Research Article

Coordination of Voluntary and Stimulus-Driven Attentional Control in Human Cortex

John T. Serences,[1] Sarah Shomstein,[1] Andrew B. Leber,[1] Xavier Golay,[2,3] Howard E. Egeth,[1] and Steven Yantis[1]

[1]Department of Psychological and Brain Sciences, Johns Hopkins University; [2]Department of Radiology, Johns Hopkins University School of Medicine; and [3]F.M. Kirby Research Center for Functional Brain Imaging, Kennedy Krieger Institute, Baltimore, MD

ABSTRACT—*Visual attention may be voluntarily directed to particular locations or features (voluntary control), or it may be captured by salient stimuli, such as the abrupt appearance of a new perceptual object (stimulus-driven control). Most often, however, the deployment of attention is the result of a dynamic interplay between voluntary attentional control settings (e.g., based on prior knowledge about a target's location or color) and the degree to which stimuli in the visual scene match these voluntary control settings. Consequently, nontarget items in the scene that share a defining feature with the target of visual search can capture attention, a phenomenon termed* contingent attentional capture. *We used functional magnetic resonance imaging to show that attentional capture by target-colored distractors is accompanied by increased cortical activity in corresponding regions of retinotopically organized visual cortex. Concurrent activation in the temporoparietal junction and ventral frontal cortex suggests that these regions coordinate voluntary and stimulus-driven attentional control settings to determine which stimuli effectively compete for attention.*

Visual attention, the mechanism by which organisms select relevant or salient visual information from scenes, can be directed by a deliberate intent on the part of the observer (voluntary or goal-directed attention), or it can be captured by salient events in the scene (stimulus-driven attention; for a review, see Yantis, 2000). When searching a visual scene for a particular target, observers often adopt a deliberate attentional set for target-defining attributes that can efficiently guide attention to items that are likely to be targets (Bacon & Egeth, 1994). However, when to-be-ignored nontarget items possess a target-defining feature, they can capture attention, leading to impairments in target detection (Folk, Leber, & Egeth, 2002; Folk, Remington, & Johnston, 1992). Such instances of *contingent attentional capture*, in which a top-down attentional set interacts with the contents of the scene, are likely to be the rule rather than the exception in everyday life. Because the precise location of a target is often not known in advance, attentional control settings that represent the target's known attributes are established, and fast but error-prone filters tuned by the control settings rapidly direct attention to items that partly or fully express the target-defining features.

Although behavioral studies of contingent attentional capture suggest that the locus of attention is often determined by an interaction between voluntary and stimulus-driven factors (Folk et al., 1992, 2002; Yantis & Jonides, 1990), most neurophysiological studies of attentional control focus solely on voluntary orienting to locations, features, or objects. A network of dorsal parietal regions (intraparietal sulcus, IPS, and superior parietal lobule) and dorsal frontal regions (frontal eye fields, FEF) is thought to mediate such instances of "pure" voluntary attentional control (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger, Buonocore, & Mangun, 2000; Liu, Slotnick, Serences, & Yantis, 2003; Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001; Yantis et al., 2002). In the present study, we used functional magnetic resonance imaging (fMRI) to investigate the neural basis of contingent attentional capture, a well-controlled instance of the interaction between voluntary attentional control and stimulus-driven attentional capture.

Address correspondence to John T. Serences, Department of Psychological and Brain Sciences, Johns Hopkins University, 3400 North Charles St., Baltimore, MD 21218; e-mail: serences@jhu.edu.

We adopted a modified version of a behavioral task introduced by Folk et al. (2002). This task required participants to identify letters of a particular color (e.g., red) embedded in a central stream of rapidly presented heterogeneously colored letters (Fig. 1a). Two additional (mostly gray) letter streams flanked the central target stream and contained occasional colored distractor stimuli; the distractors could be rendered either in the target color or in an equally salient nontarget color. The results showed that spatial attention was selectively captured by the target-colored peripheral distractors, as reflected in both decreased target detection accuracy and increased activation levels in the regions of visual cortex corresponding to the spatial location of the target-colored distractors. In addition, regions of the temporoparietal junction (TPJ) and ventral frontal cortex (VFC) were strongly activated when attention was captured by target-colored distractors. These regions have been implicated previously in stimulus-driven attentional control and the detection of salient or attended stimuli (Arrington, Carr, Mayer, & Rao, 2000; Corbetta et al., 2000; Corbetta & Shulman, 2002; Downar, Crawley, Mikulis, & Davis, 2000, 2001, 2002). The present data more specifically suggest that TPJ and VFC signal the presence of features specified by current attentional control settings, which can then trigger a redeployment of attention. These areas thus provide an interface between top-down attentional control and stimulus-driven attentional capture.

METHOD

Subjects

Twelve neurologically intact adults (all right-handed, 8 females), ages 21 to 31, gave written informed consent to participate in the study, which was approved by the Johns Hopkins University institutional review boards.

