

Spatially Selective Representations of Voluntary and Stimulus-Driven Attentional Priority in Human Occipital, Parietal, and Frontal Cortex

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When multiple objects are present in a visual scene, they compete for cortical processing in the visual system; selective attention biases this competition so that representations of behaviorally relevant objects enter awareness and irrelevant objects do not. Deployments of selective attention can be voluntary (e.g., shift or attention to a target's expected spatial location) or stimulus driven (e.g., capture of attention by a target-defining feature such as color). Here we use functional magnetic resonance imaging to show that both of these factors induce spatially selective attentional modulations within regions of human occipital, parietal, and frontal cortex. In addition, the voluntary attentional modulations are temporally sustained, indicating that activity in these regions dynamically tracks the locus of attention. These data show that a convolution of factors, including prior knowledge of location and target-defining features, determines the relative competitive advantage of visual stimuli within multiple stages of the visual system.

Keywords: fMRI, salience map, stimulus driven, visual attention, voluntary

Introduction

Visual awareness is limited to only a small subset of the available objects in a scene. This limitation is thought to be in part a consequence of the visual system's hierarchical organization. Neurons in early visual areas such as the lateral geniculate nucleus (LGN) and V1 have small spatial receptive fields (RFs) and are tuned to basic low-level features (e.g., edge orientation). Visual neurons in successively later stages of occipital, parietal, and frontal cortex tend to have RFs of increasing size that code for more abstract stimulus properties such as object identity and behavioral relevance (Bichot and others 1996; Logothetis and Sheinberg 1996; Rainer and others 1998; Schall and Thompson 1999; Bisley and Goldberg 2003). Because multiple objects often fall within the RF of a single neuron in later stages of the visual system, competition arises among stimuli to drive the response of that neuron. Selective attention biases the competition in favor of behaviorally relevant or highly salient stimuli (Desimone and Duncan 1995; Reynolds and others 1999). On this account, the role of attention is to coordinate activity between neurons in early visual areas, which provide high acuity information about basic features, and those in later visual areas, which rely on this input to selectively represent the properties of the currently attended stimulus (Desimone and Duncan 1995; Serences and Yantis 2006). Visual perception thus depends not only on raw sensory signals from the retina but also on modulatory attention signals that act upon multiple levels of the visual hierarchy to bias perceptual representations according to the behavioral relevance of locations, features, and objects in the scene.

Most psychological models assert that the locus of attention is influenced by either "voluntary" or "stimulus-driven" attentional control factors (Koch and Ullman 1985; Wolfe 1994; Yantis 2000). Purely voluntary attention shifts are based on prior knowledge about a task-relevant location (for example), whereas purely stimulus-driven attention shifts are evoked by the appearance of a physically salient stimulus—here defined as a stimulus with high local feature contrast (Yantis and Jonides 1984; Parkhurst and others 2002). Often, however, the locus of attention is determined by both factors. For example, if an observer is searching for a red object in the left visual field, other red items—including ones in the right visual field—will tend to attract attention as well (Treue and Martinez Trujillo 1999; Saenz and others 2002; Melcher and others 2005; Serences, Shomstein, and others 2005). Although this type of contingent attentional orienting is partially based on voluntary attentional control settings (e.g., search for red), it is also stimulus driven because it is dependent upon the presence of a stimulus in the scene that expresses the searched-for target feature (Folk and others 1992, 2002). Voluntary and stimulus-driven factors jointly specify relative attentional priority, which reflects the salience and the task relevance of each object in the scene. Visual search is thought to be guided by a representation of attentional priority (Koch and Ullman 1985; Wolfe 1994).

Single-cell neurophysiology in nonhuman primates has revealed that neural activity within topographically organized regions of visual cortex indexes the attentional priority of objects in the scene. For instance, neural activity in occipital cortex (e.g., V4v) and parietal cortex (the lateral intraparietal area [LIP]) reflects the current locus of attention following voluntary attention shifts and stimulus-driven attentional capture (Gottlieb and others 1998; Bisley and Goldberg 2003; Mazer and Gallant 2003; Reynolds and Desimone 2003). Similarly, the activity of spatially selective neurons in the frontal eye field (FEF) is modulated by the presentation of salient high-contrast stimuli and by stimuli that express target-defining features (Thompson and others 1997, 2005; Bichot and Schall 1999, 2002; Sato and others 2003; Thompson and Bichot 2005). Thus, neural activity in multiple cortical areas satisfies the 2 key criteria for the representation of attentional priority: spatial selectivity and sensitivity to both voluntary and stimulus-driven aspects of orienting. Furthermore, neurons in LIP and FEF project directly to motor control regions such as the superior colliculus, and are thus able to directly influence spatially targeted eye movements toward high-priority visual objects (Asanuma and others 1985; Stanton and others 1988, 1995; Fecteau and others 2004).

Although functional magnetic resonance imaging (fMRI) in humans has revealed topographically targeted attentional

modulations in occipital cortex (Gandhi and others 1999; Kastner and others 1998; Tootell and others 1998; Brefczynski and DeYoe 1999), substantially less is known about the representation of attentional priority in the human parietal and frontal cortex. Sereno and others (2001) used a delayed saccade (and memory) task to show that human intraparietal sulcus contains a topographic map of the contralateral visual hemifield. Silver and others (2005) extended this result by showing that 2 subcompartments of the intraparietal sulcus (IPS), (which they called IPS1 and IPS2) index the current locus of spatial attention following voluntary deployments to cued locations. On the other hand, although activity in the human FEF is consistently found to be modulated by eye-movement and attentional manipulations, the degree of spatial selectivity in human FEF is less well established. Some studies indicate a heightened response to contralateral stimuli or contralateral eye movements (Corbetta and others 2002; Ro and others 2002; Connolly and others 2004), whereas others fail to report signs of spatial specificity (although such effects may have been observed but not reported; Corbetta and others 2000; Corbetta and others 2005; Hopfinger and others 2000; Giesbrecht and others 2003; Kincaid and others 2005). In the most direct study to date, Hagler and Sereno (2006) demonstrated spatially selective responses in frontal cortex using a working memory task. However, no studies to our knowledge have demonstrated modulations in the human parietal or frontal cortex that reflect a spatially selective integration of both voluntary and stimulus-driven attentional control factors.

