Neural Mechanisms of Visual Attention: Object-Based Selection of a Region in Space

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Abstract

■ Objects play an important role in guiding spatial attention through a cluttered visual environment. We used event-related functional magnetic resonance imaging (ER-fMRI) to measure brain activity during cued discrimination tasks requiring subjects to orient attention either to a region bounded by an object (object-based spatial attention) or to an unbounded region of space (location-based spatial attention) in anticipation of an upcoming target. Comparison between the two tasks revealed greater activation when attention selected a region bounded by an object. This activation was strongly lateralized to the left hemisphere and formed a widely distributed network including (a) attentional structures in parietal and temporal cortex and thalamus, (b) ventral-stream object processing structures in occipital, inferior-temporal, and parahippocampal cortex, and (c) control structures in medial- and dorsolateral-prefrontal cortex. These results suggest that object-based spatial selection is achieved by imposing additional constraints over and above those processes already operating to achieve selection of an unbounded region. In addition, ER-fMRI methodology allowed a comparison of validly versus invalidly cued trials, thereby delineating brain structures involved in the reorientation of attention after its initial deployment proved incorrect. All areas of activation that differentiated between these two trial types resulted from greater activity during the invalid trials. This outcome suggests that all brain areas involved in attentional orienting and task performance in response to valid cues are also involved on invalid trials. During invalid trials, additional brain regions are recruited when a perceiver recovers from invalid cueing and reorients attention to a target appearing at an uncued location. Activated brain areas specific to attentional reorientation were strongly right-lateralized and included posterior temporal and inferior parietal regions previously implicated in visual attention processes, as well as prefrontal regions that likely subserve control processes, particularly related to inhibition of inappropriate responding. ■

INTRODUCTION

The job of visual attention is to select information to be given priority during perception. Theories of visual attention once took for granted that visual attention selects a region of space, which is then inspected for the presence of interesting or useful information. There is considerable evidence to support such a view, much of which comes from variations on Posner's spatial cueing paradigm (Posner, 1980; Posner, Snyder, & Davidson, 1980). In this task, target stimuli appear at locations spread about the visual field. A cue to the most likely location presented in advance of a target alters the speed and accuracy of target processing. Shifting of visual attention based on the cue can be measured by comparing response times and accuracy when the target appears at the cued location versus when it appears at some other location in the visual field. The typical findings in these studies have been benefits, in terms of faster and more accurate responding at or near the cued location, and costs, in terms of slower and less accurate responding at uncued locations.

Theories of visual attention built on these findings are "location-based." They propose that attention is deployed to a location defined on environmental spatial coordinates. Attention facilitates the processing of information arising at or near that location, leaving other locations unhelped or inhibited. The rate at which facilitation falls off with distance around the selected location can be varied. This gives perceivers a degree of control over the size of the facilitated region of space. The mechanism of spatial selection has been likened to a spotlight (Posner, 1980), a zoom lens (Eriksen & Yeh, 1985), or a gradient (Henderson, 1991; LaBerge & Brown, 1989) centered on the selected location.

But does visual attention always work in this fashion, selecting one spatial region at the expense of others? Groundbreaking work by Duncan (1984) showed costs for switching attention between objects that occupied the same spatial region. When asked to report the features of two overlapping stimuli, participants were slower to name two features that appeared on separate objects than to name two features of the same object. This finding suggested another way to allocate visual attention, in which perceivers sometimes select the mental representation of an object in a direct fashion, abstracted from its spatial position (Vecera & Farah, 1994; Kanwisher & Driver, 1992). Investigations of visual attention now divide into those that deal with attention to objects, those that deal with attention to space, and those that examine the relationship between these two modes of attentional deployment. The present work falls into the latter category. We focus on attention to space and how objects might play a role in guiding spatial attention.

Object-Based Spatial Attention

Location-based theories of spatial attention do not take explicit account of objects or their boundaries in describing how a spatial region is defined and selected. Nevertheless, when trying to understand how attention is allocated within space, it is useful to consider the presence of objects in the visual field. Even when they are not the imperative stimuli and no judgments are made about their properties per se, they can influence how space is perceived to be organized and may provide guidance in parsing space into regions and deploying attention to one region or another. Compelling evidence for such a phenomenon comes from Egly, Driver, and Rafal (1994), using a spatial cueing task in which targets could appear inside one of two rectangles (2-D ''objects'') presented either horizontally or vertically on the display such that the ends of a single rectangle were as far from each other as the adjacent ends of the two rectangles. When a cue was presented at one of the target locations at the end of one of the rectangles, attention appeared to conform to the object's boundaries. On trials in which the target did not appear at the cued location, the uncued target location within the rectangle was facilitated relative to regions equally distant from the cue but in another rectangle. Either attention directed to the cue ''filled'' the object, facilitating all points within its boundaries, or movement of attention from the one point to another was easier when both points lay within the same object than when an object boundary had to be crossed. A purely location-based theory of spatial attention cannot account for this finding.

The allocation of visual attention in the Egly, Driver, et al. (1994) task appears to be guided by the objects in the visual field. This use of objects to guide the allocation of spatial attention is distinct from attending to the properties of objects for their own sake, as perceivers did in the task used by Duncan (1984) in which they were asked to report features of the objects presented. We use the term ''object-based spatial attention'' to refer to the process of orienting visual attention in which objects in the visual field guide the definition and selection of a region of space. This contrasts with ''location-based spatial attention,'' which selects a region of space defined on environmental coordinates regardless of object placement. Further, the term ''object-based spatial attention'' is intended to distinguish the processes currently under investigation from other processes referenced by the more generic term ''object-based attention,'' such as processes involved in Gestalt grouping (Baylis & Driver, 1993; Kramer & Jacobson, 1991), the formation of object files (Kahneman, Treisman, & Gibbs, 1992), or Duncan's (1984) original demonstration of selecting an object—its features, parts, and their organization relative to one another—rather than the spatial region the object occupies.

