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Neural mechanisms of top-down control during spatial and feature attention

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Abstract

Theories of visual selective attention posit that both spatial location and nonspatial stimulus features (e.g., color) are elementary dimensions on which top-down attentional control mechanisms can selectively influence visual processing. Neuropsychological and neuroimaging studies have demonstrated that regions of superior frontal and parietal cortex are critically involved in the control of visual–spatial attention. This frontoparietal control network has also been found to be activated when attention is oriented to nonspatial stimulus features (e.g., motion). To test the generality of the frontoparietal network in attentional control, we directly compared spatial and nonspatial attention in a cuing paradigm. Event-related fMRI methods permitted the isolation of attentional control activity during orienting to a location or to a nonspatial stimulus feature (color). Portions of the frontoparietal network were commonly activated to the spatial and nonspatial cues. However, direct statistical comparisons of cue-related activity revealed subregions of the frontoparietal network that were significantly more active during spatial than nonspatial orienting when all other stimulus, task, and attentional factors were equated. No regions of the frontal–parietal network were more active for nonspatial cues in comparison to spatial cues. These findings support models suggesting that subregions of the frontal–parietal network are highly specific for controlling spatial selective attention.

Introduction

Coherent and adaptive human behavior is critically dependent on the ability to selectively attend to different aspects of our environment. Covert visual attention to a particular spatial location or nonspatial stimulus feature (e.g., color) leads to facilitated behavioral and neuronal responses for attended stimuli (Corbetta et al., 1990; Heinze et al., 1994; Hillyard & Münte, 1984; Kingstone, 1992; Posner, 1980; Van Voorhis and Hillyard, 1977; Woldorff et al., 1997). Theories of visual selective attention posit that this enhanced cortical activity reflects the influence of top-down control mechanisms on bottom-up sensory processing structures (Corbetta and Shulman, 2002; Desimone and Duncan, 1995; Mangun, 1995; Mangun and Hillyard, 1991; Posner and Petersen, 1990).

Neuropsychological studies of patients with brain damage and neuroimaging studies of healthy human populations have implicated regions of the superior frontal cortex and the parietal cortex in the orienting of spatial attention (Corbetta et al., 1993; Gitelman et al., 1999; Mesulam, 1990; Nobre et al., 1997; Posner et al., 1984; Yantis et al., 2002). Studies using event-related functional magnetic resonance imaging (fMRI) have shown that this frontoparietal network is involved in the *top-down control* of spatial attention (Corbetta et al., 2000; Hopfinger et al., 2000b; Kastner et al., 1998). The key component of these studies is the measurement of cortical activity in response to attention-direct-

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ing cues in covert-orienting paradigms where the cues precede task-relevant targets in each experimental trial (Posner, 1980). The inferential logic of this approach is that because the cue represents the instruction to orient to a location, those areas that are selectively activated in response to the cue, prior to presentation of the target stimulus, are those areas that are involved in top-down control of attention. This approach borrows from human electrophysiological studies of attentional control that have identified a fast and dynamic pattern of frontal and parietal activity in response to spatial cues (Harter et al., 1989; Hopf and Mangun, 2000; Yamaguchi et al., 1994). Consistent with the electrophysiological studies, these recent event-related fMRI studies (i.e., Corbetta et al., 2000; Hopfinger et al., 2000b; Kastner et al., 1998) revealed attention-directing cue-related activity in superior frontal cortex, including the frontal eye field, and superior and inferior parietal cortex, including the intraparietal sulcus.

The question addressed by the present work is whether the frontoparietal network is specific to the top-down control of covert orienting to spatial locations or whether it is more general and is also involved in the control of nonspatial orienting. Several recent studies have reported results consistent with the notion that the frontoparietal network is involved in the top-down control of nonspatial attention as well as spatial attention (Shulman et al., 1999, 2002; Weissman et al., 2002). These studies used the same conceptual approach as the studies of spatial attention described above, except that instead of measuring the cortical response to cues that direct attention to *spatial* locations, the aforementioned studies measured the cortical response to cues that direct attention to *nonspatial* stimulus features. For example, Shulman et al. (1999) instructed subjects to expect a particular direction of motion and found that parietal cortex, including the intraparietal sulcus, was activated in response to the attention-directing cues. Similarly, Weissman et al. (2002) reported activations in the frontoparietal network in response to cues that instruct subjects to attend to global or to local levels of hierarchical stimuli. Interestingly, the foci of the frontoparietal activations reported in these nonspatial cueing studies were very similar to the foci of activations observed in the studies of spatial attention described above (i.e., Corbetta et al., 2000; Hopfinger et al., 2000b; Kastner et al., 1998), suggesting that the frontoparietal network represents a generalized control system for attentional orienting (see also Wojciulik and Kanwisher, 1999).

Despite the apparent similarity in activity in frontal and parietal cortex for spatial and nonspatial attentional orienting across studies, the question of whether a single attentional orienting system subserves both forms of attention remains open, because no direct comparisons of spatial and nonspatial attentional control systems have been undertaken. None of the event-related fMRI studies that have investigated top-down control activity independently from bottom-up sensory activity (Corbetta et al., 2000; Hopfinger et al., 2000b; Kastner et al., 1998; Shulman et al., 1999, 2002; Weissman et al., 2002) have included conditions that permit the direct comparison between spatial and nonspatial control systems. Indeed, to our knowledge no human neuroimaging studies have directly compared spatial and nonspatial control systems within the same experiment and subject group. Here we investigate the generality of frontal and parietal cortex in the top-down control of visual selective attention to spatial locations and to nonspatial stimulus features using direct statistical comparisons between conditions.

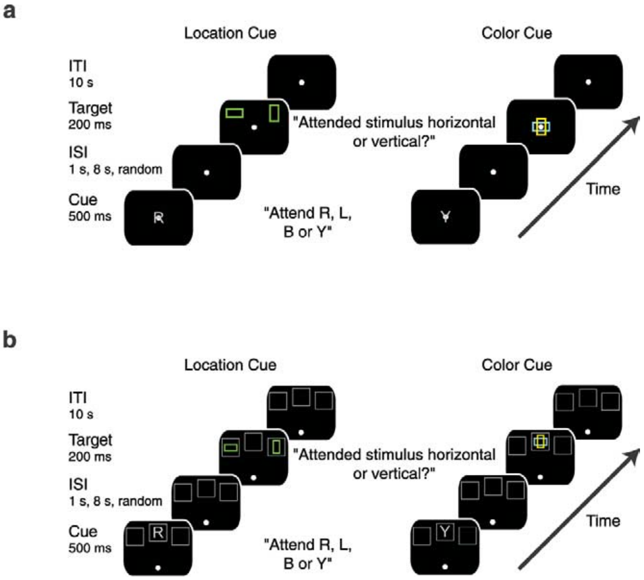


Fig. 1. Experimental task. On each trial subjects were instructed by a cue letter presented at fixation to attend to a location (right, R; left, L) or a color (blue, B; yellow, Y). After a variable interstimulus interval (ISI) of 1–8 s, a target was presented and subjects were required to indicate, with a speeded button press, the orientation of the relevant rectangle.

The present approach

To test whether the same cortical network supports top-down control of both spatial and nonspatial attention, we used event-related fMRI during a cued attention task to identify the brain systems that were engaged when attention was directed to a location versus when attention was directed to a stimulus feature. A schematic representation of the task is shown in Fig. 1. Based on instructive cues (gray letters), subjects oriented their attention covertly from trial to trial to either a spatial location or a nonspatial stimulus feature (color). In the spatial location condition, cues instructed subjects to attend to one of two relevant locations (left or right visual locations). In the nonspatial condition, cues instructed subjects to attend to one of two relevant colors (blue or yellow). After a variable interstimulus interval (ISI, 1–8 s) the target display was presented. On location-cue (i.e., spatial) trials, the display consisted of two green rectangles presented bilaterally in the upper visual field, one in each hemifield, whereas on color-cue (nonspatial) trials the display consisted of blue and yellow rectangles overlapped in the same location. The task in both conditions was to indicate the orientation (horizontal or vertical) of the rectangle of the precued dimension (i.e., left, right, blue, or yellow). Subjects performed the task well, correctly indicating the orientation of the targets on 85% of the trials (83% on location trials, 87% on color trials). The design was intended to require the subjects to use location-specific mechanisms in the spatial task and feature-specific mechanisms in the nonspatial task: That is, on spatial trials subjects were required to orient to one of two relevant locations (and not to a color) to discriminate the orientation of the rectangle at the designated location, and on nonspatial trials subjects were required to orient to one of two relevant colors to discriminate the orientation of the rectangle in the designated color, independent of spatial orienting. Thus, this paradigm matched spatial-cue and nonspatial-cue conditions for a variety of nonspecific effects (e.g., arousal, motor preparation) and cognitive operations (e.g., working memory, response selection).