Behavioral Task

The behavioral task is depicted in Figure 1a. Participants were to identify letters of a particular color (e.g., red) embedded in a central stream of heterogeneously colored distractor letters. The subjects' task was to press a button with their left hand if the target letter was in the first half of the alphabet and another button with their right hand if the target letter was in the second half of the alphabet. Flanking the target stream were two distractor letter streams located 5.25° (at a viewing distance of 65 cm) to the left and right of fixation. The peripheral distractor streams consisted mostly of gray letters, but colored distractors were presented infrequently in these streams; a distractor's color could either match the target's color or be a nontarget color that never appeared in the central target stream. For half the subjects, the target color was red and the other distractor color was green; for the remaining subjects, this mapping was

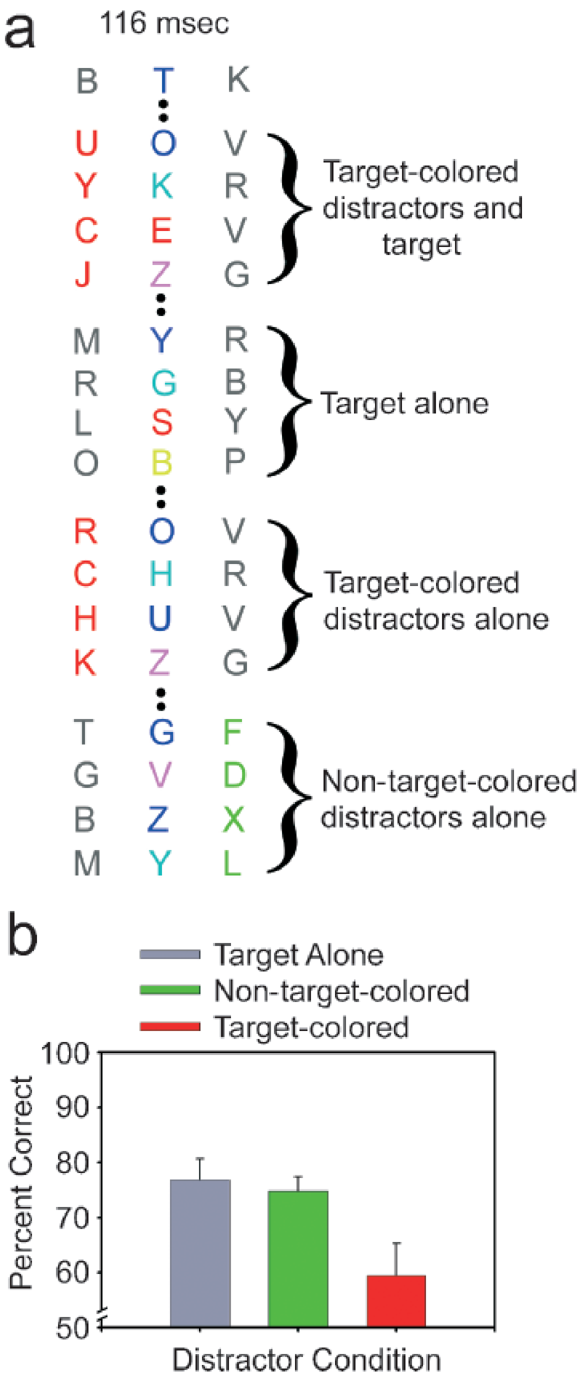

Fig. 1. Illustration of the behavioral task (a) and target discrimination accuracy (b). Subjects were instructed to continuously fixate the central letter stream, which consisted of multicolored distractor letters and an occasional target letter (red for half of the subjects, as in this illustration, and green for the other half of the subjects). The central stream was flanked by streams of mostly gray letters. On one third of the trials, target-colored peripheral distractors were presented temporally adjacent to the central target; on the remaining trials, peripheral colored distractors were presented 2,552 to 10,556 ms before or after the central targets, so that targets and colored peripheral distractors (either target-colored or non-target-colored) were temporally isolated. The graph shows the percentage of trials on which subjects responded correctly to the target, for targets presented without flanking colored distractors and targets with flanking non-target-colored and target-colored peripheral distractors.

reversed. Subjects were instructed to continuously maintain fixation on the central target stream.

In all three letter streams, all characters (simultaneously) changed identity every 116 ms (no gap), and each character subtended approximately 1° horizontally and 1.3° vertically. Each run in the scanner lasted for 340 s and included 36 target presentations. Peripheral colored distractors consisted of a color change in one of the peripheral letter streams that lasted for 464 ms (four frames). On one third of the trials, target-colored or non-target-colored distractors were presented 232 ms before the onset of the central target and lasted for 116 ms after the offset of the target. On the remaining trials, the peripheral distractors were presented 2,552 to 10,556 ms (pseudo-exponentially distributed) before or after the central target. This temporal separation permitted an assessment of behavioral responses to targets alone and of cortical activity elicited by target-colored and non-target-colored distractors alone, uncontaminated by target detection and response processes. All fMRI analyses focused on responses to peripheral distractor stimuli presented in temporal isolation from the central targets and behavioral responses.

The brief exposure duration of the stimuli and the multicolored distractor letters presented in the central stream induced subjects to adopt an attentional control setting for "target-colored letter appearing in central stream." Psychophysical evidence has shown that under these circumstances, target-colored distractors capture attention even if they appear in a peripheral distractor stream that can never contain targets (Folk et al., 2002).

fMRI Data Analysis

MRI scanning was carried out with a Philips Intera 3-T scanner. High-resolution anatomical images (1-mm^3 resolution) were acquired using an MP-RAGE T1-weighted sequence and a SENSE (MRI Devices, Inc., Waukesha, WI) head coil (TR = 8.2 ms, TE = 3.7 ms, flip angle = 8°, prepulse inversion time delay = 852.5 ms, SENSE factor = 2, scan time = 385 s). Whole-brain echoplanar functional images were acquired in 26 transverse slices (TR = 1,700 ms, TE = 30 ms, flip angle = 70°, matrix = 80 × 80, field of view = 240 mm, slice thickness = 3 mm, 1-mm gap, SENSE factor = 2).

