Cortical Mechanisms of Feature-based Attentional Control

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A network of fronto-parietal cortical areas is known to be involved in the control of visual attention, but the representational scope and specific function of these areas remains unclear. Recent neuroimaging evidence has revealed the existence of both transient (attention-shift) and sustained (attention-maintenance) mechanisms of space-based and object-based attentional control. Here we investigate the neural mechanisms of feature-based attentional control in human cortex using rapid event-related functional magnetic resonance imaging (fMRI). Subjects viewed an aperture containing moving dots in which dot color and direction of motion changed once per second. At any given moment, observers attended to either motion or color. Two of six motion directions and two of six colors embedded in the stimulus stream cued subjects either to shift attention from the currently attended to the unattended feature or to maintain attention on the currently attended feature. Attentional modulation of the blood oxygenation level dependent (BOLD) fMRI signal was observed in early visual areas that are selective for motion and color. More importantly, both transient and sustained BOLD activity patterns were observed in different fronto-parietal cortical areas during shifts of attention. We suggest these differing temporal profiles reflect complementary roles in the control of attention to perceptual features.

Introduction

Adaptive visually guided behavior requires the selection of relevant aspects of the scene through the effective deployment of attention. Investigation of the psychological and neural basis of visual selective attention has focused on two complementary factors: the effects of attention in modulating the strength of early sensory representations in striate and extrastriate cortex, and the sources of the attentional control signal in parietal and prefrontal cortex.

In the last decade, studies using single-unit recording in monkeys and functional neuroimaging in humans have provided insights about both the effects and control of visuospatial attention (for recent reviews, see Desimone and Simone, 1995; Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Yantis and Serences, 2003). For example, the effects of the deployment of spatial attention to one side of the visual field are reflected in a relative increase in the contralateral cortical response (e.g. Tootell et al., 1998; Brefczynski and DeYoe, 1999; Hopfinger et al., 2000; Yantis et al., 2002). Furthermore, the act of shifting attention from one location in space to another recruits both sustained and transient increases in parietal and prefrontal regions that are thought to reflect the sources of attentional control (e.g. Nobre et al., 1997; Hopfinger et al., 2000; Vandenberghe et al., 2001; Yantis et al., 2002).

Behavioral studies have revealed that while attention is often deployed to spatial locations (a sort of 'mental spotlight'), visual selection also operates on spatially invariant perceptual objects or perceptual feature dimensions (for a review, see Yantis, 2000). The vast majority of studies of visual selective attention have focused on the mechanisms of spatial attention; much less is known about object-based and feature-based attention. In the present study, we investigate the neural mechanisms of featurebased attentional control.

Functional imaging studies of feature-based attention have revealed that attention can modulate responses in extrastriate visual areas that specialize in processing perceptual features. For example, attending to motion enhances the activity in MT+, the human analogue of monkey MT/MST (Beauchamp *et al.*, 1997; O'Craven *et al.*, 1997), whereas attending to color increases the response of the color-sensitive area V4/V8 (Chawla *et al.*, 1999; Saenz *et al.*, 2002). Similar results have been reported for homologous areas in the monkey brain (Treue and Martinez Trujillo, 1999; McAdams and Maunsell, 2000). These studies expose the effect of attention by showing attentional modulation on the stimulus-evoked response in extrastriate areas (also see Corbetta *et al.*, 1991).

Other studies have investigated the control of attention to perceptual features. For example, the Wisconsin Card Sorting Task (WCST) and its variants require subjects to occasionally update an attentional set for the feature that define a target category. Neuroimaging studies have investigated the neural correlates of the update process (Konishi *et al.*, 1998; Nagahama *et al.*, 1998, 1999; for a somewhat similar paradigm, see Pollmann *et al.*, 2000). However, although widely used in clinical settings, the WCST is a complex task that involves many cognitive components. Furthermore, the display usually contains more than one item, potentially inducing object- and space-based attention shifts, as well as eye movements. Thus it is difficult to construct well-matched control conditions that are tightly restricted to shifts of feature-based attention using this paradigm.

