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Research Report

Pre-target activity in visual cortex predicts behavioral performance on spatial and feature attention tasks

Barry Giesbrecht^{a,*}, Daniel H. Weissman^b, Marty G. Woldorff^b, George R. Mangun^c^aDepartment of Psychology, University of California, Santa Barbara, CA 93106-9660, USA^bCenter for Cognitive Neuroscience, Department of Psychiatry, Duke University, Durham, NC 27708, USA^cCenter for Mind and Brain, Departments of Neurology and Psychology, University of California, Davis, CA 95616, USA

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ABSTRACT

Physiological studies in humans and monkeys have revealed that, in response to an instruction to attend, areas of sensory cortex that code the attributes of the expected stimulus exhibit increases in neural activity prior to the arrival of the stimulus. Models of selective visual attention posit that these increases in activity give attended stimuli a processing advantage over distracting stimuli. Here, we test two key predictions of this view by using functional magnetic resonance imaging to record human brain activity during a cued voluntary orienting task. First, we tested whether pre-stimulus modulations are observed during both cued spatial and cued feature attention. Secondly, we tested whether the magnitude of pre-stimulus modulations predicts behavioral performance. Our results indicate that cue-triggered expectation of targets with particular spatial or nonspatial features activates areas of the visual cortex selective for these features. Furthermore, the magnitude of the cue-triggered modulations correlated with behavioral measures, such that those subjects who exhibited relatively large pre-stimulus modulations of activity performed better on the behavioral task. These findings support the view that top-down control systems bias activity in sensory cortices to favor the processing of expected target features and that this bias is related to behavior.

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1. Introduction

One of the key functions of the attention system is to aid the selection and processing of task-relevant information in our environment in support of coherent goal-directed behavior. A long line of behavioral, neurophysiological, and neuroimaging studies of visual selective attention have demonstrated that voluntary covert orienting (i.e., orienting without eye movements) to a particular spatial location or to a particular nonspatial stimulus feature (e.g., color) leads to facilitated behavioral performance and to increased neuronal responses evoked by stimuli that are presented in the attended location

or that possess the attended feature (e.g., Corbetta et al., 1990; Heinze et al., 1994; Hillyard and Münte, 1984; Kingstone and Klein, 1991; Luck et al., 1994; Mangun and Hillyard, 1991; Posner, 1980; Van Voorhis and Hillyard, 1977; Woldorff et al., 1997). Neurobiological models of attention posit that the enhanced behavior and associated neuronal activity reflect the influence of top-down control mechanisms on bottom-up sensory processing in visual cortex (e.g., Corbetta and Shulman, 2002; Desimone and Duncan, 1995).

Although attention effects in sensory processing are typically observed as modulations of the neural activity evoked by the task-relevant “target” stimuli, several studies have ob-

* Corresponding author. Fax: +1 805 893 4303.

E-mail address: giesbrecht@psych.ucsb.edu (B. Giesbrecht).

served modulations in neural activity prior to, or in the absence of, the to-be-attended target stimulus. For example, single-unit recordings in monkeys have found that cells in inferior temporal cortex that are selective for a given stimulus exhibit elevated pre-stimulus baseline firing rates when that stimulus is to be fixated in an upcoming visual search display (Chelazzi et al., 1993, 1998). Similarly, Luck et al. (1997) found that some cells in visual cortex exhibit increases in pre-stimulus baseline firing rates when the visual field location that the cells represent is covertly attended. As in the single-unit studies, human neuroimaging studies have also reported increases in activity prior to the presentation of an attended target stimulus in areas of visual cortex that represent the attended location (e.g., Giesbrecht et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999; Weissman et al., 2004; Wilson et al., 2005; Woldorff et al., 2004) or the attended feature (Chawla et al., 1999).

According to one model of visual selective attention, changes in pre-stimulus activity are generated by top-down biasing signals originating from control areas in frontal and parietal cortex (Desimone and Duncan, 1995). As a consequence of these biasing signals, the attended stimulus is afforded an advantage in the competition for neural resources, resulting in a higher level of processing of the attended items relative to unattended ones. If changes in baseline activity do indeed bias processing in favor of the attended stimulus, then it follows that these changes in baseline activity should be related to behavioral performance. Consistent with this conjecture, studies of spatial attention have reported that activity in visual cortex is correlated with the outcome of perceptual decisions in highly trained observers performing a near-threshold detection task (Ress and Heeger, 2003; Ress et al., 2000). Although consistent with the theoretical conjecture, it remains unclear whether these correlations between activity in visual cortex and behavior generalize to cue-triggered, pre-stimulus modulations of neural activity and to the behavior of naive participants during suprathreshold discrimination tasks that are more commonly used when studying visual selective attention.

The present study had two main goals. First, we investigated the magnitude and time course of pre-stimulus activity in regions of visual cortex, in response to cues that directed subjects to attend to a spatial location or to a stimulus feature

prior to target presentation. Although there is evidence that attending to spatial locations or nonspatial stimulus features can result in enhanced pre-stimulus activity, the evidence comes from different studies using a variety of tasks. Therefore, it has been difficult to relate pre-stimulus modulations during spatial and feature modes of attention (but see Giesbrecht et al., 2003). Second, and most importantly, we investigated whether pre-stimulus modulations that occurred during cued spatial and cued feature attention predicted subsequent behavioral discrimination performance of a target that was presented in the cued location or possessed the cued feature.