In the present study, we used fMRI to identify regions of occipital, parietal, and frontal cortex that responded more strongly following voluntary deployments of attention to the contralateral visual field (compared with the ipsilateral visual field). Within these same cortical regions of interest (ROIs), we also observed increased activity following a stimulus-driven attention shift to the contralateral hemifield. We conclude that the joint influence of voluntary and stimulus-driven attention on neural activity within spatially selective visual areas in occipital, parietal, and frontal cortex gives rise to a distributed representation of attentional priority that integrates prior knowledge about target location with information about the presence of behaviorally relevant objects in the visual scene.

Methods

Participants

Ten neurologically intact adults (4 females), aged 19–32, gave written informed consent to participate in the study, which was approved by the Johns Hopkins University institutional review boards. Each subject participated in two 2-h scanning sessions that took place on separate days. Subjects were compensated at a rate of \$25.00/h for time spent in the scanner.

Attention Task

The behavioral task is depicted in Figure 1*a*. Three rapid serial visual presentation (RSVP) streams consisting of multicolored letters (each letter subtending 1.5° visual angle vertically) were presented on each side of fixation (falling on an imaginary circle with 10.5° radius). The 2 streams directly left and right of fixation (on the horizontal midline) contained occasional cues and targets. White numeral cues instructed subjects to shift attention voluntarily between the left and right cue/target streams. Thus, if subjects were currently attending to the left stream, they could receive a cue instructing them either to continue attending to the left stream (a “hold” cue) or to shift attention to the right stream (a “shift” cue). For six of the subjects, a 3 instructed them to attend left and a 7 instructed them to attend right; this mapping was

reversed for the remaining subjects. The locus of attention at the start of each run was cued by verbal instruction.

The subject’s task was to monitor the currently attended stream for a target letter that was defined by color (red for half the subjects, green for the rest). Subjects were to press a button held in their left hand if the target letter was in the first half of the alphabet and a button held in their right hand if the target letter was in the second half of the alphabet. On approximately two-thirds of the target appearances, red or green distractors were presented in either the middle letter stream or in all 3 streams that were contralateral to the currently attended target location. Although behavioral pilot studies suggested that the presentation of 3 distractors magnified contingent attentional capture effects, no effect of distractor number was observed on either the behavioral or the blood oxygen level-dependent (BOLD) data during the experiment carried out in the scanner. Thus, we collapsed across the 1- and 3-distractor conditions for the sake of simplicity.

If a subject was searching for a red target, then red letters in the ignored hemifield would constitute a “target-colored” distractor and green letters in the ignored hemifield would constitute a “nontarget-colored” distractor. On approximately one-third of the trials, the target was presented without an accompanying distractor (the “target-alone” condition, in which the target was flanked by a randomly chosen colored distractor that was neither red nor green). Subjects were instructed to continuously maintain fixation on a small central fixation point (subtending 0.3° degrees of visual angle). Trials on which the subject failed to make a behavioral response to a target were discarded (8% of the trials in target-alone condition, 4% in the nontarget-colored distractor condition, and 3% in the target-colored distractor condition). We speculate that because of the fast presentation rate of the stimuli (100 ms/item), subjects omitted responses more frequently on target-alone trials because there were fewer visual cues in the display indicating the presence of a target (i.e., there was no distractor to serve as an additional cue that a response was required).

Each run in the scanner included 80 events (i.e., presentations of cues, targets alone, or targets accompanied by distractors). Half of these events consisted of numerical attention cues, and the rest were target-alone or target/distractor events. Cue, target-alone, and target/distractor events were randomly interleaved and temporally jittered by 2500–5500 ms in 1000-ms intervals (evenly distributed).

In all 6-letter streams, all characters simultaneously changed identity every 100 ms (no gap). Each run in the scanner lasted for 334 s and included 40 cue presentations and 40 target presentations. Target letters presented in the attended letter stream were exposed for 1 RSVP frame (100 ms); distractors in the unattended stream consisted of 4 sequentially presented letters (each with a unique identity) that were all rendered in either the target color (a target-colored distractor) or the nontarget color (a nontarget-colored distractor), starting 200 ms before the onset of a target in the attended stream. This distractor-to-target temporal lag has previously been shown to maximize capture by target-colored distractors (Folk and others 2002). The numerical attention cues were also presented for 4 frames in the currently attended location (and the identity of the cue remained constant across all 4 frames).

Retinotopic Mapping

Retinotopic mapping data were obtained in 2–4 runs per subject using a rotating (36 s/cycle) contrast reversing checkerboard stimulus (flickering at 8 Hz and subtending 60° of polar angle, see Sereno and others 1994; Slotnick and Yantis 2003). Cross-correlation analysis was used to delineate occipital visual areas V1v, V2v, V3v, and V4v in each hemisphere of each subject based on the relative phase of the BOLD response in each voxel. In several subjects, the boundaries between V2d, V3d, and V3a could not be resolved, so data are not reported from these dorsal occipital visual areas.

fMRI Data Acquisition and Analysis

Magnetic resonance imaging (MRI) scanning was carried out on a Philips Intera 3T scanner in the F.M. Kirby Research Center for Functional Brain Imaging at the Kennedy Krieger Institute in Baltimore, MD. Anatomical images were acquired with a SENSE (MRI Devices, Inc., Waukesha, WI) parallel-imaging head coil using an magnetisation prepared rapid gradient echo (MP-RAGE) T_1 -weighted sequence that yielded images