Brain Voyager software (Brain Innovation, Maastricht, The Netherlands), along with in-house statistical software, was used for the fMRI analyses. Images from each data-collection run were slice-time and motion corrected (both within and between runs) and then high-pass (3 cycles/run) and low-pass (50 cycles/run) filtered to remove low- and high-frequency noise in the functional time series. A 4-mm full-width at half-maximum (FWHM) Gaussian kernel was used to spatially smooth the images before transformation into Talairach space (Talairach & Tournoux, 1988). Data from each participant were collected in nine separate functional runs (340 s/run) conducted in a single session. The data from four runs (one run each from 4 different subjects) were discarded because of unusually severe imaging artifacts, possibly induced by subject motion.

The hemodynamic response function for each event type was estimated using a general linear model (GLM) that included separate regressors to estimate the blood-oxygenation-level-dependent (BOLD) response at the time of event onset and at each of the next eight time points following that event (times 0–13,600 ms poststimulus; see Dale & Buckner, 1997). In this approach, the number of rows in the GLM design matrix corresponds to the number of time points in a scanning session, and each column corresponds to the relative temporal position of each model regressor with respect to the time of event onset. Each of the nine time points was modeled with a "1" in the appropriate row and column of the GLM design matrix, yielding a scaled fit coefficient (beta weight) at each modeled time point for each event (Ward, 2002).

All statistical maps were computed by subjecting the mean fit coefficients across Time Points 3 through 6 (3,400–8,500 ms poststimulus) to a two-way repeated measures analysis of variance (ANOVA) with distractor color (target-colored vs. non-target-colored) and distractor location (left vs. right) as factors. We chose to use the mean activation level across Time Points 3 through 6 in the ANOVA because this time frame reasonably reflects the range of variability in the time-to-peak of the BOLD response in different brain regions, making this analysis more general than one assuming a fixed BOLD response function (e.g., a gamma function; see Boynton, Engel, Glover, & Heeger, 1996). The single-voxel threshold for all statistical maps was set at $F(1, 11) = 9.8$, $p < .01$. A minimum cluster size of 0.405 ml (15 voxels) was adopted to correct for multiple comparisons, yielding a map-wise false-positive probability of $p < .01$ (based on 2,000 Monte Carlo simulations taking into account the 38,400 voxels that were entered into the GLM and spatially smoothed with a 4-mm FWHM kernel; Ward, 2000).

To investigate attentional modulations in extrastriate cortex evoked by contralateral target-colored distractors, we defined regions of interest (ROIs) by testing for a main effect of peripheral-distractor side, collapsed across target-colored and non-target-colored distractors (Fig. 2). This analysis identified all voxels significantly activated by any (red or green) colored distractor stimulus presented in the contralateral hemifield; therefore, the definition of the ROIs was agnostic to potential differences between responses to target-colored and non-target-colored distractors. After the ROIs were identified, paired two-tailed *t* tests were performed on the time series values from Time Point 4, the observed peak of the group-averaged hemodynamic response functions within these regions, to test for differences between contralateral target-colored and non-target-colored distractors (fit coefficients were corrected for serial autocorrelation).

To investigate BOLD modulations induced by contingent attentional capture in brain regions outside of occipital visual