The voluntary orienting task was implemented using two stimulus configurations that differed in the position of the cue and target stimuli in the display. In one configuration, referred to as the "foveal" configuration (Fig. 1a), the location cues, color cues, and the color targets were presented at fixation and the location targets were presented in the periphery (as described above). The spatial-cue condition of this configuration (i.e., foveal cues and peripheral field targets) is typical of most behavioral voluntary orienting paradigms (Posner, 1980) and, as such, provides a direct link with the existing literature. The color-cue condition (i.e., foveal cues and targets) is also like previous behavioral studies of nonspatial attention that present multiple potential target stimuli overlapped in the same location at fixation (Duncan, 1984). However, the color-cue condition is unlike previous neuroimaging studies of nonspatial attention (e.g., Fink et al., 1997; Vandenberghe et al., 2001) in that it does not require explicit invocation of spatial mechanisms to orient to the location of the cue nor to move from the location of the cue to the location of the target, and it therefore provides a relatively pure measure of nonspatial attention. Although presenting the location and color targets in peripheral and foveal positions, respectively, provides a direct link with studies of top-down control of spatial attention and provides a pure measure of nonspatial attention, there is the possibility that any observed differences between the spatial and nonspatial conditions would be due to differences in attending for peripheral and foveal events, rather than differences between spatial and nonspatial attention per se. To rule out this possibility, a second configuration, referred to as the "peripheral" configuration was employed (Fig. 1b). Here, all cues and targets were located in the periphery: the cues (location as well as color) and color targets were presented on the vertical meridian the same distance away from fixation as the location targets (which were displayed in the same lateral positions as in the foveal condition described earlier). At first glance, the peripheral configuration may appear to provide tighter control between spatial and nonspatial conditions than does the foveal condition because it removes the foveal–peripheral difference between the spatial and nonspatial trials, but it also has the limitation that it introduces the likelihood that spatial orienting mechanisms may be used in the nonspatial condition (because attention must be directed to locations away from ocular fixation). As a result, both the foveal and the peripheral conditions were necessary as complementary experimental conditions that, when considered together, control for spatial orienting during color trials, for color orienting during spatial trials, and for differences in eccentricity between conditions.

The design of the present experiment permitted the assessment of the generality and the specificity of the frontoparietal network in attentional control. Identifying the areas that respond to both the location cues and the color cues (i.e., areas of overlap) assessed the generality of the control network. Based on the prior literature in using cuing designs that separately investigate spatial and nonspatial control systems, we predicted that there would be significant overlap in the frontoparietal network across our two types of attentional cuing. Such overlap could represent a number of control operations including those that use information that is coded at a relatively abstract level (e.g., Shulman et al., 2002). In contrast, identifying the areas that differentially respond to location cues and to color cues via direct statistical contrasts assessed the specificity of the control network. This comparison would also tend to subtract away the common activity produced by generalized and nonspecific functions of the frontoparietal network in our task, revealing those areas that are specialized for the top-down control of spatial versus nonspatial (feature) attention. If the frontoparietal network is completely generalized and feature nonspecific, then no areas should show selective activation. If, however, subregions of the frontoparietal network are specialized for different types of top-down attentional control, then these areas should show selective activation during orienting to either spatial or feature cues. Here we provide evidence that although spatial and nonspatial attentional control systems rely on highly similar cortical networks involving superior frontal and parietal areas, subsets of these areas are preferentially involved in spatial orienting.

Methods

Subjects

Ten right-handed volunteers (ages 24–32 years; five women) were paid $10/hour for participating in the two-session study. Participants were informed of all the procedures and gave written consent as specified in the protocol approved by Duke University Medical Center Institutional Review Board.

Stimuli

Except as noted, the stimuli and procedure of the foveal and peripheral configurations were the same. Cues were gray uppercase letters from the English alphabet. *Foveal cues* were presented at fixation and were 0.8° × 0.6° (height × width); *peripheral cues* were presented on the vertical meridian, 5.7° above fixation, and increased in size to 1.5° × 1.1° to compensate for the lower visual acuity in the periphery. The targets were rectangles (1.75° × 1.42°) that could be horizontal or vertical in orientation. Location targets were green and were presented bilaterally in the upper left and right visual fields (5.7° from fixation). Color targets consisted of overlapping, equiluminant blue and yellow rectangles (0.88° × 0.71°). In the foveal configuration, the color targets were overlapped at fixation. In the peripheral configuration, the color targets were overlapped in the same peripheral location as the cue and were increased in size to match the peripheral location targets. All stimuli were presented on a black background.

Procedure

Each trial began with a cue (500-ms duration) that instructed subjects to covertly attend to a target location on the right or left, or to a target color blue or yellow (R, L, B, Y, respectively). The cue was followed by an ISI during which only the fixation point was displayed. The ISI was either 1000 ms (33% of trials), 8000 ms (33%), or randomized between 1900 and 7100 ms (33%). These timing parameters provided sufficient temporal jitter so that the statistical model employed for analysis could effectively deconvolve the hemodynamic responses to cues and targets. Target displays were presented for 200 ms, after which there was a 10 s fixation display before the presentation of the next cue, during which time the subjects indicated the orientation of the cued rectangle target. Both hands were used for responses (i.e., horizontal responses were made with one hand and vertical with the other) and the response-to-hand mapping was counterbalanced across subjects. Cue type was combined factorially with ISI and all trials were intermixed randomly within runs. Each of the two configuration conditions (i.e., foveal and peripheral cue configurations) consisted of nine runs of 24 trials each, presented to each subject in a random order. The order of presentation of the foveal and peripheral configurations was counterbalanced across subjects.

Subjects were instructed to maintain fixation at all times (verified by electro-oculogram; see below) and to actively use the cue information as soon as it was presented. In the peripheral configuration, subjects were instructed to maintain fixation, but attend to the upper vertical meridian for the cue. Pilot testing of the peripheral configuration indicated that it was difficult to maintain attention in the exact location of the cue, so to aid subjects the cue and target locations were indicated with gray boxes that were on the screen at all times.

Imaging methods

Functional images were acquired with a General Electric 1.5-T scanner equipped with an Advanced Development workstation for real-time echoplanar imaging. Images were acquired using a T2*-weighted gradient-echo, echoplanar imaging sequence with a repetition time (TR) of 2.0 s, echo time (TE) 40 ms, and a flip angle (FA) of 90°. Twenty-four contiguous slices were collected with a voxel size of 3.75 × 3.75 × 5.0 mm. Anatomical images were acquired using a T1-weighted sequence with a TR = 500 ms, TE = 14 ms, and FA of 90° and a voxel size of 0.94 × 0.94 × 5.0 mm.

Image processing was performed using SPM99. Functional images were corrected for differences in slice acquisition order and motion. Each subject's anatomical scan was coregistered with their functional images and then spatially normalized to stereotaxic space using the MNI template. The resulting parameters were then used to spatially normalize the functional images. The normalized functional images were spatially smoothed with an 8-mm isotropic Gaussian kernel.

Statistical analyses

The responses to the attention-directing cues were isolated by convolving a vector of onset times of the cues and targets with a synthetic hemodynamic response function that emphasized transient activity in response to the events (Friston et al., 1995, 1998; Hopfinger et al., 2000a). The general linear model was used to estimate the effects of interest and other confounding effects (e.g., session effects and estimated motion parameters) for each subject individually in each configuration; these models also used a first-order autoregressive model to estimate the temporal autocorrelations in the time series. Each individual's results were then combined across subjects (i.e., random effects). Statistical significance for the event-related responses to the cues was evaluated with a height threshold of $P < 0.005$, uncorrected. To reduce the rate of false positives, a spatial extent threshold of 10 contiguous voxels was also applied (Forman et al., 1995; Friston et al., 1994; Poline et al., 1997; Xiong et al., 1995). Areas of overlap in location- and color-cue-related activity were then identified by a conjunction analysis that multiplied the two cue-related maps (thresholded as above) within each configuration.