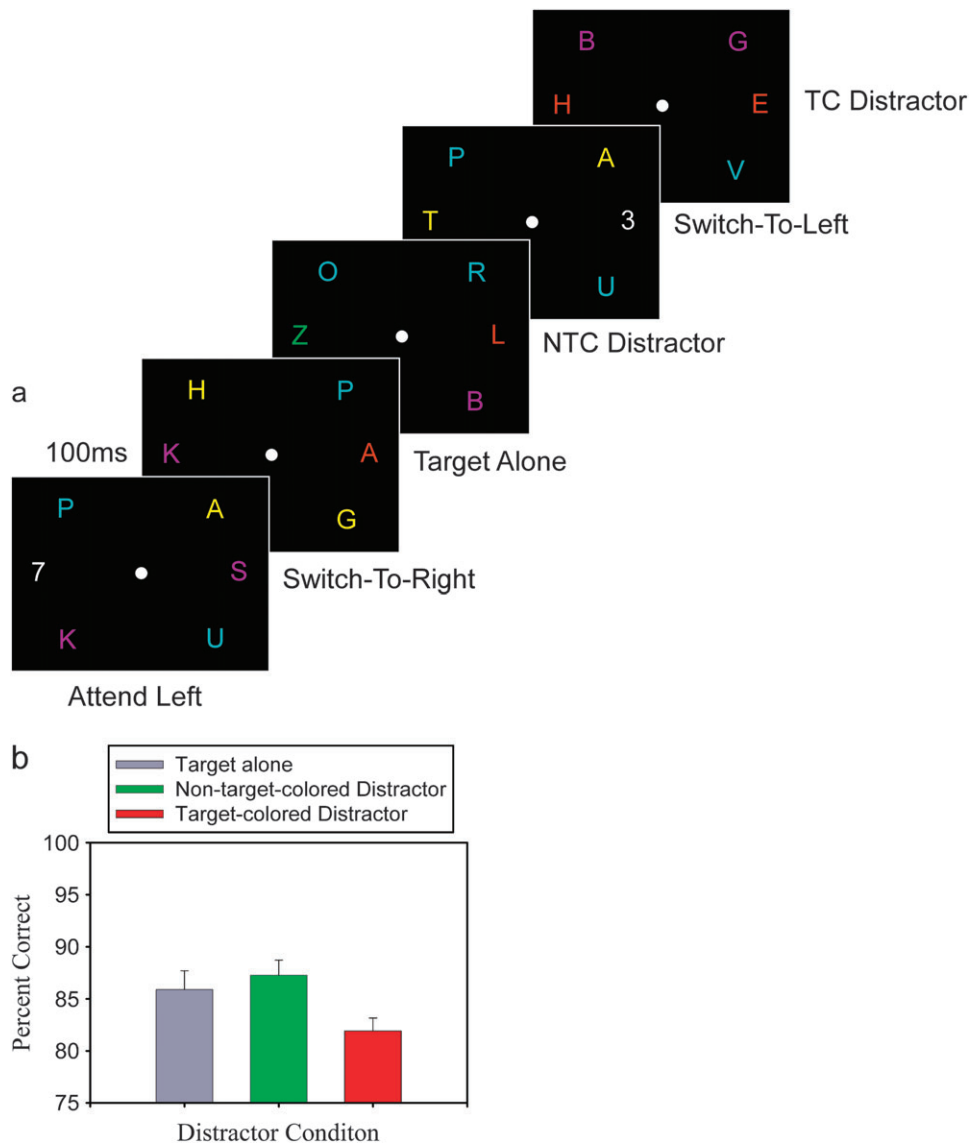


Figure 1. (a) The behavioral paradigm used in the scanner (see text for details, in this sequence, subjects are searching for a red letter in the currently attended location). The stimuli were arrayed around an imaginary circle with a radius subtending 10.5° of visual angle to improve the likelihood of observing spatially lateralized modulations in IPS and FEF, where neurons are thought to have large spatial RFs that often overlap the vertical meridian. (b) Target detection accuracy when the target was accompanied by a commonly presented color, a nontarget-colored distractor, or a target-colored distractor (only targets for which subjects made a response are considered, see Methods). Accuracy was selectively impaired when a target-colored distractor was presented, reflecting the capture of attention away from the target location. Error bars reflect group standard error of mean.

with a 1-mm isovoxel resolution (time repetition [TR] = 8.1 ms, echo time [TE] = 3.7 ms, flip angle = 8° , time between inversions = 3 s, inversion time = 748 ms). Whole-brain echo planar functional images (EPIs) were acquired in 35 transverse slices (TR = 2000 ms, TE = 30 ms, flip angle = 70° , image matrix = 64×64 , field of view = 192 mm, slice thickness = 3 mm, 1-mm gap, SENSE factor = 2). To aid in the visualization of early cortical visual areas revealed by the retinotopic mapping procedures, we projected fMRI data from occipital cortical areas onto a segmented and inflated representation of each subject's gray matter/white matter boundary.

BrainVoyager QX (v 1.6; Brain Innovation, Maastricht, The Netherlands), along with custom time series analysis software written in Matlab (v 7.1; The Math Works, Natick, MA), was used for data analysis. Data from each subject were collected in 17–19 runs across the 2 scanning sessions. All EPI time series data were slice-time corrected, motion corrected (both within and between runs), filtered with a 3-cycle/run high-pass temporal filter, and spatially smoothed (Gaussian smoothing kernel, 4.0 mm full width half maximum) before transformation into the atlas space of Talairach and Tournoux (1988).

ROI Definitions

ROIs were defined separately for each subject in occipital cortex, IPS, and FEF by comparing the magnitude of the BOLD response during epochs of contralateral attention with epochs of ipsilateral attention while subjects performed the behavioral task depicted in Figure 1a (Table 1). To identify these ROIs, a general linear model was applied to the BOLD time series with one regressor specified for temporal epochs of attention on the left and another regressor marking epochs of attention on the right. The boxcar regressors were then convolved with a gamma function ($\delta = 2.5$ s, $\tau = 1.25$ s; Boynton and others 1996), and a linear contrast was used to identify ROIs responding more strongly during contralateral compared with ipsilateral epochs of attention. All voxels within each ROI passed a minimum threshold of $P < 0.05$, corrected for multiple comparisons using the false discovery rate computation implemented in BrainVoyager. Using this procedure, we identified bilateral IPS and FEF ROIs in 9 of 10 subjects; in the remaining subject, only the left IPS and FEF were defined (see Table 1). ROIs in occipital cortex were defined as the intersection of each visual area

Table 1

Coordinates and volume of cortical ROIs identified in each subject based on voxels exhibiting a stronger response during epochs of attention to the contralateral visual field compared with the ipsilateral visual field

