

Preparatory Activity in Visual Cortex Indexes Distractor Suppression During Covert Spatial Orienting

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Serences, John T., Steven Yantis, Andrew Culbertson, and Edward Awh. Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *J Neurophysiol* 92: 3538–3545, 2004. First published July 14, 2004; doi:10.1152/jn.00435.2004. The deployment of spatial attention induces retinotopically specific increases in neural activity that occur even before a target stimulus is presented. Although this preparatory activity is thought to prime the attended regions, thereby improving perception and recognition, it is not yet clear whether this activity is a manifestation of signal enhancement at the attended locations or suppression of interference from distracting stimuli (or both). We investigated the functional role of these preparatory shifts by isolating a distractor suppression component of selection. Behavioral data have shown that manipulating the probability that visual distractors will appear modulates distractor suppression without concurrent changes in signal enhancement. In 2 experiments, functional magnetic resonance imaging revealed increased cue-evoked activity in retinotopically specific regions of visual cortex when increased distractor suppression was elicited by a high probability of distractors. This finding directly links cue-evoked preparatory activity in visual cortex with a distractor suppression component of visual selective attention.

INTRODUCTION

Visual attention is the mechanism by which behaviorally relevant information is selected from complex multielement scenes. A growing body of evidence suggests that the suppression of interference from distractors is a primary component of this selection process. For example, several studies have revealed amplified benefits of attention when there is competition from nearby distracting stimuli compared with when there is no competition (Awh and Pashler 2000; Awh et al. 2003; Doshier and Lu 2000; Kastner and Ungerleider 2001; Kastner et al. 1998; Moran and Desimone 1985; Reynolds et al. 1999; Shiu and Pashler 1994). This result implicates a distractor suppression component of attention that produces the strongest attentional modulation when significant competition from distractors must be suppressed. However, attention can also modulate visual responses in the absence of competing distractor stimuli. This finding is not easily explained by distractor suppression, and it has been taken as the strongest evidence for some form of signal enhancement (i.e., the direct enhancement of sensory responses to attended targets: Carrasco et al. 2000; Hillyard et al. 1998; Luck et al. 1996). Thus a full characterization of visual selection requires a method for measuring the unique contributions of distractor suppression and signal enhancement processes, respectively.

Neuroimaging studies of covert spatial orienting have shown that when a specific location is attended, there is a concurrent increase in activity in the parts of visual cortex that represent and process stimuli in that location, even before the target stimuli themselves are presented. This *baseline shift* in cortical activity presumably primes the relevant visual areas for the attentive processing of subsequent targets (Hopfinger et al. 2000; Kastner et al. 1999; Luck et al. 1997; Muller and Kleinschmidt 2003; Ress et al. 2000). However, the available data cannot distinguish whether this preparatory activity reflects signal enhancement at attended locations, anticipatory suppression of distractor interference, or some combination of the two.

We addressed this issue by manipulating the probability that targets would be accompanied by visual distractors and observing cortical responses after attention-directing cues. In a previous behavioral study, Awh et al. (2003) provided cues that indicated the likely location of an upcoming target as well as the probability that the target would be accompanied by a dense array of distractors. When distractors were present in the array, then the spatial cuing effect (that is, the improved target detection accuracy for validly cued vs. invalidly cued targets) was greater when distractors were probable than when they were improbable, showing that the cue supported distractor suppression in preparation for the distractor-laden display. Importantly, when distractors were not present in the array, then distractor probability had no effect on the spatial cuing effect. This pattern shows that the distractor probability manipulation selectively affected the degree of distractor suppression and had no effect on signal enhancement. If the probability manipulation had elicited increased levels of signal enhancement, then the cued targets would have enjoyed an enhanced spatial cuing effect even when distractors were absent.

In the present experiments, we used the same manipulation of distractor probability, combined with functional magnetic resonance imaging (fMRI), to assess the contribution of distractor suppression during preparatory activity in posterior visual cortex.