Another common approach in neuroimaging studies of attentional control utilizes a cue to direct attention to a target stimulus that appears after a delay lasting several seconds, in order to estimate the respective cue-related (control of attention) and target-related (effect of attention) hemodynamic responses (e.g. Corbetta *et al.*, 2000; Hopfinger *et al.*, 2000; Shulman *et al.*, 2002). However, because the deployment of attention operates on a much more rapid time scale (Egeth and Yantis, 1997), the long temporal delay between cue and target could introduce interpretational complexities. For example, because it is not necessary for subjects to immediately shift their attention upon the presentation of the cue, they could wait until just before the target appears to shift attention. Such considerations led us to adopt a different methodology in the present study. We employed a rapid serial visual presentation (RSVP) paradigm in which the sensory stimulus is constantly present, and thus could be factored out through statistical contrasts, allowing for the isolation of shift-related control signals.

Of direct relevance to the current investigation are studies comparing conditions that require shifts of attention between feature dimensions with those that do not require such shifts (e.g. Le et al., 1998; Rushworth et al., 2001; Shulman et al., 2002). These studies have found increased activation in frontal and parietal areas when shifts of feature-based attention are required. The present study differs from previous ones in four respects. First, subjects attended to different features of a single stimulus in our task, eliminating the possibility that attention may be shifted among spatial locations. Secondly, our task incorporated explicit instructional cues for attention shifts, unlike earlier studies in which subjects shifted attention based on the context of a particular trial (e.g. Nagahama et al., 1998, 1999; Pollmann et al., 2000), or studies in which there was no explicit and temporally localized shift of attention (e.g. Corbetta et al., 1995; Wojciulik and Kanwisher, 1999). This allowed us to limit our study to deliberate, top-down acts of attentional control and exclude stimulus-driven shifts of attention (for a review, see Yantis, 2000). Thirdly, we employed event-related fMRI to examine the timecourse of neural activity time-locked to shifts of attention at a finer scale than in blocked designs (Le et al., 1998; Nagahama et al., 1998; Wojciulik and Kanwisher, 1999). Finally, the cue to shift attention was embedded within a continuous stream of visual information, and served also as a target. That is, the cue was not a temporally distinct sensory event (as in e.g. Corbetta et al., 2000; Hopfinger et al., 2000; Shulman et al., 2002), permitting us to investigate the neural responses evoked by attention shifts without the influence of sensory effects.

Observers viewed an aperture containing a field of randomly arranged and uniformly colored dots, most of which moved in a single direction. Once per second, the color of all the dots and the predominant direction of motion changed simultaneously. During the course of a scanning run, subjects attended either to the color or to the direction of motion as they monitored for color and direction-of-motion targets. Two types of targets could appear: *hold targets* instructed subjects to continue attending to the currently attended feature; *shift targets* instructed them to shift attention from color to motion or vice-versa.

By contrasting the activity during attention to motion and color, we were able to observe the attentional modulation of extrastriate cortical representations of color and motion, respectively. We selected color and motion as stimulus features because distinct extrastriate areas (MT+ for motion and V4/V8 for color) have been shown to be selectively responsive to these features (Watson *et al.*, 1993; McKeefry and Zeki, 1997; Hadjikhani *et al.*, 1998). We expected to see the effects of attentional modulation in these visual areas, as an internal check that our attention manipulation was effective.

By contrasting the activity time-locked to shift and hold targets, we were able to observe the locus and timecourse of attentional control signals in parietal and prefrontal areas. Because the sensory stimulation and motor responses during the shift and hold targets were equated, this paradigm allowed us to isolate the areas involved in controlling shifts of attention from those that respond to sensory changes or to motor activity. Moreover, through the examination of the activation timecourses, different types of attentional control signals in the cortex could be disentangled (for a discussion of the logic of this approach, see Yantis *et al.*, 2002).

Materials and Methods

Subjects

Fourteen subjects (11 women), all with normal or corrected-to-normal vision, participated in the experiment (age: 24.3 ± 4.4 years old, mean \pm SD). One subject was excluded from the data analyses because their behavioral performance was more than 2 SD below the group mean. All subjects provided informed consent approved by the Institutional Review Board at Johns Hopkins University.

