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Functions of the human frontoparietal attention network: Evidence from neuroimaging

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Abstract

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.

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 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.

The interhemispheric competition account of space-based attentional control is in stark contrast to the prevailing *hemispacial theory* [11], which assumes that the right hemisphere controls attention in both visual hemifields, whereas the left hemisphere controls attention in the contralateral visual field only. This hypothesized asymmetry across hemispheres received a groundswell of support primarily from patient studies with unilateral lesions in

the inferior parietal lobule and/or the temporoparietal junction [12,13]. These patients typically exhibit symptoms of visuo-spatial hemi-neglect to the contralesional side of space, but such deficits manifest with an overwhelmingly higher rate following right, rather than left, hemispheric damage.

A similar breadth of clinical evidence in favor of interhemispheric competition is largely lacking, presumably due to the unlikely occurrence of focal lesions contained within IPS. Recently, however, two such cases were reported [14,15]. Patients H.H. and N.V. have a focal lesion confined to left posterior IPS and right middle IPS (extending into SPL), respectively, and both exhibited attention-related deficits examined in a modified Posner cuing task. Here, subjects reported the orientation of a grating following an endogenous precue; on a proportion of trials, a competing distractor appeared in the uncued location. Behavioral deficits attributed to stimulus competition were present for both H.H. and N.V. despite having lesions in opposite hemispheres. Importantly, deficits were restricted to trials in which the target appeared in the contralesional side of space.

The neuroimaging and clinical studies described above provide compelling evidence in favor of the interhemispheric competition account, but fall short of directly testing its behavioral predictions. For example, given an attentional control system in which the sum of the weights across hemispheres dictates the current locus of selection, a perturbation in form of a transitory ‘virtual lesion’ induced by transcranial magnetic stimulation (TMS) over one hemisphere should lead to an attentional shift toward the ipsilateral visual field. Conversely, bilateral stimulation should not change the overall attentional weighting balance, and hence nor the locus of selection. These predictions were recently confirmed in a study that used a multimodal approach of behavioral testing, neuroimaging and fMRI-guided TMS [16*]. First, individual differences in the estimated strengths of frontoparietal attentional weights were predictive of behavior when allocating spatial attention. Second, causal evidence in support of the account’s predictions was established by demonstrating that space-based attention could be systematically shifted toward either visual field, depending on the site (unilateral or bilateral IPS1–2, or right SPL1) of a single TMS pulse, presumably due to temporary changes to the attentional weights in underlying cortex. Thus, in the intact human brain, space-based attention appears to be controlled through competitive interactions between hemispheres.

Spatial prioritization in frontoparietal cortex

Having established a retinotopic organization of the frontoparietal network which in turn supports a contralaterally biased representation of space, an intriguing subsequent line of inquiry explored how a region of space is favorably prioritized for selection. Space-based selection is a complex process that is driven by the combination of sensory input and internal behavioral goals, the sum of which may be represented via dynamic spatial priority maps [17–19]. Such a priority map effectively grades spatial locations in accordance with top-down and bottom-up properties, and presumably, specific stimuli and task demands that gave rise to a particular pattern of prioritization should be indistinguishable within it. To test whether spatial priority maps may be localized within the frontoparietal attention network, Jerde *et al.* [19] conducted a neuroimaging study in which one group of subjects completed a

series of tasks designed to tax covert spatial attention, spatial working memory, or saccadic planning. Using a classifier trained on patterns of activation elicited from any one of the tasks, the experimenters found that spatial priorities could be accurately decoded from the remaining two tasks in both IPS2 and FEF. Neuronal populations within these two regions therefore likely signal prioritized space in a task-independent manner, such that selected locations are represented, while stimulus and task properties that drive selection are not. These findings are consistent with a growing body of literature that finds evidence for priority maps in middle IPS [20,21] as well as in distributed networks that include IPS and FEF [22]. There exists, however, a concurrent line of studies that has successfully decoded stimulus information (in particular, features) within similar control regions [23,24**,25**,26]. We turn to these studies next.