EXPERIMENT 1

Methods

SUBJECTS. Twelve neurologically intact young adults (10 females), age 20–31 yr, gave written informed consent to par-

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participate in the study, which was approved by the Johns Hopkins University institutional review boards.

BEHAVIORAL TASK. Figure 1 depicts the behavioral task. The stimuli were rendered in white on a black background and the letters and numbers were presented in Arial font. From a viewing distance of 65 cm, the letter and number stimuli subtended 1.2° visual angle in width and 1.5° in height, with an interstimulus separation of 0.3°. Target locations were 3° from the central fixation point and the distractor stimulus grid formed a square that was 8.7° on a side.

The task included equal numbers of *distractor-present* (Fig. 1A) and *distractor-absent* trials (Fig. 1B). Four cue shapes (2 circles and 2 squares) appeared in opposite diagonals of an imaginary square. For half the subjects, the squares indicated the to-be-attended locations, and for the other half, the circles indicated the to-be-attended locations (the shape of the central fixation stimulus matched that of the relevant cue). After a pseudo-exponentially distributed delay of between 2,500 and

8,500 ms (mean: 4,375 ms, SD: 2,087 ms), 4 digits appeared in the same locations as the cue shapes. The subject's task was to add the digits appearing in the 2 attended locations and to press a button in their left hand if the sum was even and a button in their right hand if the sum was odd.

For half of the subjects, when the attention cues appeared in the upper right and lower left locations, there was an 80% probability that the display on that trial would be densely populated with distractors (*distractor-probable cues*); when the cues appeared in the upper left and lower right locations this probability was 20% (*distractor-improbable cues*). This mapping was reversed for the other half of the subjects. Thus the positions of the cues provided information about 2 aspects of the upcoming display: first, where the targets would appear (with 100% validity), and second, whether distractors would be present (with 80% validity).

Exposure durations for targets in the presence and absence of distractors were independently titrated for each subject using a staircase method so that target accuracy was about 75% for each display type (see next section). This method yielded mean exposure durations of 193 ms (SD: 41 ms) for targets with distractors, and 88 ms (SD: 31 ms) for targets without distractors. These exposure durations were too brief to allow saccades between the 2 target locations. A pattern mask was presented for 581 ms after the offset of the target display.

STAIRCASE TIMING PROCEDURE. To equate the difficulty of target discrimination for each observer and each type of display, a staircase procedure was used to determine separate exposure durations for the target displays with and without distractors, respectively. This procedure prevented ceiling effects, and enabled a direct comparison of distractor probability effects in the distractor-present and distractor-absent trials. During these timing trials, distractor-probable cues were always followed by distractor-present displays and distractor-improbable cues were always followed by distractor-absent displays (that is, the 2 probabilities were 100 and 0%, rather than 80 and 20% as in the main experiment). Observers began with the exposure duration set at 1,670 ms. On each trial, exposure duration was reduced by 10% if the observer's response was correct, or increased by 30% if the observer's response was incorrect. On the day before scanning, each observer performed 8 blocks of 40 trials, and the mean exposure duration over the last 2 blocks (after exposure duration had reached asymptote) was determined for each display type. After the subjects were positioned in the scanner, 3 additional blocks of this timing procedure were run, with the starting exposure duration determined by each subject's performance during the previous session. Mean exposure duration for each display type was determined by performance during the last 2 blocks of this procedure. Small adjustments in the exposure duration were sometimes made over the course of the scanning session to keep the subjects in the appropriate accuracy range (~75%).