To address these questions, we asked participants to perform a cued attentional orienting task, while their brain activity was assessed using functional magnetic resonance imaging (fMRI). In each trial, participants were cued to covertly direct their attention to either one of two spatial locations (right or left) or one of two colors (blue or yellow). The task was to discriminate the orientation (horizontal or vertical) of a rectangle that was presented at the cued location or in the cued color (Fig. 1). Critically, the spatial and nonspatial cuing conditions were equated on a variety of nonspecific effects (e.g., arousal, motor preparation) and cognitive operations (e.g., working memory, response selection) but differed in terms of which stimulus dimension was cued. We predicted that location- and color-selective regions of the visual cortex would both exhibit selective increases in pre-target activity in response to cues to attend for the appropriate target. Moreover, we hypothesized that these increases in pre-target activity would be associated with improved performance on the location- and color-cue tasks. Consistent with these predictions, we observed activation increases in visual cortical areas selective for processing the target stimuli prior to their actual presentation, and the magnitude of these modulations was positively correlated with behavioral performance across subjects.

2. Results

2.1. Behavior

The mean proportion of correct responses in the spatial and color conditions is shown in Fig. 2. Overall, subjects performed

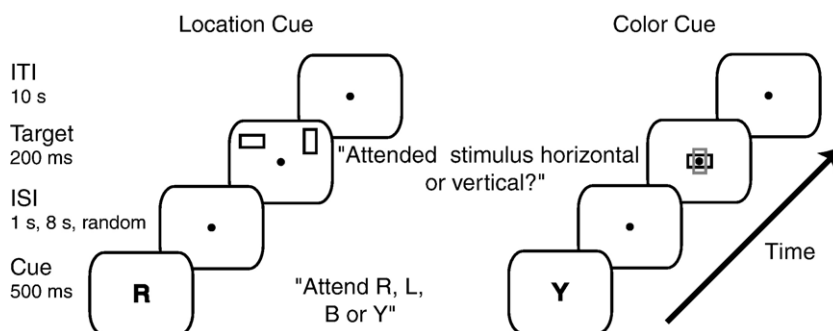


Fig. 1 – Experimental task. On each trial, subjects were instructed by a cue letter presented at fixation to attend to a location or color. After a variable interstimulus interval (1–8 s), a target was presented, and subjects were required to indicate, with a button press, the orientation of the relevant rectangle. Actual displays viewed by the participants were color on a black background: cues were gray, both location targets were green, one color target was blue, and the other was yellow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

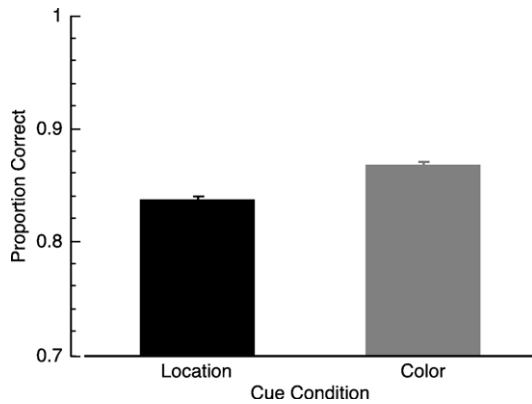


Fig. 2 – Mean proportion of correct responses on the location and color tasks. Error bars represent the standard error of the mean and are appropriate for within-subjects comparisons (Loftus and Masson, 1994).

the tasks well, with mean proportion correct being 0.85. Subjects were more accurate on the color task ($t(11) = 9.35$, $P < 0.001$), where the mean proportion correct was 0.867 (SEM = 0.003), than on the location task, where the mean proportion correct was 0.837 (SEM = 0.003).

2.2. Pre-target modulations

The areas that exhibited differential increases in pre-target activity that were significantly different from baseline (see Methods) are shown in Fig. 3a. The coordinates of the local maxima are listed in Table 1. During the location task (top row of Fig. 3a), differential pre-target modulations were observed in the anterior-medial lingual gyrus (LingG) bilaterally, which is consistent with the known retinotopic representation of the peripheral visual field in these areas (e.g., DeYoe et al., 1994; Sereno et al., 1995). During the color task (bottom row of Fig. 3a), differential pre-target modulations were observed in the fusiform gyrus (FusG) bilaterally, consistent with previous research indicating that the FusG is involved in color processing (Corbetta et al., 1990, 1991; McKeefry and Zeki, 1997; Zeki and Bartels, 1999; Zeki and Marini, 1998; Zeki et al., 1991).

Shown in the left of Fig. 3b are the hemodynamic responses to the location and color cues in areas that exhibited significant pre-target modulations shown in Fig. 3a. As hypothesized, in the areas that were selectively activated to the peripheral location targets, the foveally presented cues did not evoke a typical hemodynamic response function. In areas that were selectively activated to the foveally presented color targets, on the other hand, the foveally presented cues evoked a more typical hemodynamic response function (i.e., peaking at 4–6 s). To subtract out the sensory response to the foveally presented cues, we computed pre-target modulation difference waves in the location- and color-target-selective regions (Fig. 3b). As described in the Methods, in the location-target-selective areas, the difference wave was computed by subtracting the response to the color cue from the response to the location cue, whereas, in the color-target-selective areas, the difference wave was computed

by subtracting the response to the location cue from the response to the color cue. Computing the difference waves in this manner subtracts off the sensory response to the cues, and what should remain is the attentional modulation alone. The blue curve shows the difference wave in the location-target-selective areas, and the red curve shows the difference wave in the color-target-selective areas. In location-target-selective areas, there was an increase in differential activity in response to the location cues. Similarly, in the color-target-selective areas, there was an increase in differential activity in response to the color cues. The change in activity was significant across time, before the target occurred ($F(6,66) = 11.32$, $P < 0.001$). The magnitude of the differential modulation in pre-target activity did not differ in the location- versus color-selective areas ($F < 1$).

