

# A Common Network of Functional Areas for Attention and Eye Movements

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## Summary

Functional magnetic resonance imaging (fMRI) and surface-based representations of brain activity were used to compare the functional anatomy of two tasks, one involving covert shifts of attention to peripheral visual stimuli, the other involving both attentional and saccadic shifts to the same stimuli. Overlapping regional networks in parietal, frontal, and temporal lobes were active in both tasks. This anatomical overlap is consistent with the hypothesis that attentional and oculomotor processes are tightly integrated at the neural level.

## Introduction

We simultaneously attend to and look at objects in a visual scene by means of saccadic eye movements that rapidly bring the fovea, the retinal region of highest acuity, onto stimuli of interest. It is possible, however, to dissociate the locus of attention from the line of gaze (James, 1890), i.e., to attend to different peripheral objects while maintaining eye fixation (covert attention). Attending to a spatial location improves the detection and discrimination of stimuli presented at that location, even when eye movements are not allowed (Eriksen and Hoffman, 1972; Posner, 1980; Bashinski and Bachrach, 1984; Downing, 1988; Hawkins et al., 1988). These findings have suggested the existence of brain mechanisms for selecting information from various locations in the visual field (visuospatial attention) (Posner, 1980; Treisman and Gelade, 1980; Koch and Ullman, 1985; Ullman, 1996).

The relationship of visuospatial attention and eye movements is controversial. While the two systems can work independently, as when attention moves to a peripheral location while the eyes hold fixation, the preparation of an eye movement toward a location appears to induce a concurrent shift of attention toward the same location (Shepherd et al., 1986; Chelazzi et al., 1995; Hoffman and Subramaniam, 1995; Kowler et al., 1995; but see Klein, 1980; Posner, 1980; Remington, 1980; and

Stelmach, 1997, for a different view). One theory has proposed that attentional shifts involve covert oculomotor preparation (Rizzolatti et al., 1987). Overall, the psychological evidence indicates that attention and eye movements are functionally related, but it remains unclear to what extent these two sets of processes share neural systems and underlying computations.

At the neural level, single unit studies in awake behaving monkeys have demonstrated that attentional and oculomotor signals coexist. In many cortical and subcortical regions in which oculomotor (e.g., presaccadic/saccadic) activity has been recorded during visually guided saccadic eye movements, i.e., frontal eye field (FEF, e.g., Bizzi, 1968; Bruce and Goldberg, 1985), supplementary eye field (SEF, e.g., Schlag and Schlag-Rey, 1987), dorsolateral prefrontal cortex (e.g., Funahashi et al., 1991), posterior parietal cortex (e.g., Mountcastle et al., 1975; Robinson et al., 1978; Andersen et al., 1987), substantia nigra (e.g., Hikosaka and Wurtz, 1983a), caudate nucleus (e.g., Hikosaka et al., 1989a), and pulvinar nucleus of the thalamus (e.g., Petersen et al., 1985), the response to visual stimuli is also modulated by their behavioral relevance (Wurtz and Goldberg, 1972; Wurtz and Mohler, 1976a, 1976b; Bushnell et al., 1981; Goldberg and Bushnell, 1981; Hikosaka and Wurtz, 1983b; Petersen et al., 1985, 1987; Boch and Goldberg, 1989; Hikosaka et al., 1989b; Steinmetz et al., 1994; Robinson and Kertzman, 1995; Robinson et al., 1995; Colby et al., 1996; Kustov and Robinson, 1996; Kodaka et al., 1997). For example, in parietal cortex, stimuli presented at task-relevant locations tend to produce a different visual response than stimuli presented at task-irrelevant locations (spatially selective visual modulation) (Bushnell et al., 1981; Steinmetz et al., 1994; Robinson et al., 1995; Colby et al., 1996). Overall, the single unit data provide strong evidence that some areas mediate both attentional and oculomotor processes but do not rule out the possibility that other areas may be solely involved in one or the other function.

Neuroimaging studies in humans have activated similar regions in parietal and frontal cortex when people covertly direct their attention toward peripheral visual stimuli during detection or discrimination tasks (Corbetta et al., 1993, 1995; Vandenberghe et al., 1996, 1997; Nobre et al., 1997), or when they look at peripheral visual stimuli during oculomotor localization tasks (Fox et al., 1985; Paus et al., 1993, 1995; Petit et al., 1993, 1996, 1997; Anderson et al., 1994; Lang et al., 1994; Darby et al., 1996; Muri et al., 1996; Sweeney et al., 1996; Bodis-Wollner et al., 1997; Law et al., 1997; Luna et al., 1998). In the latter condition, attentional shifts are coupled with (and possibly precede) oculomotor shifts toward the stimulus location (e.g., Shepherd et al., 1986). It is unknown, however, if the same anatomical regions are actually recruited in the two conditions, since no experiment has directly compared them in the same group of subjects.

In a recent retrospective meta-analysis of published imaging studies on visuospatial attention and visual saccadic eye movements, all regions in parietal and frontal

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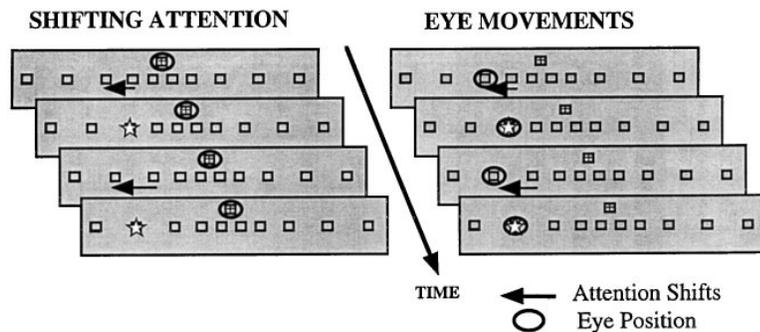


Figure 1. Diagrams of Visual Display and Task Paradigms

The probe stimulus was an asterisk displayed for 150 ms in one of the boxes, and it was followed by a variable interstimulus interval (range, 1000–2000 ms) with a mean of 1500 ms. Boxes were located at 1°, 3°, 5°, 7°, and 10° of visual angle. The arrows indicate sequential shifts of attention made on each trial in anticipation of the probe. The ovals define the position of the eyes: in the center during the shifting attention task and while moving in anticipation of the stimulus probe in the eye movement task. In the attention task, probe

stimuli appeared in the left visual field. In the eye movement task, probe stimuli appeared in the fovea, since the change of fixation preceded their presentation. In the fixation control task, the same array of boxes was displayed in the absence of stimulus probe.

cortex driven by attention were also active during visual saccades. Some segregation in the pattern of activation was also observed, with foci for attention in the frontal lobe more anteriorly located than foci for eye movements (Corbetta, 1998). This meta-analysis was limited by variability in both the experimental protocols and the underlying anatomy among different groups of subjects. To more directly compare the neural systems controlling visuospatial attention and eye movements in the same group of subjects, functional magnetic resonance imaging (fMRI) and surface-based representations of functional brain activity (flat maps) were used to study the functional anatomy of tasks in which attention was shifted to visual stimuli, with or without concurrent eye movements. If visuospatial attention and oculomotor processes share the same areas, the corresponding pattern of cortical activation should greatly overlap; conversely, if they are partially implemented through different areas, some regions related to oculomotor preparation/execution should be active only when the eyes are allowed to move.

## Results

Subjects were scanned in a blocked fMRI design on three experimental tasks. In the “shifting attention” task, subjects were instructed to maintain central fixation and sequentially shift attention along a predictive series of box locations (1°, 3°, 5°, 7°, 10°, 1°, etc.) in the left visual field, to detect the onset of a visual probe. The shift of attention was endogenously generated since it occurred prior to probe onset. We used this task in an earlier positron emission tomography (PET) experiment (Corbetta et al., 1993) to localize regions related to shifts of attention. In the “eye movement” task, subjects were instructed to sequentially shift fixation (and presumably attention) along the series of box locations in order to detect upcoming probes. As in the shifting attention task, the sequence of locations was predictive, and subjects were instructed to move the eyes to the next location prior to the onset of the visual probe. Hence, the probes were always presented at the fovea during the eye movement task, in contrast to their peripheral position in the shifting attention task. In a “fixation” control task, subjects viewed and maintained central fixation on the same array of boxes, and no probes were presented (Figure 1).

## Behavior

In a 1 hr psychophysical session, subjects were trained to maintain fixation during the shifting attention and fixation tasks and to perform accurate saccades during the eye movement task. Eye position was monitored with electro-oculogram (EOG), and feedback was given throughout the training session about the precision of fixation. Loss of fixation during fixation and shifting attention tasks was detected in <2% of the trials. The efficacy of the attentional instruction in the shifting attention task was assessed by measuring manual (speeded key presses) reaction times to visual probes appearing at expected locations, i.e., following the predictive sequence of locations (80% of trials), and at unexpected locations (20% of trials) in the same visual field. Reaction times were faster at expected than at unexpected locations (273 versus 310 ms,  $F[1,5] = 36.11$ ,  $p < 0.001$ ). The sequence of probe locations was 100% predictive in both attention and eye movement tasks during the fMRI experiment.

