



## Reviews and perspectives

## Spatial attention deficits in humans: The critical role of superior compared to inferior parietal lesions

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## ABSTRACT

According to a longstanding view, inferior as opposed to superior parietal cortex critically contributes to the spatial attentional deficits encountered following unilateral parietal ischemic lesions. We review the evidence on which this view is based and contrast it with more recent structural lesion evidence concerning the critical role of the intraparietal sulcus in spatial attention deficits. In a classical spatial cueing paradigm, focal lesions of the posterior and of the middle segment of the intraparietal sulcus give rise to a pathological invalidity effect that is indistinguishable from that seen after classical inferior parietal lesions. When a competing distracter is added to a target stimulus, the deleterious consequences of focal IPS lesions are again very similar to those classically observed following inferior parietal lesions. The deficit could not be accounted for by functional effects at a distance affecting inferior parietal cortex. These single-case lesion data establish the critical role of the posterior and the middle IPS segment in spatially selective attention and are in line with a vast amount of functional imaging evidence in the intact brain pointing to the prominent role of the intraparietal sulcus in spatial attention, along with inferior parietal cortex under specific circumstances. Functional imaging has also provided hints about the differences in functional contribution between inferior and superior parietal cortex. These hypotheses await further confirmation based on lesion evidence.

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Over the past two decades, functional imaging studies of selective attention in the intact brain have provided us with novel insights into parietal function that go far beyond what one would have predicted based on the clinical literature. In several instances, the conclusions from the 2 sources of evidence even seem *prima facie* irreconcilable. The three main functional imaging findings that were not anticipated from a clinical perspective were the spatial-attentional effects seen in the retinotopically organised areas of the posterior segment of the intraparietal sulcus (IPS) (Bressler & Silver, 2010; Sheremata, Bettencourt, & Somers, 2010; Silver & Kastner, 2009; Vandenberghe et al., 2005; Vandenberghe & Gillebert, 2009; Yantis et al., 2002), the systematic activation of the middle segment of IPS in nearly all selective attention neuroimaging paradigms (e.g. Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta & Shulman, 2002; Giesbrecht, Woldorff, Song, & Mangun, 2003; Molenberghs, Gillebert, Peeters, & Vandenberghe, 2008; Molenberghs, Mesulam, Peeters, & Vandenberghe, 2007; Nobre et al., 1997; Pollmann et al., 2003; Serences & Yantis, 2007; Woldorff et al., 2004), and activation of the superior parietal lobule (SPL) during spatial shifting (Molenberghs et al., 2007; Serences & Yantis, 2007; Shomstein & Yantis, 2004; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001a; Yantis et al., 2002).

These findings were unpredicted by overlap studies and lesion subtraction analyses in neglect and extinction which had pointed to a critical role of structural damage to cortical regions such as the right angular (Mort et al., 2003; Vallar & Perani, 1986; Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, 2010; Vossel et al., 2011) or supramarginal gyrus (Committeri et al., 2007; Golay, Schnider, & Ptak, 2008), the right posterior superior temporal gyrus (STG) (Committeri et al., 2007; Karnath, Berger, Küker, & Rorden, 2004; Karnath, Ferber, & Himmelbach, 2001; Samuelsson, Jensen, Ekholm, Naver, & Blomstrand, 1997; Verdon et al., 2010), and the right temporoparietal junction (TPJ) (Golay et al., 2008; Grandjean, Sander, Lucas, Scherer, & Vuilleumier, 2008; Karnath, Himmelbach, & Küker, 2003; Ticini, de Haan, Klose, Nägele, & Karnath, 2010). Functional effects at a distance from the structural lesion may account for this apparent discrepancy: while the structural damage is mainly affecting the inferior parietal and posterior temporal cortex, the functional effects at a distance also affect attentional networks outside the structurally lesioned zone, including e.g. the IPS which is involved in endogenous attentional control (Carter et al., 2010; Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Corbetta, Patel, & Shulman, 2008; He, Shulman, Snyder, & Corbetta, 2007). In the current review we will examine another possibility, namely that structural damage to IPS and SPL, areas implicated by functional imaging in selective attention, in effect cause spatial attentional deficits, as one would predict based on their activation during spatial attention in healthy subjects (Gillebert et al., 2011). We will also demonstrate that the lower bank of IPS is often damaged by infarctions of the inferior branches of the middle cerebral artery at the periphery of the ischemic zone and that this structural damage contributes to the spatial attentional deficits seen in these patients (Molenberghs et al., 2008).