2.3. Correlations with behavior

The results of the voxel-wise correlation between pre-target modulations and behavior are shown in Fig. 4a. The regression lines for the voxels that showed the highest r value (i.e., the local maxima) for the correlation between pre-target activity and behavior are shown in Fig. 4b. The coordinates of all the local maxima (>8.0 mm apart) are listed in Table 2.

In location-target-selective areas of both the left and the right LingG, the magnitude of the pre-target attentional modulation (i.e., computed by subtracting location-cue minus color-cue responses and averaging across post-cue time points covering a period of 8–10 s post-cue, see Methods) was positively correlated with performance on the location-cue task—that is, those subjects that showed larger pre-target modulations in these areas performed better on the task. When computed at each voxel, the maximum r value was 0.858, and, when computed averaging across all voxels that showed significant correlations with behavior, $r = 0.790$. Similarly, in color-target-selective areas of the FusG bilaterally, the magnitude of the attentional modulation (i.e., computed by subtracting color-cue minus location-cue responses and averaging across the post-cue interval from 8 to 10 s, see Experimental procedures) was positively correlated with performance on the color task. When the correlation was computed at each voxel, the maximum obtained $r = 0.887$ and when averaging across all voxels that showed significant correlations with behavior $r = 0.778$.

To assess the specificity of the correlation between pre-target activity and behavior, we also correlated the pre-target attentional modulation from within the location- and color-target areas (i.e., the same measurements of attentional modulation used above) with performance on the task that did not correspond to the type of target that defined the region of interest. For example, measures of attentional modulation taken from the location-target-selective local maximum were correlated with performance on the color task, and measures of attentional modulation taken from the color-target-selective local maximum were correlated with performance on the location task. Fig. 4c shows the regression lines for this correlation conducted using the same local maxima as were used in Fig. 4b. The correlation value between the differential