## fMRI

Different pairs of experimental tasks were randomly alternated in each fMRI scan: (1) shifting attention versus fixation, (2) eye movement versus fixation, and (3) shifting attention versus eye movement. To avoid the confounding of different effectors (hand versus eye) in the two tasks (attention versus eye movements), subjects were instructed to perform the shifting attention task as in the behavioral session, but without pressing a key to signal the detection of the visual probes.

The top row of Figure 2 shows group average regions of activation in the shifting attention task compared to fixation. In the parietal and frontal lobes, regions near intraparietal sulcus (IPS), precentral sulcus (PrCeS), posterior end of superior frontal sulcus (SFS), medial frontal gyrus (MeFG), middle frontal gyrus, and frontal operculum (latter two regions not shown) were localized bilaterally, albeit more strongly in the right hemisphere, contralateral to the stimulated/attended left visual field (Table 1 for location and magnitude). In the occipital and temporal lobes, other activations were localized in the right hemisphere in lateral occipital cortex (LO), human middle temporal (MT) complex, near the superior temporal sulcus (STS), and more dorsally at the junction between intraparietal and transverse occipital sulcus (IPS/TOS).

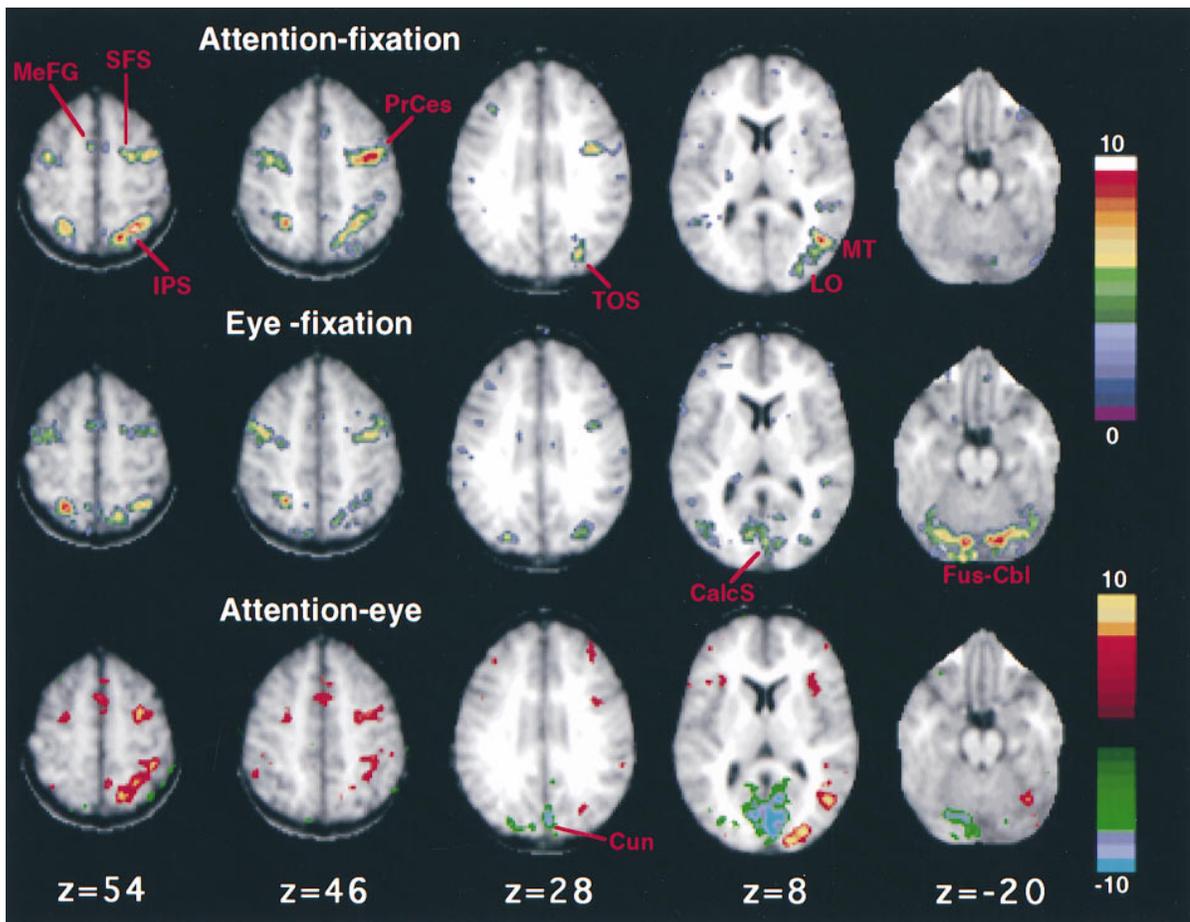


Figure 2. z Maps of BOLD Signal in Attention versus Fixation, Eye Movement versus Fixation, and Attention versus Eye Movement. Activity data superimposed onto anatomical MR images. Anatomical left is on the image left. Abbreviations: MeFG, medial frontal gyrus; SFS, superior frontal sulcus; PrCes, precentral sulcus; IPS, intraparietal sulcus; TOS, junction intraparietal/transverse occipital sulcus; STS, superior temporal sulcus-gyrus; MT, middle temporal; LO, lateral occipital; CalcS, calcarine sulcus; Ling, lingual gyrus; Fus/Cbl, fusiform gyrus/vermis cerebellum; CUN, cuneus, parieto-occipital, posterior cingulate. Note that the range of color values in the top two images is  $0 < z < 10$ ; hence, green corresponds to  $z = 5$ . In the bottom image, the range of values is  $-10 < z < 10$ , and green corresponds approximately to  $z = -5$ .

The middle row of Figure 2 shows the group average functional anatomy of the eye movement task as compared to fixation. As expected based on previous oculomotor studies, regions of activations were localized bilaterally in frontal cortex near precentral sulcus, posterior end of superior frontal sulcus, medial frontal gyrus, and parietal cortex along the intraparietal sulcus. These regions strongly overlapped with those recruited during covert shifts of attention, albeit at a lower level of activation (compare the top and middle rows of Figure 2 and the location/magnitude of foci in Table 1). In contrast to the attention task, strong activations were localized in occipital cortex along the calcarine sulcus (CalcS) and the lingual (Ling) and fusiform (Fus/Cbl) gyri. Other extrastriate visual regions driven by the attention task (see above) were also active during the eye movement task. The posterior vermis of the cerebellum (Fus/Cbl) was uniquely driven by eye movements.

The bottom row of Figure 2 shows a direct contrast between shifting attention and eye movement tasks, conducted in a separate set of scans. Frontal and parietal regions, localized in attention—fixation and eye

movement—fixation, were replicated and significantly more active in the right hemisphere (contralateral to the stimulated/attended left visual field) during the attention task (Table 1). No new regions were identified by this subtraction (with the exception of the inferior frontal gyrus, which was only weakly active in attention—fixation; see Table 1). In contrast, stronger activity was recorded in medial occipital cortex, both ventrally and dorsally, during the eye movement task. The ventral regions (calcarine, lingual, and fusiform) corresponded to those identified in the eye movement—fixation image. The dorsal regions (cuneus, parieto-occipital sulcus, posterior cingulate) corresponded to relative deactivations that were recorded in the shifting attention—fixation image (data not shown). Deactivations in these regions have been observed across many other visual processing experiments (Shulman et al., 1997). Finally, medial cerebellar regions were also significantly more active during eye movements, as observed in the first two subtractions. Overall, the contrast attention—eye movement yielded a spatial pattern of activation that was analogous to the one identified in the former two

Table 1. Regions of Activation in Group Average Images

AREAS	Hem	Attention versus Fixation			Eye Movement versus Fixation			Attention versus Eye Movement			Eye Movement versus Attention					
		x	y	z	x	y	z	x	y	z	x	y	z			
PARIETAL	R	25	-59	56	11.2	35	-57	54	7.47	37	-45	50	6.77			
	L	-25	-55	50	8.85	-23	-59	56	9.8							
	R	17	-65	54	9.38	13	-63	62	7.23	15	-67	54	7.21			
	L	-19	-63	60	7.12	-7	-77	50	5.78							
	R	27	-75	28	7.11	25	-79	30	5.45	29	-75	28	4.91			
	L	-25	-75	22	4.37	-23	-81	18	7.33							
FRONTAL	R	41	-7	46	9.4	41	-7	46	7.09	35	-5	46	5.81			
	L	-35	-9	46	6.59	-37	-7	46	6.75							
	R	35	-1	30	8.54	35	-1	30	5.82	45	-5	38	4.89			
	R	29	-3	60	6.43	29	-3	60	5.34	29	-5	54	7.11			
	L	-27	-13	46	5.67	-29	-13	46	5.03							
	L	-5	-1	58	6.63	-5	-1	56	5.66	-1	3	52	5.22			
	R	11	-11	68	5.41					3	-11	62	5.58			
	L	-35	27	30	5.89	-37	29	30	4.61							
	R	45	29	34	5.22	53	21	32	5.07	33	43	24	5.63			
	R	57	3	22	5.61	51	11	-4	5.44	47	5	20	6.16			
	R									35	9	12	6.6			
	L									-31	19	10	5.63			
TEMPORAL	R	41	-43	8	5.01	47	-39	10	6.19	59	-49	6	5.11			
OCCIPITAL	R	43	-67	8	8.78	43	-69	14	5.22	43	-67	6	7.4			
	L					-45	-71	12	7.08							
	R	27	-87	10	6.59	29	-83	4	6.57	15	-95	8	11.2			
	L									-23	-95	16	5.25			
	R	41	-75	4	6.22											
	L															
CINGULUM	R					11	-89	-4	10.8							
	L					-11	-79	2	10.5							
	R					-1	-95	-14	8.38							
	L					17	-99	-8	6.11							
	R	29	-81	-12	6.66											
	R					31	-77	-20	6.31							
	R					-23	-81	-20	7.08							
	L					41	-71	-20	5.74	39	-87	-14	5.37			
	R					-43	-79	-12	5.32							
	L															
	R					13	-83	-16	11.2							
	CEREBELLUM	Med					-11	-95	-22	7.3						
Lat										35	-67	-22	6.54			
L										-35	-47	-30	5.08			

Local maxima are determined using a search algorithm whose diameter is set at 8 mm (z dimension of voxel in functional data). Only the top focus in each region is reported.