Stimulus and Task

The visual stimulus was displayed on a rear-projection screen at the end of the scanner bore by an Epson PowerLite 5000 projector with a custom-made zoom lens (Buhl Optical, Pittsburgh, PA). Subjects viewed the screen through a tilted mirror positioned on the top of the head coil. The motion-coherence display (e.g. Newsome and Paré, 1988) consisted of a central aperture subtending 11° of visual angle that contained 350 moving dots, 75% of which moved in the same direction at a speed of 2.7°/s; the remaining dots were re-plotted in random locations inside the aperture at each screen update. Each dot subtended 0.04° of visual angle. The dots moved in one of six directions (left, upper-left, upper-right, right, lower-right and lower-left), and were rendered in one of six colors (red, green, blue, yellow, cyan and magenta; see Fig. 1). Before the scanning session, the six colors were set to be equluminant for each individual subjects via the method of heterochromatic flicker photometry (Kaiser, 1991). A fixation cross (0.2°) was displayed in the center of the screen throughout each run, and subjects were instructed to always maintain central fixation.

During the experiment, the direction of motion and the color changed abruptly and simultaneously once per second. The subject was instructed to attend either to motion or to color at any given time, and to monitor for two target colors or two target directions of motion that were memorized during practice runs outside the scanner. One target color and one target direction of motion signaled that attention should be held on the currently attended feature; the other target color and direction of motion signaled that attention should be shifted to the currently unattended feature dimension.

In the example shown in Figure 1, the subject was told that red means 'shift attention from color to motion' and green means 'hold attention on color'. Conversely, motion to the upper right means 'shift attention from motion to color' and motion to the lower left means 'hold attention on motion'. Thus in this example red and upper-right motion are 'shift targets', while green and lower-left motion are 'hold targets'. Each subject was assigned a different set of target colors and directions of motion.

The target events occurred on average every 4.5 s, with random temporal jitter ranging from 3 to 6 s. A target could only appear in the currently attended feature dimension. This promoted focused attention on only one dimension at any given moment. At the beginning of a run, a field of white dots moved in an upward direction, serving as a 'get ready' signal. The first event was triggered by the scanner at the beginning of data acquisition, and it was always a shift target, which provided an initial attention cue. This initial event was excluded from all reported analyses.

The subject held a pair of buttons in their right hand. They were told to press one button with their thumb whenever they detected a hold target and another button with the same thumb whenever they detected a shift target.

Finally, the design incorporated a sequential constraint such that a shift target was either followed by another shift target, or by two hold targets in a row followed by another shift target. This permitted a further test of the timecourse of the BOLD signal following shift events (see Results).

Scanning Protocol

Imaging was performed on a 1.5 T Philips Gyroscan ACS-NT system in the F.M. Kirby Research Center for Functional Brain Imaging. Subjects underwent extensive practice on the task before the scanning session began. During the scan, functional images were acquired with a T_2^* -weighted



Figure 1. A schematic diagram depicting the task. The subject attended either to color or to motion at any given time in order to detect one of two shift targets or two hold targets as the color and predominant direction of motion changed synchronously once per second. The arrow at the top of each frame represents the coherent direction of motion of the dots. The gray border around the frame is added here for visual clarity; it was not present in the actual experiment (for details see text).

echo planar imaging (EPI) sequence ($T_{\rm E}$ = 49 ms, $T_{\rm R}$ = 2000 ms, flip angle = 90°). Twenty-six transverse slices were acquired (FOV = 288 × 288 mm, matrix = 64 × 64, thickness = 4.5 mm, no gap). The first four EPI images in each run were discarded. Subjects completed 4 runs in the scanner, each 248 s in duration (124 functional images per run). A high-resolution anatomic image was also acquired for each subject with a T₁-weighted MPRAGE sequence ($T_{\rm R}$ = 8.1 ms, $T_{\rm E}$ = 3.7 ms, flip angle = 8°, 1 mm isotropic voxel).

