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The hybrid model of attentional control: New insights into hemispheric asymmetries inferred from TMS research

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ABSTRACT

Several competing theories on the mechanisms underlying attentional control have emerged over the years that, despite their substantial differences, all emphasize the importance of hemispheric asymmetries. Transcranial magnetic stimulation (TMS) has proven particularly successful in teasing them apart by selective perturbation of the dorsal and ventral fronto-parietal network. We here critically review the TMS literature and show that hemispheric asymmetries within the dorsal attention network differ between parietal and frontal cortex. Specifically, posterior parietal cortex seems to be characterized by a contralateral bias of each hemisphere and competition between them. In contrast, the right frontal eye field seems to be involved in shifting attention toward both hemifields, whereas left frontal eye field is only involved on shifting attention toward the contralateral hemifield. In the light of presented evidence, we propose to revise the functional-anatomical model originally proposed by Corbetta and Shulman (2011, 2002) and introduce a hybrid model of hemispheric asymmetries in attentional control.

1. Introduction

The voluntary control of attention allows prioritizing those aspects of incoming sensory information that are relevant to us. It therefore constitutes a vital prerequisite for goal-directed behavior and enables us to effectively deal with the abundance of sensory information entering the brain. Already during the beginnings of psychology and neuroscience, the importance of this selection mechanism has been recognized (James, 1890), and there is a wealth of studies investigating the effects of attention on behavior, the functional mechanisms of attentional control, and the underlying neuronal processes (Carrasco, 2011; Corbetta and Shulman, 2002; Desimone and Duncan, 1995; Reynolds and Chelazzi, 2004; Reynolds and Heeger, 2009; Ungerleider and Kastner, 2000).

Similar to the discovery of many other brain functions, neuropsychological findings regarding the behavioral consequences of brain damage have provided first evidence for the involvement of certain brain areas in attentional control and have inspired theories on their functional properties. Especially a neurological syndrome called *spatial hemineglect* has been very influential. Various models of spatial neglect have been proposed over the years and they have shaped theories on spatial attention control until the present day (Bisiach et al., 1996; Halligan et al., 2003; Milner and McIntosh, 2005; Posner et al., 1987; Robertson, 2001). Spatial hemineglect is caused by lesions to frontal, parietal, or subcortical structures and is characterized by impaired attentional processing within the space contralateral to the lesion's location (Bartolomeo et al., 2012; Corbetta et al., 2005; Duncan et al., 1999; Karnath et al., 2002; Karnath and Rorden, 2012; Mesulam, 1999). Most importantly, the phenomenon of spatial neglect is more common and severe after right hemisphere damage than after left hemisphere damage, suggesting a functional asymmetry of the mechanisms underlying spatial attention (Beis et al., 2004; Suchan et al., 2012). Based on this observation, two competing theories of spatial attention have originally emerged, namely Heilman's *hemispatial theory* and Kinsbourne's *opponent processor model*, both accounting for this asymmetry but proposing very different mechanisms (Heilman and Abell, 1980; Heilman and Valenstein, 1979; Kinsbourne, 1977). Despite the many advances in cognitive neuroscience in the last decades, it has been rather difficult to differentiate between these two models with the majority of existing methods. However, transcranial magnetic stimulation (TMS) has proven quite successful in teasing them apart, indeed revealing functional asymmetries between the left and right hemisphere with regard to spatial attention control. With the debate far from being settled, Corbetta and Shulman proposed a functional-anatomical model, strongly supported by neuroimaging data, that offered yet another explanation for the pre-dominance of spatial neglect after right hemisphere damage (Corbetta and Shulman,

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2002; Corbetta and Shulman, 2011). And again, TMS seems to be well-suited to test specific predictions derived from that model.

Here, we first present the three competing models of spatial attention control and lay out their explanatory approach to spatial hemineglect. We then review several lines of research, all based on the application of TMS in healthy volunteers, that have produced critical insights into the mechanisms underlying attentional control. We conclude that each model captures relevant aspects of the mechanisms underlying attentional control, which we here incorporate into one overarching functional-anatomical model of spatial attention control.

2. Competing models of attentional control

The pre-dominance of spatial neglect after right hemisphere damage has originally inspired two competing theories of spatial attention control. Both theories assume a functional asymmetry between the two hemispheres but propose very different mechanisms causing it. According to Heilman's hemispatial theory, the right hemisphere is dominant in spatial attention because it mediates attention shifts to both hemifields, whereas the left hemisphere only mediates attention shifts to the right hemifield (Heilman and Abell, 1980; Heilman and Valenstein, 1979). In case of left hemisphere damage, only mild attentional deficits are expected because the right hemisphere can still shift attention to both hemifields thereby compensating for the damaged left hemisphere. Consequently, the ability to shift attention to both hemifields remains largely intact. In case of right hemisphere damage, however, such overlap in function does not exist and functional compensation is impossible because the intact left hemisphere only mediates attention shifts to the right hemifield. Consequently, the ability to shift attention to the left hemifield is lost resulting in spatial neglect of the left hemifield following right hemispheric lesion.