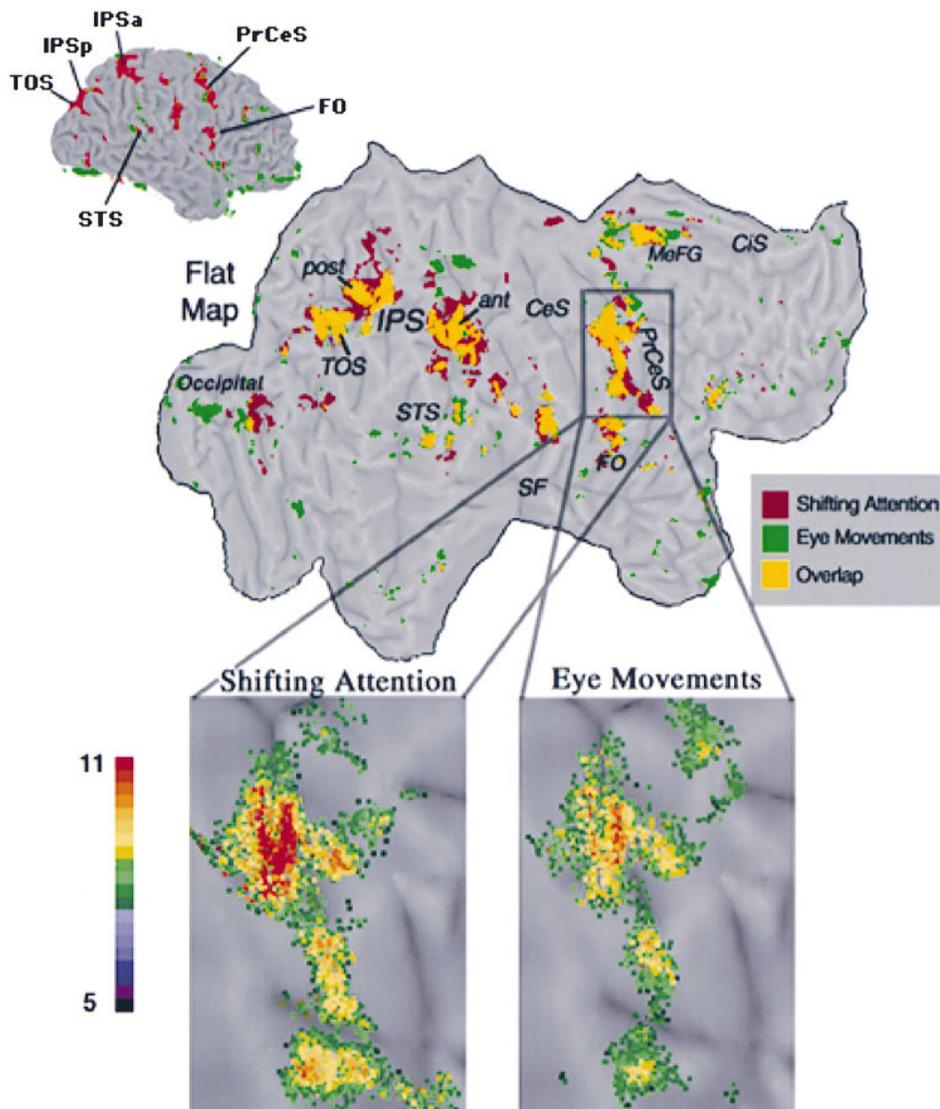


Figure 3. Three-Dimensional Surface Reconstruction and Flattened Cortical Map of the Right Hemisphere in Subject 1582

Activity data with a  $z$  score  $> 5.0$  were coregistered and colored; the shifting attention task is shown in red, the eye movement task in green, and the overlap in yellow. The inset highlights the precentral region that includes the frontal eye field (FEF). Activity data are plotted using a 42 value color scale in which red/max/ $z$  score = 11 and black/min/ $z$  score = 5.

contrasts (attention—fixation, eye movement—fixation). This provides further evidence that a highly overlapping network of cortical regions was recruited, but to different degrees, by both tasks.

#### Flat Maps

To more precisely localize functional activity in relationship to the underlying cortical geography, we computed the flattened surface representations of the cortical mantle in two subjects and projected the corresponding functional data (Drury et al., 1996; Van Essen and Drury, 1997). Cortical surface reconstructions allow the visualization of activity buried into sulci while preserving the exact topological relationship between adjacent points. In lateral frontal cortex, activity near the PrCeS was precisely localized to the posterior bank of the sulcus,

along its ventral-dorsal extent up to the intersection with the superior frontal sulcus. In medial frontal cortex, a second region was localized on the MeFG, extending into the cingulate sulcus/gyrus (CiS). Three distinct parietal regions were activated corresponding to the anterior and posterior end of the IPS and its junction with the transverse occipital sulcus (TOS). In temporal cortex, another region was localized on the anterior bank of the superior temporal sulcus and the superior temporal gyrus (STS) (Figures 3 and 4).

In both subjects, a remarkable degree of overlap was evident in the pattern of activation for shifting attention and eye movement tasks. Across the whole brain (with the exception of the occipital lobe) no region was uniquely active in one or the other condition. Table 2 shows a quantitation across the five subjects of the

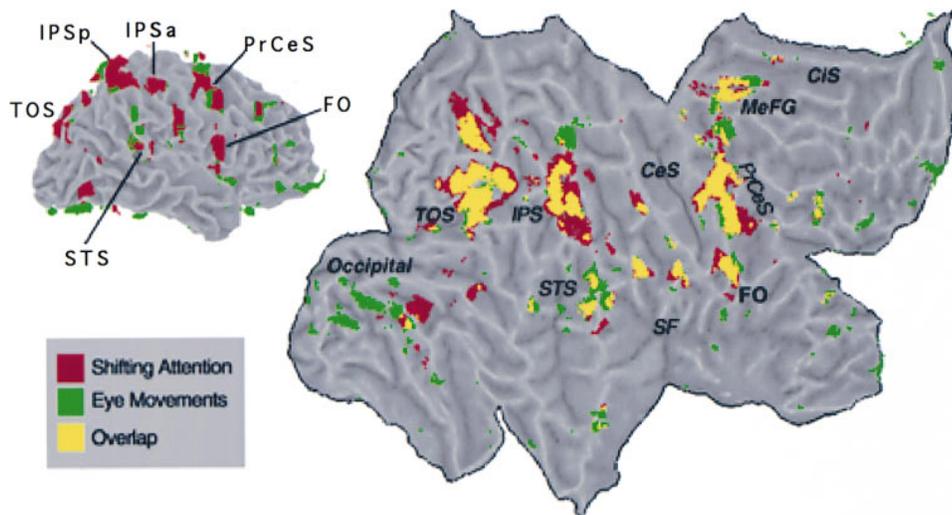


Figure 4. Three-Dimensional Surface Reconstruction and Flattened Cortical Map of the Right Hemisphere in Subject 611  
See Figure 3 legend.

functional overlap within each of the regions shown in Figures 3 and 4. Across different regions the percentage of overlap varied between 60% and 80%, i.e., in any region, at least 60% of the voxels that were significant in the least active condition were also significant in the other condition. These values underestimate the degree of regional overlap because many common voxels were found below the statistical threshold used to correct for multiple comparisons.

### Discussion

To test whether visuospatial attention and oculomotor processes share common functional areas in the human brain, fMRI and surface-based representations of the brain were used to compare the functional anatomy of two tasks in which people voluntarily shifted attention to peripheral visual stimuli, either with or without concurrent saccadic eye movements. The main finding was that a common network of functional regions in parietal, frontal, and temporal cortex was activated by the two tasks. The anatomical overlap was demonstrated at the level of group and single subject images, and by projecting the functional data on flat maps of the cortical mantle in two subjects. We first discuss the anatomical localization of these functional regions and putative homologies with areas of the macaque brain. Then, we consider possible explanations for the functional anatomical overlap of attention and eye movements.