fMRI Data Analysis

Data were analyzed in BrainVoyager (Brain Innovation, Maastricht, The Netherlands). Preprocessing of the functional data included motion correction, slice time correction, linear trend removal and temporal highpass filtering at 3 Hz. For each subject, the EPI images were then coregistered with the high-resolution anatomic image. Finally, the functional data were projected into a standard space (Talairach and Tournoux, 1988) and resampled to $3 \times 3 \times 3$ mm resolution, before they were spatially smoothed with a Gaussian kernel of 4 mm FWHM. The BOLD signal in each voxel was then modeled with a four-regressor general linear model (GLM). The model regressors corresponded to the four target types (hold on motion (hM), hold on color (hC), shift color to motion (sCM) and shift motion to color (sMC)). Only correctly identified target events were included in the model. The regressors were constructed by convolving a 1 s boxcar function for each occurrence of a target event with a standard hemodynamic response function ($\delta = 2.5$, τ = 1.25; see Boynton *et al.*, 1996). Brain activations were detected by contrasting the regressor weights (beta coefficients) associated with the conditions of interest (e.g. shift versus hold) and evaluating the statistical significance of the contrasts in a random-effects model. A spatial cluster extent threshold was used to correct for multiple comparisons in hypothesis testing. The threshold was determined by performing 10 000 Monte-Carlo simulations in a brain volume of 1.084 l with an uncorrected Pvalue of 0.005 for individual voxels (Ward, 2000). The simulation yielded a minimum volume of 405 µl for a P-value of 0.001 at the whole-brain level. Data were also analyzed using a conjunction of two statistical maps to identify transient activity. The conjunction map was constructed by taking the union of two statistical parametric maps (SPM), that is, a voxellevel AND operation. Here the same cluster extent threshold was applied, but the threshold at individual-voxel level was set at a P-value of $\sqrt{0.005} = 0.071$, to take into account the reduced probability of type-I error (see Friston et al., 1999). Although this approach is similar in some respects to a fixed-effects conjunction analysis (Friston et al., 1999), it should be noted that each individual map was obtained with a randomeffects contrast which permits conclusions that can be generalized to the population.

The timecourse of the BOLD signal within significantly activated clusters of voxels was evaluated by constructing event-related averages. For each correctly identified target event, a temporal window was defined, ranging from 6 s prior to 16 s after the event onset in which the mean BOLD timecourse was computed (~50 events were used to compute each timecourse). The mean signal in the 6 s prior to target onset was defined as baseline (0% signal change) in the event-related averages. By defining the baseline as the mean of the 6 s preceding the event, we are able to visualize changes in the BOLD signal that arise before the event in question. Furthermore, note that the positive and negative deflections in the timecourse are only relative in nature; they do not necessarily entail a positive or negative beta weight in the GLM.

Eye-tracking Procedure

A subset of the subjects (n = 8) performed the same task outside the scanner while their eye position was recorded with an Eyelink I system (SMI, Teltow, Germany). Each subject completed two runs of the task. Data were analyzed using custom software that removed blinks and detected eye movements. The number of eye movement in the 2 s window following each target event was calculated and used in the statistical analysis.

Results

Behavioral Results

The probability of correctly identifying the targets was calculated for each subject. Because subjects had ample practice before the scanning session, the performance was consistently high, with a group mean accuracy rate of 0.95 ± 0.05 . There was no significant difference between response latencies on switch and hold trials (879 versus 877 ms, respectively). This is not surprising, because (i) the responses were not speeded and (ii) even if the responses were speeded, any delays that might be due to an inserted attention shift would occur after the target was detected, and therefore not contributed to a prolonged response time.

Sustained Effects of Attention Shift

To examine whether brain areas that selectively represent motion or color were subject to sustained attentional modulation, we contrasted the regressors for 'hold motion' (hM) and 'hold color' (hC) to identify sustained attentional effects. An alternative analysis contrasting epochs during which attention was directed to motion or color revealed a very similar pattern of activation.

Subtraction of hC from hM identified areas that exhibited more tonic activity for attention to motion than to color. This contrast revealed extensive bilateral activation in superior/ inferior parietal lobule, precentral gyrus and middle/inferior temporal gyrus (Fig. 2 and Table 1). The latter two activation loci presumably contain the frontal eye fields (FEFs) and MT+, respectively, whose anatomic locations have been described before (e.g. for FEF see Paus, 1996; Corbetta *et al.*, 1998; for MT+ see Watson *et al.*, 1993; Culham *et al.*, 2001). The preference for motion over color was confirmed in the event-related BOLD timecourse analyses. To illustrate this, event-related averages of the BOLD signal are depicted in the right column of Figure 2 for three brain regions: right precentral gyrus, right superior parietal lobule and left inferior temporal gyrus. Similar BOLD timecourse patterns were observed in the other regions shown in Figure 2. Activity following the hM target was signifi-