The direct comparison of the location and color cues was restricted to regions of interest that were defined in two steps. First, the conjunction for the foveal and peripheral configurations of the color cue-related maps was obtained, as was the conjunction for the foveal and peripheral configurations of the location cue-related maps (thresholded as above). This step was intended to remove activations that were due to sensory differences between the foveal and peripheral configurations. Second, the union of these location-cue and color-cue-related statistical conjunction maps was generated to yield regions of interest (ROIs), and the direct comparison between the cues in each configuration was then performed within these ROIs. This approach created functional ROIs that reduced the search volume while maximizing sensitivity to areas activated to one cue or the other. Because this procedure was implemented to test a priori predictions, the statistical threshold for the contrasts within the ROIs was set to $P < 0.05$ (uncorrected).

Identification of areas of visual cortex that were sensitive to the direction of attention prior to target presentation were identified by directly comparing activity in response to right cues versus activity in response to left cues. These direct contrasts were restricted to regions of visual cortex that were selectively activated to the location targets in each configuration (thresholded at the same level as the cue-related maps above). Areas were considered to be activated in these direct contrasts only if they survived a conjunction between the configurations (minimum conjoined $P < 0.05$). We adopted a conjunction approach for this contrast because the location targets were in exactly the same location and therefore the cue-specific attentional modulations should be in the same location for each configuration.

Control task

Five of the subjects that participated in the orienting task described above also participated in a control task conducted in a separate session. This control task was exactly the same as the foveal configuration, with two important exceptions. First, the cue letters were changed to "P," "T," "K," and "X" and they were randomized with respect to the subsequent target display on a trial by trial basis with the constraint that each cue letter was presented an equal number of times within each block. The randomization of the pairing between any of the cue letters and the subsequent target stimulus meant that the subjects could not predict the type of target stimulus based on the cue identity. Second, the task was to press a button with their right hand when the target display was presented, regardless of the type of target displayed. Thus, the only information provided by the cues was a temporal warning signal that a target stimulus was about to be presented and otherwise was meaningless with respect to a specific instruction to orient attention to a location or a color. As a result, the control task provided a baseline measure of the activity related to the sensory processing of the cue and to attentive fixation (because the subjects still had to maintain fixation and attend for the target) while removing activity associated with instruction to orient attention to either a spatial location or a feature. Any observed differences between the orienting task and the control task were assumed to be mainly associated with the top-down control of orienting attention to a location or a feature.

Image acquisition and spatial preprocessing for this control experiment were exactly the same as described earlier. One subject was excluded from the statistical analysis because of technical problems during image acquisition. There were two differences between the statistical analysis of the control task and the analysis of the orienting task described above. First, because the cues were randomized with respect to the particular target display, there were not location cues and color cues in the control task. However, to facilitate comparison with the orienting task, the analysis of the control task divided the cues into those that preceded color (i.e., central) targets and those that preceded location targets.

Second, because of the small number of subjects in the control task, using a typical random effects analysis, as in the analysis of the orienting task, is not appropriate because the small number of degrees of freedom (i.e., $df = N - 1 = 4 - 1 = 3$) would render the analysis relatively insensitive to all but only the strongest effects. To maximize statistical sensitivity, the data from all subjects were entered into a single, or fixed effects, statistical model using the same parameters as those described above. Areas significantly activated by the cues were identified using a multisubject conjunction analysis described by Friston and colleagues (1999) that capitalizes on the statistical sensitivity of fixed effects analyses while also being able to make inferences about the population (for a detailed description of this method please see Friston et al., 1999). Using this approach, subject-specific contrasts were generated for the location cue and for the color cue conditions. Each subjects' activation maps were thresholded liberally ($P < 0.26$, uncorrected) so that the voxels surviving the conjunction across the four subjects would have a P value similar to the random effects analysis (i.e., $P < 0.26^4 = P < 0.005$). To further reduce the likelihood of false positives and to provide a close correspondence with the analysis of the orienting task, an extent threshold of 10 contiguous voxels was also applied to the resulting location and color cue conjunction maps.

Eye movement recording

Maintenance of fixation was verified by measuring electrooculograms (EOG) recorded during the training session. Horizontal eye movements were recorded with electrodes located on the skin at the outer ocular canthus of each eye, aligned horizontally with the pupil. Vertical eye movements were recorded with electrodes placed above and below the left orbit and aligned vertically with the pupil. After the training session, each subject did a calibration task that was used to estimate the voltage fluctuation produced by voluntary eye movements of 0.5°, 1°, 1.5°, and 2°, of visual angle. The analysis of the EOG data was performed offline and included dividing the continuous data into 1000-ms epochs (including a 100-ms prestimulus baseline), baseline correction, and exclusion of trials during which artifacts, such as blinks, occurred. These artifacts were identified on the vertical EOG channel using a threshold of ±75 μV. The included trials were averaged and statistical comparisons were performed on the data recorded from the horizontal EOG channel. These comparisons involved *t* tests of the mean voltage amplitude averaged across the time window of 300–900 ms after stimulus onset. This time window was used because visual inspection of the grand-average EOG in the calibration task indicated that the voltage deflection after an eye movement reached asymptote by about 300 ms and the duration between successive eye movements was about 1000 ms.

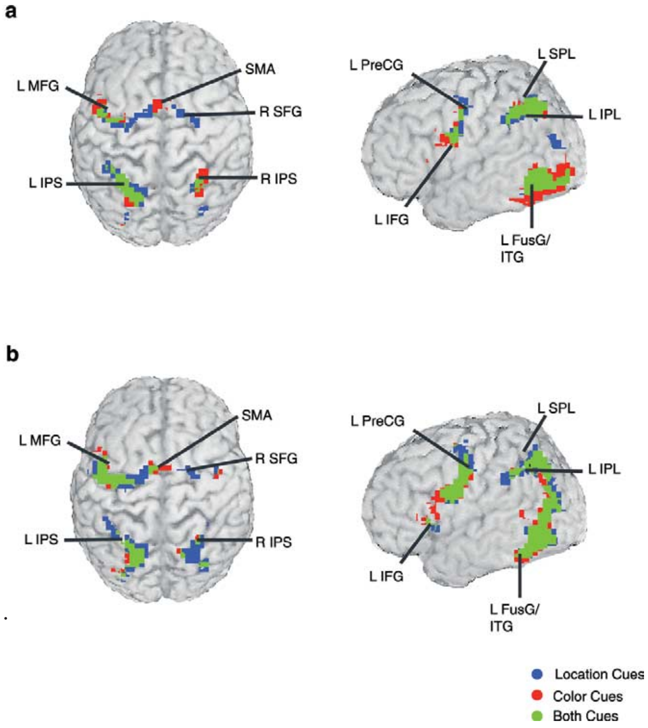


Fig. 2. Cue-related activity. Group-averaged data for brain regions significantly activated to attention-directing cues, overlaid onto a brain rendered in 3D. Areas activated in response to location cues are shown in blue, color cues are in red, and those areas activated by both cues are shown in green. Maps are displayed using a height threshold of $P < 0.005$ (uncorrected) and an extent threshold of 10 contiguous voxels. (a) Foveal configuration. (b) Peripheral configuration. Abbreviations are as in Table 1.

Results

The results of the event-related analysis of both cue-target configurations (foveal and peripheral) are shown in Fig. 2, where cortical areas that were significantly activated by location cues are shown in blue, those activated by color cues are shown in red, and those activated by both cue types are shown in green. The stereotaxic coordinates for the local maxima of the location and color cue activations are shown in Table 1 and the coordinates of frontal and parietal maxima that overlapped in the location and color cue conditions are listed in Table 2.