#### Anatomical Localization of Functional Regions for Attention and Eye Movements, and Putative Homologies with Monkey Brain

The cortical network active during shifting attention and eye movement tasks (as compared to fixation) included the superior temporal sulcus/gyrus (STS), the IPS/TOS, anterior and posterior sectors of the IPS, a large swath of tissue along the PrCeS, and a region on the MeFG. This functional anatomy closely matches earlier PET

findings on a version of the shifting attention task that required stimulus detection by key press (Corbetta et al., 1993, 1997) and other experiments on covert visual orienting (Corbetta et al., 1995; Vandenberghe et al., 1996, 1997; Nobre et al., 1997). The current fMRI data improve the anatomical localization of these functional responses in relationship to the underlying sulcal and gyral anatomy. For instance, activity in parietal cortex was clearly localized along the intraparietal sulcus (anterior and posterior sectors), which divides the inferior from the superior parietal lobule and extends ventrally into the transverse occipital sulcus, in contrast to the early localization in the superior parietal lobule (Corbetta et al., 1993). Activity in superior frontal cortex was localized to the precentral sulcus (posterior bank), as compared to the early localization to the superior frontal cortex. Finally, activity in temporal cortex was localized to the anterior bank of the superior temporal sulcus and on the superior temporal gyrus, as compared with an early localization to the superior temporal/inferior parietal cortex. These new localizations agree well with previous localizations in which PET data were coregistered with individual anatomical MRI (Nobre et al., 1997) and agree well with the anatomy of visual neglect (Vallar and Perani, 1987).

The cortical network recruited during covert visual orienting largely overlapped with regions active in the eye movement task, which involved both attentional and saccadic shifts to peripheral stimuli. These functional regions were also similar to those localized by many imaging studies of visual saccades (Fox et al., 1985; Paus et al., 1993, 1995; Petit et al., 1993, 1996, 1997; Anderson et al., 1994; Lang et al., 1994; Darby et al., 1996; Muri et al., 1996; Sweeney et al., 1996; Bodis-Wollner et al., 1997; Law et al., 1997; Luna et al., 1998). Therefore, it appears that any difference between attention and eye movement responses across groups of subjects, as in the meta-analysis by Corbetta (1998), is most easily related to anatomical variability or variability

Table 2. Degree of Anatomical Overlap in Individual Subjects between Shifting Attention and Eye Movement Tasks

Subject	Condition	MeFG	R PrCS/SFS	R IPS	R IPS/TOS	R STS
Number of significant voxels						
S1	Attention	27	51	41	63	13
	Eye	38	47	29	39	18
	AND	20	39	26	35	8
	% Overlap	74	83	90	90	62
S2		3	8	15	9	
		7	13	11	16	
		0	3	9	2	
		0	38	82	22	
S3		48	125	108	15	12
		44	82	90	9	9
		27	66	56	6	8
		61	80	62	67	89
S4		0	0	29	10	6
		17	17	29	20	8
		0	0	19	10	6
		0	66	66	100	100
S5		28	28	42	14	7
		18	18	16	22	0
		15	15	15	4	0
		83	83	94	29	
	Median %	61	80	82	82	67

Anatomical regions were chosen from the right hemisphere as in Figures 3 and 4. Abbreviations as in Figures 2, 3, and 4. S1, S2, etc. represent subject 1, subject 2, etc.; attention, number of active voxels (after multiple comparison correction) during shifting attention task; eye, number of active voxels during eye movement task; AND, number of active voxels during both eye movement and attention tasks.

in the standardization procedures used to analyze group data.

The anatomical overlap between attention and eye movement allows us to "label" more precisely these functional regions and establish putative homologies with areas in the macaque brain. For instance, the PrCeS has been proposed by many studies to be the human homolog of the FEF, based on its robust pattern of activation on a variety of oculomotor tasks and location on the lateral surface of the frontal lobe (e.g., reviewed by Paus, 1996). In ours and more recent experiments that used fMRI and single subject analysis (e.g., Petit et al., 1997; Luna et al., 1998), the precentral region includes a large swath of tissue along the ventrodorsal extent of the precentral sulcus, up to the intersection with the superior frontal sulcus. Given its considerable spatial extent, when compared to the relatively small size of FEF in macaque, the precentral region probably does not contain a single functional field. As shown in Table 1, separate peaks of activation were found in the precentral sulcus. The vector distance between the superior frontal sulcus (PrCes/SFS) and dorsal precentral (PrCeS dors) peak was 19 mm, and between the dorsal (PrCeS dors) and ventral (PrCeS ventr) peak was 18 mm (see Table 1). These distances between functional fields typically underlie separate areas (Hunton et al., 1996). This impression is reinforced by inspecting the flat map (see inset of Figure 3) in which multiple separate clusters of activity were present along the precentral sulcus.

Activity along the MeFG may correspond to the SEF given its pattern of activation during oculomotor tasks (e.g., Luna et al., 1998) and relative proximity with the homologous area in monkey (Schlag and Schlag-Rey, 1987; Shook et al., 1990). Putative homologies in parietal cortex are more ambiguous. In single subjects (e.g., see

flat maps in Figures 3 and 4), three separate functional regions, respectively in the anterior (IPSa) and posterior (IPSp) intraparietal sulcus, and at the IPS/TOS, can be consistently identified. Given the colocalization of attentional and oculomotor signals, and its strong anatomical connections with the FEF (that appears to be also active in this experiment) (Selemon and Goldman-Rakic, 1988; Andersen et al., 1990a; Colby et al., 1996), one or more of these functional fields might correspond to areas LIP and 7a in macaque. Finally, the response in the superior temporal sulcus/gyrus (STS) may correspond to the superior temporal polysensory area (STP) in macaque (Bruce et al., 1981; Hikosaka et al., 1988; Scalaidhe et al., 1997), based on its position and responsiveness during attention (see also Nobre et al., 1997), eye movements, and motion processing (Shulman et al., 1997, Soc. Neurosci., abstract). However, a strong limitation to the exercise of establishing homologies with monkey areas is that functional areas in humans can be defined only on the basis of their pattern of activation, whereas multiple and different criteria (myelo- and cytoarchitectonics, connectivity, microstimulation, physiological responses, effects of lesion or inactivation) can be used in macaque. Future studies will need to test these functional fields with a wider range of stimulation paradigms, similarly to what has been done for human MT (Tootell et al., 1995).

#### Functional Anatomical Overlap for Visuospatial Attention and Eye Movements

In order to explain the anatomical overlap between attention and eye movements, it is helpful to consider first what types of neuronal signals might drive cortical regions during the eye movement task and then to consider which of these signals might be active during the

shifting attention task. The following discussion concentrates on findings from single unit and imaging experiments.

#### **Eye Movement Task**

Single unit studies in macaque have shown that regions putatively active in this experiment, i.e., posterior parietal cortex, FEF, SEF, etc. contain several different types of signals. Neurons fire at the onset of a visual stimulus, and/or prior or during the execution of a saccadic eye movement (presaccadic/saccadic/postsaccadic activity) (Bizzi, 1968; Mountcastle et al., 1975; Robinson et al., 1978; Bruce and Goldberg, 1985; Andersen et al., 1987; Schlag and Schlag-Rey, 1987; Andersen, 1989). Moreover, visual responses for relevant stimuli, i.e., when they are the target of an eye movement, are often enhanced as compared to when the same stimuli are irrelevant, i.e., presented at task-irrelevant locations (spatially selective visual enhancement) (Wurtz and Goldberg, 1972; Wurtz and Mohler, 1976a; Goldberg and Bushnell, 1981). Finally, some neurons fire during fixation of a visual stimulus (Bizzi, 1968; Suzuki and Azanuma, 1977; Motter and Mountcastle, 1981; Bruce and Goldberg, 1985; Bon and Lucchetti, 1992; Schlag et al., 1992).

Blood oxygenation level-dependent (BOLD) fMRI responses during the eye movement task (as compared to fixation) likely reflected different neuronal signals, including visual, visual enhancement, and oculomotor (both preparatory and execution) signals. Fixation neurons were probably similarly active during the eye movement and fixation control tasks, as both required extensive periods of visual fixation. Visual neurons were probably driven by the presentation of the foveal stimuli, and their response was possibly enhanced by their behavioral significance. Finally, oculomotor neurons were active during periods in which saccades were prepared and executed. Although fMRI cannot distinguish between presaccadic and postsaccadic activity, all regions localized in this and other eye movement studies (putative FEF, SEF, LIP, etc.) contain in the monkey a combination of both signals with an apparent predominance of presaccadic activity in FEF, SEF, and LIP (Bruce and Goldberg, 1985; Schlag and Schlag-Rey, 1987; Boch and Goldberg, 1989; Andersen et al., 1990b). Interestingly, imaging studies of eye movements have not revealed consistent activations in the general region of the posterior cingulate where exclusively postsaccadic activity has been most commonly recorded in monkey (Olson et al., 1993).

#### **Attention Task**

BOLD fMRI responses during the attention task, and their striking similarities to those obtained during the eye movement task, may reflect the artifactual occurrence of saccadic eye movements during attention or a genuine overlap in the pattern of functional activation. Hereafter, we will first discuss the possibility of artifactual eye movements, then consider causes of functional overlap.