Feature-based, object-based and category-based attention mechanisms and functions

Although the majority of work on the frontoparietal attention network has focused on the control of spatial attention, a growing body of research suggests that the network is also involved in the selection of non-spatial information.

Control of feature-based attention

Studies of feature-based attention have shown that shifting attention from one feature to another [27] leads to increased activation within regions of the frontoparietal network analogous to shift-related changes in space-based attention [28–30]. Importantly, the same effect is observed when attentional shifts occur between different values of the same feature dimension [18], suggesting that shift-related activation patterns cannot be explained by potentially unique interactions between different features and space-based attention. Furthermore, regions of the frontoparietal network carry information about feature values within the current attentional set [24**,26]. Liu and colleagues [24**] instructed participants to monitor one of two overlapping motion dot fields that differed either by color or direction of motion in order to detect changes in either luminance or speed (see Figure 2d for an illustration of the color task). Attending to either color or motion led to widespread activation in topographically defined regions along the IPS, as well as frontal regions, and retinotopically defined early visual areas (Figure 2e). Although overall response amplitude in these regions did not differ across within-feature conditions (e.g., attending to green versus attending to red), activation patterns could nonetheless be used to reliably decode the attended feature value (Figure 2f). Finally, the patterns of classifier weights that resulted in successful decoding differed between the attend-to-motion task and the attend-to-color task. This suggests that directing attention to different feature dimensions is controlled by distinct subpopulations of neurons within the same network.

Control of object-based attention

A number of studies have now also implicated the frontoparietal attention network in the control of object-based attention [31,32]. Analogous to the increased activation observed following the re-direction of space-based [28–30] or feature-based attention [23,27], shifting attention in between two spatially overlapping objects increases responses in frontoparietal

areas including SPL, IPS and the superior frontal sulcus [31]. In addition to controlling shifts in object-based attention, the frontoparietal network appears to be involved in the maintenance of object-based attentional sets. In a recent study [25**], participants were instructed to detect luminance changes in one of two spatially superimposed triangles. Luminance changes could occur anywhere on the attended triangle, precluding the possibility of using a space-based attention strategy for target detection. Relative to a passive viewing condition, deploying object-based attention resulted in widespread activation in early visual and occipitotemporal cortex as well as in regions of the frontoparietal network. Across all regions of interest (ROIs), overall response magnitude did not reflect which of the two triangles was currently task-relevant. In contrast, multivariate classification analyses revealed that distributed patterns of activity in a number of ROIs, including IPS and FEF, did differ depending on which triangle was attended. Akin to theories of space-based and feature-based attention, these results support the hypothesis that source regions in the frontoparietal network generate object-specific biasing signals that modulate sensory processing of objects in visual cortex. However, future studies utilizing methods such as TMS that allow for stronger causal inferences regarding the functional relationship between frontoparietal and visual regions are needed to further corroborate this supposition.

Control of category-based attention

To date, there are no published studies that implicate the frontoparietal attention network in the selection at the level of object categories. However, it is conceivable that at least a subset of regions within the network are also involved in the generation of category-specific control signals. For instance, a series of monkey physiology studies using a delayed-match-to-category paradigm has revealed that neurons in LIP can flexibly encode information about category membership [33–35]. Interestingly, category-specific responses were maintained during a delay period, in the absence of any visual stimulation, reminiscent of an attention signal. Further support that the network is involved in the control of category-based attention derives from a preliminary report that activation patterns within posterior IPS regions carry information about the current attentional set during a real-world visual search task [K.N. Seidl-Rathkopf. *et al.*, abstract 43.562, 14th Annual Meeting of the Vision Sciences Society, St. Pete Beach, FL, May 2014].