In general, similar networks of brain areas were activated in response to each type of cue (i.e., green areas), regardless of stimulus configuration. For location cues, activity was observed bilaterally in dorsal frontal areas (superior and middle frontal gyri, extending into the precentral gyrus) and in both superior and inferior parietal areas (including the intraparietal sulcus). The activation of this frontoparietal network in response to attention-directing cues replicated our previous work and that of others using spatial cuing paradigms (Corbetta et al., 2000; Hopfinger et al., 2000b; cf. Kastner et al., 1998) and is consistent with the notion that the frontoparietal network plays a major role in directing spatial attention (e.g., Mesulam, 1981).

As with location cues, the color cues in both configurations also activated a frontoparietal network, which largely overlapped with the location-orienting network. Additional color cue-related activity was observed in the inferior frontal gyrus/insular cortex (IFG/Ins), bilaterally. Thus, in a cuing paradigm that permitted brain activity to attention-directing cues to be distinguished from subsequent target and response processes, we observed highly similar neural networks to be engaged when attention was oriented to spatial locations and to nonspatial stimulus features. In the renderings presented in Fig. 2, however, there are some regions that appear to be specific for orienting to one dimension and not the other (i.e., red and blue areas), thus raising the question of whether there are specific spatial and feature attentional control areas.

To investigate this possibility, activity in response to location and color cues was compared directly in a separate statistical contrast (Fig. 3 and Table 3). Areas that were more active to location cues than color cues included only

Table 1
Event-related activations to location and color cues for foveal (a) and peripheral (b) stimulus configurations (local maxima).

Cue type	Region	Area	Coordinates (mm)			*T* value	*P* value
			x	*y*	*z*		
(a) Foveal stimulus configuration							
Location	Frontal	L SMA	−8	0	55	4.37	<0.001
		L PreCG	−49	−4	30	12.43	<0.05*
		R MFG	26	−8	50	4.96	<0.0005
	Parietal	L SPL	−23	−71	50	9.3	<0.00001
		L IPL	−38	−45	40	7.59	<0.00005
		R IPL	26	−56	45	5.58	<0.0005
	Occipitotemporal	L FusG	−49	−64	−10	7.61	<0.00005
		L FusG	−23	−94	−10	5.43	<0.0005
		R AngG	38	−79	30	7.38	<0.00005
		R MOG	34	−83	15	6.00	<0.0005
		R IOG	38	−86	−15	6.67	<0.00005
	Other	L Ins	−38	15	5	5.65	<0.0005
Color	Frontal	L SFG	−4	4	55	4.34	<0.001
		L PreCG	−34	−8	50	4.64	<0.001
		L MFG	−53	0	30	7.13	<0.00005
		R IFG	45	8	25	3.77	<0.005
	Parietal	L SPL	−23	−68	45	8.20	<0.00001
		R IPL	30	−56	40	11.28	<0.00001
	Occipitotemporal	L IOG	−26	−90	−5	10.17	<0.00001
		L FusG	−41	−68	−10	9.95	<0.00001
		R MOG	38	−83	−15	8.43	<0.00001
		R FusG	45	−60	−20	11.82	<0.00001
	Other	L Ins	−34	19	10	5.58	<0.0005
		L PHG	−19	−38	−5	3.89	<0.005
(b) Peripheral stimulus configuration							
Location	Frontal	L SMA	−11	0	55	5.02	<0.0005
		L MFG	−26	−11	50	6.25	<0.0001
		L PreCG	−45	−8	35	9.48	<0.00001
		L IFG	−49	4	30	9.05	<0.00001
		R MFG	45	0	45	4.61	<0.001
	Parietal	L SPL	−23	−68	45	7.86	<0.00005
		R PreCun	26	−64	35	7.65	<0.00005
	Occipitotemporal	L FusG	−41	−68	−15	11.76	<0.05*
		R MOG	34	−83	15	9.30	<0.00001
		R STG	49	−56	10	4.58	<0.001
	Other	L Ins	−34	15	5	5.89	<0.0005
		R Ins	34	23	5	4.90	<0.0005
Color	Frontal	L PreCG	−8	0	55	4.95	<0.0005
		R IFG	45	−4	45	4.69	<0.001
		L SMA	−41	−8	40	11.94	<0.05*
		L PreCG	−45	4	30	5.84	<0.0005
	Parietal	R PreCun	15	−68	50	4.42	<0.001
		R SPL	26	−56	45	5.03	<0.0005
	Occipitotemporal	R STG	49	−49	15	8.00	<0.00005
		R MTG	53	−64	5	6.40	<0.00005
		L FusG	−53	−64	−10	9.96	<0.00001
		R FusG	41	−56	−20	5.04	<0.0005
		L FusG	−41	−53	−25	11.32	<0.00001
	Other	L Ins	−38	15	10	6.33	<0.0001

Note. Abbreviations: L, left; R, right; AngG, angular gyrus; FusG, fusiform gyrus; IFG, inferior frontal gyrus; IOG, inferior occipital gyrus; IPL, inferior parietal lobe; ITG, inferior temporal gyrus; Ins, insula; LingG, lingual gyrus; SMA, medial frontal gyrus; MFG, middle frontal gyrus; MOG, middle occipital gyrus; MTG, middle temporal gyrus; PHG, parahippocampal gyrus; PreCG, precentral gyrus; PreCun, precuneus; SFG, superior frontal gyrus; SOG, superior occipital gyrus; SPL, superior parietal lobe; STG, superior temporal gyrus; SPL, superior parietal lobule; Coordinates: *x,* left/right; *y,* posterior/anterior; *z,* inferior/superior in the reference frame of the MNI brain in SPM99.

* Significant when corrected for multiple comparisons ($P < 0.05$).

dorsal cortical regions (Figs. 3a and c): left superior and middle frontal gyri (SFG/MFG) along the superior frontal sulcus extending to the intersection with the precentral sulcus, left superior parietal lobe (SPL), and the right inferior parietal lobe (IPL). Areas that were more active to color cues than location cues, on the other hand, were mainly ventral cortical areas (Figs. 3b and d): more specifically, greater activity for color cues was observed in fusiform gyrus (FusG), bilaterally, extending anteriorly and laterally into portions of inferior temporal gyrus (ITG).

Although these patterns of selectivity were virtually identical in both configuration conditions, there were two minor variations to this pattern in the peripheral configuration. First, the superior frontal and parietal areas appeared to be slightly less location selective in the peripheral configuration. Additional analyses suggest that this result was due to greater activity in these areas in response to color cues in this configuration, in line with the idea that spatial attention was also engaged when the color targets were presented in the periphery, a predicted consequence of the peripheral cue configuration that necessitated the inclusion of the foveal condition in the original design. Second, the ventral color selective areas in the peripheral configuration were more anterior and lateral than in the corresponding activations in the foveal configuration. This shift in color-selective activation is consistent with other studies that suggest that the peripheral color representation is located in more anterior portions of the fusiform gyrus (Zeki and Bartels, 1999). These minor variations notwithstanding, the strikingly similar patterns of selectivity in the different configurations (foveal vs. peripheral) suggest that the differential activations for spatial and nonspatial attentional orienting are due to differences in spatial and nonspatial attention mechanisms per se and are not due to differences between attending to foveal versus peripheral events. Thus, this direct statistical comparison revealed areas that were more active to one type of cue than the other, while subtracting away any regions that were activated in common by the two types of attention-directing cues.

The selective activation of fusiform gyrus to color cues observed here is consistent with previous studies of nonspatial attention that show increased activity in feature selective areas of visual cortex prior to the presentation of the attended target (Chawla et al., 1999). However, several studies of spatial attention have also reported location-specific modulations of pretarget activity in visual cortex (Kastner et al., 1999; Ress et al., 2000), including increased activity in retinotopically organized extrastriate areas contralateral to the direction of attention indicated by spatial cues (Hopfinger et al., 2000b). These spatially specific modulations are thought to reflect the influence of frontal and parietal top-down control systems on visual processing (Desimone and Duncan, 1995; Giesbrecht and Mangun, 2002; Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000; Posner and Petersen, 1990). If the selective activation of superior parietal and frontal areas in response to location cues observed here represents the operation of attentional control systems preferential to spatial attention, then one might predict that spatially specific modulations of activity should be apparent in response to the cue and before the target. To assess whether spatially specific influences in response to attention-directing cues on visual cortex activity were also present in our paradigm, we directly compared extrastriate cortical activity in response to right cues versus activity in response to left cues. The results of this direct comparison are shown in Fig. 4. Activity in the medial lingual gyrus and portions of fusiform gyrus was sensitive to the direction of attention, such that the left visual cortex was more active in response to right cues relative to left cues, whereas the right visual cortex was more active in response to left cues relative to right cues. Thus, consistent with previous studies (Hopfinger et al., 2000b; Kastner et al., 1999; Ress et al., 2000) demonstrating that spatial attention can modulate activity in visual cortex in a spatially specific manner prior to the presentation of an expected, behaviorally relevant target, likely reflecting the influence of top-down control systems on sensory processing structures.