Figure 2. Brain activations revealed in the contrast of 'hold motion' greater than 'hold color' (hM-hC). Talairach-transformed brain volumes are averaged across the subjects for visualization of functional activations. Shown here are clusters of active voxels exceeding the statistical threshold in a random-effects GLM (n = 13). Event-related averages of the BOLD response are shown in the right column for three brain areas (for notations see Table 1). These graphs plot the mean of the event-related average across subjects. Error bar shown is the mean of the standard error of all the time points on a curve. Time 0 is the moment the target event occurred, and baseline (0% signal change) is the mean signal level in the 6 s window preceding each target type.

cantly higher than activity following the hC target and remained so for several seconds, confirming a preference for motion in these areas. Furthermore, the timecourses from these activated

Brain regions showing sustained activity associated with attention shift

Table 1

contrast	Area	х, ү, г	Volume (µl)	t(12)	
hM-hC	R PCG	22, -13, 48	3456	4.27	
	L PCG	-24, -15, 47	4401	4.17	
	R SPL/IPL	27, –53, 47	12906	4.34	
	L SPL/IPL	-28, -50, 41	11106	4.43	
	R ITG	49, -63, -1	1337	4.18	
	L ITG	-45, -65, 2	1485	4.28	
	R MTG	47, –50, 7	540	4.07	
	L MTG	-42, -52, 7	675	4.19	
hC-hM	R SFG	4, 38, 34	486	4.48	
	R Fus	26, -55, -7	594	4.01	

The Talairach coordinates of the center of each cluster, the size of the cluster, and the mean *t*-values of the voxels in each cluster are reported. L: left; R: right; PCG: precentral gyrus; SPL: superior parietal lobule; IPL: inferior parietal lobule; ITG: inferior temporal gyrus; MTG: middle temporal gyrus; SFG: superior frontal gyrus; Fus: fusiform gyrus.

clusters following shift targets exhibited a crossover pattern: sMC targets produced an initial increase followed by a decrease, whereas the reverse pattern is evident for sCM targets.

Subtraction of hM from hC revealed significant activation in only two areas: the right medial superior frontal gyrus and the right fusiform gyrus (Fig. 3 and Table 1). Timecourses from these two regions are shown in Figure 3 (right). These regions exhibit a color preference in that activity following the hC target is greater than that following the hM target. Furthermore, the timecourses for the shift targets exhibit a weak crossover pattern: activity following sMC targets increased, while activity following sCM targets decreased over time.

One signature of the sustained timecourse is the difference in activity at time 0 between the hold targets (see also Yantis *et al.*, 2002; J.T. Serences *et al.*, submitted for publication). Here we see similar patterns: the event-related average for hM and hC targets has already diverged at time 0, the moment of target onset. This is due to the fact that a hold target on a featural dimension is always preceded by a shift target to that dimension; that is, attention is already directed toward that dimension at time 0.

Transient Effects of Attention Shift

An area that initiates shifts of attention between feature dimensions should exhibit greater activity following shift than hold



Figure 3. Brain activations revealed in the contrast of 'hold color' greater than 'hold motion' (hC-hM). Event-related averages of the BOLD response are shown for the two brain areas (for notations see Table 1).

targets. Furthermore, such a pattern should hold true for both feature dimensions if the control area in question is not featurespecific in its operation. A conjunction of two contrasts was performed to identify brain areas showing such a pattern of activity. First, a subtraction of 'hold color' from 'shift color to motion' (sCM-hC) was made to isolate brain areas that were more active following shift targets than hold targets in the color dimension. This contrast is appropriate because both events consist of color targets; the only difference between them is whether the subject was cued to hold or shift attention. Similarly, a subtraction of 'hold motion' from 'shift motion to color' (sMC-hM) was made to isolate greater activity associated with shifting attention in the motion dimension. Then a conjunction was performed between the resulting two statistical maps. The threshold for the conjunction map was adjusted accordingly (see Materials and Methods). This conjunction revealed regions whose increase in activity following shift targets did not depend on the dimension from which the switch occurred.