Distributed connectivity profiles across the frontoparietal control network

In many of the imaging studies described above — spanning all forms of top-down selection — broad swaths of the frontoparietal network are implicated as contributors to attentional control [6**,24**,25**]. This suggests that these complex attention mechanisms are likely supported by distributed networks across sites of control. A handful of human studies have utilized either functional or structural connectivity methods in an effort to elucidate distributed networks within frontoparietal cortex [36–41], and often broad connectivity patterns between FEF and IPS are revealed. However, in many cases IPS is not fully parcellated (as with, e.g., topographic mapping), limiting the interpretability of the results. When attempts to (partially) subdivide IPS are made (either defined topographically, via probabilistic tractography, or using previously published coordinates), FEF is commonly

observed to be functionally connected with IPS2 [38,40,42**], IPS3 [37,38,40], and SPL [38,42**].

While this suggests a seemingly broad connectivity pattern between PPC and FEF, separable pathways may be functionally distinct. Evidence for functional specialization distributed within the frontoparietal network has been found in a study that examined connectivity patterns of different network nodes [42**]. Two pathways between frontal cortex and PPC were identified using diffusion tensor imaging (DTI) and probabilistic tractography, and functional interactions of activity evoked during attention tasks: first, a lateral pathway connecting FEF and IPS2 and second, a medial pathway connecting the supplementary eye field (SEF) and SPL1 (Figure 3). Intriguingly, these two pathways appear to mediate different functions. The IPS2-FEF pathway supports attentional selection in retinotopic, or viewer-centered spatial coordinates, whereas the SEF-SPL1 pathway supports attentional selections based on an object-centered spatial reference frame. Thus, the multiple topographic representations in PPC may code for attentional priorities in different spatial reference frames.

Conclusions

In sum, a growing body of research demonstrates the broad involvement of frontoparietal cortex in space-based, feature-based, object-based, and category-based selection, consistent with the possible existence of domain-general control centers within the human control network (see Figure 2). An important question that remains unresolved is how a single network can flexibly generate a diverse range of control signals depending on current task demands. Further studies are needed to determine whether separable selection mechanisms are subserved by true domain-general neuronal populations or whether each mechanism recruits distinct subpopulations of neurons within the same regions [23,26].

Relatedly, it remains an open question what individual roles subregions within the network may play in the generation of attentional control signals. The existence of 14 topographic representations in human PPC alone seems, on the face of it, excessive and redundant. As such, an investigation into potential functional dissociations between subunits is warranted. DTI studies lend some support to this line of inquiry, as IPS can be largely subdivided based on structural connectivity patterns alone [37,40]. Given that the functional properties of a brain region are necessarily constrained by its anatomical connections, these data imply that subunits of IPS may very well be functionally distinct, but carefully implemented imaging studies are necessary to confirm this hypothesis. Encouragingly, a number of recent studies investigating both spatial [6**,16*,19] and non-spatial [24**,25**,26] selection mechanisms have adopted a topographically defined approach in individual subjects. Continuing such a systematic approach will help uncover the potentially distinct contributions of individuated control subunits.

This review has deliberately focused on the cortical attention network, but it bears noting that subcortical regions also likely play critical roles in top-down attentional control. In particular, there is first evidence that the pulvinar nucleus of the thalamus, which has direct connections to both visual cortex and PPC [43,44], coordinates the routing of visual

information across cortical maps [44]. It will be an important venue for future neuroimaging studies to further explore the role of the pulvinar and other thalamic nuclei in attentional selection, in particular with regard to its interactions with the frontoparietal attention network.

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Box 1**Topography in frontoparietal cortex**

Topographic representations are ubiquitous in the brain and reflect the spatial layout of the sensory receptors; in the case of the visual system, retinal locations are organized in multiple retinotopic maps (Figure 1a,b). The advent of neuroimaging mapping techniques used to define these topographic representations in individual subjects has greatly facilitated the study of functional specialization of visual areas. This approach has been successfully extended in recent years to higher-order cortex. Using a cognitive mapping approach that utilizes periodic memory-guided saccade or spatial attention tasks, topographic organization has been found in a number of areas in parietal and frontal cortex. To date, seven topographically organized areas have been described in bilateral posterior parietal cortex (PPC): six of these areas form a contiguous band along the intraparietal sulcus (IPS0-IPS5), and one area extends medially into superior parietal lobule (SPL1) (Figure 1c,d; [5,45,46]). Each of these topographic areas contains a continuous representation of the contralateral visual field and is delineated from neighboring areas according to alternating representations of the upper and lower vertical meridian (Figure 1a,b). Topographic maps have also been identified in frontal cortex [47,48]. One such map is located in the superior branch of precentral cortex (PreCC), in the approximate location of the human frontal eye field (FEF), and a second one in the inferior branch of PreCC (Figure 1c,d).

