

Identifying the neural systems of top-down attentional control: A meta-analytic approach

Barry Giesbrecht & George R. Mangun
Center for Mind & Brain
University of California, Davis

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Correspondence should be addressed to:

Barry Giesbrecht, Ph.D.
Center for Mind & Brain
University of California
One Shields Avenue
Davis, California 95616
TEL: 530-297-4409
FAX: 530-792-1489
Email: giesbrecht@ucdavis.edu (B.G.)

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Abstract

Several recent neuroimaging studies have investigated the brain systems involved in the control of voluntary orienting of selective visual attention by measuring the cortical response to attention-directing cues. Although these studies have provided strong evidence for frontal and parietal involvement in attentional control, it has proven difficult to unambiguously isolate attentional orienting responses from other cognitive operations evoked by the cue. Here we present a meta-analysis of a series of voluntary orienting studies from our lab. Across the studies, the only common mental operation is attentional orienting. We predicted that if regions of frontal and parietal cortex subserve top-down control of voluntary orienting specifically, then overlap between all studies should be observed. Consistent with this prediction, focal areas of superior frontal sulcus and intraparietal sulcus of both hemispheres were activated across all studies. We suggest that these subregions are critical players in the top-down control of attentional orienting.

I. Introduction

The visual environment is extremely complex. One way in which observers handle this complexity is by selectively attending to information relevant to their current goals. Understanding the selective nature of visual attention and its importance for coherent behavior has been one of the most extensively studied issues of psychology and neuroscience. Of particular interest is the notion that selective stimulus processing is mediated by the interaction between top-down executive control functions and bottom-up sensory processing systems. A key cognitive operation that is involved in this top-down interaction is voluntary covert orienting (e.g., Posner, 1980). Recent event-related functional magnetic resonance imaging (fMRI) studies of visual attention have focused on identifying the brain systems that support the control of voluntary covert attentional orienting (e.g., Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Giesbrecht, Woldorff, Song, & Mangun, 2003; Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). These fMRI studies have identified a distributed network of brain areas that support voluntary orienting, including both cortical and subcortical structures. The key cortical structures, which are the focus of the present work, are portions of superior frontal cortex, near the human homologue of the frontal eye fields (FEF), and posterior parietal cortex (PPC), along the intraparietal sulcus (IPS).

Much of what is known about voluntary orienting comes from studies of selective attention that use the so-called cueing paradigm (Posner, 1980; Figure 1). In these studies participants are presented with a cue stimulus that directs attention to a particular location or feature (e.g., color, form, motion) in order to make a discrimination of a subsequently presented target stimulus that either does or does not occur at the cued location or contain the cued feature. Implication of frontal and parietal cortex in top-down control of selective attention in this task requires the dissociation of orienting responses from other cognitive operations. One approach to this dissociation, first reported by Harter et al. (Harter, Miller, Price, LaLonde, & Keyes, 1989) using electroencephalography, is to measure the cortical response to attention-directing cues in the cueing paradigm. The validity of dissociating control mechanisms from other information processing stages via the measurement of cue-related responses rests on the logic that

if an attention-directing cue engages cognitive operations that prepare the system for incoming information, then by measuring the cortical response to the cue separately from the target one can dissociate those systems that are involved in the control of orienting to task-relevant targets from those involved in selectively processing the targets themselves.

Although identifying top-down control systems by measurement of cue-related cortical activity has intuitive appeal because of its elegant simplicity, effective application of the approach is a complex endeavor. This complexity is rooted in the fact that attention-directing cues not only evoke activity in brain systems that control attentional orienting, but they evoke activity in perceptual, cognitive, and motor stages of processing in order to prepare the system for the task. Within a simple cognitive framework, these stages include: 1) sensory processing of the cue, 2) extraction of an abstract/linguistic code from the cue-symbol, 3) mapping of the code onto the task instruction (e.g., the arrow means attend right), 4) covertly orienting to the relevant stimulus feature or location, 5) maintaining the task instruction during the cue-target interval, and 6) preparing to respond. It is worthwhile underscoring that this framework is simple and that each of these stages may be subdivided to a more refined scale, e.g., sensory processing = orientation detection + edge detection + color processing; orienting to a location = disengage + move + engage. Thus, despite the intention of using cue-related activity to identify the brain areas that subserve orienting (i.e., stage 4), areas that are activated by the cue could, in principle, support any one of, or some combination of all these processing stages. Therefore, in order to understand the mechanisms that mediate voluntary orienting (i.e., stage 4) using the cue-related approach, one can not simply measure activity evoked by the cue-related activity alone, but one must dissociate orienting activity from activity that is related to other sensory, motor and cognitive operations.