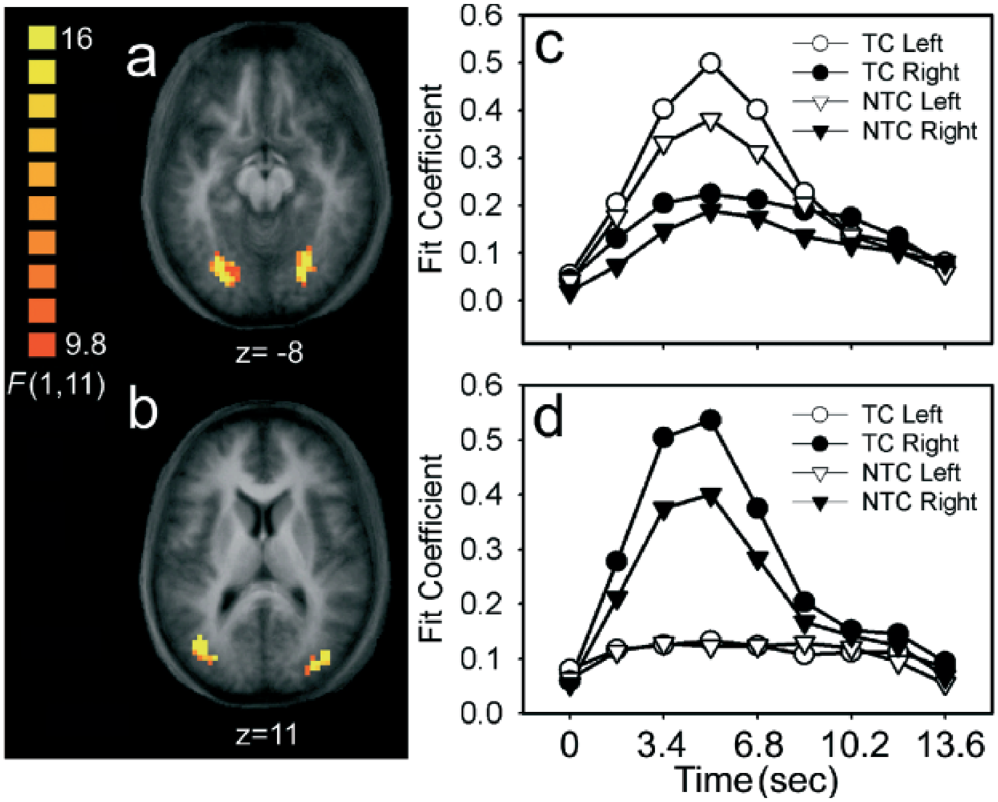

Fig. 2. Regions of right and left extrastriate visual cortex showing a greater response to any colored (i.e., nongray) peripheral distractor presented on the contralateral side of space (a, b) and event-related time course of the response in these regions (c, d). Only colored peripheral distractors that were presented 2,552 to 10,556 ms from the target were considered in this analysis. The graph in (c) shows results for right extrastriate cortex ($x = 32$, $y = -69$, $z = 10$; volume = 7.5 ml), separately for target-colored (TC) and non-target-colored (NTC) distractors presented in the left (contralateral) and right (ipsilateral) letter streams. The graph in (d) shows results for left extrastriate cortex ($x = -26$, $y = -69$, $z = 0$; volume = 3.3 ml). Coordinates are based on Talairach and Tournoux (1988).

cortex, we tested for a main effect of target-colored versus non-target-colored distractors, collapsed across distractor side (Fig. 3). The estimated time series were then corrected for serial autocorrelation before the mean fit coefficients across Time Points 3 through 6 from each region were submitted to repeated measures ANOVA with distractor color and distractor side as factors (see Table 1).

RESULTS

The behavioral data corroborated previous behavioral results (Folk et al., 2002): Targets were missed more frequently when they were flanked by a target-colored distractor than when they were flanked by an equally salient non-target-colored distractor or than when they were presented in temporal isolation from a colored distractor (Fig. 1b), $F(2, 22) = 8.82$, $p < .005$, $\eta^2 = .22$, Tukey's *HSD* $ps < .01$. In addition, discrimination accuracy when the target was flanked by gray letters was well below ceiling, confirming that the task required attention to be highly focused on the central letter stream.

To isolate the neural mechanisms of contingent attentional capture from target- and response-related processing, we focused our fMRI analyses on signal changes due to peripheral distractors that were presented in temporal isolation from the target stimuli. We first checked whether the target-colored distractors captured spatial attention even when they were separated in time by 2,552 to 10,556 ms from a central target. We defined sensory ROIs in extrastriate visual cortex that responded to any colored distractor (red or green) in the contralateral visual field (Figs. 2a and 2b; see Method). These ROIs were in regions of occipital cortex that correspond to the retinotopic location of the two flanking letter streams. Within the ROI in right visual cortex, there was a greater BOLD response to contralateral (left) target-colored distractors than to contralateral non-target-colored distractors at Time Point 4, paired $t(11) = 2.21$, $p < .05$, two-tailed (Fig. 2c). The complementary pattern was observed in the left visual cortex ROI for distractors appearing on the right, $t(11) = 2.34$, $p < .05$ (Fig. 2d). Such increases in visual cortex activity are often seen as a consequence of voluntary attention shifts (Hopfinger et al., 2000; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Serences et al., 2004; Yantis et al., 2002) and

