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Functions of the human frontoparietal attention network: Evidence from neuroimaging

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Human frontoparietal cortex has long been implicated as a source of attentional control. However, the mechanistic underpinnings of these control functions have remained elusive due to limitations of neuroimaging techniques that rely on anatomical landmarks to localize patterns of activation. The recent advent of topographic mapping via functional magnetic resonance imaging (fMRI) has allowed the reliable parcellation of the network into 18 independent subregions in individual subjects, thereby offering unprecedented opportunities to address a wide range of empirical questions as to how mechanisms of control operate. Here, we review the human neuroimaging literature that has begun to explore space-based, feature-based, object-based and category-based attentional control within the context of topographically defined frontoparietal cortex.

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Introduction

Human cognitive systems are constrained by set capacities, such that the number of co-occurring stimuli that can be processed simultaneously is limited. Selecting behaviorally relevant information among the clutter is therefore a critical component of routine interactions with complex sensory environments. In the visual domain, such selections are completed via several interacting mechanisms based on different criteria, including spatial location (e.g., a spectator of a soccer match may restrict attention to any activity within the penalty area), a specific feature (e.g., the spectator may attend only to soccer players in white jerseys), a specific object (e.g., the spectator may direct attention to the soccer ball), or even a category of objects (e.g., the spectator may attend to any soccer player regardless of identity or team affiliation).

In the primate brain, attentional selection in the visual domain is mediated by a large-scale network of regions within the thalamus, and occipital, temporal, parietal and frontal cortex [1,2]. This network can be broadly subdivided into first, control regions ('sources') in frontoparietal cortex and the thalamus that generate modulatory signals and second, sensory processing areas ('sites') in occipitotemporal cortex where these modulatory signals influence ongoing visual processing [3,4]. Here, we will focus on recent advances in our understanding of functions of the source regions, particularly in the human frontoparietal network, as explored using neuroimaging techniques.

Space-based attention mechanisms and functions

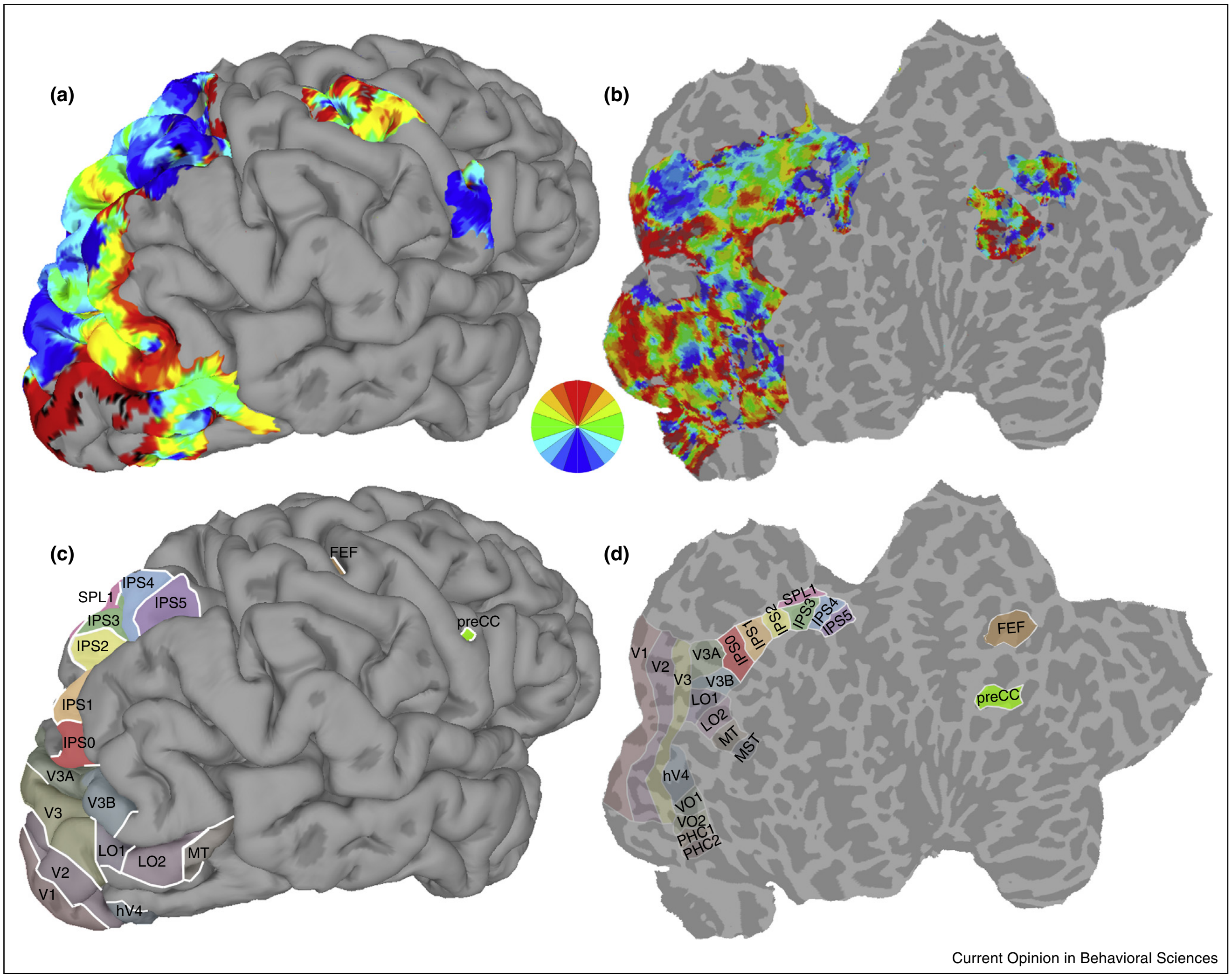
Of the different selection methods described in the introduction, space-based attention has been the focus of the vast majority of neuroimaging studies directed at the control network to date. This line of research has been facilitated by a clear understanding of spatial representations within higher-order cortex [5]. Importantly, there is a great amount of overlap between the attention-related activations in frontoparietal cortex and the topographically organized frontal and parietal areas (see Figure 1 and Box 1), which permits the systematic study of attentional control systems in individual subjects. This approach holds the promise to yield a more complete understanding of the neural underpinnings of cognitive control processes related to selective attention.