Subject	Right IPS	Left IPS	Right FEF	Left FEF
KB	26, -59, 42 (2.56 ml)	-25, -56, 39 (8.27 ml)	31, -4, 42 (1.89 ml)	-39, -3, 40 (3.88 ml)
CC	— ^a	-27, -63, 48 (2.32 ml)	— ^a	-36, -5, 37 (0.24 ml)
ME	25, -55, 45 (0.89 ml)	-20, -56, 44 (1.24 ml)	31, -6, 42 (0.43 ml)	-36, 3, 24 (0.24 ml)
TJ	27, -47, 41 (0.73 ml)	-26, -54, 42 (2.21 ml)	34, -2.2, 37 (1.0 ml)	-36, -6, 42 (0.35 ml)
WJ	26, -67, 44 (5.27 ml)	-24, -52, 39 (9.96 ml)	32, -5, 31 (1.26 ml)	-39, 5, 37 (6.19 ml)
HL	25, -42, 43 (3.75 ml)	-24, -45, 44 (3.02 ml)	31, -1, 34 (4.46 ml)	-36, 2, 37 (2.0 ml)
OM	19, -57, 46 (0.71 ml)	-20, -61, 36 (7.29 ml)	40, -9, 41 (0.73 ml)	-36, -10, 46 (5.48 ml)
YN	25, -46, 42 (1.65 ml)	-23, -65, 42 (6.76 ml)	30, -7, 46 (1.49 ml)	-37, 8, 32 (4.77 ml)
SR	28, -52, 48 (7.4 ml)	-26, -49, 44 (9.29 ml)	35, 2, 37 (3.62 ml)	-39, 3, 37 (10.27 ml)
MT	27, -56, 49 (4.67 ml)	-36, -47, 44 (9.67 ml)	43, -10, 49 (0.97 ml)	-40, -3, 40 (6.78 ml)
Mean	25, -53, 44 (3.07 ml)	-25, -55, 42 (6 ml)	34, -5, 40 (1.76 ml)	-37, -1, 37 (4.02 ml)
Standard deviation	3, 8, 3 (2.36)	5, 7, 3 (3.45)	5, 4, 6 (1.37)	2, 6, 6 (3.34)

Note: All left hemisphere ROIs responded more strongly when attention was directed to the right visual field; the reverse was true for all right hemisphere ROIs. Coordinates based on the atlas of Talairach and Tournoux (1988).

^aIndicates that no ROI could be identified.

(V1-V4v) and the regions found to show a heightened response during epochs of contralateral attention.

The mean coordinates of the FEF ROIs defined in the present study are slightly lateral and inferior to the coordinates reported in previous studies that identified FEF using saccadic tasks as functional localizers (mean x, y, z : 34, -5, 40 and -37, -1, 37 for right and left FEF in the present study compared with a mean of 26, -7, 48 and -29, -8, 47 reported in 4 recent studies [Paus 1996; Connolly and others 2000, 2002, 2004]). The reason for this apparent discrepancy is not clear. It may reflect normal variability in the locus of FEF across subjects, or there may be functional subdivisions of FEF that are relatively more sensitive to saccade preparation versus changes in the current locus of attention. In the present report, we refer to these frontal cortex activations as FEF. The mean coordinates of the IPS ROIs reported in the present study correspond well to previous reports; they are slightly medial to the regions reported by Sereno and others (2001) and slightly anterior to the regions reported by Silver and others (2005).

To estimate the magnitude of the event-related BOLD response within the spatially lateralized ROIs defined for each subject, we first normalized the time series from each run by converting the data to a measure of percent signal change by dividing the signal magnitude at each time point by the mean value of that run, subtracting 1, and then multiplying by 100. The event-related BOLD responses to each event type were then averaged within a temporal window extending from 0–24 s after event onset. Using this approach, the “0” point on the y axis of the event-related average plots represents the mean signal across all runs (see data plots in Figs 2–4); positive and negative deviations from 0 should therefore be interpreted as relative increases or decreases compared with the mean signal intensity. The event-related responses were then collapsed across left and right cortical ROIs (when bilateral ROIs were available; otherwise, only the unilaterally defined ROI was used for that subject, see Table 1) and then averaged across subjects to obtain an estimate of the group response. The magnitude of the peak event-related BOLD response in the group was used to quantitatively assess differences between the evoked responses to different event types.

Eye Tracking

Eye position was monitored in 6 of the 10 subjects during scanning using a custom-built MRI-compatible video camera that provided input to viewpoint eyetracker software (Arrington Research, Inc., Scottsdale, AZ). We first computed the mean gaze position during epochs of attention to the left and right sides of space; no differences were found (Supplementary Table 1). We also computed the mean gaze position during the 500 ms following target-colored and nontarget-colored distractors, reasoning that attention-capturing target-colored distractors might induce eye movements. No differences in gaze position were observed (Supplementary Table 1). Finally, note that if reflexive saccades made toward target-colored distractors were responsible for driving the differential BOLD responses, then the BOLD responses evoked by the targets should have been affected as well. This pattern

was not observed, which, in conjunction with the eye tracking results, strongly argues against a role for systematic eye movements in biasing the reported data.

Results

Behavioral Data

The behavioral task is depicted in Figure 1*a*. Corroborating previous results (Folk and others 2002; Serences, Shomstein, and others 2005), target discrimination accuracy was lower when the target was accompanied by a target-colored distractor compared to when it was accompanied by a nontarget-colored distractor or when it was presented alone (Fig. 1*b*; 1-way repeated measures analysis of variance [ANOVA], $F_{2,18} = 8.6$, $P < 0.005$, $\eta^2 = 0.491$). The discrimination deficit reflects the capture of attention away from the currently attended location by a target-colored distractor, which partially matches the subjects' attentional control settings (Folk and others 1992, 2002). In addition, target discrimination accuracy was well below ceiling in all conditions, confirming that the task was attentionally demanding.

Defining Cortical ROIs

In the visual system, incoming sensory information from the left visual hemifield projects primarily to the right cortical hemisphere, and sensory information from the right hemifield projects primarily to the left hemisphere. Based on this anatomical organization, we identified ROIs (Table 1) separately for each subject in occipital, parietal, and frontal cortex that exhibited a heightened response during temporal epochs of focused attention in the contralateral visual field (see Methods). RFs of neurons in IPS and FEF are generally thought to be larger than those in early occipital visual areas (e.g., V1), so the stimuli were placed relatively far in the periphery (10.5°) in an attempt to minimize their projection to neurons with RFs overlapping the vertical meridian. This choice was inspired in part by a previous observation that regions of IPS and FEF show relatively small spatial laterality effects when stimuli are placed closer to the fovea (e.g., Serences, Shomstein, and others 2005).