*Eye Movements during Attention.* It is very unlikely that eye movements occurred during the shifting attention task. All subjects showed reliable fixation within the resolution of the EOG just prior to the imaging session, and none reported any difficulty in holding fixation in the MR environment. The visual probe stimuli were suprathreshold, and the attention task did not require high

visual acuity. This task has been extensively investigated in our laboratory over many years (Corbetta et al., 1993, 1995), and it is our experience that no lateralized eye movements occur within the resolution of measurement when subjects shift attention to peripheral stimuli under these conditions. Finally, the pattern of activations in many regions was consistent with the hypothesis that subjects moved their eyes only in the eye movement task. In the eye movement task, subjects moved the eyes sequentially along a prespecified sequence of locations (1°, 3°, 5°, 7°, 10°, 1°, etc.) in the left visual field and detected visual probes at the fovea after each saccade. The medial cerebellum, typically recruited by eye movements, was uniquely active in the eye movement task. Visual cortex (calcarine sulcus, lingual and fusiform gyri) was also more strongly active during eye movements, a logical consequence of the foveal position of the probes. In general, all activations were more bilateral during eye movements, and more contralateral during shifts of attention. This can be explained in the eye movement task by the foveal position of the stimuli, and the execution of bidirectional saccades in left visual field, i.e., foveofugally (1° > 3° > 5° > 7° > 10°) on four out of five of the trials and foveocentrically (10° > 1°) on one out of five of the trials, which in turn should drive both hemispheres. In the attention task, the visual probes/attended locations were strictly contralateral; the presence of stronger contralateral activations irrespective of direction of shifts replicate earlier findings (Corbetta et al., 1993).

*Causes of Functional Overlap.* The functional anatomical overlap between attention and eye movements indicates that the same areas are active when people covertly attend to peripheral visual stimuli or actually perform directed saccadic eye movements to the same stimuli. Therefore, the possibility that separate regions mediate visuospatial attention and visual saccadic eye movement can be ruled out. The functional anatomical overlap is consistent with the hypothesis that attentional and oculomotor processes involve the same neural mechanisms (Rizzolatti et al., 1987), but the imaging data do not directly demonstrate this identity. Since separate populations of neurons can be driven by different signals within the same cortical region, visuospatial attention and saccadic eye movement processes may be using entirely different neuronal (or computational) mechanisms within the same anatomical area.

Hemodynamic responses in the attention task may have reflected a variety of neuronal signals that also occurred in the eye movement task. We argue that visual fixation (and associated saccadic suppression signals) and visual sensory signals cannot explain the observed functional overlap. Rather, the overlap reflects both attentional modulations of the visual response and preparatory oculomotor activity associated with covert shifts of attention.

*Fixation and Saccadic Suppression Signals.* Periods of active fixation occurred in all three tasks, i.e., throughout the duration of a scan for fixation control and shifting attention tasks, and in between saccades during the eye movement task. However, it is possible that the attention task might have required a more intense fixation signal to suppress unwanted eye movements. Fixation signals have been recorded by several groups from

regions similar to the one identified in the present experiment. For instance, Petit and colleagues recorded activity in the precentral region (FEF), medial frontal gyrus (SEF), and cingulate cortex during active fixation in the dark (as compared to rest) (Petit et al., 1995). Law et al. (1997) recorded activity in FEF, SEF, and posterior parietal cortex during visual fixation in the presence of peripheral distractors (as compared to fixation alone), and interpreted this activity as "inhibitory" to prevent reflexive saccades to the peripheral stimuli.

However, hemodynamic changes in the shifting attention task cannot exclusively be related to fixation signals, since the hemodynamic changes produced by visual fixation are weaker when compared with those produced by visual orienting and/or saccadic preparation/execution. For example, Corbetta and colleagues (Corbetta et al., 1993) presented subjects with peripheral visual stimuli while they maintained central fixation under three different conditions: (1) peripheral attention (shifts of attention), (2) foveal attention, and (3) no active task (passive). In the passive condition, attention was presumably automatically drawn by the sudden appearance of the peripheral stimuli (Yantis and Jonides, 1990). The level of activation in FEF was higher when the peripheral stimuli were voluntarily attended (shifting attention) than when they were ignored (central detection) or automatically attended (passive). Since all three tasks required central fixation and suppression of reflexive saccades, activity in parietal and frontal cortex is better explained in terms of attentional orienting than fixation or saccadic suppression. Law and coworkers (Law et al., 1997) estimated blood flow in FEF and SEF during various oculomotor tasks, including real and imagined saccades to visual targets (conditions that also involve saccadic and attentional shifts) and central fixation without or with peripheral stimuli, which, similar to our passive task, may induce reflexive orienting. Blood flow in both regions was highest when the stimuli were task relevant (real and imagined saccades), intermediate during reflexive orienting (fixation with distractors), and least active during simple visual fixation. Again, this profile demonstrates these regions are more active during orienting and saccadic preparation/execution than fixation or saccadic suppression.

*Visual Sensory Signals and Related Attentional Modulations.* The functional anatomical overlap between attention and eye movement tasks might also reflect only the effect of visual stimulation during attention and eye movement tasks, i.e., it may be entirely unrelated to the mechanisms involved in shifting attention and preparing/executing eye movements. Several single unit studies have shown that passive visual stimuli drive both parietal (LIP, 7a) and frontal (FEF, SEF) regions (Bizzi, 1968; Mountcastle et al., 1975; Robinson et al., 1978; Bruce and Goldberg, 1985; Andersen et al., 1987; Schlag and Schlag-Rey, 1987; Andersen, 1989). However, we have previously shown that responses in parietal cortex and FEF during shifts of attention to peripheral stimuli can be found after controlling for sensory activity (Corbetta et al., 1993, 1997). For example, we (Corbetta et al., 1993) presented peripheral visual stimuli while enforcing central fixation (and monitoring eye movements with EOG) under conditions in which (1) attention was directed to the periphery (shifting attention) or (2) attention

was directed to the fovea. Activity in both posterior parietal and FEF was greater during peripheral than foveal attention, even though the stimulus was constant. Similar results showing effects of peripheral attention on parietal and frontal regions, after controlling for sensory activity, have been reported by Vandenberghe and colleagues (Vandenberghe et al., 1996, 1997). These data indicate that attentional signals contributed to the activity recorded in parietal and FEF regions during the shifting attention task of the current experiment.

The presence of visual attentional modulations in posterior parietal cortex is entirely consistent with a large body of physiological results (Robinson et al., 1978; Bushnell et al., 1981; Steinmetz et al., 1994; Colby et al., 1995; Robinson and Kertzman, 1995). In contrast, the presence of modulations in the human FEF during covert attention differs from early single unit experiments, which showed enhancement of visual responses in FEF only in relationship to the execution of saccadic eye movements (Wurtz and Mohler, 1976a; Goldberg and Bushnell, 1981). However, recent single unit experiments have reported selective modulations of the visual response in both FEF (Kodaka et al., 1997) and SEF (Bon and Lucchetti, 1997) during peripheral attention tasks that do not require a saccadic response. Kodaka et al. (1997) noted that while attention was directed to peripheral locations throughout a block of trials in their study (and in ours as well), it was divided between a peripheral and a central location in the earlier studies.

*Oculomotor Signals.* Finally, covert shifts of attention may require saccadic preparation and hence drive oculomotor neurons. In our experiment, the predictive spatial sequence of probe positions enabled subjects to shift attention in anticipation of the probe stimulus. The neuronal signal implementing a shift of attention (control signal) therefore preceded the sensory event (the probe stimulus). It has been proposed that shifting attention to a peripheral location corresponds to the intention to make an eye movement toward it (Rizzolatti et al., 1987). Accordingly, single unit experiments show that attended locations can be coded in parietal cortex in terms of directional motor activity (Andersen, 1995; Snyder et al., 1997). A similar mechanism seems to be operative in the superior colliculus, in which voluntary and reflexive covert shifts of attention amplify the saccadic movement vector induced by the micro-electrical stimulation of neurons in the deep layer (Kustov and Robinson, 1996). Hence, in parietal cortex and superior colliculus, there is some evidence that covert shifts of attention could be related to the intention of preparing an eye movement.

Voluntary covert shifts of attention and overt saccadic movements are closely intergrated in everyday life and require the coordination of visual, visuomotor, and attentional signals. Our experiment demonstrates that these processes recruit a common set of functional areas in frontal, parietal, and temporal cortex. These imaging data are in line with psychological findings that support a functional relationship between attention and eye movement processes (Shepherd et al., 1986; Rizzolatti et al., 1987; Chelazzi et al., 1995; Hoffman and Sbramiam, 1995; Kowler et al., 1995). They are also consistent with single unit data in macaque showing that both saccadic and attentional signals can be recorded from many cortical areas (e.g., LIP, 7a, SEF, FEF)

(Bushnell et al., 1981; Petersen et al., 1987; Robinson et al., 1995; Colby et al., 1996; Bon and Lucchetti, 1997; Kodaka et al., 1997) and even from the same neurons within an area (Colby et al., 1996). Finally, our imaging data are consistent with lesion analysis demonstrating that damage of similar cortical regions in humans and monkey produces both attentional and oculomotor deficits (Mesulam, 1981; DeRenzi, 1982; Posner et al., 1984; Pierrot-Deseilligny et al., 1995).