Underlying Neural Mechanisms

Both lesion studies (Petersen, Robinson, & Morris, 1987; Posner, Cohen, & Rafal, 1982; Posner, Walker, Friedrich, & Rafal, 1987) and neuroimaging studies (Gitelam et al., 1999; Rosen et al., 1999; Nobre et al., 1997; Corbetta, Miezin, Shulman, & Petersen, 1993) suggest that attention to space is implemented by a network of posterior cortical and subcortical structures. According to Posner et al. (Posner & Petersen, 1990; Posner & Raichle, 1994), three operations are involved in deploying spatial attention: *disengage*, which releases attention from its current location; *move*, which shifts attention from the current location to the new one; and *engage* or *enhance*, which creates a new focus of attention centered on the new location. The result is to reduce or inhibit processing of information from the original location and facilitate processing at the new location. Within this model, each operation is thought to have its own anatomical support, with posterior parietal cortex associated with the ''disengage'' function, superior colliculus with ''move,'' and pulvinar nucleus of the thalamus crucial to ''enhance.'' More contemporary models emphasize that spatial attention involves a much wider system of neural structures, including anterior cortical brain regions. Nevertheless, the Posner model provides useful guidance in thinking about the functional anatomy of spatial attention.

Like the spotlight, zoom lens, and gradient theories at the psychological level, this neural theory takes no account of objects in the visual field. However, data from neglect patients with left- or right-hemisphere lesions suggests a specialized neural substrate for using object boundaries to guide spatial attention (Egly, Driver, et al., 1994). While right temporoparietal damage produced severe performance deficits in Egly et al.'s rectangles task described earlier, sensitivity to object boundaries was preserved. Left temporoparietal damage, however, eliminated sensitivity to object boundaries. A separate study using the same paradigm with a split-brain patient found converging evidence for a left-hemisphere role in orienting to object boundaries (Egly, Rafal, Driver, & Starrveveld, 1994). In addition, neuroimaging studies using PET have found left-hemisphere activity when attention is directed to the features of an object rather than to the space defined by the object (Fink, Dolan, Halligan, Marshall, & Frith, 1997; Vandenberghe et al., 1997). Thus, the left hemisphere may take the lead in deploying attention to the objects themselves, as well as in deploying object-based spatial attention.

The Present Study

We used event-related functional magnetic resonance imaging (ER-fMRI) to study the neural substrates of location-based and object-based deployment of spatial attention. The development of ER-fMRI has provided researchers with a methodology able to better capture the separable mental components of cognitive tasks than the block design methodologies used in PET and standard fMRI studies (Rosen, Buckner, & Dale, 1998). One benefit of ER-fMRI is the ability to present intermixed or randomized trial types within a single imaging run and then separately analyze the MR signal changes associated with the different trial types. While convergent findings between standard and ER-fMRI methods may be desirable (Buckner et al., 1996), evidence suggests that blocked versus randomized presentation of trials can have a dramatic influence on the engagement of particular neural processes in otherwise similar tasks and consequently influence the results of imaging studies employing the two methods (D'Esposito, Zarahn, & Aguirre, 1999). In standard behavioral studies of visual attention using the Posner spatial cueing task, validly and invalidly cued trials are randomly mixed to insure that perceivers' expectations about cue validity are equated for the two trial types and thus allow for the analysis of the processes involved in reorienting attention when an invalid cue violates an expectation about cue validity. ER-fMRI allows this standard methodology to be employed during imaging, as well as allowing for a more complete separation of neural activity associated with validly and invalidly cued trials. In the current study, we take advantage of ER-fMRI methodology in two ways. First, when comparing location-based and object-based cueing, we are able to examine activity associated with only the validly cued trials. The analysis of location-based versus object-based cueing is therefore uncontaminated by invalid trials that include the orienting of attention to the target, which is located at a new location that may or may not be inside an object. Second, we can address the specific question of what neural structures are involved in the processes associated with the reorienting of attention following invalid cueing by comparing validly cued versus invalidly cued trial types. This question has recently been of interest to researchers using neuroimaging techniques to study attention (Corbetta, Kincade, Olligner, McAvoy, & Shulman, 2000; Nobre, Coull, Frith, & Mesulam, 1999).

Imaging data were collected while participants completed a variant of the Posner spatial cueing task in which both location-based and object-based cueing could be implemented (Figure 1). In this letter-discrimination task, prior to target onset, attention was cued either by an arrow pointing in the direction of the most likely target positions, or by a geometric shape drawn to contain the most likely target positions within its boundary. Every display contained both the arrow and the shape cues. Whether the arrow (location-based cueing) or the shape (object-based cueing) was predictive of target location varied between blocks of trials and participants were given instructions as to which cue to attend to in each block. To prevent the shape from capturing attention exogenously, the luminance of the object cue was increased gradually. Thus, attentional cueing was manipulated across imaging runs while other task variables—perceptual input, the decision about target identity, and response require-