The fMRI studies that have implicated frontal and parietal involvement in the control of attentional orienting via the assessment of cue-related activity have attempted to isolate the orienting response from other cognitive operations by direct comparison of cue-related activity versus a reference condition. The assumption of such comparisons is that the reference condition shares many cognitive operations with the condition of interest, but ideally differs from the condition of interest only in terms of

a single cognitive operation. Thus, when the condition of interest and reference condition are compared directly, the shared operations cancel or subtract out, and only those brain areas that support the cognitive operation of interest should remain. Several studies have used the subtraction approach, but in many cases the reference condition has not been ideal for isolating orienting from the other cognitive operations evoked by the cue. For instance, some studies have identified frontal and parietal top-down control systems by comparing cue-related activity to baseline activity (Corbetta et al., 2000; Hopfinger et al., 2000; Kastner et al., 1999). However, applying the cognitive framework outline above and the subtraction approach suggests that the activity cannot be uniquely associated with voluntary orienting, but rather represents orienting and additional cognitive operations involved in processing the cue. A more complex contrast between conditions was used by Hopfinger et al. (2000), where target-related activity was used as a reference. Although this contrast controls for many basic cognitive operations, it unfortunately introduces other important differences between the cue and reference conditions particularly in terms of response related operations. Thus, although cue-related fMRI studies clearly indicate that portions of frontal and parietal cortex are activated in response to attention-directing voluntary orienting cues, the precise function of these areas remains unclear because the statistical comparisons have not completely dissociated the orienting response from other operations evoked by the cue.

In order to investigate which specific areas of frontal and parietal cortex support voluntary attentional orienting, we conducted a meta-analysis of published and unpublished attentional cuing studies from our lab. Cue-related contrasts from these studies were divided into three categories (see Methods). These categories differed in terms of the nature of the reference condition and therefore differed in terms of the cognitive operations that were revealed by the contrast. Critically, the only cognitive operation that the three categories had in common was the involvement of voluntary orienting, either to a location or to a feature (e.g., color). The analytical approach was based on the following simple logic. If the only mental operation that these comparisons have in common is the involvement of voluntary orienting, then by overlaying the activations onto a single cortical representation, those areas

that are activated in all of the studies should be those areas that are involved in the control of voluntary orienting of selective attention. The results of this meta-analysis demonstrate that posterior portions of the superior frontal sulcus (SFS) and portions of IPS were common to the three categories of cue-related comparisons, suggesting that these areas are therefore critically involved in the control of voluntary orienting of selective attention.

II. Method

A. Details of included studies

Studies conducted in our lab were included if they were a) published in a peer-reviewed journal or b) presented at a scientific meeting. Each study used an attentional cueing paradigm (e.g., Fig. 1). In these tasks subjects were cued to attend to a location, nonspatial stimulus feature (e.g., color or global/local), or a particular spatial reference frame. Table 1 lists the studies that were included and the details about the conditions.

B. Meta-analysis

Cue-related contrasts were divided into three categories. The categories differed in terms of the cognitive operations that were revealed by the statistical comparison based on the cognitive framework and subtraction approach outlined above. One category, the cue versus baseline (CvsB) category, included contrasts that compared cue activity versus baseline activity (as defined by either precue activity or by mean level of activity across the fMRI time-series). Areas revealed by this category of contrast could, in principle, support any one of the putative cognitive operations (i.e., stages 1-6). A second category, the cue versus passive (CvsP) category, included contrasts that compared activity evoked by attention-directing cues versus passive cues that did not direct attention nor prepare subjects to respond. Because passive cues require sensory processing, extraction of a linguistic code, and mapping of the code onto the instruction (i.e., "do nothing") just like attention-directing cues, but not orienting and motor related processes, direct comparison of passive cue activity with cue-related activity should cancel out

those areas that are involved in the common operations (steps 1-3), but leave those areas that support stages 4-6. Finally, the third category, referred to as the cue versus active (CvsA) category, included activations that were revealed by comparing cue-related activity to another "active" cue condition. For example, an active cue condition could be a neutral cue that does not direct subjects to orient, but does require the maintenance of a task instruction during the cue-target interval and response preparation processes. Relative to the other two categories, areas revealed by this type of contrast are likely to reflect a pure voluntary orienting response because all other operations have been roughly equated between the cue-related condition of interest and the active reference condition.