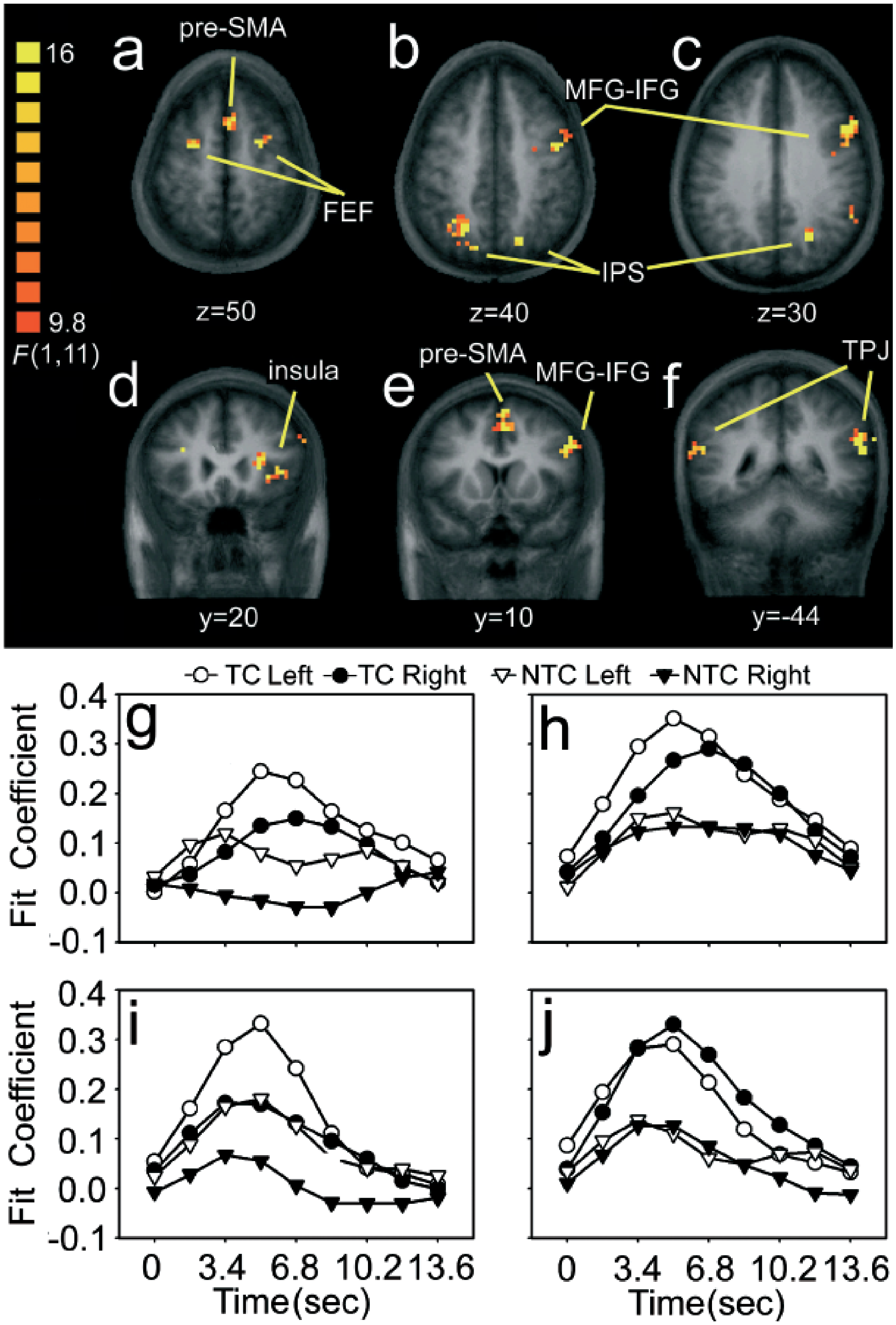

Fig. 3. Regions of cortex showing a larger response to target-colored (TC) distractors than to non-target-colored (NTC) distractors (a–f) and event-related time series of response from the right temporoparietal junction (TPJ; g), right middle and inferior frontal gyri (MFG-IFG; h), right frontal eye field (FEF; i), and left intraparietal sulcus (IPS; j). Only distractors that were presented in temporal isolation from the targets were considered in this analysis. The axial views in (a) through (c) depict the activations in the right and left FEF, anterior supplementary motor area (pre-SMA), right MFG-IFG, and right and left IPS. The coronal views in (d) through (f) depict the activations in the right insula, right MFG-IFG, medial pre-SMA, and right and left TPJ. See Table 1 for additional data.

presumably underlie behavioral observations that peripheral target-colored distractors capture spatial attention (Folk et al., 2002, and the present study).

For half the subjects, the target color was red and the non-target color was green, and this mapping was reversed for the remaining subjects; therefore, the lateralized attention effects in

TABLE 1

Brain Regions Showing a Greater Response to Target-Colored Distractors Than to Non-Target-Colored Distractors During Time Points 3 Through 6 (3,400–8,500 ms Poststimulus)

			Analysis of variance results		
Brain region	Talairach coordinates (x, y, z)	Volume (ml)	Color $F(1, 11)$	Side $F(1, 11)$	Color × Side $F(1, 11)$
		Right hemisphere			
TPJ	55, −44, 24	1.22	28.2***	14.5***	0.1
MFG-IFG	45, 6, 33	2.27	28.9***	1.2	0.3
FEF	26, −2, 47	0.810	75.3***	14.2**	0.01
Lateral insula	35, 21, 5	0.432	21.5***	1.01	0.001
Medial insula	22, 18, 14	0.459	22.9***	0.02	0.6
IPS	15, −69, 41	0.621	29.0***	10.4**	0.02
Posterior IPS	22, −59, 29	0.486	41.8***	14.0***	0.01
Pre-SMA	4, 10, 48	0.756	36.6***	3.2	0.12
		Left hemisphere			
TPJ	−55, −41, 17	0.918	19.4***	0.21	3.1
Insula	−26, 16, 18	0.486	17.9***	2.7	0.77
IPS	−20, −60, 41	1.78	27.5***	1.5	0.16
Posterior IPS	−26, −71, 20	0.432	18.3***	12.5**	0.03
FEF	−22, −3, 49	0.540	17.7***	1.1	0.07

Note. Coordinates reflect positions relative to the atlas of Talairach and Tournoux (1988). F values are from repeated measures analyses of variance performed on the mean fit coefficients across Time Points 3 through 6 for each region with distractor color and distractor side as factors. The main effect of distractor color defined the regions depicted in Figure 3. FEF = frontal eye field; IPS = intraparietal sulcus; MFG-IFG = medial and inferior frontal gyri; pre-SMA = anterior supplementary motor area; TPJ = temporoparietal junction.
$^{**}p < .01$. $^{***}p < .005$.