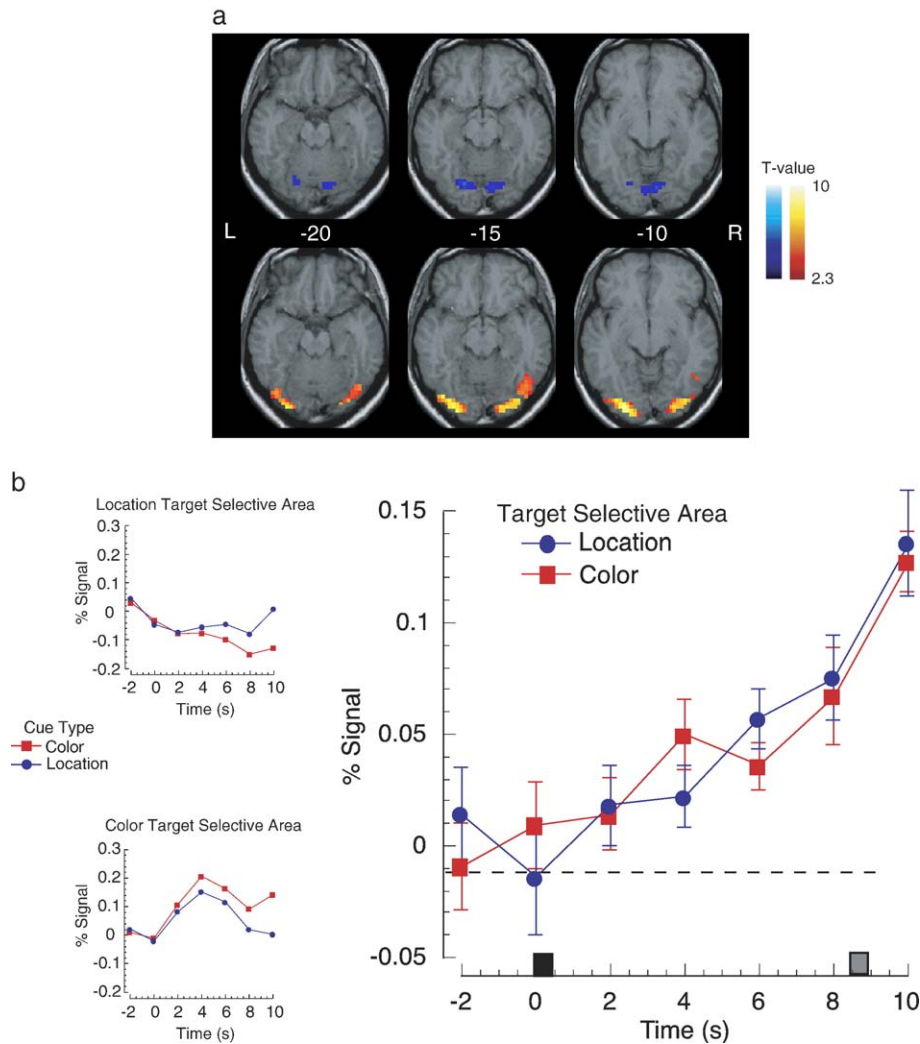


Fig. 3 – Pre-target modulations. (a) Group average data for brain regions that showed significant modulations in pre-target activity in location-target-selective areas (top row; location vs. color cue contrast) and color-target-selective areas (bottom row; color vs. location cue contrast). Activations were thresholded at $t(11) = 2.3$ ($P < 0.025$) and are overlaid onto key slices of a single subject's anatomical image that includes ventral visual cortex ($z = -10, -15, -20$ mm). (b) Time course of the hemodynamic response averaged across activated voxels shown in panel a. On the left is the response to the location cues (blue curves) and color cues (red curves) averaged across voxels that showed significant pre-target modulations in location-target-selective areas (top) and color-target-selective areas (bottom). On the right is the time course of the differential attentional modulation in terms of percent signal change averaged across the activated voxels shown in panel a. Black and gray boxes on the x axis indicate the onsets of the cue and target, respectively. Error bars represent the standard error of the mean and are appropriate for within-subjects comparisons (Loftus and Masson, 1994).

attentional modulation in the location-target-selective areas at the local maximum and performance on the color task was $r = 0.031$ (n.s.). The correlation between the differential attentional modulation in the color-target-selective areas at the local maximum and performance on the location task was $r = 0.229$ (n.s.).

To test whether these values were different than those obtained by the original correlations between pre-target activity and behavior (i.e., those shown in Fig. 4b), we conducted hypothesis tests using Fisher's r -to- Z transformation and using the original r values as the expected values of ρ under the null hypothesis (Hays, 1994). These hypothesis tests revealed that the r values of the secondary correlations

were significantly different from the r values obtained from the initial correlations between the attentional modulation in the target-selective areas and performance on the corresponding task (e.g., modulation in location-target-selective areas with performance on the location task). Specifically, in location-target-selective areas, the r value of 0.031 resulting from the correlation of pre-target modulation with color-task behavior was significantly different than (i.e., lower than) the value observed when correlating pre-target modulation and location-task behavior ($r = 0.858$, $P < 0.0001$). Similarly, in color-target-selective areas, the r value of 0.229 resulting from the correlation between pre-target modulation with location-task behavior was significantly different than

Table 1 – Local maxima of regions showing significant pre-target modulations

Contrast	Region	n voxels	t	P<	x mm	y mm	z mm	
Color > location	L FusG	102	9.38	0.002 ^a	-22	-90	-5	
			6.94	0.04 ^a	-30	-86	-15	
			6.73	0.05 ^a	-411	-79	-15	
Location > color	R FusG	106	5.93	0.0001	38	-82	-15	
			5.42	0.001	19	-90	-15	
	R ITG			3.73	0.002	45	-68	-15
				4.58	0.0005	-19	-75	-15
	L LingG	56	2.84	0.01	-8	-82	-10	
			4.50	0.0005	8	-79	-10	
3.54			0.003	15	-79	-15		

Abbreviations: FusG, fusiform gyrus; IOG, inferior occipital gyrus; ITG, inferior temporal gyrus; LingG, lingual gyrus; L, left; R, right.
^a Corrected for multiple comparisons.

(i.e., lower than) the value observed when correlating the color-target modulation and color behavior ($r = 0.887$, $P < 0.0001$).

3. Discussion

The purpose of the present investigation was to investigate (a) pre-target modulations of activity during cued selective attention and (b) the relationship between pre-target modulations during cued selective attention and subsequent behavioral performance on the attention task. We hypothesized that areas of visual cortex that selectively responded to the location and feature targets would exhibit increases in activity in response to cues to attend to a location or a feature, but before the presentation of the relevant target. We also hypothesized that the magnitude of these pre-target modulations should be correlated with performance on both the spatial and feature tasks. Consistent with these predictions, we found evidence for significant increases in activity in visual cortex prior to the presentation of the attended targets, and the magnitude of these modulations was positively correlated with performance. In the following, we will discuss how these findings inform our understanding of top-down influences of attention on activity in visual cortex.

First, we predicted that areas of visual cortex should exhibit increases in activity in preparation for an upcoming target stimulus. This prediction was based on previous studies of spatial attention that have shown that activity in visual cortex can be modulated in preparation for an upcoming target stimulus (e.g., Giesbrecht et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999; Weissman et al., 2004; Wilson et al., 2005; Woldorff et al., 2004). Critically, these pre-target modulations occur in areas of visual cortex that represent the attended location or feature. Consistent with these findings, we observed that areas of visual cortex that were selective for the location target stimuli showed cue-triggered increases of activity in response to an instruction to attend to the location before the target stimulus was presented. The anatomical locations of these increases in activity were consistent with our previous findings of contralateral pre-

target attention effects when attending to right versus left peripheral visual field locations (Giesbrecht et al., 2003; Hopfinger et al., 2000; Wilson et al., 2005; Woldorff et al., 2004). Furthermore, the presence of pre-target biasing activity in these areas fits nicely with other findings indicating systematic increases in activity in retinotopically organized visual cortex in the absence of visual stimulation (e.g., Kastner et al., 1999).