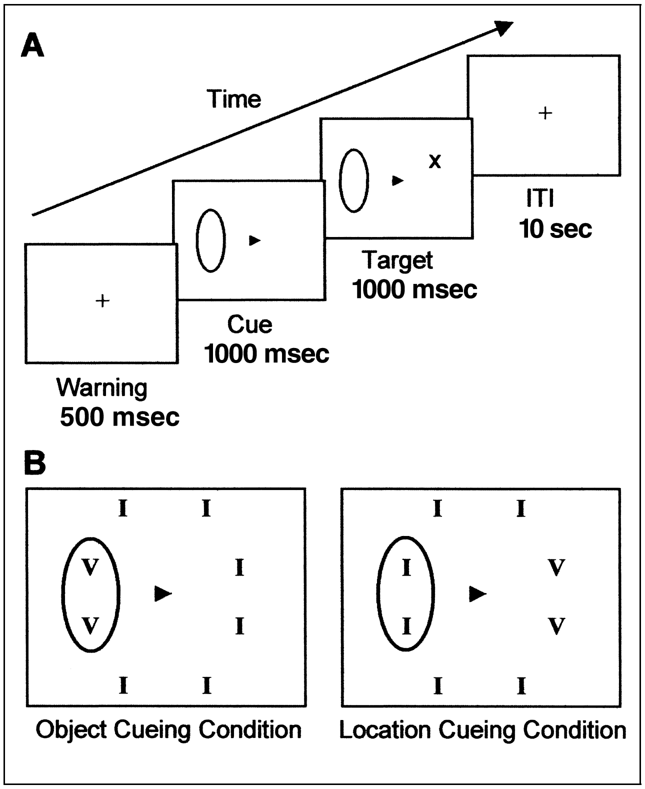

Figure 1. (A) Trial line for cued discrimination task, showing the sequence and timing of the warning signal, cue, target, and intertrial fixation point. For each trial, the subject made a manual response indicating the identity of the target letter. Display elements are not drawn to scale. Within an imaging run, either the object (object-based cueing) or the arrow (location-based cueing) was 80% predictive of target location. Valid (V) and invalid (I) target locations are illustrated in (B).

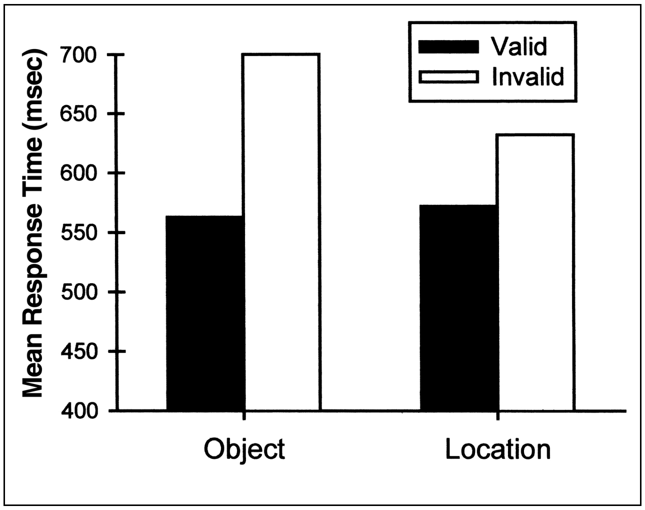

Figure 2. Mean response times for correct responses in the object-based and location-based cueing conditions.

ments—remained constant. This experimental design allowed any difference between cueing conditions to be attributed to processes elicited by the different types of cueing.

RESULTS

Behavioral Results

Mean correct response times were faster when the target occurred in the cued region (valid trials) than when the target appeared at an uncued location (invalid trials), $F(1, 11) = 19.5$, $p < .05$ (Figure 2). The interaction of attentional condition and cue validity was significant, $F(1, 11) = 15.4$, $p < .05$, such that the validity effect was larger with object-based than location-based cueing. However, planned comparisons of the cue validity effect showed significant cueing effects for both conditions when tested individually, $t(11) = 4.8$, $p < .05$, and $t(11) = 2.6$, $p < .05$, for object-based and location-based cueing, respectively. Thus attention was successfully manipulated by both cue types. Reanalysis of the location-based condition found no differences as a function of whether the target was inside or outside the shape, indicating that gradual shape onset was successful in preventing exogenous attraction of attention by the shape when the arrow was the designated cue.

Functional Imaging Results: Location-Based Versus Object-Based Deployment

The detailed description of the ER-fMRI analysis procedures are given in the Methods. In the analysis designed to identify differences between location-based and object-based spatial attention, only validly cued trials were used to avoid including activation associated with processes involved in reorienting attention on invalid trials. Statistical comparisons among the attentional conditions were made on a voxel-wise basis using a one-way repeated-measures ANOVA followed by pooled-variance t tests comparing results between conditions. A statistical threshold of $t(11) = \pm 2.8$, $p < .01$ and a minimum cluster size threshold of 0.37 ml was applied after transformation into the Talairach coordinate space.

Table 1 presents volumes and center of mass coordinates in the Talairach space for areas of activation that

Table 1. Areas of Activation: Object- > Location-Based Cueing

			CM			
Region	*Side*	*BA*	*x*	*y*	*z*	*Volume (ml)*
Parietal lobe						
Inferior parietal lobule (IPL)	L	40	−30	−35	41	0.39
Postcentral gyrus (PoCG)	L	1, 2	−40	−27	52	0.85
Temporal lobe						
Superior/middle temporal gyrus (STG/MTG)	L	21, 22	−62	−34	5	0.37
Inferior temporal gyrus (ITG)	L	20	−44	−25	−21	0.45
Parahippocampal gyrus (pHIPP)	L	30	−16	−33	−4	0.37
Frontal lobe						
Superior frontal gyrus (SFG)	L	8, 9	−16	36	36	1.00
Medial frontal gyrus (MdFG)	B	10	1	42	−8	0.76
Inferior frontal gyrus (IFG)	L	47	−31	37	1	0.82
Occipital lobe						
Dorsal extrastriate (DE)	B	18	6	−73	15	2.48
Striate cortex	L	17	−11	−69	11	0.40
Fusiform gyrus (FG)	R	19	15	−69	−11	0.37
Lingual gyrus (LG)	R	19	11	−51	0	0.44
Lingual gyrus (LG)	L	19	−13	−48	−3	0.66
Subcortical regions						
Pulvinar (PULV)	L	–	−22	−29	2	[a]
Cerebellum (CER)	R	–	11	−49	−39	0.98

CM = center of mass, Talairach and Tournoux (1988) coordinate space; BA = Brodmann's area.