It is important to note that anatomical integration between attention and eye movement systems holds only for the set of conditions used in this experiment (voluntary visual shifts of attention and eye movements) and may or may not generalize to other behavioral conditions such as reflexive visual orienting, orienting to auditory stimuli, or orienting in the dark. Moreover, one should be cautious to emphasize the link between oculomotion and spatially selective attention. It may turn out that, although the functional relationship between these two processes enjoys a privileged status, similar functional relationships and sharing of neuronal machinery may exist between spatial attention and any other system for the programming and execution of sensory controlled motor responses, such as reaching, grasping, and navigation (Snyder et al., 1997). Furthermore, some of the same regions may be involved in attentional control functions that extend beyond the computation of spatial locations (Shulman et al., 1997, Soc. Neurosci., abstract; Buchel et al., 1998; Le et al., 1998; Lumer et al., 1998).

### Conclusions

A largely overlapping network of cortical regions including putative FEF, SEF, and several parietal and temporal regions was recruited during voluntary covert shifts of attention and overt saccadic (and attentional) movements. These functional anatomical data indicate that attention and eye movement processes are not only functionally related, as originally suggested by psychological studies, but also share functional anatomical areas in the human brain.

### Experimental Procedures

#### Subjects

Six subjects (three females, three males) between the ages of 18 and 37 were recruited from the local Washington University community. All subjects were strongly right handed as measured by the Edinburgh handedness inventory (Raczkowski et al., 1974), were without any significant abnormal neurological history, and were normal or corrected-to-normal in visual acuity. Subjects were paid \$25 for each hour of their participation and gave informed consent in accordance with guidelines set by the Human Studies Committee of Washington University. One subject did not complete the imaging session, and her data were therefore disregarded.

#### Display

Subjects viewed a display (white stimuli on black background) in which multiple locations along the horizontal meridian ( $1^\circ$ ,  $3^\circ$ ,  $5^\circ$ ,  $7^\circ$ , and  $10^\circ$  of visual angle in each visual field) were marked by box outlines ( $1^\circ \times 1^\circ$  size). The probe stimulus was an asterisk displayed for 150 ms in different boxes of the left visual field, with a variable interstimulus interval (range, 1000–2000 ms; mean, 1500 ms). The sequence of stimulated locations was predictive according to the sequence  $1^\circ$ ,  $3^\circ$ ,  $5^\circ$ ,  $7^\circ$ ,  $10^\circ$ ,  $1^\circ$ , etc. Three tasks were performed as earlier described: (1) shifting attention, (2) eye movement, and (3) fixation.

### Functional Imaging, Experimental Design, and Data Analysis

Stimuli were generated by an Apple Power Macintosh computer and projected to subjects with a Sharp LCD projector (model XGE850) onto a screen positioned at the head end of the bore. Subjects viewed the screen through a mirror mounted on the head-coil. Imaging was performed on a Siemens 1.5 Tesla Vision System (Erlangen, Germany). Structural images were acquired using isotropic high resolution sagittal MP-RAGE images, optimized for contrast-to-noise ratio and resolution (Epstein et al., 1994) (repetition time TR = 9.7 ms, echo time TE = 4 ms, flip angle  $\alpha = 12^\circ$ , inversion time TI = 300 ms, voxel size =  $1 \times 1 \times 1$  mm). These images were also used for the surface reconstruction (see below). Functional images were collected in runs using an asymmetric spin-echo echo-planar sequence sensitive to blood oxygenation level-dependent (BOLD) contrast (T2\*) (TR = 2360 ms, T2\* evolution time = 50 ms,  $\alpha = 90^\circ$ ). During each functional run, 120 sets of 16 contiguous, 8 mm thick axial images were acquired ( $3.75 \times 3.75$  mm in-plane resolution), allowing complete brain coverage at a high signal-to-noise ratio (Conturo et al., 1996, Soc. Neurosci., abstract). Functional images were acquired parallel to the AC-PC plane in each subject after prescribing slice position based on automatic measurements of rotation, translation, and tilt of the initial images to an averaged ( $n = 12$ ) MP-RAGE anatomical image (target) representative of the atlas of Talairach and Tournoux (1988).

The fMRI design was "blocked" with various conditions alternating every 42.5 s, and each scan lasted 4 min and 43 s. Their order was counterbalanced within and across subjects. The beginning of each task period during a scan was signaled by a visual cue respectively either by a 750 ms change in the color of a random peripheral box (red for attention, green for eye movement), indicating the location of the first probe stimulus in a series, or by a change in the luminance of the central fixation box (fixation). Fifteen runs of functional data (five per comparison) were acquired in a 2.5 hr session.

Functional data were realigned within and across runs allowing unrestricted head motion, normalized for global fluctuation in intensity, and coregistered with the anatomical data (Friston et al., 1994; Snyder, 1995). Atlas registration was accomplished by a 12 parameter linear (affine) transformation of the T1-weighted MP-RAGE image (source) to match an averaged ( $n = 12$ ) MP-RAGE anatomical image (target) representative of the atlas of Talairach and Tournoux (1988). Time series obtained in different scans during pairs of experimental task conditions (e.g., eye movement versus fixation) were averaged in each subject. The Wilcoxon paired rank sum test was applied in each subject to the averaged time series to create z maps of different paired comparisons (e.g., saccade versus fixation). For group analysis, individual z maps were summed and divided by the square root of  $n$  in atlas space and then corrected for multiple comparisons based on voxel intensity and cluster size (Ollinger, 1997). This correction rejects single voxel regions and ensures that  $p < 0.001$ , where  $p$  is the probability of a single erroneous activation in the image volume. For individual analysis, z maps were standardized to atlas space and corrected for multiple comparisons. For comparison, Bonferroni correction across the whole volume was also calculated and corresponded to a z value of 4.8. An automated peak-search algorithm (Mintun et al., 1989) identified the location of peak activations based on z value and cluster size.

The analysis of anatomical overlap in individual subjects for functional regions active during attention and eye movement tasks involved: (1) counting the number of significant voxels, i.e., after multiple comparison correction, in each region in the shifting attention and eye movement conditions; (2) counting the number of significant voxels in each region in an "AND" (attention + eye movement) image, where voxels were displayed if they were significant and common in both attention and eye movement tasks; and (3) computing a ratio of overlap in each region according to the formula "number of voxels in AND image divided by number of voxels in the least active condition." Each region was defined based on its relationship with specific anatomical landmarks (e.g., precentral sulcus or intraparietal sulcus) that were easily visualized in each subject. All significant voxels within a region were used for the analysis.

### Surface Reconstruction

Surface reconstructions were computed from the MP-RAGE structural images. In one hemisphere (Figure 3A), contours were drawn

manually in NIH image and were reconstructed to form a wire-frame tessellation using Nuages software (Geiger, 1993). In the other hemisphere (Figure 3B), a semiautomatic segmentation algorithm was used to reconstruct the cortical surface (Teo et al., 1997). Images were manually edited to ensure correct topology of sulcal and gyral anatomy. Using software developed for the reconstruction and flattening of cortical surfaces (Drury et al., 1996), flat maps were computed for two subjects. The activation volume was resampled from  $3.75 \times 3.75 \times 8$  mm voxels to  $1 \text{ mm}^3$  voxels to yield an interpolated map of z statistics. Functional activity above a statistical threshold of  $z > 5.0$  was coregistered and projected onto the flattened anatomical representations to localize regions of activation in the various conditions.