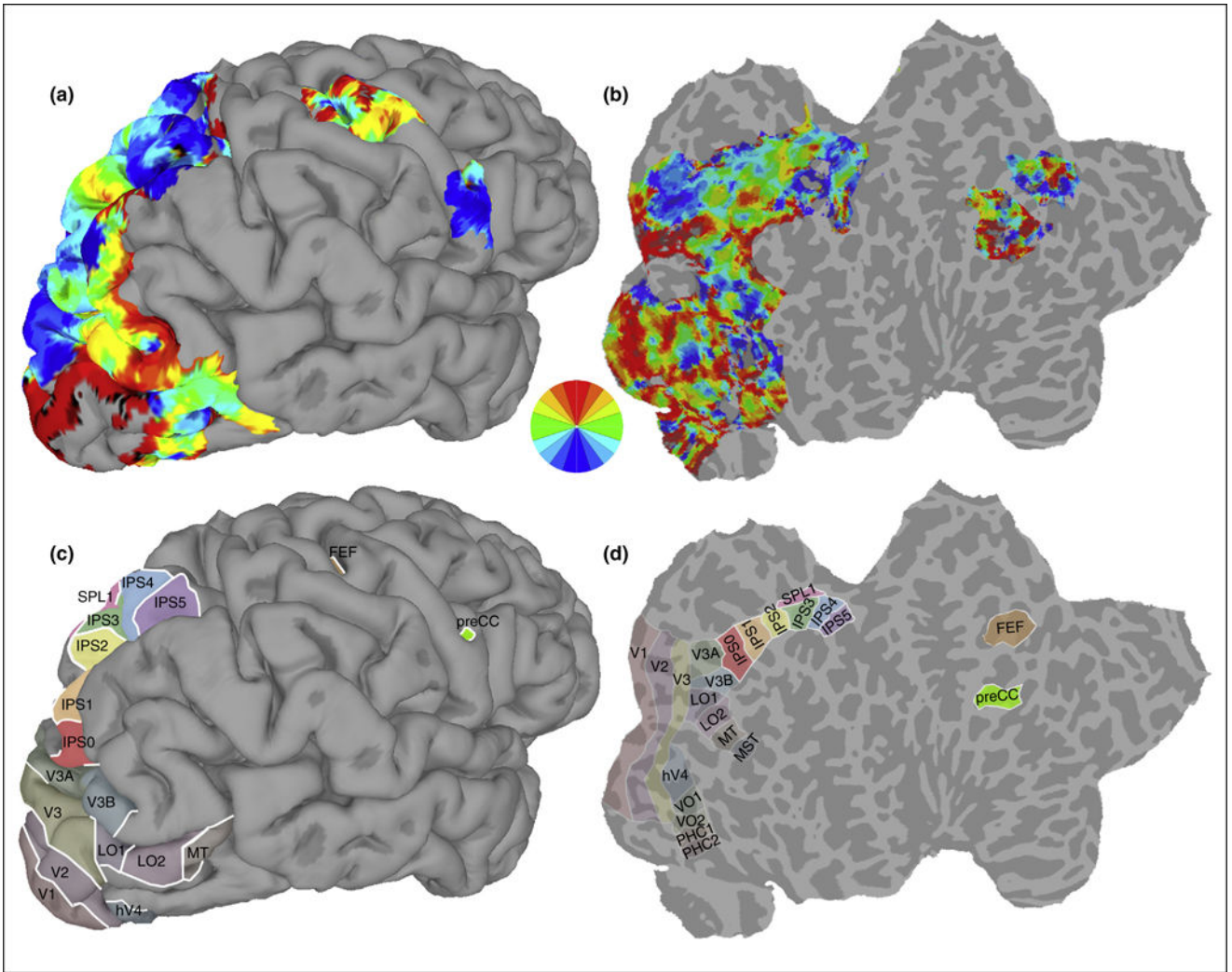