This analysis yielded significant activation in several brain areas, including precuneus, left intraparietal sulcus, left precentral gyrus and bilateral calcarine sulcus (Fig. 4 and Table 2). Representative event-related BOLD timecourses from four areas are shown in the right column of Figure 4. In contrast to the sustained activity observed before, activity in these regions showed a transient increase for both shift targets and a small relative decrease for both hold targets. There was no crossover between the timecourses for the two shift targets; instead, both functions peaked at about the same time. Furthermore, unlike



Figure 4. Brain activations revealed in the conjunction of 'shift color to motion' versus 'hold color' and 'shift motion to color' versus 'hold motion.' Event-related averages of the BOLD response are shown for four brain areas (for notation see Table 2).

Table 2 Brain regions showing transient activity associated with attention shift

Contrast	Area	х, у, г	Volume (µl)	t ₁ (12)	$t_2(12)$
sCM-hC (1) and sMC-hM (2)	l PCG	-55, -5, 21	621	2.62	2.99
	Precu	2, -71, 36	3132	4.28	2.55
	L IPS	-25, -72, 32	3321	3.32	2.68
	L Calc	-9, -73, 3	2403	3.00	2.61
	R Calc	9, –73, 3	2403	3.05	2.56

The Talairach coordinates of the center of each cluster, the size of the cluster, and the mean *t*-values of the voxels in each cluster in the two contrasts are reported. L: left, R: right. PCG: precentral gyrus, Precu: precuneus, IPS: intraparietal sulcus, Calc: calcarine sulcus.

the sustained response, the greater activity for shift targets than for hold targets was absent at time 0 (the difference, if any, was in the opposite direction). Greater shift activity only emerged about 2-4 s after target onset.

Because the target sequence contained either two shift events in a row, or one shift events followed by two hold events (see Methods), it permitted a further test of the transient nature of neural activity. Event-related averages were generated for the four possible combinations of target sequences and were shown in Figure 5 for the precuneus and IPS activation. BOLD responses for both 'shift-shift' events and 'shift-hold-hold' events showed an initial increase. However, the latter showed a prompt decrease toward baseline, whereas the former had a more prolonged and sometimes bimodal response. The prolonged response is consistent with linear summation of two transient neural signals time-locked to the two sequential shifts in attention. Such a response pattern corroborates the transient nature of neural activity in these brain regions.

Eye Movement Results

For each subject, the average number of eye movements in the 2 s window after each target event was calculated. The group mean of the number of eye movements for the four target types were: 1.45 (sMC), 1.41 (sCM), 1.53 (hM) and 1.41 (hC). A one-way repeated-measures ANOVA with target type as factor revealed no significant difference between conditions [F(3,21) < 1].

Discussion

The results will be discussed in terms of the effects and control of feature-based attention, respectively. Our discussion draws on previous literature on selective feature processing and attentional control in the brain. Thus we consider extrastriate visual areas as the recipient of attentional control signals, showing the effects of attention and fronto-parietal areas as the source of such signals, exerting control over attention.

The Modulatory Effects of Feature-based Attention

Previous studies have demonstrated enhanced neural activity as a result of attending to a feature dimension (e.g. O'Craven *et al.*, 1997; Chawla *et al.*, 1999). In the present study, we corroborated and extended these results with our observation that feature-specific cortical activity is modulated by the attentive state of the subject. As in previous studies, because both feature dimensions were continuously present throughout the task, the

Figure 5. Event-related averages of the BOLD response from two areas in Figure 4 (Precu and L IPS).

observed modulation of cortical activity must be attributed exclusively to top-down attentional factors.

When the subject attended to motion, greater activity was observed in bilateral MT+ (Fig. 2). In addition to an enhanced activity for hM over hC targets, a crossover pattern for the two shift targets was also evident. The crossover pattern is a clear signature of a motion-processing mechanism that is modulated by the attentive state of the subject. An area in the right fusiform gyrus was more active when attention was directed to stimulus color than to motion (Fig. 3). This area is slightly anterior to the previously identified human color-sensitive area, V4/V8 (McKeefry and Zeki, 1997; Hadjikhani et al., 1998), although it is very close to the anterior color-selective area found in a study using a color discrimination task (Beauchamp et al., 1999). The unilateral activation is probably due to the relatively strict threshold adopted - at a slightly lower statistical threshold, a corresponding area in the left fusiform gyrus was also observed. Although activity was greater for hC than hM targets, timecourses for the shift targets did not follow a clear crossover pattern seen in motion-selective areas. One possibility is that stimulus motion is a more salient feature than its color. Thus it might be difficult to maintain attention only on its color, without also attending to its motion. This might explain the somewhat small and brief peak in the timecourse for hC targets.