[a] Parahippocampal gyrus activation contiguous with pulvinar activation.

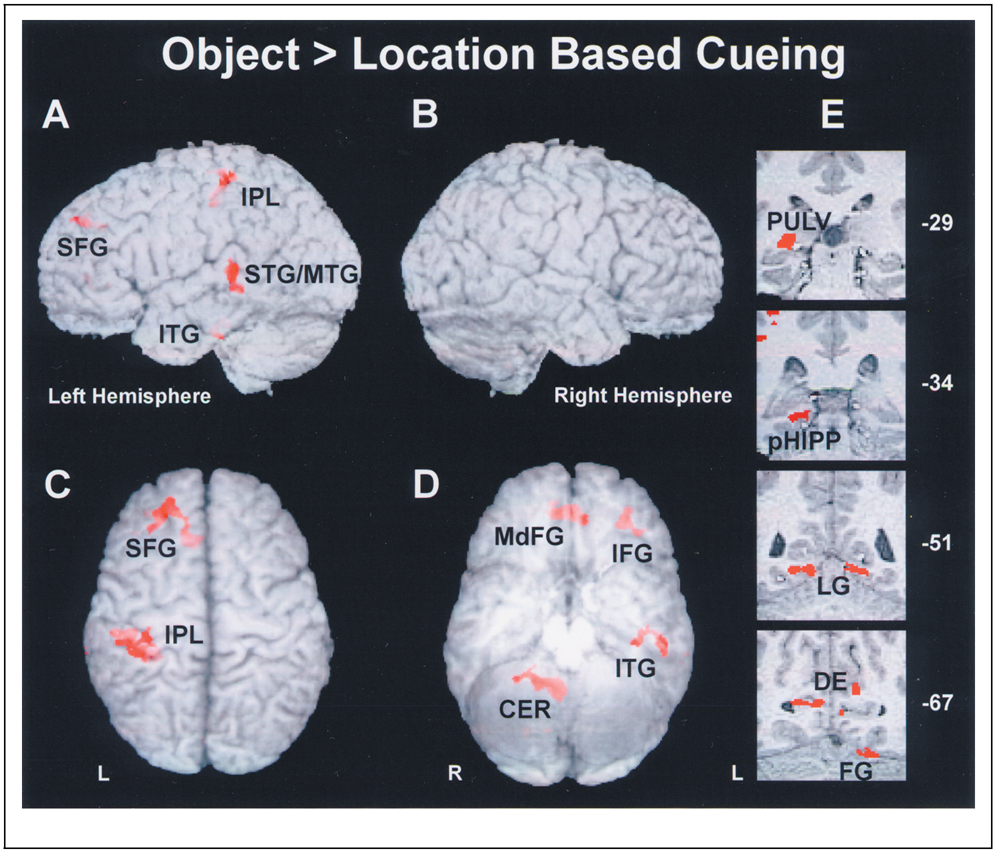

Figure 3. Brain areas showing significantly greater activity associated with object-based cueing relative to location-based cueing (see Table 1 for abbreviations of brain regions). Functional data were generated by planned comparisons of the Location-Valid and Object-Valid conditions across the 12 subjects. Cortical activation is projected on the (A) left, (B) right, (C) superior, and (D) inferior surfaces of the brain. Lighter shading indicates areas of activation positioned deeper in the cortical sulci. (E) Subcortical areas of activation are shown in the coronal plane ($z = -29$, -34, -51, and -67). There were no brain areas showing significantly greater activity associated with location-based cueing relative to object-based cueing.

met these criteria in the comparison of Location-Valid and Object-Valid trial types, the comparison that speaks most directly to the question of different neural substrates underlying the two modes of deploying attention. In this comparison of the location-based and object-based cueing conditions, all significant differences resulted from greater activation in the object-based condition than in the location-based. No areas were observed in which location-based cueing showed greater activation than object-based cueing.

Figure 3 shows the major areas of cortical activation from the comparison of location-based and object-based spatial attention. These areas of activation were widely distributed and were primarily left-lateralized, involving the superior frontal, inferior frontal, parietal, superior and middle temporal, inferior temporal (including the anterior fusiform gyrus), parahippocampal, and thalamic (pulvinar nucleus) areas. Bilateral activity was found in the medial frontal, lingual, and extrastriate regions. The only strictly right-lateralized areas of activation were in the posterior fusiform gyrus and inferior cerebellum.

Functional Imaging Results: Reorienting After Invalid Cueing

To determine neural regions involved in reorienting attention after invalid cueing, a 2 × 2 (location-based vs. object-based by valid vs. invalid) repeated-measures ANOVA was performed on a voxel-by-voxel basis. The diffuse condition was not included since it contains neither valid nor invalid trials. A statistical cutoff of $F(1, 11) = 3.1$, $p < .01$ and minimum cluster size threshold of 0.37 ml were applied. The main effect of cue validity produced six areas of activation that met these criteria. In every case, differential activity resulted from greater activity in the invalid condition. Figure 4 shows the primary areas of activation, which were highly right-lateralized and included large areas of activity in the temporoparietal junction and inferior-frontal cortex. as well as smaller regions in the middle-temporal and middle-/superior-frontal gyri. Table 2 reports the volumes and Talairach coordinates for the center of mass of each area of activation.