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#### References

- Andersen, R.A. (1989). Visual and eye movement functions of the posterior parietal cortex. *Annu. Rev. Neurosci.* **12**, 377–403.
- Andersen, R.A. (1995). Encoding of intention and spatial location in posterior parietal cortex. *Cereb. Cortex* **5**, 457–469.
- Andersen, R.A., Essick, G.K., and Siegel, R.M. (1987). Neurons of area 7 activated by both visual stimuli and oculomotor behavior. *Exp. Brain Res.* **67**, 316–322.
- Andersen, R.A., Asanuma, C., Essick, G., and Siegel, R.M. (1990a). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *J. Comp. Neurol.* **296**, 65–113.
- Andersen, R.A., Bracewell, R.M., Barash, S., Gnadt, J.W., and Fogassi, L. (1990b). Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.* **10**, 1176–1196.
- Anderson, T.J., Jenkins, I.K., Brooks, D.J., Hawken, M.B., Frackowiack, R.S.J., and Kennard, C. (1994). Cortical control of saccades and fixation in man. *Brain* **117**, 1073–1084.
- Bashinski, H.S., and Bachrach, V.R. (1984). Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Percept. Psychophys.* **28**, 241–248.
- Bizzi, E. (1968). Discharge of frontal eye field neurons during saccadic and following eye movements in unanesthetized monkeys. *Exp. Brain Res.* **6**, 69–80.
- Boch, R.A., and Goldberg, M.E. (1989). Participation of prefrontal neurons in the preparation of visually guided eye movements in the rhesus monkey. *J. Neurophysiol.* **61**, 1064–1084.
- Bodis-Wollner, I., Bucher, S.F., Seelos, K.C., Paulus, W., Reiser, M., and Oertel, W.H. (1997). Functional MRI mapping of occipital and frontal cortical activity during voluntary and imagined saccades. *Neurology* **49**, 416–420.
- Bon, L., and Lucchetti, C. (1992). The dorsomedial frontal cortex of the macaca monkey: fixation and saccade-related activity. *Exp. Brain Res.* **89**, 571–580.
- Bon, L., and Lucchetti, C. (1997). Attention-related neurons in the supplementary eye field of the macaque monkey. *Exp. Brain Res.* **113**, 180–185.
- Bruce, C.J., and Goldberg, M.E. (1985). Primate frontal eye fields. I. Single neurons discharging before saccades. *J. Neurophysiol.* **53**, 603–635.
- Bruce, C.J., Desimone, R., and Gross, C.G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus. *J. Neurophysiol.* **46**, 369–384.
- Buchel, C., Josephs, O., Rees, G., Turner, G., Frith, C.D., and Friston, K.J. (1998). The functional anatomy of attention to visual motion. *Brain* **121**, 1281–1294.
- Bushnell, M.C., Goldberg, M.E., and Robinson, D.L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective attention. *J. Neurophysiol.* **46**, 755–772.
- Chelazzi, L., Biscaldi, M., Corbetta, M., Peru, A., G.T., and Berlucchi, G. (1995). Oculomotor activity and visual spatial attention. *Behav. Brain Res.* **71**, 81–88.
- Colby, C., Duhamel, J., and Goldberg, M. (1995). Oculocentric spatial representation in parietal cortex. *Cereb. Cortex* **5**, 470–482.
- Colby, C.L., Duhamel, J.R., and Goldberg, M.E. (1996). Visual, pre-saccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. *J. Neurophysiol.* **76**, 2841–2852.
- Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems. *Proc. Natl. Acad. Sci. USA* **95**, 831–838.
- Corbetta, M., Miezin, F.M., Shulman, G.L., and Petersen, S.E. (1993). A PET study of visuospatial attention. *J. Neurosci.* **13**, 1202–1226.
- Corbetta, M., Shulman, G.L., Miezin, F.M., and Petersen, S.E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* **270**, 802–805.
- Corbetta, M., Shulman, G.L., Conturo, T.E., Snyder, A.Z., Akbudak, E., Petersen, S.E., and Raichle, M.E. (1997). Functional magnetic resonance imaging (fMRI) of visuospatial attention: group and single subject analysis. *Neuroimage* **5** (suppl.), 85.
- Darby, D.G., Nobre, A.C., Thangaraj, V., Edelman, R., Mesulam, M.M., and Warach, S. (1996). Cortical activation of the human brain during lateral saccades using epistar functional magnetic resonance imaging. *Neuroimage* **3**, 53–62.
- DeRenzi, E. (1982). *Disorders of Space Exploration and Cognition* (New York: John Wiley and Sons).
- Downing, C.J. (1988). Expectancy and visual-spatial attention effects on vision. *J. Exp. Psychol. Hum. Percept. Perform.* **14**, 188–197.
- Drury, H.A., Van Essen, D.C., Anderson, C.H., Lee, C.W., Coogan, T.A., and Lewis, J.W. (1996). Computerized mappings of the cerebral cortex: a multiresolution flattening method and a surface-based coordinate system. *J. Cogn. Neurosci.* **8**, 1–28.
- Epstein, F.H., Mugler, J.P.I., and Brookeman, J.R. (1994). Optimization of parameter values for complex pulse sequences by simulated annealing: application to 3D MP-RAGE imaging of the brain. *Magn. Reson. Med.* **31**, 164–177.
- Eriksen, C.W., and Hoffman, J.E. (1972). Temporal and spatial characteristics of selective encoding from visual displays. *Percept. Psychophys.* **12**, 201–204.
- Fox, P.T., Fox, J.M., Raichle, M.E., and Burde, R.M. (1985). The role of cerebral cortex in the generation of voluntary saccades: a positron emission tomographic study. *J. Neurophysiol.* **54**, 348–369.
- Friston, K., Jezzard, P., and Turner, R. (1994). Analysis of functional MRI time-series. *Hum. Brain Mapping* **7**, 153–171.
- Funahashi, S., Bruce, C.J., and Goldman-Rakic, P.S. (1991). Neuronal activity related to saccadic eye movements in the monkey's dorsolateral prefrontal cortex. *J. Neurophysiol.* **65**, 1464–1483.
- Geiger, B. (1993). Three dimensional modeling of human organs and its application to diagnosis and surgical planning. Institute National de Recherche Informatique et Automatique. Technical Report 2105.
- Goldberg, M.E., and Bushnell, M.C. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *J. Neurophysiol.* **46**, 773–787.
- Hawkins, H.L., Shafto, M.G., and Richardson, K. (1988). Effects of target luminance and cue validity on the latency of visual detection. *Percept. Psychophys.* **44**, 484–492.
- Hikosaka, O., and Wurtz, R.H. (1983a). Visual and oculomotor functions of monkey substantia nigra pars reticulata. I. Relation of visual and auditory responses to saccades. *J. Neurophysiol.* **49**, 1230–1253.

- Hikosaka, O., and Wurtz, R.H. (1983b). Visual and oculomotor functions of monkey substantia nigra pars reticulata. III. Memory-contingent visual and saccadic responses. *J. Neurophysiol.* *49*, 1268–1284.
- Hikosaka, K., Iway, E., Saito, H., and Tanaka, K. (1988). Polysensory properties of neurons in the anterior bank of the caudal superior temporal sulcus of the macaque monkey. *J. Neurophysiol.* *60*, 1615–1637.
- Hikosaka, O., Sakamoto, M., and Usui, S. (1989a). Functional properties of monkey caudate neurons. I. Activities related to saccadic eye movements. *J. Neurophysiol.* *61*, 780–798.
- Hikosaka, O., Sakamoto, M., and Usui, S. (1989b). Functional properties of monkey caudate neurons. III. Activities related to expectation of target and reward. *J. Neurophysiol.* *61*, 799–913.
- Hoffman, J.E., and Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Percept. Psychophys.* *57*, 787–795.
- Hunton, D.L., Miezin, F.M., Buckner, R.L., van Mier, H.I., Raichle, M.E., and Petersen, S.E. (1996). An assessment of functional-anatomical variability in neuroimaging studies. *Hum. Brain Mapping* *4*, 122–139.
- James, W. (1890). *Principles of Psychology*, Volume 2 (New York: Henry-Holt).
- Klein, R. (1980). Does oculomotor readiness mediate cognitive control of visual attention? In *Attention and Performance VII*, R.S. Nickerson, ed. (Hillsdale, NJ: Erlbaum), pp. 259–276.
- Koch, C., and Ullman, S. (1985). Shifts in visual attention: toward the underlying circuitry. *Hum. Neurobiol.* *4*, 219–227.
- Kodaka, Y., Mikami, A., and Kubota, K. (1997). Neuronal activity in the frontal eye field of the monkey is modulated while attention is focused on to a stimulus in the peripheral visual field, irrespective of eye movement. *Neurosci. Res.* *28*, 291–298.
- Kowler, E., Anderson, E., Doshier, B., and Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Res.* *35*, 1897–1916.
- Kustov, A.A., and Robinson, D.L. (1996). Shared neural control of attentional shifts and eye movements. *Nature* *384*, 74–77.
- Lang, W., Petit, L., Hollinger, P., Pietrzyk, U., Tzourio, N., Mazoyer, B., and Berthoz, A. (1994). A positron emission tomography study of oculomotor imagery. *Neuroreport* *5*, 921–924.
- Law, I., Svarer, C., Holm, S., Paulson, O.B. (1997). The activation pattern in normal humans during suppression, imagination, and performance of saccadic eye movements. *Acta Physiol. Scand.* *161*, 419–434.
- Le, T.H., Pardo, J.V., and Hu, X. (1998). 4 T-fMRI study of nonspatial shifting of selective attention: cerebellar and parietal contributions. *J. Neurophysiol.* *79*, 1535–1548.
- Lumer, E.D., Friston, K.J., and Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science* *280*, 1930–1934.
- Luna, B., Thulborn, K.R., Strojwas, M.H., McCurtain, B.J., Berman, R.A., Genovese, C.R., and Sweeney, J.A. (1998). Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. *Cereb. Cortex* *8*, 40–47.
- Mesulam, M.M. (1981). A cortical network for directed attention and unilateral neglect. *Ann. Neurol.* *10*, 309–315.
- Mintun, M.A., Fox, P.T., and Raichle, M.E. (1989). A highly accurate method of localizing regions of neuronal activation in the human brain with positron emission tomography. *J. Cereb. Blood Flow Metab.* *9*, 96–103.
- Motter, B.C., and Mountcastle, V.B. (1981). The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: foveal sparing and opponent vector organization. *J. Neurosci.* *7*, 154–176.
- Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H., and Acuna, C. (1975). Posterior parietal association cortex of the monkey: command function for operations within extrapersonal space. *J. Neurophysiol.* *38*, 871–908.
- Muri, R.M., Iba-Zizen, T.M., Derosier, C., Cabanis, E.A., and Pierrot-Deseilligny, C. (1996). Location of the human posterior eye field with functional magnetic resonance imaging. *J. Neurol. Neurosurg. Psychiatry* *60*, 445–448.
- Nobre, A.C., Sebestyen, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiack, R.S.J., and Frith, C.D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* *120*, 515–533.
- Ollinger, J.M. (1997). Correcting for multiple comparisons in fMRI activation studies with region-size dependent thresholds. *Int. Soc. Magn. Reson. Med. Fifth Sci. Meeting* *2*, 1672.
- Olsen, C.R., Musil, S.Y., and Goldberg, M.E. (1993). Posterior cingulate cortex and visuospatial cognition: properties of single neurons in the behaving monkey. In *Neurobiology of Cingulate Cortex and Limbic Thalamus: a Comprehensive Handbook*, B.A. Vogt and M. Gabriel, eds. (Boston: Birkhauser), pp. 366–380.
- Paus, T. (1996). Location and function of the human frontal eye-field: a selective review. *Neuropsychologia* *34*, 475–483.
- Paus, T., Petrides, M., Evans, A.C., and Meyer, E. (1993). Role of the human anterior cingulate cortex in the control of oculomotor, manual, and speech responses: a positron emission tomography study. *J. Neurophysiol.* *70*, 453–469.
- Paus, T., Marrett, S., Worsley, K.J., and Evans, A.C. (1995). Extraretinal modulation of cerebral blood flow in the human visual cortex: implications for saccadic suppression. *J. Neurophysiol.* *74*, 2179–2183.
- Petersen, S.E., Robinson, D.L., and Keys, W. (1985). Pulvinar nuclei of the behaving rhesus monkey: visual responses and their modulation. *J. Neurophysiol.* *54*, 867–886.
- Petersen, S.E., Robinson, D.L., and Morris, J.D. (1987). Contributions of the pulvinar to visual spatial attention. *Neuropsychologia* *25*, 97–105.
- Petit, L., Orrsaud, C., Tzourio, N., Salamon, G., Mazoyer, B., and Berthoz, A. (1993). PET study of voluntary saccadic eye movements in humans: basal ganglia–thalamocortical system and cingulate cortex involvement. *J. Neurophysiol.* *69*, 1009–1017.
- Petit, L., Tzourio, N., Orssaud, C., Pietrzyk, U., Berthoz, A., and Mazoyer, B. (1995). Functional neuroanatomy of the human visual fixation system. *Eur. J. Neurosci.* *7*, 169–174.
- Petit, L., Orrsaud, C., Tzourio, N., Crivello, F., Berthoz, A., and Mazoyer, B. (1996). Functional anatomy of a prelearned sequence of horizontal saccades in man. *J. Neurosci.* *16*, 3714–3726.
- Petit, L., Clark, V.P., Ingeholm, J., Haxby, J.V. (1997). Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. *J. Neurophysiol.* *77*, 3386–3390.
- Pierrot-Deseilligny, C., Rivaud, S., Gaymard, B., Muri, R., and Vermersch, A.I. (1995). Cortical control of saccades. *Ann. Neurol.* *37*, 557–567.
- Posner, M.I. (1980). Orienting of attention. *Q. J. Exp. Psychol.* *32*, 3–25.
- Posner, M.I., Walker, J.A., Friedrich, F.J., and Rafal, R.D. (1984). Effects of parietal injury on covert orienting of attention. *J. Neurosci.* *4*, 1863–1874.
- Raczkowski, D., Kalat, J.W., and Nebes, R. (1974). Reliability and validity of some handedness questionnaire items. *Neuropsychologia* *12*, 43–47.
- Remington, R. (1980). Attention and saccadic eye movements. *J. Exp. Psychol. Hum. Percept. Perform.* *6*, 726–744.
- Rizzolatti, G., Riggio, L., Dascola, I., and Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* *25*, 31–40.
- Robinson, D.L., and Kertzman, C. (1995). Covert orienting of attention in macaques. III. Contributions of the superior colliculus. *J. Neurophysiol.* *74*, 713–721.
- Robinson, D.L., Goldberg, M.E., and Stanton, G.B. (1978). Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J. Neurophysiol.* *91*, 910–932.
- Robinson, D.L., Bowman, E.M., and Kertzman, C. (1995). Covert orienting of attention in macaques. II. Contributions of parietal cortex. *J. Neurophysiol.* *74*, 698–721.
- Schlag, J., and Schlag-Rey, M. (1987). Evidence for a supplementary eye field. *J. Neurophysiol.* *57*, 179–200.