Table 2
Coordinates of local maxima in frontal and parietal cortex that survived the conjunction of location and color cues for each configuration

Configuration	Region	Area	Coordinates (mm)		
			x	*y*	*z*
Foveal	Frontal	L PreCG	−49	−4	30
		L MFG	−30	−11	45
		L SMA	−8	0	55
		L IFG	−30	26	−5
	Parietal	R SPL	30	−56	45
		L SPL	−30	−56	45
		L IPL	−38	−45	40
Peripheral	Frontal	L SMA	−11	0	55
		L MFG	−34	−8	50
		L PreCG	−45	−8	40
		L IFG	−49	4	30
		R MFG	45	0	45
	Parietal	L PreCun	−8	−56	45
		R SPL	26	−56	45

Note. Abbreviations are as in Table 1.

Control task

Fig. 5 shows those areas that were activated in response to the cues in the control task. As described under Methods, for purposes of comparison with the results of the orienting task (e.g., Fig. 2), the trials were divided into two groups

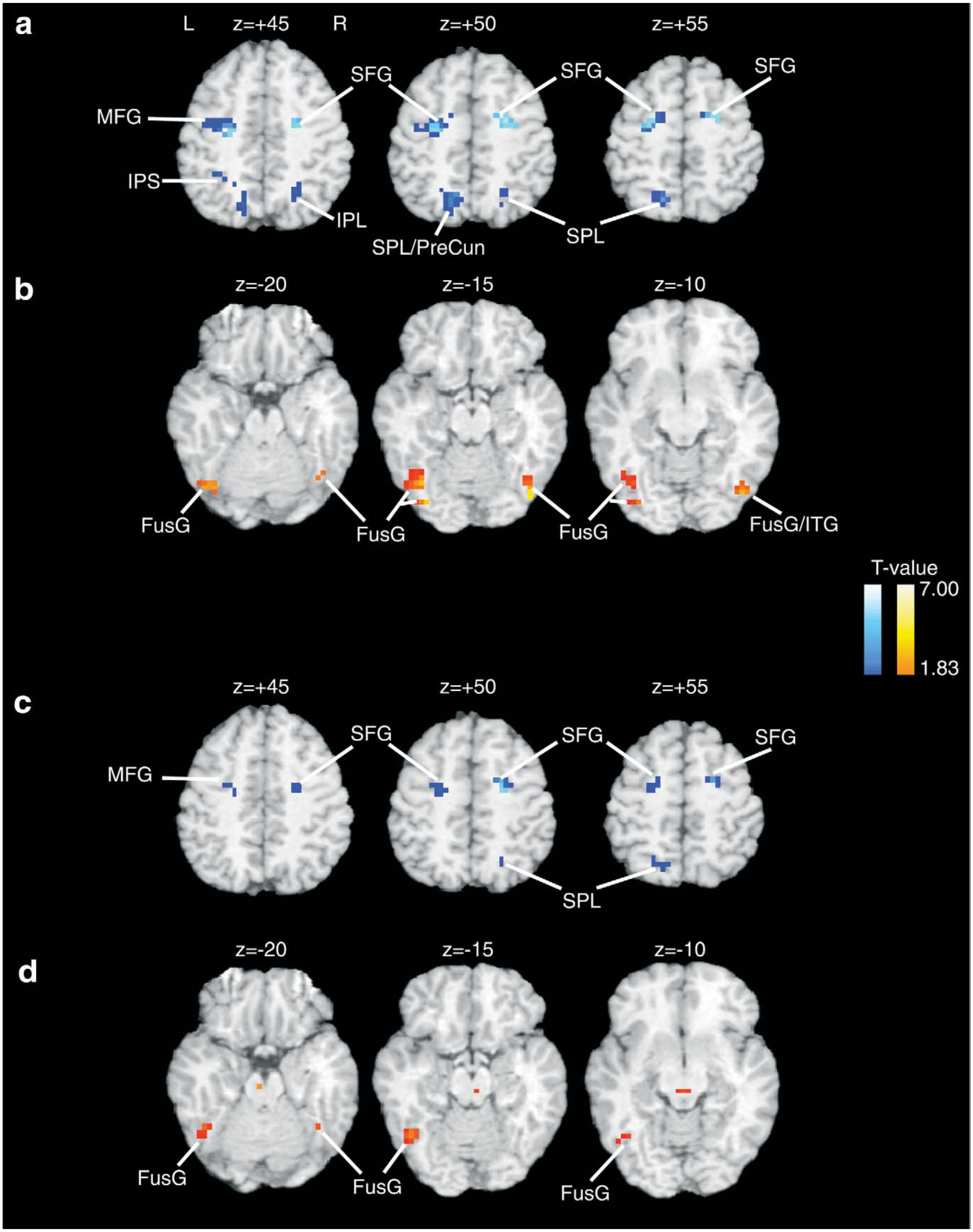
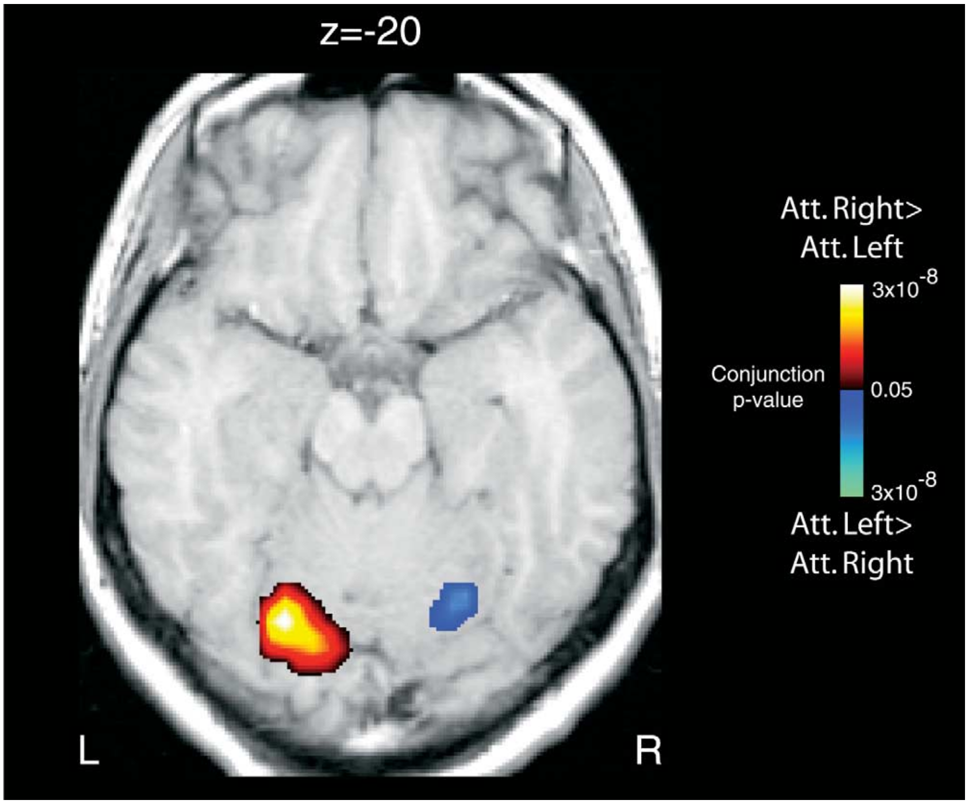


Fig. 3. Feature-specific activity. (a) Group-average data for brain regions more active to location cues than color cues in the foveal configuration overlaid onto key slices of a single subject's anatomical image cutting through superior cortex (z = 45, 50, and 55 mm). (b) Brain regions more active to color cues than location cues in the foveal configuration overlaid onto representative slices of ventral cortex ($z = -20, -15, -10$ mm). (c) Brain regions more active to location cues than color cues in the peripheral configuration overlaid onto the same slices as used in (a). (d) Brain regions more active to color cues than location cues in the peripheral configuration overlaid onto the same slices as used in (b). Maps for these a priori comparisons are displayed at $P < 0.05$ (uncorrected). Abbreviations are as in Table 1.