The interaction effect of cue validity and cueing condition reached significance in four regions indicating that differences in responding to valid and invalid cueing varied for location-based and object-based spatial orienting. The four regions (center of mass in Talairach coordinates) were bilateral extrastriate cortex (5, −81, 21), left middle frontal gyrus (−40, 40, 11), left-insular cortex, (−32, −8, 5), and left cerebellum (−13, −57, −41). Further post hoc comparisons of the valid versus invalid trials were conducted for each cueing condition. However, within the regions where the interaction term was significant, these individual comparisons failed to

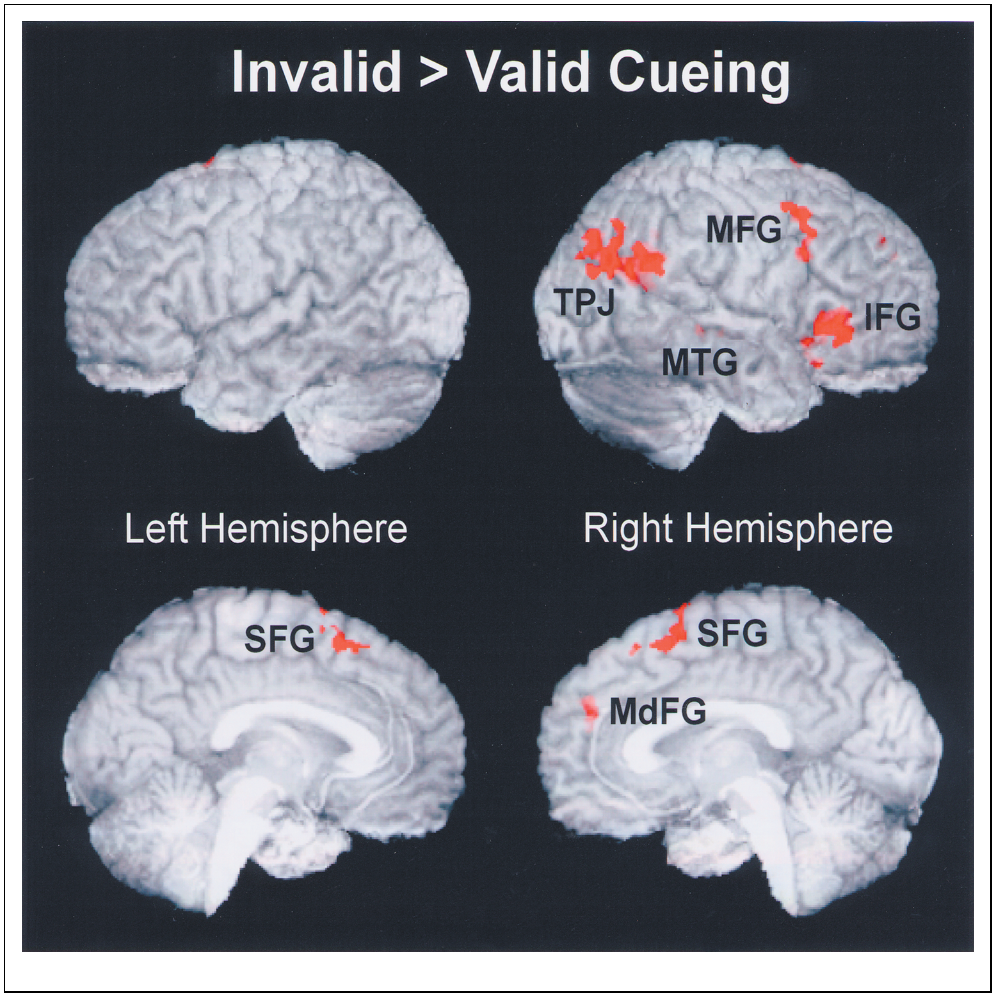

Figure 4. Brain areas showing significantly greater activity associated with invalid cueing relative to valid cueing (see Table 1 for abbreviations of brain regions). Cortical activation is projected on the lateral and medial surfaces of the brain. Lighter shading indicates areas of activation positioned deeper in the cortical sulci. There were no brain areas showing significantly greater activity associated with valid cueing relative to invalid cueing.

Table 2. Areas of Activation: Invalid > Valid Cueing

			CM			
Region	*Side*	*BA*	*x*	*y*	*z*	*Volume (ml)*
Temporal/Parietal Lobes						
Temporoparietal junction (TPJ)	R	39, 40	47	−62	26	3.50
Middle temporal gyrus (MTG)	R	21	46	−28	−6	0.59
Frontal Lobe						
Medial frontal gyrus (MdFG)	R	9	11	47	26	0.63
Superior frontal gyrus (SFG)	B	8	1	15	54	0.65
Middle frontal gyrus (MFG)	R	9	44	11	38	0.85
Inferior frontal gyrus (IFG)	R	47	42	22	−1	2.01

show cue validity effects that met our threshold for statistical significance and cluster size. The lack of significant effects in these individual analyses may result from the small number of trials available for these analyses (five invalid trials per imaging run, three runs per condition); as such, the interaction effects are sufficiently difficult to interpret and will not be considered further.