Models of space-based selection

Utilizing such advanced mapping techniques, a recent functional magnetic resonance imaging (fMRI) study (see Figure 2a for an illustration of the task) found attention signals (see Figure 2b) in topographic frontal and parietal areas to be spatially specific: response magnitude was significantly greater when attention was directed to objects in the contralateral, relative to the ipsilateral, visual field [6••]. With the exception of an area in the left superior parietal lobule, known as SPL1, each topographic area in frontal and parietal cortex individually generated this contralateral spatial bias that was on average balanced between the two hemispheres (Figure 2c).

The results above provide empirical evidence in support of and a neural basis for an *interhemispheric competition*

Figure 1



Topographic maps in the human visual system. **(a)** A single subject's activation pattern displayed on an inflated view of the right hemisphere (here, activation has been restricted to emphasize frontoparietal cortex), derived from a memory-guided saccade task. The task utilizes a traveling wave paradigm that combines covert shifts of attention, working memory and saccadic eye movements (see [48,46] for a detailed description of the design and analysis). The color wheel at center indicates the region of visual space to which each color in the activation map corresponds. **(b)** Same as (a), but presented on a flat surface, thereby depicting the topographic organization of the entire visual system. **(c)** Parcellated regions in frontoparietal cortex with drawn boundaries, based on topographic mapping. The boundaries between intraparietal sulcus (IPS) regions as well as superior parietal lobule (SPL1) are defined according to reversals in the representation of space along the upper and lower vertical meridians (see text in Box 1). Retinotopically mapped regions in visual cortex are included as well to illustrate the anatomical relationship between sources of attentional control and modulation sites (see section 'Introduction'). **(d)** Same as (c), but presented on a flat surface.

account of space-based attentional control [7,8]. Nearly every topographic region of the left and right hemisphere contributes to the control of space-based attention across the visual field by generating a spatial bias, or 'attentional weight' [9] in favor of the contralateral hemifield. The sum of the weights contributed by all areas within a hemisphere constitutes the overall spatial bias exerted over contralateral space, and the net output of the two hemispheres is similar, resulting in a balanced system. This balance of attentional weights across the hemispheres may be achieved through reciprocal interhemispheric inhibition of corresponding areas [10]. However, the higher-order control system appears to be somewhat complicated by right SPL1's unique role in spatial attention, as the attentional weight generated by this area was not found to be counteracted by left SPL1. Instead, the left frontal eye field (FEF) and left intraparietal sulcus (IPS) areas IPS1-*2* generated stronger attentional weights than the corresponding regions in the right hemisphere. Thus, the control system likely requires the cooperation of several distributed subcomponents in order to achieve balance across the two hemispheres.