Analogous to the spatial attention effects, we observed that areas of visual cortex selective for the color target stimuli exhibited increases in activity in response to an instruction to attend for an upcoming color stimulus. This finding is consistent with the idea that nonspatial attentional mechanisms can bias feature-selective regions of visual cortex in a manner similar to spatial attentional mechanisms (e.g., Desimone and Duncan, 1995). Together, these findings provide strong support for the hypothesis that top-down attentional control systems can modulate activity in areas of visual cortex that represent task-relevant information.

In the context of the present paradigm where the location targets and color targets are presented in different locations, one cannot completely rule out the involvement of spatial attention in the color task. Nevertheless, there are two factors that suggest that these color-cue-triggered pre-target modulations cannot be accounted for by spatial attention mechanisms alone. First, because the color-target display consisted of blue and yellow rectangles overlapping at the same physical location, cue-triggered selection of the task-relevant rectangle could not be done solely on the basis of spatial location. Rather, in order for the participants to perform well on the task, they needed to select the rectangle that was presented in the cued color. Thus, it is clear that color-selective attention needed to be engaged for the color task. Second, the finding that activity in FusG systematically increased in response to color cues prior to the target is consistent with previous studies showing that the FusG is selective for color processing (Corbetta et al., 1990, 1991; Hadjikhani et al., 1998; McKeefry and Zeki, 1997; Zeki and Bartels, 1999; Zeki and Marini, 1998; Zeki et al., 1991) and that it can be activated when attending to color even in the absence of a color stimulus (Chawla et al., 1999). Indeed, the coordinates of the local maxima are very close to the coordinates revealed by investigations of human color vision (e.g., McKeefry and Zeki, 1997). Based on these converging lines of evidence, we would argue that the color-task pre-target modulations included a reflection of nonspatial, feature-based attention mechanisms. Regardless of whether spatial or nonspatial mechanisms were involved in the color task, however, our most important finding was that cue-triggered activity in target-selective regions of the visual cortex predicted upcoming behavior, as we discuss in more detail next.

Our second main prediction was that the magnitude of the differential modulations in location- and color-target-selective areas of visual cortex should be correlated with better performance on the location and color tasks, respectively. This prediction was based on models of visual selective attention that postulate that modulations of pre-target activity in visual cortex give attended objects a processing advantage over unattended objects in the competition for