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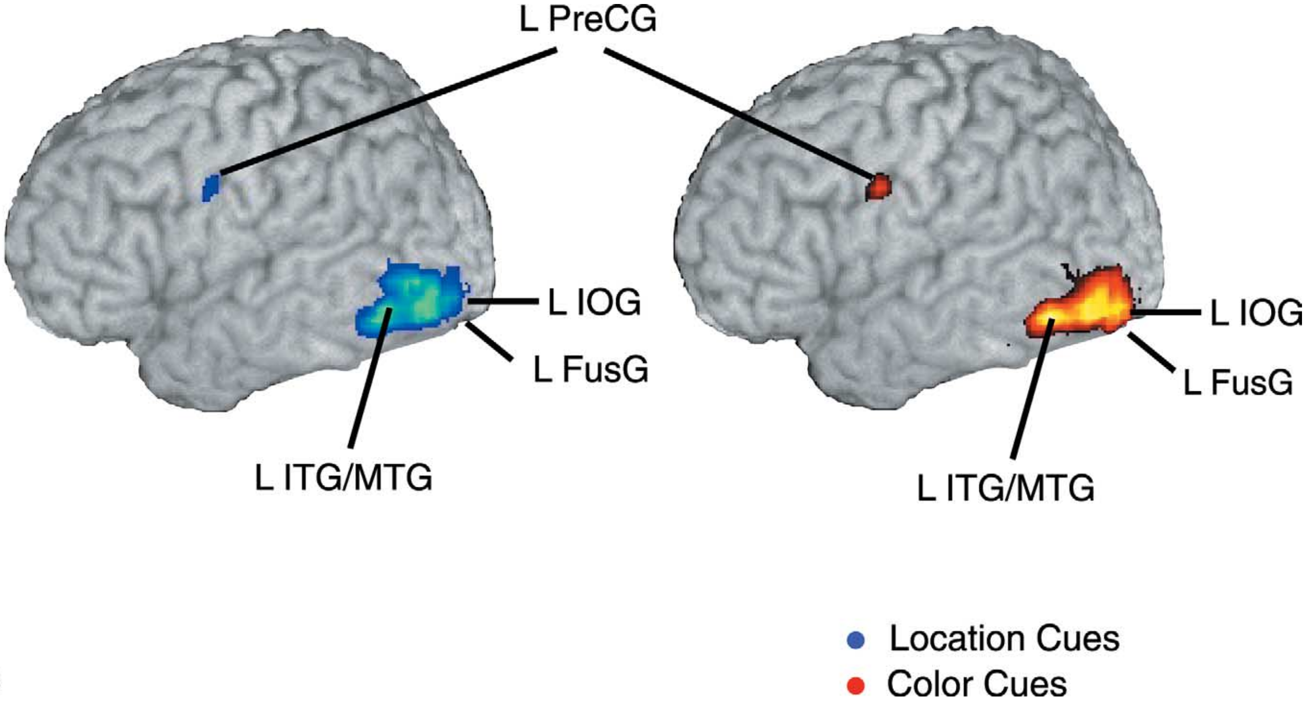

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Fig. 4. Lateralized cue-related attentional modulations. Group-average data for brain regions more active to right cues versus left cues (red) and left cues versus right cues (blue) overlaid onto a single slice of a single subject's anatomical image cutting through ventral visual cortex ($z = -20$ mm). Those areas activated are those that survived the conjunction of the direct comparisons between the two location cue conditions across the foveal and peripheral configurations (thresholded with a conjoined $P < 0.05$). Coordinates of local maxima (*x y z* mm): right cue > left cue, −23 −71 −20; left cue > right cue, 26 −64 −20.

Fig. 5. Cue-related activity in control task. Group-averaged data for brain regions significantly activated to meaningless cue letters overlaid onto a brain rendered in 3D. Those areas activated are those that survived the conjunction across subjects ($P < 0.26$, uncorrected for each subject = conjoined $P < 0.005$, extent threshold of 10 contiguous voxels). Areas activated in response to letters that preceded location targets are shown in blue on the left; those areas activated in response to letters that preceded color targets in red on the right. Local maxima for each condition (area, *x y z* (mm), minimum T value across subjects) are as follows: location: L IOG, −41 −79 −10, T=4.69; R IOG, 30 −90 −15, $T = 3.85$; L FusG, −38 −49 −30, $T = 2.05$; R FusG, 45 −56 −25, $T = 2.41$; L MOG, −45 −79 0, $T = 4.63$; R MOG, 49 −79 −10, $T = 4.50$; L MTG, −41 −64 −10, $T = 4.88$; R ITG, 45 −60 −10, $T = 2.37$; L PreCG, −45 0 30, $T = 2.58$. Color: L IOG, −45 −79 −10, $T = 4.79$; R IOG, 30 −90 −15, $T = 3.99$; L FusG, −41 −49 −25, $T = 2.02$; R FusG, 45 −60 −25, $T = 2.56$; L MOG, −41 −68 0, $T = 1.9$; R MOG, 45 −79 −15, $T = 3.02$; L PreCG, −41 −4 35, $T = 2.93$. Abbreviations are as in Table 1.

based on whether the target that followed the cue was a location target or a color target. Note that the cues themselves provided no information regarding the type of target. Because of the high degree of overlap between the conditions, the activations shown in Fig. 5 are presented on separate renderings, with those areas activated in response to the cues on location-target trials shown on the left in blue and those activated in response to the cues on color-target trials shown on the right in red. The critical result in this analysis is that the main areas of activation in both conditions were visual cortex, including FusG and IOG, extending into ITG and MTG. Although only the left hemisphere activations are shown in Fig. 5, the effects in visual cortex were symmetrical. The only other area activated by the cues in the control task was PreCG of the left hemisphere. No other areas of the frontoparietal network were activated in response to the noninstructive cues. These results provide further support that the frontoparietal network is involved in the control of orienting visual attention and is not simply passively responding to the cue stimulus.

Eye movements

The results of the eye movement recordings during the training of the experimental task and the eye movement calibration task are illustrated in Fig. 6. Shown in Fig. 6a is the grand average horizontal EOG time-locked to the onset of left and right location cues. Shown in Fig. 6b is the grand average horizontal EOG time-locked to the onset of blue and yellow color cues. Overlaid in each panel are the results of the calibration task. Each trace represents the voltage deflection that corresponds to eye movements ranging from 0.5° of visual angle to 2.0°. Negative deflections represent leftward eye movements and positive deflections represent rightward movements. The statistical analysis of these data revealed no differences in mean amplitude between left and right cues ($t(9) = 0.74$, $P < 0.48$) or between blue and yellow cues ($t(9) = 0.42$, $P < 0.67$). Comparison between location and color cues did not reveal differences in mean amplitude between the attention conditions ($t(9) = 0.14$, $P < 0.89$). Finally, and perhaps most critically, the mean amplitudes in the location and color conditions were not significantly different from 0 (location, $t(9) = 0.03$, $P < 0.98$; color, $t(9) = -0.11$, $P < 0.91$), but were both significantly smaller than the mean amplitude evoked in response to the smallest instructed eye movement of 0.5° executed during the calibration task (0.5° movement vs. location, $t(9) = 8.12$, $P < 0.0001$; 0.5° movement vs. color, $t(9) = 7.71$, $P < 0.0001$). Thus, these results demonstrate that during training, which preceded the scanning sessions, subjects did not move their eyes in response to the attention-directing cues.