The meta-analysis was performed by selecting the coordinates of the local maxima in frontal and parietal cortex from each of the contrasts, projecting these foci onto the surface of a brain spatially normalized to the same stereotactic space (i.e., Montreal Neurological Institute), and then rendered on an inflated cortical representation (Van Essen, 2002). In order to compare brain activations revealed by the different contrasts, each focus was surrounded by an 8 mm radius. The application of this radius accounts for variability in the location of the foci that can be introduced by standard image processing techniques (e.g., spatial normalization, spatial smoothing) and differences in mean anatomical variability across the studies (Van Essen & Drury, 1997).

III. Results

The results of eleven cue-related contrasts from five independent studies were included in the meta-analysis. There were a total of 97 frontal and parietal foci which are shown in Figure 2. Across all studies attention directing cues activated large portions of frontal and parietal cortex in both hemispheres. Despite the generally wide distribution of foci, several concentrations of foci can be observed. These concentrations included the IPS of both hemispheres and dorsolateral prefrontal cortex of both hemispheres including the SFS, middle frontal gyrus (MFG), and superior frontal gyrus (SFG). Other clusters of activity appeared lateralized to the left hemisphere and included the posterior aspect of

the inferior frontal sulcus (IFS) spreading to the precentral sulcus (PreCS), and the medial frontal gyrus (MedFG) including the supplementary motor area (SMA).

The eleven contrasts were divided into the three categories of cue contrast described in the Method (see Table 1). The classification scheme resulted in 6 contrasts being assigned to the CvsB group; 2 to the CvsP group; and 3 to the CvsA group.

In order to identify areas of overlap between the three categories of contrasts, the anatomical location of each focus was smoothed (8 mm, see Methods) and then painted onto the inflated representation of cortex, shown in Figure 3. In this representation, the key areas are those common to all three contrasts which are shown in white; non-white areas represent CvsB (red), CvsP (green), CvsA (blue), or some combination of two of the three categories (magenta, yellow, and cyan). There were five areas that were common to all categories of cue-related contrasts. In frontal cortex, there was overlap in both hemispheres in the posterior portions of the SFS near the junction with the PreCS. In addition, there was overlap in medial prefrontal regions, including the SMA of the left hemisphere (not shown in the figure). In parietal cortex, the only area of overlap was in the IPS, bilaterally. Interestingly, the overlap in IPS appeared in both anterior and posterior portions of IPS in each hemisphere.

IV. Discussion

A central issue in the study of visual attention is the identification of the neural systems that control the selective orienting of attention to relevant locations, features and objects. Here we used a meta-analytic analysis across several studies from our laboratory to investigate whether specific areas of frontal and parietal cortex could be related to the mental operation of attentional orienting. We approached this by searching for brain regions that were consistently activated across three different types of contrasts between cue-related brain activity and reference conditions of varying complexity. Based on a simple cognitive framework we hypothesized that because these contrasts had a single stage of processing in common, namely attentional orienting, then those areas that were commonly activated by the contrasts should be those areas that subserve the top-down control of attentional orienting. The

present results demonstrated that focal areas of activation in frontal and parietal cortex were common to all contrasts. These areas were the posterior aspect of the SFS and along the IPS of both hemispheres and the SMA of the left hemisphere. Therefore we propose that these specific regions of frontal and parietal cortex are critically involved in the top-down control of voluntary orienting of selective visual attention. Importantly, because the studies utilized in this analysis involved orienting of spatial and non-spatial attention, these brain regions should be considered to be related to focusing of general attentional resources in vision rather than for a specific form of attentional orienting; we discuss this in more detail below.