Voluntary Attentional Deployments

Figure 2*a–c* depicts the group mean event-related time course in the V4v, IPS, and FEF ROIs following cues instructing

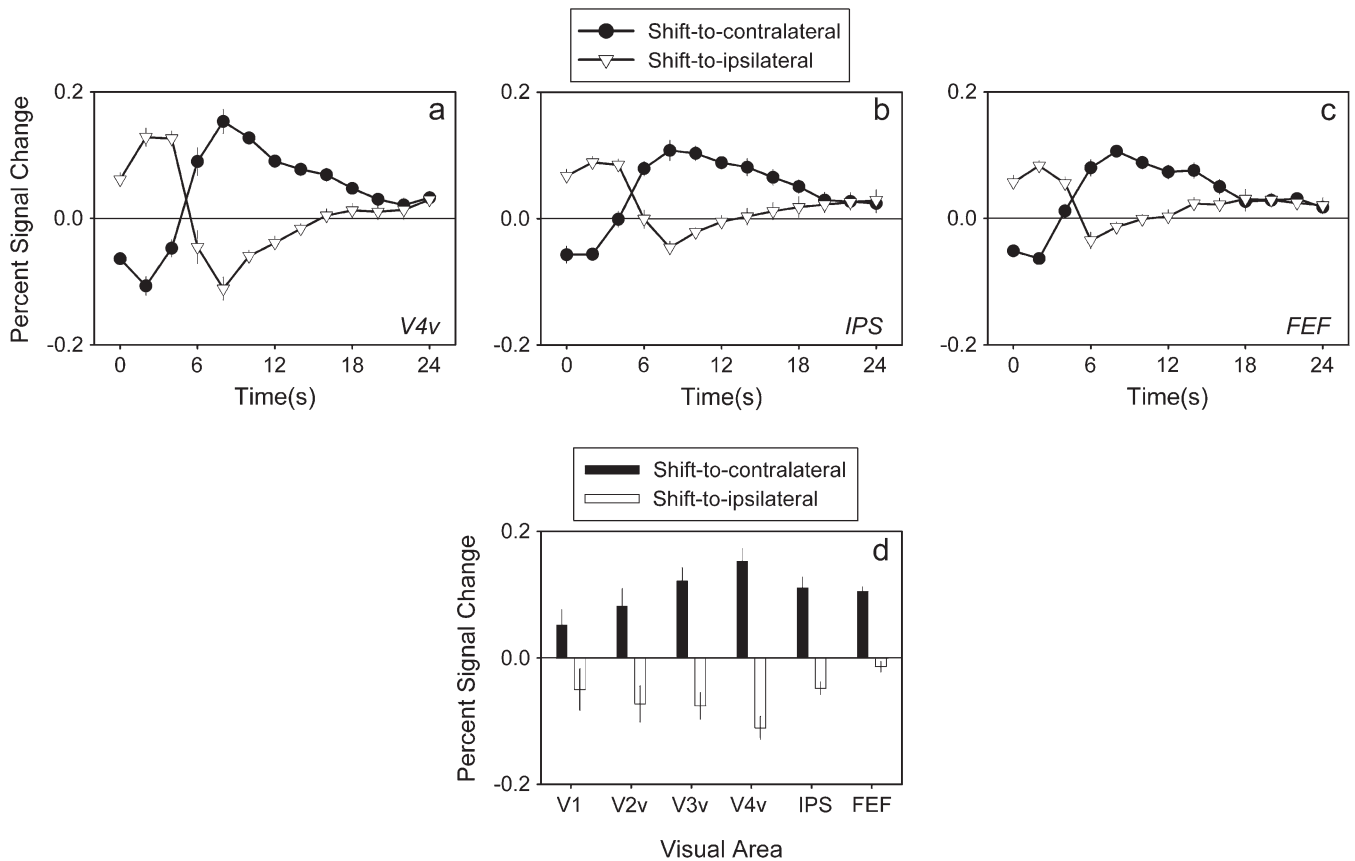


Figure 2. (a–c) Mean group event-related time courses depicting the magnitude of the BOLD response in V4v, IPS, and FEF following cues to shift attention to the contralateral hemifield (filled circles) and following cues to shift attention to the ipsilateral hemifield (open triangles) during the main attention task depicted in Figure 1a. (d) Mean peak group BOLD response (8 s poststimulus) across all measured visual areas. Error bars reflect ± 1 standard error of mean.

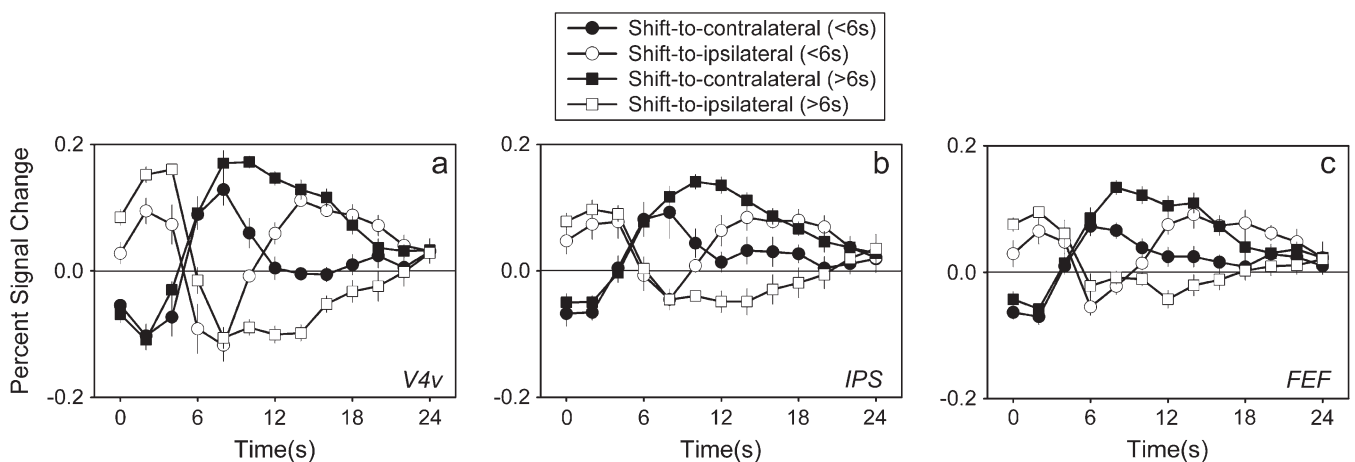


Figure 3. (a–c) Mean group event-related time courses from V4v, IPS, and FEF depicting the BOLD response following cues to shift attention between the left and right target streams. Same data that are depicted in Figure 2, but the event-related averages were generated by binning the evoked responses based on the amount of time spent attending to either the contralateral or ipsilateral hemifield following each attention cue (either less than 6 s, circles, or longer than 6 s, squares). Error bars reflect ± 1 standard error of mean.

observers to voluntarily shift attention from the ipsilateral to the contralateral side of space or vice versa. As expected, based on the definition of the ROIs, all regions exhibited a similar response profile: the BOLD signal started low and increased following a voluntary shift of attention from the (nonpreferred) ipsilateral hemifield to the (preferred) contralateral hemifield