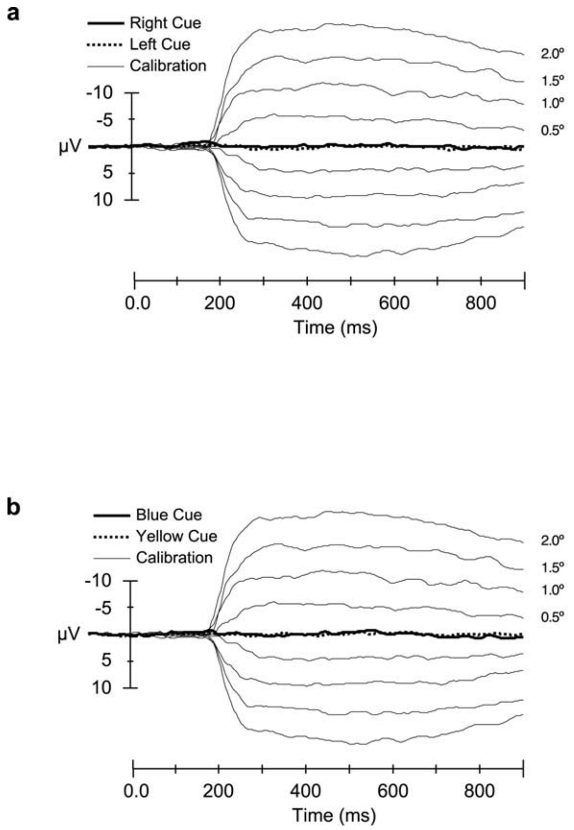

Fig. 6. Eye movement recordings. (a) Grand average horizontal electrooculogram (HEOG) in response to left and right location cues displayed with the results of the calibration task. (b) Same as (a), except for blue and yellow color cues. Each trace of the calibration task corresponds to a 0.5° step in visual angle. Positive deflections are rightward movements; negative deflections are leftward movements.

Discussion

The present study investigated the neural correlates of spatial and nonspatial attentional control using event-related fMRI in a cuing paradigm that identified the cortical areas activated when attention was precued to either the location or the color of an upcoming target stimulus. We found that both location and color cuing led to increased activity in superior frontal and posterior parietal cortex. In direct statistical comparisons of these effects, we observed that spatial attention induced greater activity in circumscribed subregions within superior frontal and superior parietal cortex than did feature attention. The observed overlap and selectivity will be discussed with respect to two critical aspects of the top-down control of selective visual attention: (1) the generality of frontal and parietal areas in attentional control and (2) the specificity of the frontoparietal network in top-down control.

Table 3
Statistical contrasts between location and color cues for foveal (a) and peripheral (b) stimulus configurations (local maxima)

Cue contrast	Region	Area	Coordinates (mm)			*T* value	*P* value
			x	*y*	*z*		
(a) Foveal stimulus configuration							
Location > color	Frontal	L MFG	−26	−4	55	5.11	<0.0005
		R SFG	23	0	50	6.27	<0.0001
		L SFG	−30	−11	45	6.99	<0.05*
		L PreCG	−45	−4	40	4.06	<0.005
	Parietal	L SPL	−15	−64	55	3.75	<0.005
		L SPL	−34	−45	45	3.08	<0.01
		R IPL	23	−56	45	2.95	<0.01
	Occipital	R SOG	34	−79	25	4.96	<0.0005
Color > location	Occipitotemporal	R ITG	49	−71	−5	3.22	<0.01
		L MOG	−34	−83	−15	3.40	<0.005
		L FusG	−38	−68	−15	3.22	<0.01
		R MOG	45	−79	−15	4.26	<0.005
		R FusG	41	−64	−20	2.6	<0.05
	Other	L Ins	−34	26	0	2.07	<0.05
(b) Peripheral stimulus configuration							
Location > color	Frontal	L SFG	−23	−8	50	3.06	<0.01
		R SFG	23	−8	50	4.72	<0.001
	Parietal	L SPL	−15	−64	55	2.50	<0.05
		R PreCun	23	−60	50	1.99	<0.05
		R IPL	38	−79	35	2.96	<0.01
Color > location	Occipitotemporal	L MTG	−45	−64	0	2.37	<0.05
		L FusG	−45	−60	−15	2.53	<0.05
	Other	L Ins	−34	4	25	2.84	<0.01
		L Ins	−38	11	5	2.52	<0.05

Note. Abbreviations are as in Table 1.
* Significant when corrected for multiple comparisons ($P < 0.05$).

Overlap in the frontoparietal network

Within the context of the present study, the overlap in activity produced by location and color attention-directing cues likely reflects the neural systems engaged in common mental operations. In both location and color cue trials, subjects were presented with a cue letter that was followed by a variable ISI and then a target that required discrimination and response. These trials were designed so that sensory processing, extraction of a linguistic code from the cue letter, mapping of that code to the relevant task instruction (i.e., attend to location or color), executing the task instruction (i.e., orient attention selectively to location or color), maintaining that information during the ISI, and preparing to respond were the same for both location and color cue trials. Therefore, at one level of interpretation, the overlap in the frontoparietal network reflects these common operations. For example, areas of left lateral frontal cortex, especially inferior frontal gyrus, are often activated in verbal encoding tasks (Awh et al., 1996; Buckner and Koustaal, 1998; Heun et al., 1999; Kelley et al., 1998; for reviews see, Cabeza and Nyberg, 1997, 2000; Fletcher and Henson, 2001), as well as in attention tasks that use words or letters as cues (Shulman et al., 2002; Weissman et al., 2002; Woldorff et al., 2001). It is noteworthy that activation is not typically seen in left inferior frontal gyrus in experiments that use nonlinguistic stimuli (e.g., arrows) as attention-directing cues (Corbetta et al., 2000; Hopfinger et al., 2000b; Shulman et al., 1999). Thus the overlap in this area observed in the present study likely reflects the encoding of the linguistic information contained in the spatial and nonspatial cue letters. In contrast, areas of parietal cortex have been observed to be activated in a variety of attention and working memory tasks (Awh and Jonides, 2001; Awh et al., 1999; Gitelman et al., 1999, 2000; Jonides et al., 1998; LaBar, 1999; Le et al., 1998; Nobre et al., 1997; Vandenberghe et al., 2001; Wojciulik and Kanwisher, 1999), suggesting that the overlap in parietal cortex we observed may reflect the coding and maintenance of the task relevant dimension (Kanwisher and Wojciulik, 2000). Similarly, the overlap in PreCG likely reflects the preparation for a motor response. Consistent with this interpretation, left PreCG was the only nonvisual area to be activated by both cues in the control task during which responses were prepared and executed with the right hand, but attention was not directed to a particular location or feature. Thus, the significant overlap of activity in response to attention directing cues in the frontoparietal network suggests that much of this control network is not specific to the orienting of spatial attention, but rather consists of a more general executive control network that is activated in the service of spatial and nonspatial attention.

The hypothesis that portions of the frontoparietal network generalize over multiple dimensions was recently proposed by Shulman and colleagues (2002). These authors report that posterior inferior frontal cortex and portions of parietal cortex, particularly in the left intraparietal sulcus, were similarly engaged by word cues instructing subjects to attend to the direction of motion or color of a subsequent target stimulus. Shulman et al. (2002) argued that the areas of cortex that were recruited similarly by their color and motion cues perform the functions of coding and maintaining the relevant information in a sufficiently abstract from so that it can be used regardless of the nature of the behaviorally relevant dimension. Here we show that this generalization within the frontoparietal network not only holds across different nonspatial features, such as motion and color, but also holds across spatial and nonspatial feature dimensions.

Some prior neuroimaging studies investigating selective attention have also observed overlapping patterns of brain activity during spatial and nonspatial attention tasks (Fink et al., 1997; Vandenberghe et al., 2001; Wojciulik and Kanwisher, 1999). Critically, however, unlike the present experiment, such studies were not designed in a manner that enabled separation of attentional control activity from subsequent target processing operations, and therefore could not directly test whether spatial and nonspatial attention shared common neural control systems. Of those prior studies that could extract activity in response to attention-directing cues from activity related to target processing (Corbetta et al., 2000; Hopfinger et al., 2000b; Kastner et al., 1998; Shulman et al., 1999), none were designed to directly compare spatial and nonspatial attention in a design where all other stimulus, task, and response requirements were equivalent. Nonetheless, consideration of the patterns of activity in frontal and parietal cortex across different published studies is in line with our current finding that spatial and nonspatial attentional control mechanisms activate largely overlapping regions of cortex.

