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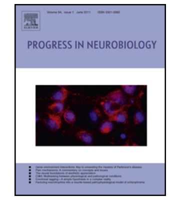

The cross-functional role of frontoparietal regions in cognition: internal attention as the overarching mechanism

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Neuroimaging studies have repeatedly reported findings of activation in frontoparietal regions that largely overlap across various cognitive functions. Part of this frontoparietal activation has been interpreted as reflecting attentional mechanisms that can adaptively be directed towards external stimulation as well as internal representations (internal attention), thereby generating the experience of distinct cognitive functions. Nevertheless, findings of material- and task-specific activation in frontal and parietal regions challenge this internal attention hypothesis and have been used to support more modular hypotheses of cognitive function. The aim of this review is twofold: First, it discusses evidence in support of the concept of internal attention and the so-called dorsal attention network (DAN) as its neural source with respect to three cognitive functions (working memory, episodic retrieval, and mental imagery). While DAN activation in all three functions has been separately linked to internal attention, a comprehensive and integrative review has so far been lacking. Second, the review examines findings of material- and process-specific activation within frontoparietal regions, arguing that these results are well compatible with the internal attention account of frontoparietal activation. A new model of cognition is presented, proposing that supposedly different cognitive concepts actually rely on similar attentional network dynamics to maintain, reactivate and newly create internal representations of stimuli in various modalities. Attentional as well as representational mechanisms are assigned to frontal and parietal regions, positing that some regions are implicated in the allocation of attentional resources to perceptual or internal representations, but others are involved in the representational processes themselves.

Contents

Abbreviations: DAN, dorsal attention network; dlPFC, dorsolateral prefrontal cortex; DMN, default mode network; FEF, frontal eye fields; FPCN/MDS, frontoparietal control network/multiple demand system; IFG, inferior frontal gurus; IPL, inferior parietal lobe; IPs, intraparietal sulcus; ITC, inferior temporal cortex; MFG, middle frontal gyrus; MTL, medial temporal lobe; PMC, premotor cortex; SMA, supplementary motor area; SMG, supramarginal gyrus; SPL, superior parietal lobe; TMS, transcranial magnetic stimulation; TPJ, temporoparietal junction; VAN, ventral attention network; VC, visual cortex.

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1. Introduction

In cognitive science, concepts like working memory, episodic memory, and mental imagery have generally been investigated in isolation, independent from one another. In neuropsychology, they are assessed with rather different test batteries, and efforts have been made to assign the discrete cognitive functions to separate brain regions (Lezak, 2012). However, findings from brain imaging indicate that the structural and functional make-up of the human brain does not comply with these conceptual differentiations. A major review of brain imaging studies has shown that many cognitive functions appear to share common brain circuits, as they are all associated with the activation of highly similar brain regions when investigated with positron emission tomography or functional magnetic resonance imaging (fMRI; Cabeza and Nyberg, 2000). This finding challenges our understanding of the cognitive concepts under inspection. While the various cognitive functions had up to that point been considered as largely independent processes, the results of the review suggest that especially higher cognitive functions share certain overarching mechanisms and may thus not be as fundamentally different as they are treated on the cognitive-behavioural level.

A network of frontal and parietal brain regions comprising the presumed human homologue of the frontal eye fields (FEF) and the intraparietal sulcus (IPs) extending into the superior parietal lobe (SPL) represents a prime example of such a scenario, as it appears to be involved in mental imagery (e.g., Formisano et al., 2002; Ganis et al., 2004; Ishai et al., 2000; Sack and Schuhmann, 2012; Sack et al., 2008, 2002) working memory (e.g., Collette et al., 2007; Curtis, 2006; Gordon et al., 2012; Linden et al., 2012; Majerus et al., 2010; Owen et al., 2005; Passaro et al., 2013; Pessoa et al., 2002; Postle et al., 2004; Rottschy et al., 2012), and episodic memory retrieval (e.g., Burianová et al., 2012; Ciaramelli et al., 2010; Kim, 2010; Kragel and Polyn, 2014; Kwok et al., 2012; Ranganath et al., 2005; see Fig. 1 for overlapping patterns of activation across tasks).

This suggests that this network supports one broader mechanism that is needed for the execution of all these functions, rather than several task-specific processes. The challenge is to identify the mechanism that underlies these functions in their essence and to understand how this cognitive-behavioural essence is represented in the brain. A likely candidate for this overarching mechanism is that of attention, more specifically top-down attentional orienting or attentional control. For one thing, in neuroscience, the activation of FEF and IPs has been strongly implicated in specific processes of attentional orienting (Corbetta and Shulman, 2002) and is quite consensually labelled the dorsal attention network (DAN; see Corbetta et al., 2008; Power et al., 2011). Furthermore, from a purely cognitive perspective, attention can be considered one of the most basic mechanisms, likely to be involved in the successful execution of almost all cognitive tasks. It thus seems plausible to assume that the recurring activation of the FEF and IPS (as a network) across cognitive tasks is related to the attentional demands these tasks entail.

The finding of DAN activation across tasks involving the internal maintenance or representation of task material has nurtured a set of neurocognitive models that focus on attentional orienting as a central mechanism in the field of working memory (*internal attention;* e.g., Lepsien and Nobre, 2007; Nobre et al., 2004), episodic retrieval (*attention to memory*; e.g. Cabeza et al., 2008; Ciaramelli et al., 2008), and mental imagery (*top-down control*; e.g., Kosslyn, 2005; Sack and Schuhmann, 2012; Zimmer, 2008).

The common quintessence of these accounts is that the respective cognitive functions are all assumed to involve the orienting of attentional resources towards internal representations of task-relevant material. On the neural level, this task-relevant material is assumed to be represented in the brain regions initially involved in the sensory processing of that same material, and the attentional mechanism originating in the DAN is conceptualised as a top-down modulation or biasing of these sensory processing regions to maintain or reactivate the neural activation that encodes the material. Rather than proposing a multitude of functionally specific modules within the brain, these models thus suggest a more parsimonious view of brain function, where the same attentional mechanisms can be adaptively applied to a multitude of external and internal processes. In line with this, the past decade of fMRI studies has furthermore brought forward accumulating evidence that the execution of working memory, episodic retrieval, and mental imagery tasks is associated with activation in regions involved in sensory processing of the material used during the tasks (e.g., Majerus et al., 2010; van de Ven and Sack, 2013; Borst and Kosslyn, 2008, for working memory, episodic retrieval, and working memory, respectively) and that this activation is sustained in the absence of sensory stimulation and likely modulated by the DAN (e.g., Lee and D'Esposito, 2012). Over and above, there is evidence that the same visuospatial attentional mechanisms that are applied to external events can also be directed to internal representations of visual material (e.g., Griffin and Nobre, 2003).

In spite of the above summarised evidence in support of attention-based conceptualisations of cognitive functions, these concepts have repeatedly been challenged by proponents of the more traditional (and originally cognitive) models of the three cognitive functions that adhere to process-specific modules and material-specific stores or buffers, particularly in the field of episodic memory and working memory research (Atkinson and Shiffrin, 1968; Baddeley, 2000; Baddeley and Hitch, 1974; see also Jonides et al., 2008). In trying to transfer these models to neuroscience, several researchers have set forth to link the modules (or "boxes") and processes described in their models to specific circumscribed brain regions. Indeed, neuroimaging has provided evidence for process- and material-specific activation in frontal and parietal association cortex during working memory (Rottschy et al., 2012; Smith and Jonides, 1998; Smith et al., 1996),