(filled circles) and the inverse pattern was observed when subjects shifted from the contralateral hemifield to the ipsilateral hemifield (open triangles). Figure 2d shows the mean peak BOLD response (8 s postcue) from all ROIs. A 2-way repeated measures ANOVA (locus of attention \times visual area) confirmed the heightened BOLD response when attention was directed to

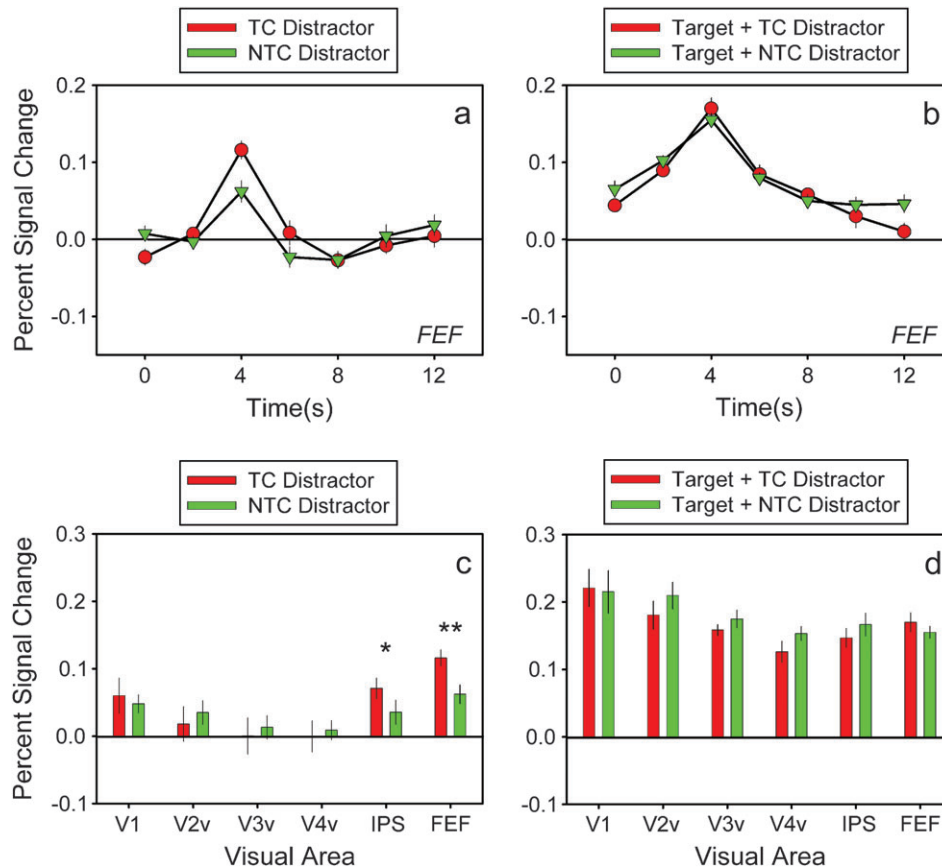


Figure 4. (a) Mean group event-related time courses depicting the BOLD response in FEF evoked by contralateral target-colored (red circles) and nontarget-colored (green triangles) distractors. (b) Mean event-related time courses depicting the BOLD response in FEF evoked by contralateral targets when they were accompanied by either target-colored distractors (red circles) or nontarget-colored distractors (green triangles) on the opposite side of the display. (c, d) Group mean peak responses (4 s poststimulus) from each visual area (* $P < 0.05$, ** $P < 0.01$). Error bars reflect ± 1 standard error of mean.

the contralateral versus the ipsilateral hemifield ($F_{1,9} = 225.5$, $P < 0.001$, $\eta^2 = 0.96$), collapsed across visual areas. Furthermore, an interaction between locus of attention and visual area revealed that the magnitude of the attention effects varied across visual areas, reaching a peak in V4v ($F_{5,45} = 8.8$, $P < 0.001$, $\eta^2 = 0.5$).

Temporally sustained attention signals

During the course of an experimental run in the scanner, subjects were required to shift and maintain attention voluntarily to the left and right sides of the display for variable periods of time. To determine if the attentional modulations depicted in Figure 3a-c depended on the duration of an epoch of contralateral attention, event-related BOLD responses were sorted into 2 separate time bins depending on the locus of attention (contralateral or ipsilateral to the ROI) and the duration of the attention epoch (≤ 6 s or > 6 s). Figure 3a-c shows the results of this analysis from the V4v, IPS, and FEF ROIs. In all three of these regions, deployments of attention to the contralateral side of space resulted in a sustained increase in the BOLD response, whereas deployments to the ipsilateral side of space resulted in a sustained relative decrease in the BOLD response. Qualitatively similar results were observed in V1, V2v, and V3v (not shown).

The results revealed spatially specific and temporally sustained modulations of the BOLD signal in regions of occipital

cortex, IPS, and FEF when attention was shifted voluntarily to the preferred contralateral hemifield compared with the non-preferred ipsilateral hemifield. These modulations were induced by changes in the internal attentive state of the observer because sensory aspects of the display were held constant as observers shifted attention between the left and the right RSVP streams. The magnitude of the attention effects increased across occipital cortical regions (e.g., from V1 to V4v), consistent with previous reports of voluntary attentional modulations (Kastner and others 1998; Silver and others 2005). Finally, the temporally sustained and spatially selective nature of the responses in IPS and FEF mirrors the sustained activity often observed in the monkey LIP and FEF during visual search and saccade preparation (e.g., reviewed in Colby and Goldberg 1999; Schall and Thompson 1999).

Stimulus-Driven Attentional Shifts

We next examined spatially lateralized modulations of the BOLD signal evoked by target-colored distractors. Recall that on most trials, targets and distractors were temporally yoked. For example, if a target was presented on the left side of the display, either a target-colored or a nontarget-colored distractor was concurrently presented on the right side of the display. Thus, we could separately measure the BOLD responses evoked by distractors and targets within the spatially lateralized cortical ROIs.

At least 3 patterns of cortical activity could arise when target-colored distractors capture attention. First, the evoked responses to target-colored distractors might be larger than the evoked responses to nontarget-colored distractors (see also Serences, Shomstein, and others 2005). Second, the capture of attention away from the currently attended target location by a target-colored distractor might result in an attenuated response to the target stimulus. Finally, the capture of attention by target-colored distractors might result in both an enhanced response to target-colored distractors and a corresponding decrease in the response to targets. To evaluate these 3 possibilities, we separately assessed the responses to distractors as a function of color (i.e., the responses to target-colored compared with nontarget-colored distractors), as well as the response to targets as a function of distractor color (i.e., the responses to targets that were accompanied by target-colored distractors compared with the responses to targets accompanied by nontarget-colored distractors).