visual cortex cannot be attributed to differences in sensory properties. Note that there was a strong evoked response to all colored (i.e., nongray) distractors presented in the contralateral hemifield; however, this sensory response was additionally magnified for target-colored distractors compared with non-target-colored distractors. In addition, the observation of lateralized attention effects suggests that subjects were successfully fixating the central target stream throughout the task, as deviations from fixation would have resulted in a nonlateralized cortical representation of the distractor stimuli. When taken together with the behavioral data discussed previously, this result verifies that the target-colored distractors captured spatial attention away from the central stream, both when they appeared simultaneously with a target (as shown by the behavioral result) and when they appeared in temporal isolation from a target (as shown by the enhancement of the contralateral BOLD response).

We next tested for brain regions outside of occipital visual cortex that showed a greater response to target-colored distractors than to non-target-colored distractors. Shown in Figure 3 are regions of IPS, FEF, anterior supplementary motor area (pre-SMA), TPJ, the middle and inferior frontal gyri (MFG, IFG), and insula that exhibited an increased BOLD response following target-colored distractors compared with non-target-colored distractors (MFG, IFG, and insula are henceforth referred to as VFC; see Table 1). Right TPJ exhibited an increased response when any nongray distractor was presented in the contralateral visual field. However, in the right TPJ and in all other areas listed in Table 1, target-colored distractors evoked a larger response than non-target-colored distractors on both sides of space (i.e., distractor side and distractor color did not interact; Table 1 and Figs. 3g–j). In contrast to this pattern, extrastriate regions (Fig. 2) exhibited a spatially selective signal enhancement for target-colored distractors only when they were presented on the contralateral side of space, functionally dissociating the pattern of activations in parietal and frontal cortices from those in early visual cortex.

DISCUSSION

The presentation of target-colored distractors led to selective decrements in target-detection accuracy, even though the distractors appeared in to-be-ignored peripheral locations. The selective accuracy impairment caused by target-colored distractors but not by equally salient non-target-colored distractors is consistent with behavioral data showing that many salient but task-irrelevant features do not capture attention in a stimulus-driven fashion (Yantis & Egeth, 1999). Target-colored distractors also led to increases in the BOLD signal in regions of visual cortex that represent the distractor locations, demonstrating that spatial attention was captured away from the central letter stream by the target-colored distractors. Finally, we observed increased activation levels in regions of TPJ, VFC, and anterior insula when attention was drawn to an irrelevant peripheral location by a target-colored distractor.

Corbetta and Shulman (2002) have proposed that TPJ and VFC are recruited when attention is captured by a stimulus presented in an unexpected location (Corbetta et al., 2000; Corbetta & Shulman, 2002). However, previous studies did not distinguish intrinsic stimulus salience (e.g., local feature contrast) and top-down attentional control settings as factors that may influence attentional capture; in these studies, the capturing stimuli were both physically salient and behaviorally relevant (Arrington et al., 2000; Corbetta et al., 2000). For instance, Downar et al. (2001) presented continuous visual and auditory stimuli; every 10 to 14 s, a brief change occurred either in the visual stream (a small rotation of a square) or in the auditory stream (an increase in frequency of a sinusoidal tone). Observers were instructed to selectively attend to and respond to the changes in one modality, and to ignore and not respond to changes in the unattended modality. An attended change evoked a larger BOLD response in the TPJ-VFC circuit than an unattended change (see also Downar et al., 2000, 2002). This result shows that an attended target stimulus evokes a larger response in the TPJ-VFC circuit than does a salient but ignored stimulus. This activation could reflect increased signal gain associated with attended stimuli (Hillyard, Vogel, & Luck, 1998; Reynolds & Desimone, 2003), the preparation and production of an overt response to the attended stimulus, or a role in identifying a salient stimulus that matches the current attentional control settings.

In the present study, peripheral target-colored distractors—which were always to be ignored—evoked a heightened response in TPJ-VFC compared with equally salient non-target-colored distractors because they possessed a target-defining feature, not because observers were overtly instructed to attend to or respond to these peripheral distractors. Thus, we suggest that the TPJ-VFC regions play a role in filtering visual input for features specified in the current attentional control settings, signaling the need to selectively shift attention to any stimulus that possesses a target-defining feature. We conclude that TPJ and VFC coordinate existing top-down attentional control settings with the contents of the scene to guide attention efficiently.

Although we focus here on the role of TPJ-VFC, we also observed activations in pre-SMA following attentional capture by target-colored distractors. Several previous studies have also demonstrated increased activations in this region following the presentation of salient or attended stimuli (Downar et al., 2000, 2001, 2002). Thus, as more data are collected, the proposed circuit for coordinating voluntary and stimulus-driven attentional control may be extended to include medial premotor areas of cortex as well.