According to Kinsbourne's opponent processor model, each hemisphere causes a natural attention bias to the contralateral hemifield with the rightward bias of the left hemisphere being stronger than the leftward bias of the right hemisphere (Kinsbourne, 1977). Under normal conditions, the two hemispheres are kept in balance due to inter-hemispheric inhibition. In spatial neglect patients, damage to either hemisphere leaves the contralesional intact hemisphere unopposed. As a result of this reduced inhibition, the contralesional hemisphere becomes overactivated and causes an ipsilesional attention bias. Note how impaired attention in one hemifield goes hand in hand with enhanced attention in the opposite hemifield. In case of left hemisphere damage, only mild attentional deficits are expected because the leftward bias of the right hemisphere is relatively small. Consequently, the ability to shift attention to both hemifields remains largely intact. In case of right hemisphere damage, however, the strong rightward bias of the left hemisphere is uncovered and attention is strongly biased to the right hemifield. Consequently, the ability to shift attention to the left hemifield is suppressed resulting in spatial neglect of the left hemifield following right hemispheric lesion.

Finally, Corbetta and Shulman (2002, 2011) have proposed a functional-anatomical model of attentional control that revolves around two distinct but interacting networks comprising frontal and parietal brain areas. On the one hand, they posit a bilateral dorsal fronto-parietal network including the frontal eye field (FEF) and posterior parietal cortex (PPC). This network is directly related to shifts of spatial attention and modulates sensory areas in a top-down way. On the other hand, there is a right-lateralized ventral fronto-parietal network including the temporo-parietal junction (TPJ) and ventral frontal cortex (VFC). This network acts as a circuit breaker of the dorsal network in case an unexpected or salient stimulus occurs that requires reorienting of attention. Importantly, it is argued that lesions to the ventral fronto-parietal network are the primary cause of spatial neglect. The principal idea then is that damage to the ventral network also indirectly affects the dorsal network due to dysfunctional interactions between both networks, resulting in attentional deficits. Because the ventral network is right-lateralized, right hemisphere damage will have a stronger (indirect) effect on the dorsal network than left hemisphere damage, explaining the predominance of spatial hemineglect after right hemisphere lesion.

In general, Heilman's and Kinsbourne's theory make rather global claims regarding hemispheric asymmetries whereas the model proposed by Corbetta and Shulman provides a more detailed functional-anatomical framework of spatial attention control. The latter model is well-supported by neuroimaging data and the relevance of the ventral network in spatial heminegelct seems to fit well with lesion studies. Importantly, even though the dynamics of dorsal and ventral interaction are still largely unknown (but see Corbetta et al., 2008), there are several TMS studies that support the notion that disruption of the ventral network can indeed influence attentional processes. For example, TMS over TPJ has been shown to have effects on visual extinction (Meister et al., 2006), exogenous cueing (Chica et al., 2011), and re-orienting in an attentional capture paradigm (Chang et al., 2013). At present, no strong conclusion can be drawn from this, but it certainly seems promising to further investigate the remote effects of ventral network stimulation on the dorsal network. Having said that, the lateralization of the ventral network to the right hemisphere does not imply that there are no additional hemispheric asymmetries that play a role in attentional control. At least on a conceptual level, the three models described above are not mutually exclusive. For example, hemispheric asymmetries as they are posited by Heilman's hemispatial theory and Kinsbourne's opponent processor model might very well apply to the dorsal fronto-parietal network, and nevertheless, the proposed role of the ventral network in spatial hemineglect might still hold. In the following, we will provide a detailed review of hemispheric asymmetries in the dorsal fronto-parietal network, presenting evidence obtained with various experimental paradigms.

3. Line bisection

Among the pen-and-paper tasks that are widely used to assess attentional deficits in clinical settings is the line bisection task that requires patients to mark the perceived midpoint of horizontal lines. Neglect patients typically report a strong deviation from the objective midpoint and, due to neglect of the contralesional hemifield, misplace it toward the ipsilesional hemifield (Albert, 1973). Computerized and adapted versions of this task have been developed that led to the discovery of small attention biases even in healthy volunteers, called pseudoneglect (Jewell and McCourt, 2000). Importantly, it has also been used in several TMS studies, revealing neglect-like attentional deficits after parietal and frontal cortex stimulation (dorsal fronto-parietal network).

To begin with, Fierro et al. (2000) applied trains of high-frequency TMS over left or right posterior parietal cortex (P5/P6 electrode position) time-locked to the presentation of transected lines. The critical finding was that TMS over the right hemisphere caused a rightward shift of attention compared to sham stimulation, whereas TMS over the left hemisphere had no effect. In a follow-up experiment (Brighina et al., 2002), this effect of TMS over right parietal cortex was replicated and extended to frontal areas (F3/F4 electrode position). Again, only TMS over the right hemisphere caused a rightward shift of attention compared to