While previous studies have revealed activation in distributed regions of frontal and parietal cortex by attention-directing cues (e.g., Corbetta et al., 2000; Hopfinger et al., 2000; Kastner et al., 1999), the precise control operations supported by these areas remains unclear based on the previous data alone. The uncertainty remains because the studies that have implicated posterior SFS and IPS in attentional orienting have either a) reported large areas of activation that have included these regions as well as several neighboring regions and/or b) revealed these regions via statistical contrasts that do not specifically isolate the mental operation of attentional orienting. Nevertheless, the results from previous studies are entirely consistent with the present result that specific regions of frontal and parietal cortex are involved in executive control. However, the meta-analytic approach adopted here offers a more precise picture of frontoparietal function in attentional control. This refinement stems from the fact that the data came from independent studies and that the different classes of cue-related activations from the different studies have only a single major operation in common, yet overlapping areas between the contrasts were still observed. These results, unlike the individually reported data, provide strong converging evidence that posterior portions of the SFS and the IPS are indeed critically involved in the top-down control of *orienting* of selective attention.

According to one prominent model of attention, orienting involves three discrete stages, disengagement, movement, and engagement of attention (Posner & Petersen, 1990). If this theoretical framework is brought to bear on the present results, then the following question can be raised: Can one

be more precise about which of these three orienting operations is supported by posterior SFS and anterior IPS? When the present results are considered with other published data, there is suggestive evidence that one can indeed be more precise about the involvement of these areas in attentional orienting. For instance, evidence suggests that the disengagement of attention is subserved by temporal-parietal and ventrolateral prefrontal areas (Corbetta et al., 2000; Corbetta & Shulman, 2002) and not SFS and IPS. Therefore, it is unlikely that SFS and IPS are involved in the disengagement of attention. Similarly, attentional engagement is thought to be revealed as increased neuronal excitability in attended sensory representations (e.g., Giesbrecht et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999), not in the frontoparietal network. Thus, the only operation that remains is that of 'moving' attention to a new focus.

Use of the term 'orienting' to describe the cognitive operation subserved by posterior SFS and IPS tends to summon the idea that these areas are involved in spatial shifts of attention. While there is little doubt that this is true, there is solid evidence that these areas are also involved in nonspatial attentional orienting. Specifically, several of the contrasts included in the present meta-analysis were from studies that cued subjects to attend to nonspatial stimulus features, such as color or to the global or local levels of hierarchical stimuli (Giesbrecht et al., 2003; Kenemans et al., 2002; Weissman, Giesbrecht, Song, Mangun, & Woldorff, in press; Weissman, Woldorff, Hazlett, & Mangun, 2002). Thus, these regions appear to be amodal in the sense that they generalize beyond the attended stimulus dimension. The hypothesis that portions of the frontoparietal network generalize over multiple dimensions was recently proposed by Shulman and colleagues (Shulman, d'Avossa, Tansy, & Corbetta, 2002). These authors argue that amodal parts of the frontoparietal network are involved in coding and maintaining relevant information in an abstract form. The present results suggest that portions of frontal and parietal cortex are also amodal in terms of their support attentional orienting.

V. Concluding remarks

Previous neuroimaging and neuropsychological studies have identified a distributed network of brain areas that supports visual selective attention. The meta-analysis presented here suggests that focal regions of this distributed network, specifically posterior SFS, anterior and posterior IPS, and medial frontal areas (SMA) subserve voluntary orienting that occurs in response to attention-directing cues present in the external environment. However, external sources of information are not the only mediators of attentional control processes. Indeed, multiple sources of information contribute to these control functions, including current expectations, emotions, task demands, past experience, knowledge, and arousal. Therefore, future investigations of top-down control functions must identify how these multiple sources of information mediate selective visual attention processes in order to reveal a precise picture of how information in our external world is represented in cortex, influences behavior, and reaches awareness.

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Table 1. Cue-related fMRI investigations included in the meta-analysis. Shown are the reference for the study, the issue addressed by the study, the specific cue-related contrast, the number of frontal and parietal foci included in the meta-analysis, and the classification for the meta-analysis based on the scheme described in the Method.

Study	Issue	Cue-related contrast	# Foci	Classification
Giesbrecht et al., 2003	spatial vs. feature attention	central location cue vs. baseline	6	CvsB
		central color cue vs. baseline	6	CvsB
		central location cue vs. central color cue	7	CvsA
		peripheral location cue vs. baseline	7	CvsB
		peripheral color cue vs. baseline	6	CvsB
		peripheral location cue vs. peripheral color cue	5	CvsA
Kenemans et al., 2002	feature attention	color cue vs. neutral cue	13	CvsA
Weissman et al., 2002	global vs. local attention	all cues vs. passive cues	13	CvsP
Weissman et al., in press	global vs. local Attention	all cues vs. passive cues	11	CvsP
Wilson & Mangun, 2002	viewer-centered vs. object-centered reference frames	viewer centered cues vs. baseline	10	CvsB
		object centered cues vs. baseline	13	CvsB