Regions of dorsal parietal and frontal cortex (i.e., IPS and FEF) also exhibited an increased response following attentional capture by target-colored distractors. These regions are commonly thought to be part of a network for implementing voluntary control over the locus of visual attention (Bisley & Goldberg, 2003; Corbetta et al., 2000; Corbetta & Shulman, 2002; Hopfinger et al., 2000; Kastner & Ungerleider, 2000; Liu et al., 2003; Serences et al., 2004; Vandenberghe et al., 2001), and recent evidence from neuroimaging and single-cell recording studies suggests that FEF and IPS regions may maintain a spatial attentional priority map (Shulman, Ollinger, Linenweber, Petersen, & Corbetta, 2001; Shulman et al., 2002). For instance, neurons in monkey FEF whose receptive fields are driven by stimuli that share features with the target are more active than neurons whose receptive fields are driven by irrelevant distractors (Bichot & Schall, 1999; Thompson, Bichot, & Schall, 1997). This graded response reflects the priority of each stimulus during visual search. In addition, if a monkey makes a saccade that brings a stimulus into the receptive field of a neuron in the lateral intraparietal area (LIP), then the response is magnified if the stimulus was made behaviorally relevant prior to the saccade (Gottlieb, Kusunoki, & Goldberg, 1998). Finally, recent evidence suggests that the current locus of attention may be represented by a population code within LIP, supporting the idea that this region comprises an attentional priority map (Bisley & Goldberg, 2003).

Three accounts of the activity we observed in dorsal areas following stimulus-driven attentional capture can be postulated. First, the ventral regions (TPJ and VFC) might modulate the impact of a stimulus on the attentional priority maps because it matches the current attentional set, thereby recruiting the voluntary control circuit in contingent attentional capture. In the current study, subjects searched the display for target-colored stimuli in the central stream; the appearance of target-colored distractors may have modified the attentional priority maps in IPS and FEF, causing a shift of attention. According to this account, changes in IPS and FEF activity provide reentrant feedback signals to the appropriate extrastriate cortical areas that represent the spatial locations and the features of the visual stimuli (e.g., Fig. 2). Alternatively, IPS and FEF might participate only in purely voluntary shifts of attention back to the center target stream after attention is captured by a target-colored distractor. Finally, these areas are known to be activated in both pro- and antisaccade tasks (Connolly, Goodale, Menon, & Munoz, 2002; Corbetta et al., 1998); thus, it is possible that spatial attention was selectively captured by the target-colored distractors, and that this capture of attention in turn initiated the preparation (and suppression) of a reflexive eye movement. These three possibilities cannot be distinguished on the basis of the present results because of temporal limitations of the neuroimaging technique. However, the data from extrastriate visual cortex indicate that spatial attention was captured by the target-colored distractors. Thus, even if eye movement preparation and suppression play a contributing role, FEF and IPS are likely to be activated by both the capture of attention in the periphery and a subsequent attention shift back to the center target stream.

These findings support a theoretical framework for understanding visual deficits (e.g., unilateral visual neglect or extinction) that are caused by lesions to cortex (Karnath, Ferber, & Himmelbach, 2001; Mesulam, 1999; Vallar & Perani, 1986). For instance, neglect induced by damage to dorsal parietal cortex, FEF, and pre-motor cortex can lead to a reduction in the ability to exert voluntary attentional control and to generate exploratory movements to the neglected side of space (Friedrich, Egly, Rafal, & Beck, 1998; Mesulam, 1999; Vallar, 1998). In contrast, patients with damage to ventral parietal cortex typically have impaired visual awareness for stimuli appearing on the affected side of space; this lack of awareness can result in reduced orienting to stimuli that would otherwise capture attention (Driver & Mattingley, 1998). Thus, although the relationship between lesion anatomy and functional aspects of neglect is not perfectly specified, the literature generally supports a distinction between a dorsal frontoparietal network that participates in voluntary aspects of attentional control and a ventral frontoparietal network that participates in reorienting attention to potentially relevant aspects of the visual scene (Corbetta, Kincade, & Shulman, 2002). In the context of this theoretical account, the present results suggest that damage to the TPJ may give rise to neglect because stimuli in the neglected portion of space are not evaluated as behaviorally relevant and thus cannot influence the attentional priority maps maintained in dorsal parietal and frontal cortex. The neglected stimuli are therefore denied attention and thus access to visual awareness (Desimone & Duncan, 1995; Driver & Mattingley, 1998).

Acknowledgments—We thank Terri Brawner and Kathy Kahl for assistance with data acquisition. This work was supported by National Institutes of Health Grant R01-DA13165 to S.Y. and by a National Science Foundation graduate research fellowship to J.T.S.

REFERENCES

Arrington, C.M., Carr, T.H., Mayer, A.R., & Rao, S.M. (2000). Neural mechanisms of visual attention: Object-based selection of a region in space. *Journal of Cognitive Neuroscience*, *12*(Suppl. 2), 106–117.

Bacon, W.F., & Egeth, H.E. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics*, *55*, 485–496.

Bichot, N.P., & Schall, J.D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature Neuroscience*, *2*, 549–554.

Bisley, J.W., & Goldberg, M.E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, *299*, 81–86.

Boynton, G.M., Engel, S.A., Glover, G.H., & Heeger, D.J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience*, *16*, 4207–4221.

Connolly, J.D., Goodale, M.A., Menon, R.S., & Munoz, D.P. (2002). Human fMRI evidence for the neural correlates of preparatory set. *Nature Neuroscience*, *5*, 1345–1352.

Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., Linenweber, M.R., Petersen, S.E., Raichle, M.E., Van Essen, D.C., & Shulman, G.L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*, 761–773.

Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., & Shulman, G.L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, *3*, 292–297.

Corbetta, M., Kincade, J.M., & Shulman, G.L. (2002). Two neural systems for visual orienting and the pathophysiology of unilateral spatial neglect. In H.O. Karnath & D. Milner (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 259–273). London: Oxford University Press.

Corbetta, M., & Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

Dale, A.M., & Buckner, R.L. (1997). Selective averaging of rapidly presented individual trials using fMRI. *Human Brain Mapping*, *5*, 329–340.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.

Downar, J., Crawley, A.P., Mikulis, D.J., & Davis, K.D. (2000). A multimodal cortical network for the detection of changes in the sensory environment. *Nature Neuroscience*, *3*, 277–283.

Downar, J., Crawley, A.P., Mikulis, D.J., & Davis, K.D. (2001). The effect of task relevance on the cortical response to changes in visual and auditory stimuli: An event-related fMRI study. *NeuroImage*, *14*, 1256–1267.

Downar, J., Crawley, A.P., Mikulis, D.J., & Davis, K.D. (2002). A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. *Journal of Neurophysiology*, *87*(1), 615–620.

Driver, J., & Mattingley, J.B. (1998). Parietal neglect and visual awareness. *Nature Neuroscience*, *1*, 17–22.

Folk, C.L., Leber, A.B., & Egeth, H.E. (2002). Made you blink! Contingent attentional capture produces a spatial blink. *Perception & Psychophysics*, *64*, 741–753.

Folk, C.L., Remington, R.W., & Johnston, J.C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 1030–1044.

Friedrich, F.J., Egly, R., Rafal, R.D., & Beck, D. (1998). Spatial attention deficits in humans: A comparison of superior parietal and temporal-parietal junction lesions. *Neuropsychology*, *12*(2), 193–207.

Gottlieb, J.P., Kusunoki, M., & Goldberg, M.E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, *391*, 481–484.

Hillyard, S.A., Vogel, E.K., & Luck, S.J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society of London: Series B. Biological Sciences*, *353*, 1257–1270.

Hopfinger, J.B., Buonocore, M.H., & Mangun, G.R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*(3), 284–291.

Karnath, H.O., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, *411*, 950–953.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L.G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, *282*, 108–111.

Kastner, S., & Ungerleider, L.G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, *23*, 315–341.

Liu, T., Slotnick, S.D., Serences, J.T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral Cortex*, *13*, 1334–1343.

Mesulam, M.M. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London: Series B. Biological Sciences*, *354*, 1325–1346.

Reynolds, J.H., & Desimone, R. (2003). Interacting roles of attention and visual salience in V4. *Neuron*, *37*, 853–863.

Serences, J.T., Schwarzbach, J., Courtney, S.M., Golay, X., & Yantis, S. (2004). Control of object-based attention in human cortex. *Cerebral Cortex*, *14*, 1346–1357.

Shulman, G.L., Ollinger, J.M., Linenweber, M., Petersen, S.E., & Corbetta, M. (2001). Multiple neural correlates of detection in the human brain. *Proceedings of the National Academy of Sciences, USA*, *98*, 313–318.

Shulman, G.L., Tansy, A.P., Kincade, M., Petersen, S.E., McAvoy, M.P., & Corbetta, M. (2002). Reactivation of networks involved in preparatory states. *Cerebral Cortex*, *12*, 590–600.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

Thompson, K.G., Bichot, N.P., & Schall, J.D. (1997). Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *Journal of Neurophysiology*, *77*, 1046–1050.

Vallar, G. (1998). Spatial hemineglect in humans. *Trends in Cognitive Sciences*, *2*(3), 87–97.

Vallar, G., & Perani, D. (1986). The anatomy of unilateral neglect after right-hemisphere stroke lesions: A clinical/CT-scan correlation study in man. *Neuropsychologia*, *24*, 609–622.

Vandenberghe, R., Gitelman, D.R., Parrish, T.B., & Mesulam, M.M. (2001). Functional specificity of superior parietal mediation of spatial shifting. *NeuroImage*, *14*, 661–673.

Ward, B. (2000). *Simultaneous inference for FMRI data*. Retrieved December 1, 2000, from http://afni.nimh.nih.gov/afni/docpdf/AlphaSim.pdf [Now available: http://afni.nimh.nih.gov/pub/dist/doc/manuals/AlphaSim.pdf]

Ward, B. (2002). *Deconvolution analysis of FMRI time series data*. Retrieved August 1, 2002, from http://afni.nimh.nih.gov/afni/docpdf/3dDeconvolve.pdf [Now available: http://afni.nimh.nih.gov/pub/dist/doc/manuals/3dDeconvolve.pdf]

Yantis, S. (2000). Goal-directed and stimulus-driven determinants of attentional control. In S. Monsell & J. Driver (Eds.), *Attention and performance XVIII* (pp. 73–103). Cambridge, MA: MIT Press.

Yantis, S., & Egeth, H.E. (1999). On the distinction between visual salience and stimulus-driven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 661–676.

Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, *16*, 121–134.

Yantis, S., Schwarzbach, J., Serences, J.T., Carlson, R.L., Steinmetz, M.A., Pekar, J.J., & Courtney, S.M. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience*, *5*, 995–1002.

(Received 1/30/04; Revision Accepted 3/18/04)