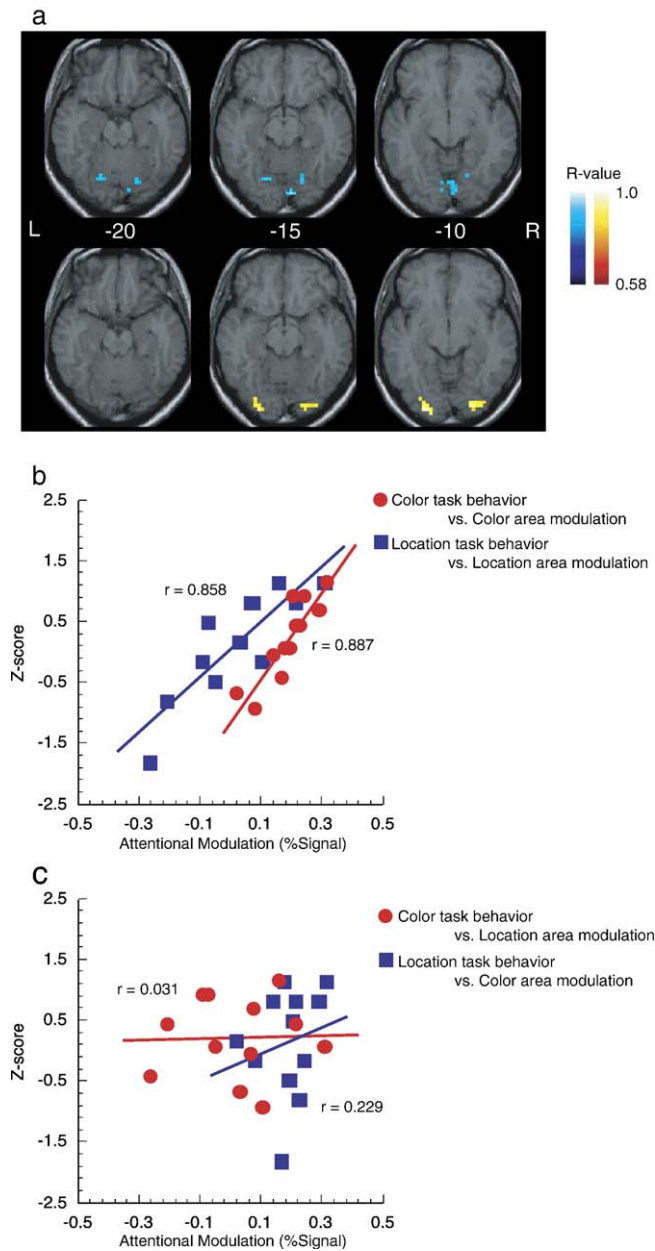


Fig. 4 – Correlation between pre-target activity and behavior. (a) Brain regions that showed significant correlations between pre-target modulation and behavior across subjects. The top row shows the correlation between performance on the location task and pre-stimulus modulations in the location-target-selective regions when attending to location. The bottom row shows the correlation between performance on the color task and pre-target modulations in the color-target-selective regions areas when attending to color. Activations were thresholded at $r = 0.576$ ($P < 0.025$) and are overlaid onto key slices of a single subject's anatomical image that represents ventral visual cortex ($z = -10, -15, -20$ mm). (c) Scatter-plot and regression lines for the correlation between pre-target activity and behavioral performance on the corresponding task. The blue squares and the blue line show results of the correlation between location-target-selective pre-target activity at the local maximum (x, y, z mm = 8, -86, -15) and location-task behavior. The red circles and red line show the results of the correlation between color-target-selective pre-target activity at the local maximum (x, y, z mm = 22, -94, -10) and color-task behavior. (c) Scatter-plot and regression lines for the correlation between pre-target activity and behavioral performance on the noncorresponding task. The red circles and red line show the results of the correlation between location-target-selective pre-target activity at the local maximum (x, y, z mm = 8, -86, -15) and color-task behavior. The blue squares and blue line show the results of the correlation between the correlation between color-target-selective pre-target activity at the local maximum (x, y, z mm = 22, -94, -10) and location-task behavior.

Table 2 – Local maxima of regions showing significant correlations between pre-stimulus modulation and behavioral performance across subjects

Correlation	Region	n voxels	r	P	x mm	y mm	z mm
Color activity/color performance	L FusG	14	0.887	0.0001	-22	-94	-10
			0.609	0.02	30	-82	-15
	R FusG	36	0.834	0.0005	22	-90	-10
Location activity/location performance	L LingG	7	0.734	0.005	30	-82	-0
			0.736	0.004	-19	-71	-15
	R LingG	21	0.858	0.0005	8	-86	-15
	R LingG	8	0.751	0.003	0	-75	-5
0.631			0.02	19	-75	-20	

Abbreviations as in Table 1.

awareness (Desimone and Duncan, 1995). Consistent with this prediction, we observed that the magnitude of attentional modulation was correlated with better performance across subjects during both spatial and nonspatial attention. To our knowledge, this is the first study to demonstrate that attentional modulations of visual cortical activity in response to cues to attend to a location or color are related to improved behavioral performance on a suprathreshold discrimination task.

The finding that there is a significant correlation between cue-triggered activity and behavior provides support for models of selective attention that posit that top-down control mechanisms aid relevant stimuli in their competition with irrelevant stimuli for neural resources (Desimone and Duncan, 1995). However, it could be argued that the significant relationship between activity and performance in both the location and color conditions observed here represents a nonspecific relationship between behavior and activity in all potentially task-relevant areas of visual cortex, perhaps due to some generalized strategy that is applied to both the location and color tasks. In other words, according to this

view, the relationship between activity and performance is not specific to the task-relevant dimension (i.e., location or feature). This argument, however, can be firmly ruled out in the present experiment. Within the present context, if the relationship between pre-stimulus activity and performance represents a nonspecific effect, then when we correlated attentional modulations from one area (e.g., location-selective) with performance on the other task (e.g., color), there should still be a correlation. In stark contrast to this alternative argument, however, there was not a significant correlation between pre-target activity in one target-selective area and performance on the other task. Moreover, not only were these correlations not significantly different from zero, but they were significantly different than the values obtained when correlating pre-target modulations with performance on the corresponding task. Thus, our results provide support for the conclusion that the correlation between pre-target attentional modulation and performance observed here does not reflect a nonspecific relationship, but rather reflects a relationship between pre-target activity in areas of visual cortex that represent task-relevant information and behavioral performance on tasks that require selective attention to that information.

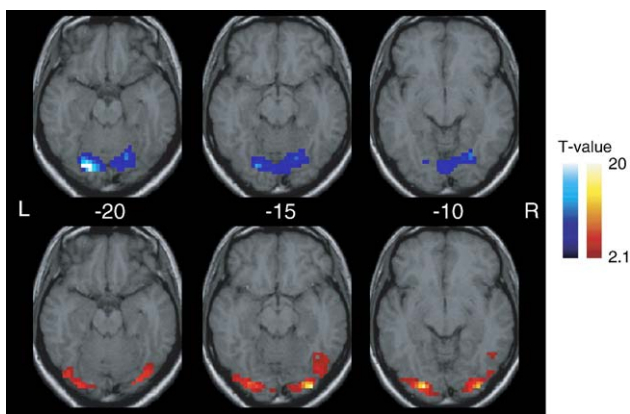


Fig. 5 – Target-selective activity in the localizer task. Group-average data for brain regions more active to location targets than color targets (top row) and brain areas more active to color targets than location targets (bottom row). Activations are overlaid onto key slices of a single subject's anatomical image, which includes the ventral visual cortex ($z = -10, -15, -20$ mm). Clusters are significant at $P < 0.05$, corrected, using a combined height and extent threshold (Poline et al., 1997).