DISCUSSION

Deployment of Spatial Attention to Object-Based Regions

All areas of activation that distinguished between object- and location-based cueing conditions showed greater activity when the object cue was being used to guide attention. This pattern suggests that more constrained deployment of attention, conforming to the precisely defined boundary of the object cue, is gained by adding to or supplementing the brain activity needed to allocate attention to a similarly situated but fuzzily bounded spatial region defined by environmental coordinates rather than object shape. In the process, attention may be more concentrated within the object's boundaries, as well as more constrained by them, since knowing that the object defines the cued region increases the certainty with which any given point in space can be designated as "cued" or "uncued." Such concentration of attention would account for the larger behavioral effect of object cues seen in the reaction time data.

Both cue types predicted target location and were intended to elicit endogenous orienting. However, the arrow was presented at fixation, whereas the shape was peripherally positioned. Peripheral cues are known to capture attention exogenously via abrupt onset (Yantis, 1993; Posner, 1980), and one might be concerned that this process rather than object-based spatial attention created the differential activation in the object-based condition. Several factors argue against such an interpretation. First, recent fMRI studies comparing exogenous peripheral versus endogenous central cueing have shown highly overlapping neural systems (Kim et al., 1999; Rosen et al., 1999) with endogenous central cues producing greater and more widespread cortical activation than exogenous peripheral cues (Rosen et al., 1999). Second, in our work the onset of the shape's luminance was gradual to reduce the likelihood of exogenous orienting. The efficacy of this procedure was confirmed by the absence of a behavioral impact of the location of the shape in conditions in which the arrow was the relevant cue. Finally, the particular structures that showed increased activity during object-based deployment suggest direct connections with the need to use object information to guide attention. We turn next to the distribution of these structures and what is known about their functional involvement in other tasks.

The brain areas showing increased activity during object-based deployment were widely distributed posterior to anterior, and in mid-cortical regions were strongly left-lateralized. Almost all of the structures found to be more active during object-based spatial attention have been found by previous neuroimaging or lesion studies to be involved in tasks requiring object recognition, scene perception, or visual attention. We consider this evidence structure by structure, moving roughly posterior to anterior.

Deficits in shape discrimination arise from bilateral damage in posterior extrastriate cortex, whereas deficits in localizing objects arise from bilateral damage in extrastriate regions somewhat more anterior and superior (Warrington, 1986). These are just the areas of visual cortex in which we saw bilateral activity during object-based selection. The extrastriate, lingual, fusiform, and inferior-temporal areas all lie in the ventral pathway for object processing (Haxby et al., 1991; Ungerleider & Mishkin, 1982; Ungerleider & Haxby, 1994). The fusiform and inferior-temporal gyri show activity in neuroimaging studies of a variety of different tasks involving objects and faces and activity tends to be greater on the left with objects (Aguirre & D'Esposito, 1997; Rees, Frackowiak, & Frith, 1997). The increased activity in these structures when participants were deploying spatial attention within object boundaries suggests a modulation of activity in object-processing systems due to attention. Evidence from both neuroimaging and single-cell recording studies have suggested such a modulatory role for attention (Brefczynski & DeYoe, 1999; Chawla, Rees, & Friston, 1999; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Wise & Desimone, 1988). Recent work by Kastner et al. found modulatory effects of attention in visual cortex both in the presence and absence of visual stimulation, leading to the suggestion that such top-down modulation or biasing is an important mechanism of visual attention (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Kastner & Ungerleider, 2000). Kastner et al. further speculated that the baseline activity shifts occurring in the absence of visual stimulation may be based on the spatial location of expected targets, while the modulation of activity associated with visual stimulation may be more object-based in nature. This suggests a further separation of location-based and object-based attentional effects in addition to those considered in the present experiment.

In the more medial portion of the temporal lobe is a distinct region of activation in the left-parahippocampal gyrus, which is contiguous with activation in the thalamus. Recent fMRI work indicates that parahippocampal cortex is involved in the representation of the spatial layout of organized visual scenes (Epstein & Kanwisher, 1998), and, certainly, the spatial layout of items in the visual display is important in the current task.

Activation of parietal, superior/middle temporal, and thalamic areas suggests a network of structures already heavily implicated in deployment of visual attention. The inferior parietal lobe and posterior superior and middle temporal cortex around the temporoparietal junction are often compromised in lesion damage that creates spatial neglect (for reviews, see Heilman, Watson, & Valenstein, 1994; Vallar, 1993). Indeed, all of these areas evidenced damage in the CT scans of the left-parietal patients who showed disrupted object-based cueing (Egly, Driver, et al., 1994), though not all areas were damaged in all patients. Bilateral parietal and temporo parietal region involvement in attentional tasks has further been confirmed in recent neuroimaging studies (Corbetta et al., 2000; Gitelam et al., 1999). The thalamus, in particular, the pulvinar nucleus, is thought to initiate perceptual processing at a selected spatial focus—the engage operation—and other research supports a role for the thalamus in connecting the attention system to the object processing system (LaBerge & Buchsbaum, 1990; Petersen et al., 1987). The present data indicated that the activity in these various structures already known to be associated with spatial attentional processes intensifies in the left hemisphere when selection must conform to a region defined by object boundaries.

Frontal activations are likely to be control structures that maintain the object and keep its boundary active to constrain attentional deployment. In particular, the large region spanning medial and dorsolateral prefrontal cortex invites such an interpretation. Midline and dorsolateral prefrontal structures are implicated in executive control and working memory by a variety of investigations with both humans and monkeys (Smith et al., 1995; Wilson, Scalaidhe, & Goldman-Rakic, 1993; Posner, Petersen, Fox, & Raichle, 1988; Posner & Petersen, 1990). A recent PET study of human brain function during an attention-demanding visual search task found activity in dorsolateral prefrontal cortex (Rees et al., 1997). The researchers suggested that this dorsolateral activation may be associated with top-down attentional control modulating activity in other brain areas. This argument is much like ours, but the dorsolateral activation they observed was right- rather than left-lateralized. Many studies of attentional control have reported dorsolateral-prefrontal activity, but it remains to be determined under what conditions this activation is left- or right-lateralized.