Figure 4*a* shows the mean event-related BOLD responses evoked by target-colored and nontarget-colored distractors from FEF (e.g., the response measured in left FEF when a target-colored distractor was presented in the right RSVP stream). Recall that when distractors appeared, they were always presented on the unattended side of space, and as a result, the responses to the distractors start below baseline. To evaluate the BOLD responses evoked by the distractors, a 2-way repeated measures ANOVA was performed on the peak response (4 s poststimulus) with distractor color (target colored or nontarget colored) and visual area as factors. Collapsed across all visual areas, the magnitude of the BOLD response evoked by target-colored distractors did not differ from that evoked by nontarget-colored distractors ($F_{1,9} = 0.59$, $P = 0.46$, $\eta^2 = 0.06$, Fig. 4*c*). However, activity within the IPS and FEF ROIs did exhibit a selectively heightened response to contralateral target-colored distractors ($F_{5,45} = 4.12$, $P < 0.005$, $\eta^2 = 0.31$; t -tests, $t_9 = 3.0$, $P < 0.025$ in IPS and $t_9 = 3.4$, $P < 0.01$ in FEF). The enhanced BOLD response in IPS and FEF to target-colored distractors suggests that the target-colored distractors enjoyed relatively high priority in these regions, which may account for the behavioral evidence that they captured spatial attention away from the currently attended target location (Folk and others 2002; Serences, Shomstein, and others 2005). Because the target color was red for half the subjects and green for the rest, the observed effects must be attributed to the fact that the target-colored distractors matched the subject's current attentional set and not to differences in physical stimulus salience. Finally, we did not observe a significantly heightened response to target-colored distractors in regions of extrastriate cortex, as we reported in a previous study (Serences, Shomstein, and others 2005). The reason for this discrepancy is not entirely clear; however, one possibility is that we measured activity in a region anterior to V4v in our previous study as no retinotopic mapping data were collected. Alternately, it is possible that our sensitivity to stimulus-driven attentional modulations was relatively attenuated in the present study because the stimuli were presented so far in the periphery. This later explanation is consistent with a comparison of the behavioral data between the 2 studies; a much larger drop in accuracy was induced by target-colored distractors when the stimuli were approximately 5° in the periphery (Serences, Shomstein, and others 2005) compared with when the stimuli were presented approximately 10° in the periphery, as in the present study.

Figure 4*b* shows the mean event-related BOLD responses evoked by targets in FEF when the target was accompanied by either a target-colored or a nontarget-colored distractor, respectively. Targets were always presented on the attended side of space, and so the BOLD responses depicted in Figure 4*b* start above baseline. Although there was a general trend toward a smaller response evoked by the targets when they were accompanied by a target-colored distractor, this difference did not reach significance in any visual area.

Based on the separate analyses of distractor and target responses, the data suggest that there was a selectively enhanced response to target-colored distractors in IPS and FEF, with no significant modulation of the response evoked by targets. However, to directly test the specificity of the enhanced response to target-colored distractors, a separate ANOVA was performed on the data from IPS and FEF to compare the magnitude of the distractor- and target-related modulations. The heightened response to target-colored distractors (compared with nontarget-colored distractors), combined with nonsignificant differences between target responses, lead to a significant interaction in both regions (IPS: $F_{1,9} = 10.9$, $P < 0.01$, $\eta^2 = 0.55$; FEF: $F_{1,9} = 6.18$, $P < 0.05$, $\eta^2 = 0.41$).

Note that the peak latency of the distractor-evoked responses occurs 4 s poststimulus, whereas the voluntary attentional modulations depicted in Figure 2 peak later in time (at approximately 8 s poststimulus). This difference in latency occurs because the voluntary attention cues mark the onset of a sustained epoch of voluntary attention that varies in duration (with a minimum duration of 2500 ms). In contrast, the distractors are presented for a relatively brief period of time (four 100-ms frames) and are presumably followed by a shift of attention back to the target RSVP stream. Thus, the event-related response to the cues should be temporally extended relative to the event-related response evoked by the distractors, giving rise to differences in the shape and the peak latency of the respective response functions.

The data presented in Figure 4 demonstrate that in parietal and frontal visual areas (IPS, FEF) target-colored distractors evoked a larger BOLD response than nontarget-colored distractors, reflecting stimulus-driven attentional capture. These transient distractor-evoked modulations rode on top of the lower frequency modulations induced by voluntary deployments of attention depicted in Figures 2 and 3. We might also have expected to see a corresponding decrease in the response to targets when attention was captured in the opposing hemifield by a target-colored distractor; however, this pattern did not reach significance in any visual area. Overall, these data suggest that the behavioral impairment caused by target-colored distractors operates primarily by momentarily increasing the robustness of the cortical representation of the to-be-ignored RSVP stream; the nonsignificant trends toward attenuated target responses can only hint at a "push-pull" interaction between the representations of the 2 visual fields (see also Bisley and Goldberg 2003).

Discussion

The locus of selective attention is influenced by both voluntary and stimulus-driven factors, and previous reports have shown that subregions of occipital cortex, IPS, and FEF exhibit enhanced responses during voluntary (e.g., Kastner and others 1999; Corbetta and others 2000; Hopfinger and others 2000;

Nobre and others 2000; Giesbrecht and others 2003) and stimulus-driven shifts of spatial attention (Kim and others 1999; Rosen and others 1999; Mayer and others 2004; Peelen and others 2004; Serences, Shomstein, and others 2005, reviewed in Corbetta and Shulman 2002). However, the functional role that these brain regions play in attentional control is not well understood, and the interaction between voluntary and stimulus-driven control has not previously been investigated. We provide new evidence showing that these areas exhibit a spatially specific and temporally sustained response enhancement when attention is directed to the contralateral visual field following either voluntary or stimulus-driven attention shifts, extending several reports from monkey neurophysiology that collectively converge on a similar conclusion (e.g., Bichot and Schall 1999; Bisley and Goldberg 2003; Thompson and others 2005). Modulations in these spatially selective regions thus reflect changes in dynamic representations of attentional priority that index the location of currently selected objects in the scene and may serve to guide spatially targeted motor interactions with the environment (Andersen and Buneo 2002).