4. Conclusion

A central issue in recent neuroimaging studies of visual attention has been to identify the brain systems and mechanisms that control selective attention. Emerging from these studies is the view that portions of frontal and parietal cortex are involved in the control of attentional orienting to spatial locations, spatial reference frames, objects, and other nonspatial stimulus features (Corbetta et al., 2000; Giesbrecht et al., 2003, 2005; Hopfinger et al., 2000; Shulman et al., 2002a, 2002b; Weissman et al., 2002; Wilson et al., 2005; Woldorff et al., 2004; Yantis et al., 2002). When these studies of attentional control are considered together with the present results, they are consistent with the notion that top-down systems can bias activity, via re-entrant connections, in specific areas of visual cortex in preparation for an upcoming stimulus. Critically, however, what the present results demonstrate is that the top-down modulations of pre-stimulus visual cortical activity are related to performance, supporting the idea that the role of these top-down modulations is to facilitate the neuronal

Table 3 – Local maxima for the functional localizer task

Contrast	Region	P (cluster)<	n voxels	t	P<	x mm	y mm	z mm
Color target > location target	L FusG	0.005 ^a	124	12.41	0.0001	-23	-90	-5
				3.82	0.01	-38	-75	-25
	L IOG	0.004 ^a	129	2.40	0.04	-8	-98	0
	R FusG			8.39	0.0005	34	-90	-15
				2.91	0.02	15	-90	-15
R ITG		2.61	0.025	49	-56	-10		
Location target > color target					0.0000			
	L LingG	0.001 ^a	196	23.52	5	-23	-79	-20
	R LingG			5.16	0.002	19	-71	-20
				5.10	0.002	26	-68	-10

Abbreviations as in Table 1.

^a Corrected for multiple comparisons.

processing of the attended information in order to support coherent, goal-directed behavior.

5. Experimental procedures

5.1. Subjects

Sixteen subjects (8 female; ages 24–32) gave informed consent before participating in accordance with the guidelines of the local Institutional Review Board. The data from ten of these subjects were the subject of a previously published article addressing a different theoretical question (Giesbrecht et al., 2003).

5.2. Stimuli

Cues were gray uppercase letters from the English alphabet presented at fixation and were $0.8 \times 0.6^\circ$ (height \times width). The targets were rectangles ($1.75^\circ \times 1.42^\circ$) that could be horizontal or vertical in orientation. Location targets were green and were presented in the upper left and right visual fields (5.7° from fixation, 4.0° from the horizontal and vertical meridia). Color targets consisted of blue and yellow (colors were equiluminant) rectangles ($0.88^\circ \times 0.71^\circ$) overlapped at fixation. The different rectangle size in the two conditions was employed to adjust for the cortical magnification factor (Serenio et al., 1995). All stimuli were presented on a black background.

5.3. Procedure

5.3.1. Attention task

The task used in the present experiment was exactly the same as that used in our previous work investigating the cortical systems of attentional control (i.e., the central cue condition described in Giesbrecht et al., 2003). Each trial began with a visual cue letter (500 ms duration) that instructed subjects to covertly attend either to a target location on the right or left (R or L, respectively) or to a particular target color that could be blue or yellow (B or Y, respectively). The cue was followed by an ISI during which only the fixation point was displayed. The ISI was either 1000 ms (33% of trials), 800 ms (33%), or random between 1900 and 7100 ms (33%). The timing parameters provided enough temporal jitter so that the statistical model could effectively deconvolve the hemodynamic responses to cues and targets (e.g., Burock et al., 1998; Dale, 1999), while ensuring a sufficient number trials at the longest ISI to study pre-target modulatory effects on the raw fMRI signal in target-selective areas. Target displays were presented for 200 ms, after which there was a 10 s fixation display, or inter-trial interval (ITI), before the presentation of the next cue. Cue type was combined factorially with ISI, and equal numbers of trials for each of the conditions were intermixed randomly within runs. The

session was divided into nine runs of 24 trials each, presented to each subject in a randomized order.

Subjects were instructed to maintain fixation at all times (verified by electro-oculograms recorded during training, Giesbrecht et al., 2003) and to actively use the cue information as soon as it was presented. Their task was to indicate the orientation of the cued rectangle when it appeared as accurately as possible.

5.3.2. Functional MRI localizer runs

The purpose of the functional MRI localizer runs was to identify areas of visual cortex that selectively responded to the location and color targets used in the attention task, but without requiring focused attention to a particular location or color. The functional localizer runs were similar to the attention task in that before each target display a letter was presented at fixation. However, unlike the attention task where a specific letter was paired with a particular instruction to attend and a particular target display (see Fig. 1), in the functional localizer runs, the cue letters were randomized with respect to the subsequent target display. Moreover, the cue letters were different than those used in the attention task, being instead P, T, K, and X. The randomization of the pairing between the letters and the subsequent target display meant that subjects could not predict the type of target stimulus based on the cue identity. Consequently, the cue served only as a warning signal that the target display was about to be presented and did not direct subjects to attend to a specific location or color. The task was to press a button with the index finger of the right hand when the target display was presented. The functional localizer task included 8 runs, just like the attention task, that were performed in a separate session. Six of the 16 subjects who also performed the attention task performed the functional localizer task. To mitigate potential order effects, half of the subjects ($n = 3$) performed the functional localizer task before the attention task.

5.4. Imaging methods

Functional images were acquired with a General Electric 1.5 T scanner equipped with an Advanced Development Workstation for real-time echo-planar imaging. Images were acquired using a T2*-weighted gradient-echo, echo-planar imaging sequence with a repetition time (TR) of 2.0 s, an echo time (TE) of 40 ms, and a flip angle (FA) of 90° . Twenty-four contiguous slices were collected with a voxel size of $3.75 \times 3.75 \times 5$ mm. Anatomical images were acquired using a T1-weighted sequence (TR = 500 ms, TE = 14 ms, FA = 90° , and voxel size of $0.94 \times 0.94 \times 5$ mm).