Reorienting After an Invalid Cue

All activity that distinguished between valid and invalid cueing resulted from greater activity in the invalid condition. It appears that all of the brain circuitry involved in orienting attention on valid trials is also involved in orienting on invalid trials, plus additional regions that contribute specifically to the reorienting of attention. Logical analysis of the task's structure suggests why this should be so. Until the target appears, valid and invalid trials are identical. The cue appears, the subject orients in response to the cue and awaits the target. When the target appears on valid trials, the subject decides its identity and responds. On invalid trials, the subject must reorient attention to the target's location before decision and response. The difference between valid and invalid trials can be represented as the insertion of an extra step in the invalid trials, and the pattern of activation that we find in this comparison is the neural signature of the inserted reorienting process. In the current data, we found activation associated with invalid cueing to be highly right-lateralized with both posterior and anterior components. The right hemisphere has long been emphasized in theories of visual attention (Mesulam, 1990) based on the prevalence of spatial neglect following right-hemisphere damage. The distributed posterior and anterior areas of activation suggest that successful reorienting of attention may require several task components.

A major demand imposed by invalid cueing is the need to give up a commitment the attention system has just made in preparation for shifting to the new location. This process requires the disengage operation and, thus, the theory of Posner et al. predicts that parietal cortex ought to play a prominent role on invalid trials. The specific neuroanatomy of the disengage operation is uncertain. Posner et al. placed its locus in the superior aspect of the posterior parietal lobe (Posner, Walker, Friedrich, & Rafal, 1984). This proposed locale was supported by neuroimaging work in a task that required moving attention from location to location in a predictable sequence (Corbetta et al., 1993). However, our comparison of valid versus invalid cueing did not show activity in the superior parietal cortex, but rather indicated the involvement of more inferior areas, in particular, a large region located at the temporoparietal junction, including areas of inferior parietal cortex posterior to the temporoparietal junction and an area of middle temporal cortex anterior to the temporoparietal junction. This finding appears to be in agreement with recent lesion studies (Friedrich, Egly, Rafal, & Beck, 1998) and neuroimaging studies (Corbetta et al., 2000) that emphasize the role of the inferior parietal cortex around the temporoparietal junction in the disengage operation. Friedrich et al. compared lesion patients with superior parietal damage to patients with more widespread damage encompassing the temporoparietal junction. In both groups, they sought evidence of an "extinction-like" pattern of reaction times in a Posner spatial cueing task. This pattern involves relatively spared performance on valid trials in which the advance cue accurately places the location of the upcoming target in the "good" visual field ipsilateral to the lesion, accompanied by substantially impaired performance on invalid trials when the good field is cued, but the target appears in the "bad" field contralateral to the lesion. The inordinately slowed reaction time to these invalidly cued targets is thought to specifically diagnose damage to the disengage operation (Posner et al., 1984). According to Friedrich et al.'s results, only patients with temporoparietal junction involvement showed the extinction-like pattern. In an ER-fMRI study, Corbetta et al. have more closely examined the specific roles of different regions within parietal cortex during various stages of attentional orienting. Using a Posner cueing task, they found activation in the region of the intraparietal sulcus associated with voluntary orienting of attention in response to the presentation of the cue and more inferior activation in the region of the temporoparietal junction associated with the presentation of the target, particularly when the target appeared outside of the cued location on invalid trials.

Invalid cueing also activated right prefrontal regions in our experiment, both lateral and midline. Extrapolating from studies of other tasks, these prefrontal regions might serve executive control processes, coordination of attention with eye movements, and inhibition of inappropriate responding while the redeployment is being implemented (Gitelam et al., 1999; Corbetta, 1998). The largest of these areas of frontal activation was located in the posterior portion of the inferior frontal gyrus. This region has previously been implicated in reorienting attention following invalid cueing. As part of a larger PET study of spatial and temporal orienting, Nobre et al. compared blocks of trials that contained either 100% valid trials or 60% valid and 40% invalid trials (Nobre et al., 1999; Coull & Nobre, 1998). In the later condition, they found anterior areas of increased activation, which they located in orbitofrontal cortex. The activation seen in that experiment was positioned somewhat more anteriorly than that reported here and was bilateral rather than right-lateralized. Evidence from several experiments using go/no-go tasks suggests that the inferior frontal region may be involved in the inhibition of responding. Two studies using a go/no-go task found activation in the same right inferior frontal area, one somewhat more anterior to the present locus (Garavan, Ross, & Stein, 1999) and one somewhat more superior (Konishi et al., 1999). In a developmental study using a go/no-go task, Casey et al. (1997) found a wider range of frontal cortex involved in the task than either of these later studies, including middle and superior frontal areas similar to ours. Thus, a variety of experiments can be taken to implicate anterior areas of the right hemisphere in withholding action while switching spatial attention.

Conclusion

Comparison of valid trials between the two cueing conditions shows largely left-lateralized differences in the neural substrates that implement object-based and location-based spatial attention, providing strong support for the hypothesis derived from lesion evidence that the left hemisphere is differentially specialized for object-based deployment of spatial attention. This finding presents another piece of evidence converging with research from a number of paradigms that suggest a general left-hemisphere involvement in object and object-based processing. Further, the application of ER-fMRI methodology to an attentional cueing task allowed for the comparison of valid versus invalid trial types. The reorienting of attention following invalid cueing appears to engage largely right-hemisphere structures involved in the disengagement of attention from the original focus and inhibition of inappropriate responding until the reorientation is accomplished.