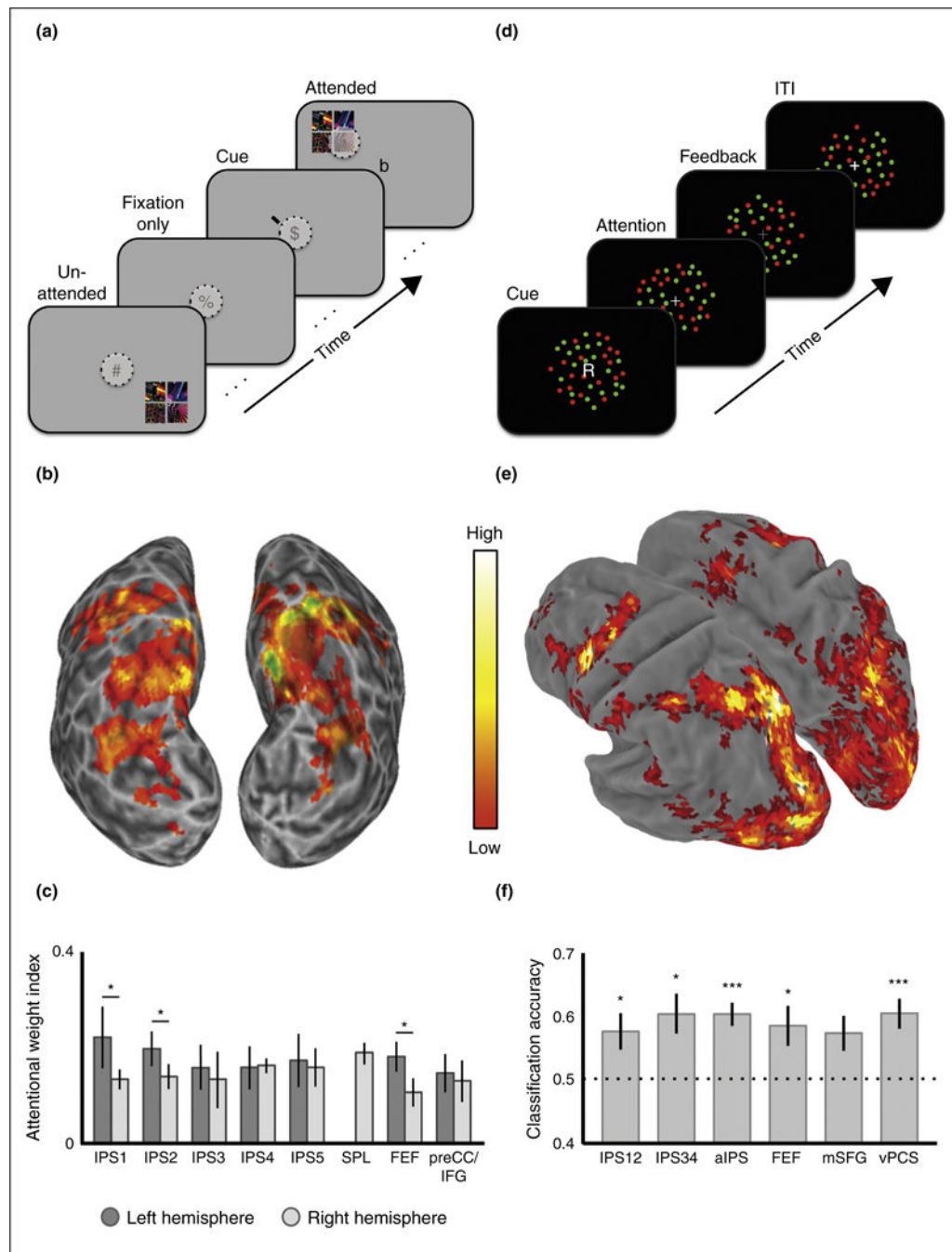