Image processing was performed using SPM99 (Friston et al., 1995). Functional images were corrected for differences in slice acquisition order and motion. One subject exhibited motion in excess of 6 mm and as a result was excluded from all subsequent analyses. The remaining subjects' ($n = 15$) anatomical scans were coregistered with their functional images and then spatially

normalized to stereotactic space using the MNI template. The resulting parameters were then used to spatially normalize the functional images. The normalized functional images were spatially smoothed with an 8-mm isotropic Gaussian kernel.

5.5. Statistical analyses

5.5.1. Behavior

Mean proportion correct was computed in both the attend location and attend color conditions. Because overall performance was high, the data were arcsin-transformed to ensure that they conformed with the underlying assumptions of the hypothesis tests that would be carried out (Hogg and Craig, 1995). To facilitate correlation with the fMRI data and to put the performance from both conditions on the same scale, each subject's accuracy on the spatial and feature tasks was standardized by transforming to a z score using the mean and standard deviation across all subjects, but within each cue condition. Three subjects were excluded from the analysis due to behavioral performance that was greater than 2.5 standard deviations from the group mean. This ensured that the correlations with the fMRI signal (see below) were not skewed by outliers. The remaining 12 subjects were included in all remaining stages of the analysis.

5.5.2. Functional MRI localizer runs

The first step was to identify areas of visual cortex that selectively responded to the target stimuli in the functional MRI localizer runs. This was done by convolving a vector of onset times of the cues and targets (collapsing across ISI) with a synthetic hemodynamic response function that emphasized transient activity in response to the events (Friston et al., 1995, 1998). The general linear model was used to estimate the effects of interest and other confounding effects (e.g., session effects and magnetic field drift) for each subject individually; these models also used a first order auto-regressive model to estimate the temporal autocorrelations in the data and adjust the degrees of freedom accordingly. The results from each of the six subjects were then used to perform random-effects analyses. It should be noted that all of the subjects included in this analysis were also included in all stages of the analysis of the attention task (that is, none of the subjects excluded due to head motion or behavioral performance performed the functional MRI localizer task). In the random-effects analysis of the six subjects, we identified target-selective areas of visual cortex by directly contrasting location and color target activity using SPM99. Target-selective voxels were those that survived a combined height ($P < 0.01$) and extent threshold of 20 contiguous voxels, which resulted in a $P < 0.05$, corrected image-wise false-positive rate (Poline et al., 1997). The resulting target-selective activations are shown in Fig. 5, and the coordinates of the local maxima are listed in Table 3.

5.5.3. Pre-target modulations

The activations that were revealed by the functional localizer runs were used as regions of interest (ROIs). Within these target-selective ROIs, the event-related hemodynamic time course evoked by the cues in the attention task was calculated for each subject and condition. The time courses for each voxel were converted to percent signal change relative to a baseline of the averaged signal intensity at the cue onset time point and the immediately preceding time point. These averages were computed by averaging the left and right cue conditions in the location task and the blue and yellow cue conditions in the color task. Because we were looking at the selective averages in response to the cue, we used only those trials in which the cue and the target were separated by 8 s in order to minimize the hemodynamic overlap between the cue and the target. Since both cues were simple gray letters, we reasoned that computing the difference wave between the responses to the different cues should subtract out basic sensory processing of the cues, thereby revealing differences

caused by attentional modulation alone. Thus, in areas that were selective to the color targets, the difference wave was computed by subtracting the response to the location cue from the response to the color cue. Similarly, in areas that were selective to the location targets, we subtracted the response to the color cues from the response to the location cue (see Fig. 3b). A 2-factor r (cue type: color, location; time: 8 post-cue time points, -2 s to $+10$ s) repeated-measures ANOVA was used to test for differences between these difference waves (see Results), using the Greenhouse–Geisser correction for the degrees of freedom where appropriate.

To identify voxels that exhibited increases in pre-target activity, we defined pre-target activity as the average activity in the difference waves (computed as described in the preceding paragraph) at the last time point before target presentation and the time point that included target presentation. Our rationale for using these time points instead of the typical peak points of the hemodynamic response (i.e., 4–6 s) was that the later time points should be the point of maximal attentional modulation. The time point of the target presentation was included because it should not contain target-related activity because the hemodynamic response does not peak until about 4–6 s post-stimulus. This index of the magnitude of the pre-target activity was computed at each voxel in the color-target-selective ROI and the location-target-selective ROI. A one-sample t test, restricted to only those voxels within the ROIs, was used to determine whether the pre-target activity was different from zero (i.e., baseline), and the resulting map was thresholded at $t(11) = 2.3$, $P < 0.025$.

5.5.4. Correlations with behavior

To assess whether pre-target modulations of sensory cortical activity predicted behavioral performance, the magnitude of the differential pre-target modulation in the location-selective and color-selective areas (computed as described above) was correlated with standardized behavioral performance in the location-cue and color-cue conditions. This correlation was computed across subjects within the pre-defined ROIs selective for the cued target. For instance, pre-target modulation in the location-target-selective ROI was correlated with standardized performance on the location task, and pre-target modulation in the color-target-selective ROI was correlated with standardized performance on the color task. The correlation was restricted to only those voxels that were significant at a corrected level in the functional MRI localizer task, and, as a result, the maps of r values were thresholded at $r = 0.576$, $P < 0.025$.

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