METHODS

Experimental Task

Twelve right-handed, neurologically normal adults gave informed consent. Stimuli were projected to a screen, which the subject viewed through prism glasses. The trial line, shown in Figure 1A, lasted 2.5 sec, with an intertrial interval of 10 sec during which subjects were told to maintain fixation on a central cross. The trial began with a 500 msec enlargement of the fixation marker as a warning signal. The cue display contained two elements, an arrow at fixation and a geometric shape (oval or rectangle) in the periphery, which appeared gradually over a 198-msec interval to minimize reflexive orienting toward the shape. After another 802 msec, the target (an X or an O) appeared for 1,000 msec. Subjects pressed one of two buttons to indicate the target's identity as rapidly as possible. The target appeared in one of eight possible regions centered on the points of an invisible octagon, with two target regions in each quadrant of the visual field. Target regions were located $\sim 2^\circ$ visual eccentricity from fixation. To avoid spatial certainty, exact target positions were made unpredictable by randomly offsetting each target from the center of the region in which it appeared, and by having each cue indicate two possible target regions.

Type of cueing was manipulated between blocks of 25 trials by telling subjects which cue would predict target location. During location-based cueing, the arrow pointed halfway between two target regions indicating that the target was 80% likely to appear in one of these two target regions. During object-based cueing, the shape indicated that the target was 80% likely to occur in one of two regions enclosed by the shape. Valid and invalid trials were presented randomly within each block. The cue/target relationships for valid and invalid trials for each cueing condition are shown in Figure 1B. Placement of the two cue elements was uncorrelated, so that there was no contingency between the location of the target and the uninformative cue. Subjects completed three imaging runs each of location-based cueing, object-based cueing and a control condition in which neither cue element predicted target location (diffuse condition). Subjects were told to maintain eye fixation on the central cross throughout the imaging run.

Eye movements could not be monitored in the MR scanner. Therefore, five additional subjects participated outside the scanner with eye position monitored by infrared eye tracker. The task was identical to the main experiment except for a shortened ITI. Eye movements were detected on less than 6% of the trials, and within that small subset of trials, the relative frequencies of eye movements in the location-based and object-based conditions did not differ, $t(4) = 1.6$, $p > .15$. Thus differences in brain activation patterns were unlikely to be caused by differential eye movements in the two conditions rather than by differences in allocation of attention.

Image Acquisition

Whole-brain ER-fMRI was conducted on a commercial 1.5 T scanner (Signa, General Electric Medical Systems) equipped with a 30.5 cm i.d. three-axis local gradient head coil and an elliptical encapped quadrature radiofrequency coil (Medical Advances, Milwaukee). Echo-planar images were collected using a single-shot, blipped, gradient-echo echo-planar pulse sequence in 17 contiguous 7-mm sagittal slices [repetition time (TR) = 2.5 sec, echo time (TE) = 40 msec, flip angle = 90°, field of view (FOV) = 240 mm, matrix size = 64 × 64, voxel size = 3.75 × 3.75 × 7 mm]. High-resolution, 3-D spoiled gradient-recalled at steady-state (SPGR) anatomical images were collected [TE = 5 msec, TR = 24 msec, flip angle = 40°, number of excitations = 1, slice thickness = 1.1, 1.2, or 1.3 mm, FOV = 240 mm, resolution = 256 × 192].

Image Analysis

Data processing was accomplished with the Analysis of Functional NeuroImages (AFNI) software (Cox, 1996). Each image time series was spatially registered in-plane to reduce the effects of head motion using an iterative linear least squares method (Keren, Peleg, & Brada, 1988). Linear drift in the time series was removed using a regression analysis. The fMRI signal provides a measure of the brain's local hemodynamic response to task-related increases in neural activity. The 12.5-sec separation between the start of each trial of the experimental task allowed time for the hemodynamic responses to rise from baseline, peak 5–7 sec after trial onset, and fall back to baseline by the start of the next trial. Thus, the five whole-brain images collected during each 12.5-sec epoch captured the task-related activation for each trial. Task-related activity for each trial was detected by subtracting a local baseline image (average of the images taken at times 0 and 12.5 sec posttrial onset) from an activation image (average of the images taken 5 and 7.5 sec posttrial onset). For each trial type (Object-Valid, Object-Invalid, Location-Valid, Location-Invalid, Diffuse), difference images were averaged within each subject.

Individual anatomical (SPGR) scans and functional difference images were linearly interpolated to volumes with 1-mm^3 voxels, coregistered, and transformed into standard stereotaxic space (Talairach & Tournoux, 1988). To compensate for normal variation in anatomy across subjects, the stereotaxically resampled 3-D difference images were spatially averaged with a 4-mm full-width at half-maximum (FWHM) filter. These data sets were then subjected to voxel-wise repeated-measures analysis of variance (ANOVA) and post hoc t statistics to examine comparisons involving object-based and location-based cueing (Object-Valid vs. Location-Valid) and comparisons involving valid and invalid cueing (Object-Valid and Location-Valid vs. Object-Invalid and Location-Invalid). An individual voxel probability threshold of $p = .01$ and a minimum cluster size threshold (Forman et al., 1995) of 0.37 ml was established based on 10,000 Monte Carlo simulations that take into consideration an average brain volume of 1,404 ml and 4 mm FWHM spatial averaging. The chance probability of obtaining a significant cluster for an entire volume (Type I error) equals $p = .05$ (final per-voxel $p = .000016$).

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The data reported in this experiment have been deposited in National fMRI Data Center (http://www.fmridc.org). The accession number is 2-2000-1116E.

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