Kincade and others (2005) recently demonstrated attentional modulations in IPS and FEF during voluntary attention shifts (in response to a central cue) and during stimulus-driven attention shifts elicited by targets that were presented in unexpected locations (invalidly cued targets). In the present study, we extend their findings by showing that regions of human IPS and FEF respond in a spatially selective manner to both voluntary and stimulus-driven attentional control factors, thus forming a representation of attentional priority that indexes the current locus of attention in the visual field. In addition, the stimulus-driven orienting condition employed by Kincade and others (2005) involved directing attention to a target that was presented in an unexpected location, which likely involves both voluntary and stimulus-driven factors because the stimulus that “captures” attention is also the target of search. Thus, the observed modulations following the appearance of an invalidly cued target are likely the result of both stimulus-driven attentional capture (e.g., by the target’s abrupt onset) and voluntary attention shifts to identify the target before making a response. The present study circumvents this issue by inducing stimulus-driven attention shifts by distractors that were always presented in a location that must be completely ignored because it could not contain a target during that epoch of voluntary attention. Any attentional deployments caused by the target-colored distractors are therefore strictly involuntary.

Distinction between Initiating and Maintaining a Locus of Attention

We have previously reported evidence showing that regions of medial superior parietal cortex (the precuneus and parts of the superior parietal lobule [SPL]) are transiently active during voluntary shifts of attention between locations, features, objects, and sensory modalities (Yantis and others 2002; Liu and others 2003; Serences and others 2004; Shomstein and Yantis 2004; Serences, Liu, and Yantis 2005). However, these transient shift signals do not vary substantially as a function of the particular location or stimulus to which attention is shifted. For example, the magnitude of the shift response observed in medial SPL does not depend on the direction of a spatial attention shift (Yantis and others 2002), on whether an object-

based attention shift is directed to a face or a house (Serences and others 2004), on whether a feature-based shift is directed to motion or color (Liu and others 2003), or on whether a shift between modalities is targeted toward vision or audition (Shomstein and Yantis 2004). Instead, these transient shift-related modulations appear to reflect a domain-independent signal associated with shifts of attention (see also, Vandenberghe and others 2001).

In contrast, the results of the present study suggest that activity in distinct, more lateralized, regions of IPS depends on whether attention is directed to a preferred region of space. An examination of the mean Talairach coordinates of the IPS ROIs reported here reveals that they are situated laterally in parietal cortex with respect to the medial SPL regions reported in previous studies that exhibited transient shift-related signals. The medial SPL coordinates, averaged across Yantis and others (2002), Liu and others (2003), Serences and others (2004), and Shomstein and Yantis (2004), are (x, y, z : 4, -63, 48), whereas the average left IPS coordinates from the present study are (-25, -55, 42) and the average right IPS coordinates are (25, -53, 44). Thus, we tentatively suggest that parietal cortex supports multiple functional modules that subserve potentially dissociable roles in 1) initiating shifts of attention (via the transient shift signal observed in SPL; Yantis and others 2002; Liu and others 2003; Serences and others 2004; Shomstein and Yantis 2004; Serences, Liu, and Yantis 2005) and 2) indexing the current locus of attention (via the spatially specific modulations observed in the present study). This functional parcellation is consistent with reports suggesting that more lateral regions of IPS and FEF, similar to those reported in the current study, play a role in continuously representing current task demands during working memory delay periods and during attentive visual search (e.g., Sala and others 2003; Shulman and others 2003).

It is not yet clear what the boundary conditions are for observing spatially lateralized attentional modulations in regions of IPS and FEF. One possibility is that the stimuli must be presented relatively far from the vertical meridian, as RFs are thought to be large in IPS and FEF and some neurons may therefore respond to stimuli presented on the ipsilateral side of space (Ben Hamed and others 2001). In the present study, the stimuli were arrayed around an imaginary circle with a radius subtending 10.5° visual angle, which is comparable with a previous study showing clear spatial organization in human IPS (in which the stimuli were presented ~13.5° in the periphery, Sereno and others 2001). Previous studies in our laboratory with stimuli close to the vertical midline have not revealed robust bilateral spatially specific modulations (Yantis and others 2002). Another factor may be statistical power; subjects in the present study were run in multiple sessions, permitting a relatively large amount of data to be collected. Supporting this notion, Silver and others (2005) observed spatially specific attentional modulations in human IPS using relatively small displays (~3° visual angle) when subjects were run in repeated scanning sessions (~4 sessions/subject). However, neither variable (eccentricity or statistical power) seems to fully account for the pattern of laterality effects observed across experiments.

Continuum of Sensitivity to Sensory and Attentional Factors

In the present study, the magnitude of voluntary attentional modulations varied across visual areas, reaching a peak in V4v but still highly significant in IPS and FEF. Stimulus-driven

attentional modulations, indexed by a spatially selective response to target-colored distractors, were most evident in regions of IPS and FEF. This response pattern suggests that the degree to which a given cortical region is influenced by low-level image features or by attentional demands varies more or less continuously from the earliest regions of the visual system (e.g., V1) to later regions (IPS and FEF). For instance, V1 exhibited a roughly equivalent response to both target-colored and nontarget-colored distractors, which were matched for sensory properties across subjects (see Fig. 4c). In contrast, spatially selective modulations in IPS and FEF were evident during both voluntary attention shifts (Figs 2 and 3) and stimulus-driven attention shifts induced by target-colored distractors (Fig. 4). Thus, modulations in these later visual areas increasingly reflect attentional factors (see also Silver and others 2005).

The graded attentional modulations observed across visual cortex suggest that different regions play complimentary roles in selective object perception. For instance, visual neurons in occipital cortex respond to basic feature elements (e.g., orientation, color, simple shapes) within a spatially restricted RF. These early visual areas provide the precise spatial information about low-level object features that is necessary to support more complex object representations that are maintained in later visual areas. On the other hand, neurons in IPS and FEF show less spatial and feature selectivity (Bichot and others 1996) and instead code more abstract stimulus properties such as task relevance and subjective value (Bichot and Schall 1999; Platt and Glimcher 1999; Bisley and Goldberg 2003; Dorris and Glimcher 2004; Thompson and others 2005). On this account, neural activity in any single cortical area is insufficient to provide both high-fidelity spatial information and information about the behavioral relevance of a particular object. Rather, coherent activity across anatomically distributed regions of visual cortex is necessary to support selective perception of attended objects and to guide efficient motor interactions with the environment (Desimone and Duncan 1995; Duncan and others 1997; Serences and Yantis 2006).

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

Notes

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