Specificity in the frontoparietal network

Whereas the overlap in activation in response to the attention-directing cues reflects generalized operations, we propose that regions showing selectivity in response to location or color cues reflect specialized top-down control systems. In the direct statistical contrast of location and color cue-related activity, we found that dorsal areas of the frontoparietal network were clearly more active when orienting attention to locations than colors. The organization of these spatial attention selective activations, namely the greater activity in superior frontal and parietal cortex, parallels classic findings in the neuropsychological literature demonstrating that patients suffering from damage to either or both of these areas have severe difficulties in orienting attention in space (Mesulam, 1981, 1990; Posner et al., 1984; cf. Karnath et al., 2001) and is also consistent with prior functional imaging studies implicating a role for these areas in the control of covert orienting to spatial locations (e.g., Corbetta et al., 1993, 2000; Gitelman et al., 1999, 2000; Hopfinger et al., 2000b; Kastner et al., 1998; Nobre et al., 1997; Yantis et al., 2002). Moreover, the increased activity in retinotopically organized visual areas contralateral to the attended location indicated by the spatial cues, and prior to the targets, is in line with previous studies that suggest that the frontoparietal network can modulate cortical activity in a spatially specific manner prior to the presentation of a behaviorally relevant stimulus (Hopfinger et al., 2000b; Kastner et al., 1999; Ress et al., 2000). What our direct comparison between location and color cues suggests, however, is that subregions of the frontoparietal network are not merely involved in top-down control of attention in a generalized manner, but that they are *preferential,* and perhaps specific to, the control of covert orienting to spatial locations.

One plausible hypothesis for the existence of these spatially selective areas of the frontoparietal network is that these subregions (i.e., superior parietal and superior frontal areas) are recruited because they map spatial coordinates for covert and overt orienting. Evidence for the coding of spatial information in frontal and parietal cortex comes from monkey single unit recording studies and from human neuroimaging studies demonstrating a strong relationship between the oculomotor and attention systems. In monkey cortex, a number of studies have shown that neurons in the lateral intraparietal area (LIP) and the frontal eye field (FEF) are sensitive to the specific location to which an eye movement is to be executed, before the movement is made (Bruce and Goldberg, 1985; Duhamel et al., 1992; Schall & Hanes, 1993; Schall et al., 1995). Critically, the activity of neurons in these areas is not predicated on the execution of eye movements. For instance, LIP neurons respond when a location within their receptive field is attended, but no eye movement is made (Bushnell et al., 1981) or even when an eyemovement is planned for a location that is not within the attended receptive field (Bisley and Goldberg, 2003). Similarly, microstimulation of the FEF that is below the threshold that would evoke an eye movement is nevertheless associated with enhanced behavioral performance for targets presented in the receptive field of the neuron (Moore and Fallah, 2001) and can also modulate activity in extrastriate neurons representing the same location (Moore and Armstrong, 2002).

In line with the monkey neurophysiological results described above, meta-analyses of human neuroimaging studies have shown that there is a high degree of overlap in reported activations under conditions of covert orienting of attention and overt orienting of the eyes, particularly in superior frontal and parietal cortex, suggesting a tight coupling of the oculomotor and spatial attention systems in these areas (Cabeza and Nyberg, 2000; Corbetta, 1998; see also Paus, 1996). Moreover, the results of recent human transcranial magnetic stimulation studies suggest a functional link between the parietal lobe and the frontal eye fields in covert orienting of visual attention in space (Grosbras and Paus, 2002; Hilgetag et al., 2001). Thus it appears likely that the pattern of selective activations in response to location cues observed here reflects the recruitment of regions of superior frontal and parietal cortex that are specialized in the control of covert orienting to spatial locations because they are able to code behaviorally relevant locations in the visual field.

The activation of frontal and parietal areas that are known to be closely linked with the oculomotor system raises the alternative hypothesis that the selective activations to location cues observed here are not due to specialized attentional operations, but rather are due to overt eye movements. There are three notable reasons to believe that eye movements were not responsible for the observed pattern of activations. First, during training and before the scanning sessions, eye movements were recorded. The analysis of these data revealed that none of the subjects moved their eyes in response to the cues (Fig. 6). It is worth emphasizing that these recordings were done before the scanning session, while the subjects were getting used to the task. As a result, it seems reasonable that if subjects did not move their eyes when they were *inexperienced* with the task, that they did not move their eyes when were *experienced* with the task—i.e., during scanning. Second, studies have shown that when ocular position was measured during scanning the exact same portions of the frontal eye fields and superior parietal areas are active in spatial attention tasks regardless of whether subjects moved their eyes or not (Gitelman et al., 1999, 2000). Finally, stimulation of these areas with transcranial magnetic stimulation modulates behavioral indices of spatial attention in the absence of eye movements (Grosbras and Paus, 2002; Hilgetag et al., 2001). Therefore, it is our contention that the selective activations in the frontoparietal network in the location-cue condition observed here were not due to overt eye movements, but rather reflects a specialization for these areas in the top-down control of covert spatial orienting.

Although we did not observe *selective* activations in the frontoparietal network in response to color cues, we did observe nonspatial selectivity in ventral extrastriate and posterior inferior temporal areas in response to the cues and prior to the targets. Could this reflect activity in specialized nonspatial attentional control structures in ventral posterior cortex? Our study cannot definitively resolve this question, but we believe that the answer is "no." Rather, we interpret this pattern of selectivity in response to the color cues in visual cortex as reflecting the enhancement of color-specific areas in preparation for the target display (e.g. Chawla et al., 1999), rather than reflecting color-specific top-down control operations. This interpretation is based in part on the sensitivity of the selective activations to the retinotopic location of the cue (compare Figs. 4b and d). Indeed, this sensitivity to the location of the cue is more consistent with what is known about attentional enahancements that have been observed in retinotopic and feature selective areas rather than with what is known about the locus of attentional control mechanisms (Anllo-Vento et al., 1998; Chawla et al., 1999; Clark et al., 1997; Corbetta et al., 1990; Heinze et al., 1994; Mangun, 1995; Martínez et al., 1999; Saenz et al., 2002; Woldorff et al., 1997; Yantis et al., 2002). In addition, the areas that were selectively activated to the color cues were also those areas that were activated by sensory processing of the cue letters as indicated by the pattern of activation in response to the meaningless cues in the control task. Moreover, none of the empirical studies reviewed here implicate a role for visual areas in attentional control, whether subjects are cued to a location or a feature (e.g., Corbetta et al., 2000; Hopfinger et al., 2000b; Shulman et al., 1999, 2002; Weissman et al., 2002). Finally, to our knowledge, there is no published model of attentional control that implicates feature selective areas of visual cortex as being a specific *source* of top-down signals. Thus, while there is the possibility that there are, as yet unknown, control operations subserved by feature specific areas of visual cortex, the pattern of selective activation in response to nonspatial cues observed here is, on the whole, more likely to reflect the attentional priming of visual cortex—i.e., the *consequences* of attention—rather than top-down control mechanisms themselves.

Conclusion

A central issue in the study of visual attention revolves around the nature of top-down control mechanisms. Here we investigated one component of this issue, namely whether top-down control systems operate by generalizing across spatial and nonspatial dimensions or by recruiting specialized systems. When considered together, the patterns of overlapping cue-related activity and the selectivity observed here are consistent with models that posit that top-down control of orienting is subserved by a brain network that is responsible for generalized functions such as cue symbol interpretation and maintenance of the task relevant representations (Corbetta and Shulman, 2002; Kanwisher and Wojciulik, 2000; Shulman et al., 2002; Wojciulik and

Kanwisher, 1999; Woldorff et al., 2001). Our results show that in addition to performing these generalized operations, this network may also recruit specialized systems necessary for orienting visual attention in space (Corbetta and Shulman, 2002; Posner and Petersen, 1990). The critical question for future investigations is to identify how these generalized and specific components of top-down control interact to support orienting to, and selection of, behaviorally relevant stimuli that are not defined by independent sources of information, but rather are defined by the more realistic conjunction of information across spatial and nonspatial domains.

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