- Schlag, J., Schlag-Rey, M., and Pigarev, I. (1992). Supplementary eye field: influence of eye position on neural signals of fixation. *Exp. Brain Res.* *90*, 302–306.
- Selemon, L.D., and Goldman-Rakic, P.S. (1988). Common cortical and subcortical target areas of the dorsolateral prefrontal and posterior parietal cortices in the rhesus monkey: evidence for a distributed neural network subserving spatial guided behavior. *J. Neurosci.* *8*, 4049–4068.
- Scalaidhe, S.P., Rodman, H.R., Albright, T.D., and Gross, C.G. (1997). The effects of combined superior temporal polysensory area and frontal eye field lesions on the eye movements in the monkey. *Behav. Brain Res.* *84*, 31–46.
- Shepherd, M., Findlay, J.M., and Hockey, R.J. (1986). The relationship between eye movements and spatial attention. *Q. J. Exp. Psychol.* *38*, 475–491.
- Shook, B.L., Schlag-Rey, M., and Schlag, J. (1990). Primate supplementary eye field. I. Comparative aspects of mesencephalic and pontine connections. *J. Comp. Neurol.* *301*, 618–642.
- Shulman, G.L., Fiez, J.A., Corbetta, M., Buckner, R.L., Miezin, F.M., Raichle, M.E., and Petersen, S.E. (1997). Common blood flow changes across visual tasks. II. Decreases in cerebral cortex. *J. Cogn. Neurosci.* *9*, 648–663.
- Snyder, A.Z. (1995). Difference image versus ratio image error function forms in PET–PET realignment. In *Quantification of Brain Function Using PET*, R. Myer, V.J. Cunningham, D.L. Bailey, and T. Jones, eds. (San Diego: Academic Press), pp. 131–137.
- Snyder, L.H., Batista, A.P., and Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. *Nature* *386*, 167–170.
- Steinmetz, M.A., Connor, C.E., Constantinidis, C., and McLaughlin, J.R. (1994). Covert attention suppresses neuronal responses in area 7a of the posterior parietal cortex. *J. Neurophysiol.* *72*, 1020–1023.
- Suzuki, H., and Azanuma, M. (1977). Prefrontal neuronal activity during gazing at a light spot in the monkey. *Brain Res.* *126*, 497–508.
- Sweeney, J.A., Mintum, M.A., Kwee, S., Wiseman, M.B., Brown, D.L., Rosenberg, D.R., and Carl, J.R. (1996). Positron emission tomography study of voluntary saccadic eye movement and spatial working memory. *J. Neurophysiol.* *75*, 454–468.
- Talairach, J., and Tournoux, P. (1988). *Co-Planar Stereotaxic Atlas of the Human Brain*, M. Rayport, transl. (New York: Thieme Medical Publishers).
- Teo, P.C., Sapiro, G., and Wandell, B.A. (1997). Ceating connected representations of cortical gray matter for functional MRI visualization. *IEEE Trans. Med. Imaging* *16*, 852–863.
- Tootell, R.B.H., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R., and Belliveau, J.W. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* *15*, 3215–3230.
- Treisman, A.M., and Gelade, G. (1980). A feature-integration theory of attention. *Cogn. Psychol.* *12*, 97–136.
- Ullman, S. (1996). *High Level Vision: Object Recognition and Visual Cognition* (Cambridge, MA: MIT Press).
- Vallar, G., and Perani, D. (1987). The anatomy of spatial neglect in humans. In *Neurophysiological and Neuropsychological Aspects of Spatial Neglect*, M. Jeannerod, ed. (New York: Elsevier Science Publishers), pp. 235–258.
- Van Essen, D.C., and Drury, H.A. (1997). Structural and functional analyses of human cerebral cortex using a surface-based atlas. *J. Neurosci.* *17*, 7079–7102.
- Vandenbergh, R., Dupont, P., Debruyne, B., Bormans, G., Michiels, J., Mortelmans, L., and Orban, G.A. (1996). The influence of stimulus location on the brain activation pattern in detection and orientation discrimination—a PET study of visual attention. *Brain* *119*, 1263–1276.
- Vandenbergh, R., Duncan, J., Dupont, P., Ward, R., Poline, J.-B., Bormans, G., Michiels, J., Mortelmans, L., and Orban, G.A. (1997). Attention to one or two features in left and right visual field: a positron emission tomography study. *J. Neurosci.* *17*, 3739–3750.
- Wurtz, R.H., and Goldberg, M.E. (1972). Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J. Neurophysiol.* *35*, 560–574.
- Wurtz, R.H., and Mohler, C.W. (1976a). Enhancement of visual responses in monkey striate cortex and frontal eye fields. *J. Neurophysiol.* *39*, 766–772.
- Wurtz, R.H., and Mohler, C.W. (1976b). Organization of monkey superior colliculus: enhanced visual response of superficial layer cells. *J. Neurophysiol.* *39*, 745–765.
- Yantis, S., and Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *J. Exp. Psychol. Hum. Percept. Perform.* *16*, 121–134.