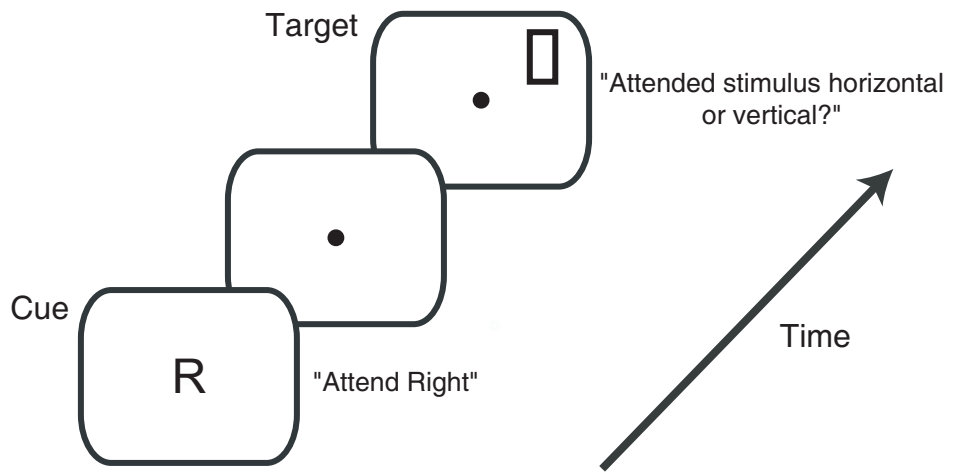
Abbreviations: C = cue; B = baseline; P = passive; A = active.

Figure Captions

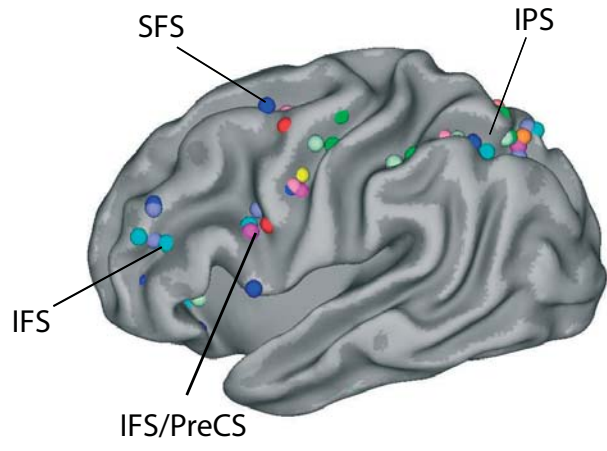
Figure 1. A schematic representation of a voluntary orienting paradigm. The cue provides an instruction to attention to a location. After a variable interval, the target stimulus is presented, for which a response is required.

Figure 2. Foci included in the meta-analysis. Each color represents a different study and contrast (see Table 1). The foci are projected onto an inflated representation of the left and right hemispheres of a brain that was normalized to stereotactic space. Abbreviations: SFS, superior frontal sulcus; IPS, intraparietal sulcus; IFS, inferior frontal sulcus; PreCS, precentral sulcus.

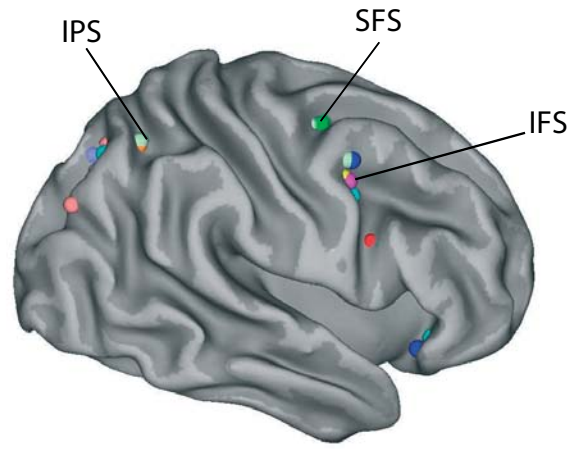
Figure 3. Anatomical overlap between the three categories of contrasts. Each focus was categorized into either the Cue vs. Baseline (red), Cue vs. Passive (green), or Cue vs. Active (blue) groups, projected onto the inflated brain, smoothed (8 mm), and painted onto the surface. White represents the intersection of all three categories. Abbreviations are as in Figure 2.