Figure 1.

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.

**Figure 2.**

Space-based and feature-based attention in the frontoparietal network. **(a)** Schematic of the experimental design for a space-based attention task [6**]. Subjects were precued to alternately attend to a peripheral stimulus in one of four quadrants (*attend* condition), or to attend to fixation and ignore the stimulus (*unattend* condition). **(b)** Activation pattern resulting from a contrast of the ‘attend’ and ‘unattend’ conditions. **(c)** Attentional weight indices from each topographic frontoparietal region ($N = 9$), defined as the difference of the peak BOLD response from the contralateral and ipsilateral attend conditions, divided by the

sum. Note that all regions, apart from left SPL1, exhibit significant contralateral biases (see section ‘Models of space-based selection’). **(d)** Schematic of the experimental design for a feature-based attention task [24**]. Subjects were precued to attend to either the red (‘R’) or green (‘G’) dots or neither (‘N’). The task was to detect small luminance increments in the cued color. **(e)** Brain areas modulated by feature-based attention. **(f)** Mean classifier accuracy ($N=6$) in the color experiment. All ROIs but medial superior frontal gyrus (mSFG) carried information about which color was currently held in the attentional set. aIPS = anterior intraparietal sulcus; vPCS = ventral precentral sulcus. (a–c) adapted from [6**]. (d–f) adapted from [24**].

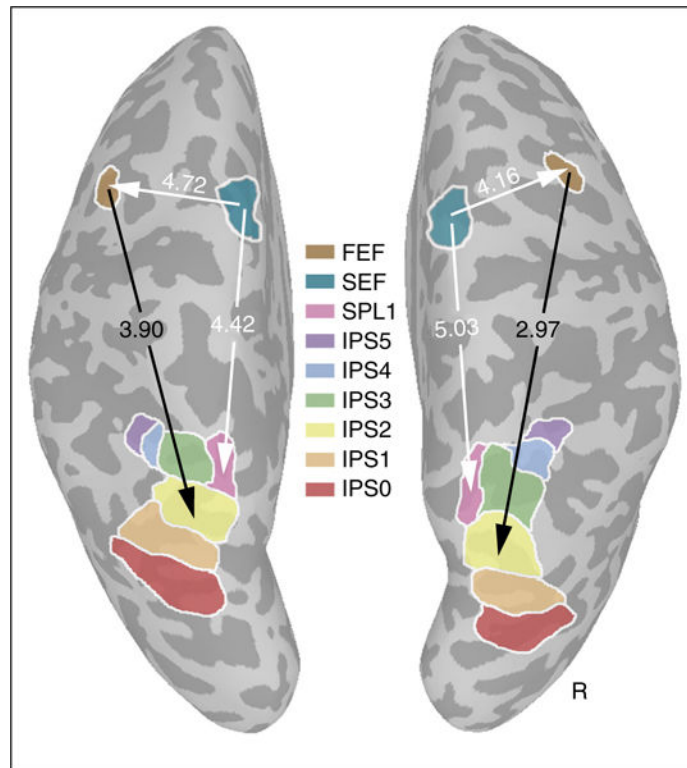


Figure 3.

Functional separation in the frontoparietal network. An adaptation of the functional connectivity results described in Figure 2 of [42**] (see section ‘Distributed connectivity profiles across the frontoparietal control network’ for more details of the experiment). Directional connectivity was estimated using multivariate autoregressive modeling (MVAR). Black lines and corresponding values reflect significant MVAR patterns within the control network with respect to viewer-centered representations (arrow endpoint indicates the direction of causal influences). Conversely, white lines and corresponding values reflect significant MVAR patterns with respect to object-centered representations. These results suggest that topographic subregions of the frontoparietal network represent space in multiple reference frames.