Overall, the observed modulations in extrastriate visual areas confirm that our attentional manipulation was effective, and therefore provides an adequate paradigm for our further explorations of the attentional control signals.

The Control of Feature-based Attention

Compared to previous studies, the task used in the present study has the advantage of equating sensory stimulation and motor responses between 'shift' and 'hold' conditions. More importantly, it incorporates explicit instructional cues to direct subjects' attention. These design features allow us to better isolate shift-related neural activity. Furthermore, the design offers the opportunity to distinguish two patterns of temporal dynamics: sustained and transient activity. We have argued previously that the neural implementation of attention shifts can assume either of these two mechanisms (Vandenberghe *et al.*, 2001; Yantis *et al.*, 2002; Yantis and Serences, 2003; J.T. Serences *et al.*, submitted for publication). An area with sustained activity maintains the goal of attention by providing a continuous biasing signal, whereas an area with transient activity sends out brief neural 'pulses' to alter the observer's attentive state, regardless of what is being attended.

By this logic, we found both transient and sustained activity during attention shifts between color and motion. Sustained activity in bilateral PCG and SPL/IPL regions showed a sustained pattern for motion (Fig. 2), while sustained activity for color was observed in the medial SFG (Fig. 3). These areas may be sources of sustained biasing signals for motion and color, respectively. This hypothesis is consistent with recent studies by Shulman et al. (1999, 2002), who found activation in a left posterior parietal region when the subject was given a directional cue for an upcoming motion discrimination task. More extensive cortical areas, including bilateral SPL and MT+, exhibited attentional modulation for motion processing during the subsequent stimulus epoch. The pattern of activation for attention to motion is very similar to that in the present study. In addition, we also found an area in medial SFG exhibiting attentional modulation for color processing. However, we do not know any previous study that reported this area to be involved in maintaining attention to color.

In contrast to sustained activity, we observed transient neural activity in several other brain areas (Fig. 4). We suggest that left PCG, precuneus and left IPS may be the source of an abrupt signal that initiates shifts of attention between motion and color. This transient signal is issued whenever there is an attention shift, irrespective of the attended feature dimension. These areas are similar to those that have been reported in previous studies of feature-based attention using other paradigms (Corbetta et al., 1995; Le et al., 1998; Nagahama et al., 1998, 1999; Rushworth et al., 2001; Shulman et al., 2002). The most consistent finding across these studies is the activation in superior parietal cortex and precuneus when attention is deployed in feature space. Our paradigm also revealed the involvement of left PCG and left IPS. Although previous studies have strongly implicated these areas in feature-based attention, our results reveal that their activation assumes a transient, rather than sustained, temporal profile.

We did not find significant activity in the inferior/middle frontal areas, which are often seen during cognitive set-shifting tasks (e.g. Konishi et al., 1998; Brass and von Cramon, 2002; Shulman et al., 2002). This might be due to the somewhat more rigorous control condition - the hold trials - employed here. In the current RSVP paradigm, subjects must continuously hold two tasks in mind and maintain a high degree of attention throughout the experiment. Thus frontal activation related to task specification and preparation might be constantly active and hence subtracted out in our contrast. This interpretation is supported by the observation that subjects in our task did not produce significantly longer RTs on switch trials compared to hold trials, a behavioral effect typically observed in set shifting studies. It should be noted that we did not emphasize speed of response in the instruction, and subjects were well practiced on the task. Further study is needed to clarify the relationship between task specification/preparation and attention shifting.