## 1. Functional imaging of the intact brain

### 1.1. Retinotopically organized areas in posterior IPS

Recent human brain mapping evidence has highlighted the presence of retinotopic representations of left and right hemifield in

the posterior segment of IPS contralaterally, called IPS0/1 and IPS2 (Silver & Kastner, 2009; Silver, Ress, & Heeger, 2005; Swisher, Halko, Merabet, McMains, & Somers, 2007; Wandell, Dumoulin, & Brewer, 2007). In posterior IPS, activity levels vary with the direction of attention, leftward or rightward (Bressler & Silver, 2010; Silver & Kastner, 2009; Vandenberghe et al., 2005; Vandenberghe & Gillebert, 2009; Yantis et al., 2002). The exact monkey homologue of these posterior IPS regions is still under debate (Koyama et al., 2004; Orban et al., 2006; Tootell et al., 1998). Cognitive effects of lesions restricted to IPS0/1 and IPS2 in humans had not been reported until recently (Gillebert et al., 2011).

### 1.2. Ubiquitous activation of middle IPS in attentional paradigms

The omnipresence of the middle segment of the intraparietal sulcus in neuroimaging studies of selective attention sharply contrasts with its seeming near-absence from traditional lesion studies of spatial attentional deficits. The middle segment of IPS is activated in spatial cueing paradigms (Corbetta et al., 1993; Giesbrecht et al., 2003; Kim et al., 1999; Nobre et al., 1997; Woldorff et al., 2004), e.g. when subjects have to direct attention covertly to a peripheral stimulus as opposed to a foveal stimulus (Kelley, Serences, Giesbrecht, & Yantis, 2008; Vandenberghe et al., 1996), when subjects have to attend to a target and a distracter is added (Molenberghs et al., 2008; Vandenberghe et al., 2005), during epochs in which predictable sequences of attentional shifts have to be made (Corbetta et al., 1993) and during the delay phase of spatial cueing paradigms (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000) etc. It is involved not only in spatial cueing but equally in visual search (Nobre, Coull, Walsh, & Frith, 2003; Pollmann et al., 2003; Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001b) and during foveal attention (Coull, Frith, Frackowiak, & Grasby, 1996; Wojciulik & Kanwisher, 1999). Furthermore, a nearby or identical area is also activated during conscious compared to subliminal processing (Beck, Rees, Frith, & Lavie, 2001) and during visual short-term memory tasks (Jonides et al., 1993; Todd & Marois, 2004).

The middle IPS may be the human homologue of the Lateral Intra Parietal (LIP) area in nonhuman primates (Koyama et al., 2004; Sereno, Pitzalis, & Martinez, 2001) (for review see Vandenberghe and Gillebert (2009)). Based on this putative homology and other human fMRI studies (Molenberghs et al., 2007, 2008; Vandenberghe et al., 2005), we have previously postulated that, like LIP (Bisley & Goldberg, 2003, 2010; Gottlieb, Kusunoki, & Goldberg, 1998), the middle IPS segment is involved in the compilation of an attentional priority map (Molenberghs et al., 2008; Vandenberghe et al., 2005; Vandenberghe & Gillebert, 2009). The attentional priority map, or saliency map, is a topographic representation of the distribution of attentional weights (Itti & Koch, 2001; Koch & Ullman, 1985; Ptak, in press). In the presence of perceptually similar targets and distractors (Duncan & Humphreys, 1989), the calibration of attentional weights (Bundesen & Habekost, 2008) allows the observer to resolve the competition between simultaneously presented stimuli and will activate IPS more than when a single perceptually salient stimulus is presented (Molenberghs et al., 2007, 2008; Vandenberghe et al., 2005; Vandenberghe & Gillebert, 2009). This priority map should probably be viewed as emerging from activity in distributed networks, including functionally specialized areas within IPS but also e.g. the frontal eye fields (Ptak, in press),

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