Left Hemisphere

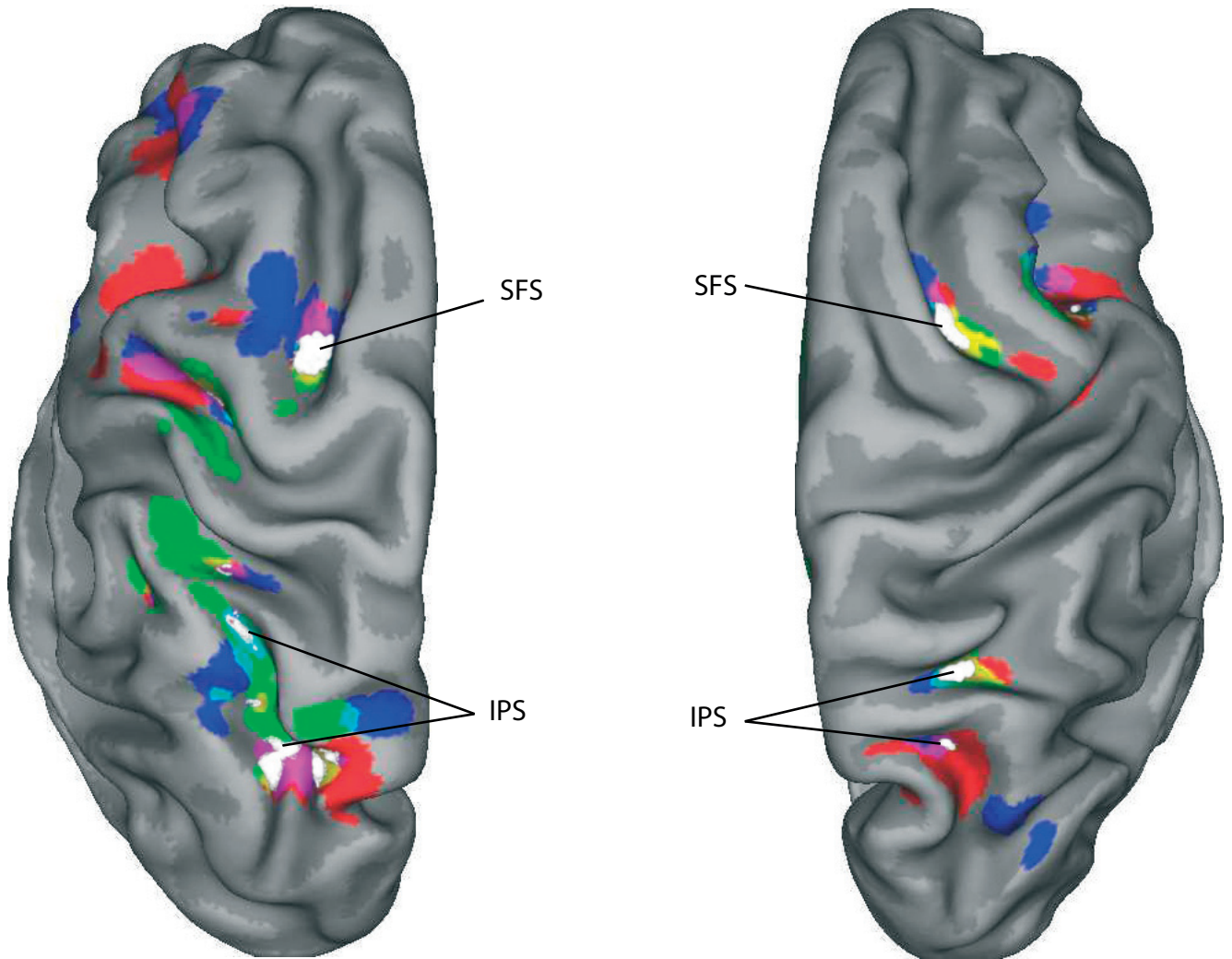


Right Hemisphere

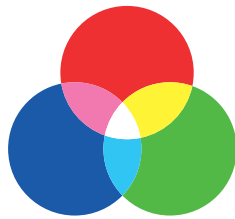


Left Hemisphere

Right Hemisphere



Cues vs. Baseline



Cues vs. Active

Cues vs. Passive