one possible cause underlying these striking individual differences might lie in the structural organization of frontoparietal pathways subserving visuospatial attention. Thus, the current study employed diffusion tractography to examine the relationship between the variability in the structural organization of the SLF and the individual differences in attentional shifts induced by a modified cTBS ($cTBS_{mod}$; triplets of pulses at 30 Hz, repeated at 6 Hz) applied over the IPS, as measured by a line bisection task. Consistent with previous studies, on a group level, $cTBS_{mod}$ applied over the right intraparietal sulcus (IPS) triggered a rightward bisection bias shift, and there were no significant effects of $cTBS_{mod}$ applied over the left IPS. However, further analyses demonstrated that both handedness and structural variability (as assessed based on hindrance modulated orientational anisotropy) within the middle and the ventral branches of the SLF predicted individual differences in the $cTBS_{mod}$-induced attentional shifts. Our study thus suggests that the effects of $cTBS_{mod}$ over the IPS may depend on intra-hemispheric interactions between cortical loci controlling visual attention. To conclude, our findings provide converging evidence for the notion

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put forward previously that inter-individual variability in the structural organization of intra-hemispheric frontoparietal connections has important implications for the functional models of human visual attention. Moreover, we hypothesize that this may also be relevant for the understanding of attentional disorders and their rehabilitation.

1. Introduction

A considerable amount of evidence suggests that visuospatial attention is asymmetrically organized in the human brain, with a right-hemispheric dominance (Corbetta & Shulman, 2002; Kinsbourne, 1987, 1993; Mesulam, 1981). The empirical support for hemispheric asymmetries in visuospatial attention stems from behavioural and functional neuroimaging studies in healthy controls, and from neuropsychological studies in right-hemispheric stroke patients suffering from hemispatial neglect syndrome (Corbetta & Shulman, 2002, 2011; Shulman et al., 2010). Neglect patients fail to direct attention towards the side of space contralateral to the damaged (most commonly right) hemisphere (Corbetta & Shulman, 2011; Heilman & Valenstein, 1979; Heilman & Van Den Abell, 1980; Vallar, 1998). In contrast, healthy participants generally respond faster to targets appearing in the left visual field, and/or display a variable degree of leftward deviation (so-called pseudoneglect) when identifying the midpoint of a line (Jewell & McCourt, 2000; McCourt & Jewell, 1999; Sosa, Teder-Salejarvi, & McCourt, 2010). It has been suggested that – during visuospatial tasks – a preferential activation of the dominant, right hemisphere leads to the above-mentioned leftward attentional bias in healthy participants, and that a pathological hyperactivity of the contralesional, left hemisphere results in the neglect syndrome (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Corbetta & Shulman, 2002, 2011; Shulman et al., 2010).

Human visuospatial attention relies on the function of the so-called dorsal and ventral attention networks (Corbetta & Shulman, 2002; Mesulam, 1981, 1990), subserved by three branches of a long frontoparietal association pathway, the superior longitudinal fasciculus (SLF); (Thiebaut de Schotten et al., 2011). The projections of the first and third branches of the SLF (SLF I and SLF III) interconnect cortical areas within the dorsal and ventral attention networks, respectively, whereas the middle branch of the SLF (SLF II) provides connections between both networks (Bartolomeo, Thiebaut de Schotten, & Doricchi, 2007; Doricchi, Thiebaut de Schotten, Tomaiuolo, & Bartolomeo, 2008; Schmahmann et al., 2007; Thiebaut de Schotten et al., 2011). Numerous studies, both structural (diffusion imaging studies) and functional magnetic resonance imaging (fMRI studies), indicate that the dorsal network is organized bilaterally, whereas the ventral network is strongly lateralized towards the right hemisphere (Corbetta & Shulman, 2002; Doricchi, Macci, Silvetti, & Macaluso, 2010; Shulman et al., 2010; Thiebaut de Schotten et al., 2011). Nevertheless, while this right-hemispheric dominance in visuospatial attention suitably reflects general principles of the human brain organization, it fails to account for the observed individual differences in spatial biases. Reports of rightward biases in healthy controls, and of neglect affecting the right side of space following left-hemispheric damage suggest that, indeed, this general model is not invariable across the human population (Cai, Van der Haegen, & Brysbaert, 2013; Chechlacz, Gillebert, Vangkilde, Petersen, & Humphreys, 2015; Jewell & McCourt, 2000; Petit et al., 2015; Suchan, Rorden, & Karnath, 2012; Thiebaut de Schotten et al., 2011). Subsequently, it has been suggested that both the extent of lateralization and the lateralization patterns in the human attention networks (i.e., left- or right-hemispheric dominance, or bilateral organization) not only determine the degree of behavioural asymmetries on the individual level, but also the susceptibility to lateralized attentional deficits following unilateral brain lesions. Recent studies demonstrated that the individual structural variability in the organization of the SLF is linked to behavioural attentional asymmetries (Chechlacz, Gillebert et al., 2015; Marshall, Bergmann, & Jensen, 2015; Thiebaut de Schotten et al., 2011). Moreover, the extent of fronto-parietal disconnections – emerging as a result of SLF damage – has been associated with the severity of neglect symptoms and with the degree of neglect recovery (Lunven et al., 2015; Thiebaut de Schotten et al., 2014). Finally, while some studies suggest that the degree of hemispheric lateralization of the attentional networks might be causally linked to handedness, other reports strongly contradict such a link, or at least indicate that this relationship is not straightforward (Bryden, Hecaen, & DeAgostini, 1983; Cai et al., 2013; Chechlacz, Gillebert et al., 2015; Floel, Buyx, Breitenstein, Lohmann, & Knecht, 2005; Floel, Jansen et al., 2005; Mazoyer et al., 2014; Petit et al., 2015; Somers, Shields, Boks, Kahn, & Sommer, 2015; Szaflarski et al., 2002; Szczepanski, Pinsk, Douglas, Kastner, & Saalmann, 2013; Whitehouse, Badcock, Groen, & Bishop, 2009; Willems, Van der Haegen, Fisher, & Francks, 2014).

Transcranial magnetic stimulation (TMS) provides a powerful tool to study the functional organization of the brain, and this technique has been frequently used to investigate basic principles of visuospatial attention control (for a review see Szczepanski & Kastner, 2009). TMS can be employed to temporarily interfere with cortical processing, in a so-called "virtual lesion" approach. The application of TMS over the right posterior parietal cortex (PPC) has been used to alter the spatial allocation of visual attention, and to induce neglect-like behaviour in healthy participants (Cazzoli, Wurtz, Muri, Hess, & Nyffeler, 2009; Fierro et al., 2000; Hilgetag, Theoret, & Pascual-Leone, 2001; Hung, Driver, & Walsh, 2005; Sack et al., 2007). On the other hand, in stroke patients, TMS applied over the intact, left PPC has been used to ameliorate neglect symptoms, by reducing the pathological