We also observed transient cortical activity bilaterally in the calcarine sulcus (Fig. 4), the site of primary visual cortex (Horton and Hoyt, 1991). Because this is an early sensory area, it is unlikely that the observed activity represents the source of an attentional control signal. We suggest that this activity may reflect a 'refocusing' of attention. First, note that V1 is not specialized for specific feature dimensions; it is known to represent both color and motion, among other dimensions. When subjects maintain their attention on a feature dimension for an

extended time, some adaptation may accrue (e.g. Engel and Furmanski, 2001). With a shift of attention to the other dimension, the neural response to the newly attended dimension is 'refreshed' through the act of attention, resulting in increased activity. This account is post-hoc and speculative, and more data are needed to resolve the nature of the observed activity in primary visual cortex.

Having made the distinction between transient and sustained activity, we now turn to the relationship between them in attentional control. Our data show that these two types of neural activity act in concert during attention shifts. The precise nature of their interaction, however, remains unknown. One possibility is that the sustained activity in frontal areas maintains the goal of attentional focus. These areas then send out control signals to posterior parietal areas, which in turn issue a transient signal to modulate sensory areas in extrastriate cortex. At present, this scenario is highly speculative. Further investigation on this issue probably requires imaging techniques with much higher temporal resolution than fMRI, such as event-related potential recording.

Eye Movements

Because the production of eye movements activates regions of fronto-parietal cortex similar to those reported here (e.g. Corbetta *et al.*, 1998; Beauchamp *et al.*, 2001), we must rule out the possibility that our results could be caused by overt eye movements, rather than covert attention shifts, as we have claimed. Results from the eye-tracking procedure revealed no significant difference in the number of eye movements following each target type. Thus the observed neural activity is unlikely caused by systematic eye movement behavior during the experiment.

Other Modes of Attentional Control

Previous neuroimaging studies of attentional control have emphasized spatial attention (e.g. Kastner *et al.*, 1999; Corbetta *et al.*, 2000; Hopfinger *et al.*, 2000), perhaps reflecting the fundamental importance of space in vision more generally. These studies have revealed a network of fronto-parietal cortical areas involved in top-down, voluntary, attentional control (reviewed in Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002).

The present study revealed similar activation loci as these previous studies in the domain of feature-based attention. Such a similarity argues for a domain-general mechanism for attentional control in the cortex (as suggested by Wojciulik and Kanwisher, 1999). Two other studies from our group also bear on this issue. Using paradigms that are similar to that used in the present study, we have investigated control mechanisms for space- and object-based attention (Yantis et al., 2002; J.T. Serences et al., submitted for publication). These two studies have also uncovered a network of frontal-parietal areas associated with attention shifts between spatial locations and superimposed objects. The most consistent finding in this series of studies is the transient nature of cortical activity in medial SPL/precuneus time-locked to shifts of attention (see also Vandenberghe et al., 2001). These results strongly implicate a role of this region in controlling voluntary shifts of visual attention in multiple representational domains.

However, a detailed comparison of the atlas coordinates in the three studies suggests that the precise locations of the transient activity vary from one study to the next. Table 3 shows the

Table 3

Talairach coordinates of the parietal activation loci in the Yantis et al. (2002) and the present study

Yantis <i>et al.</i> (2002)	Present study
SPL (11, -60, 55)	Precu (2, -71, 36)
IPL (46, -31, 28)	IPS (-25, -72, 32)

SPL: superior parietal lobule; IPL: inferior parietal lobule; Precu: precuneus; IPS: intraparietal sulcus.

Talairach coordinates of parietal activations from the Yantis *et al.* (2002) and the present study. Shifting spatial attention (Yantis *et al.*, 2002) activated more dorsal regions in the superior parietal areas than shifting feature attention (present study), whereas the inferior parietal activations were in different hemispheres across the two studies. This relatively large anatomic separation of cortical activity suggests that the posterior parietal cortex may be functionally segregated into subregions that control different modes of attention shifts. But we would caution that a direct within-study or within-subject comparison has yet to be made, so this conclusion remains tentative.

Conclusion

The present results reveal both a transient and sustained pattern of BOLD activity during attention shifts between feature dimensions. These two temporal profiles of activity were observed in distinct areas of the fronto-parietal cortex during attention shifts. We suggest that these areas play different, yet complementary, roles in attentional control. Furthermore, the characterization of brain activity in terms of transient and sustained temporal dynamics provides a useful framework in which mechanisms of attentional control can be tested.

Notes

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