FMRI DATA ANALYSIS. MRI scanning was carried out with a Philips Intera 3T scanner in the F. M. Kirby Research Center for Functional Brain Imaging at the Kennedy Krieger Institute, Baltimore, MD. Anatomical images were acquired using an MP-RAGE T1-weighted sequence that yielded images with a 1-mm isovoxel resolution [repetition time (TR) = 8.1 ms, echo time (TE) = 3.7 ms, flip angle = 8°, time between inversions = 3 s; inversion time = 748 ms]. Whole brain echoplanar

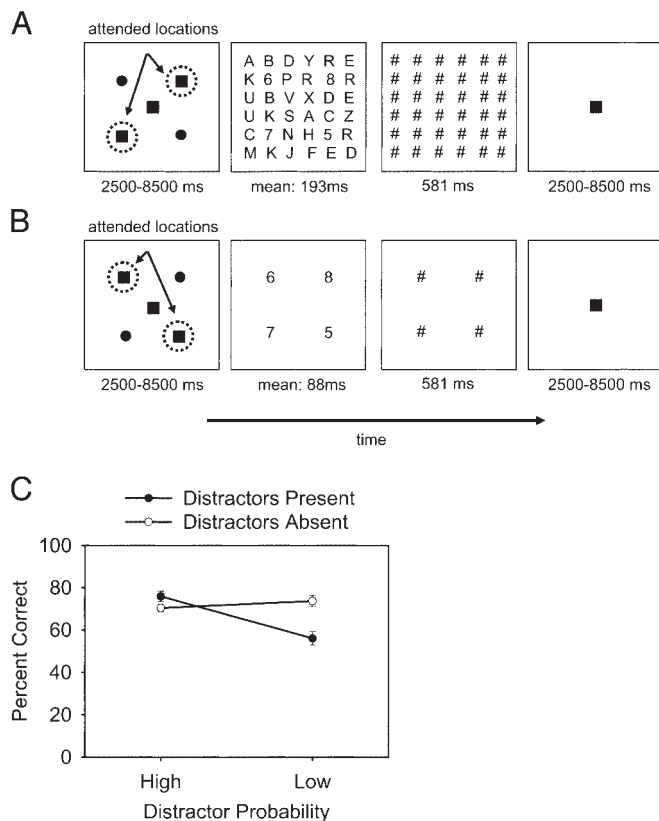


FIG. 1. Schematic of behavioral task on (A) distractor-present and (B) distractor-absent trials. Attended locations were defined by square cues for half the subjects and circles for the other half. Central fixation stimulus was the same shape as the relevant cue object. Location of the cues provided information about 2 aspects of the upcoming display: first, where the targets would appear (with 100% validity), and second, whether distractors would be present (with 80% validity). Exposure durations for targets in the presence and absence of distractors were independently titrated for each subject using a staircase method so that target accuracy was about 75% for each display type. Subject's task was to add the digits appearing in the attended locations; they pressed a button in their left hand if the sum was even and pressed a button with their right hand if the sum was odd. **C:** accuracy on the behavioral task (data collected in the scanner). In locations that had a low probability of distractor interference, subjects were selectively impaired at discriminating targets with distractors. This probability manipulation had a small and nonsignificant effect on target discrimination in the absence of distractors.

functional images (EPI) were acquired with a SENSE (MRI Devices, Waukesha, WI) head coil in 26 transverse slices [TR = 1,830 ms, TE = 30 ms, flip angle = 70°, matrix = 80 × 80, field of view (FOV) = 240 mm, slice thickness = 3 mm, 1 mm gap, SENSE factor = 2]. The same EPI parameters were used for the functional localizer scans, except that the TR was changed to 2,000 ms.

Brain Voyager software (Brain Innovation, Maastricht, The Netherlands) was used for the fMRI analyses. EPI images were slice-time and motion corrected (both within and between runs) and a 3 cycles/run high-pass temporal filter was applied to remove low-frequency components in the time series.

Data from the functional localizer scans were collected in 2 runs that consisted of 88 volume acquisitions each. Digits flickering at 8 Hz were presented in each pair of diagonal target

locations for alternating 20-s blocks. No distractors were presented during the localizer scans. Regressors were specified for each pair of target locations separately for each subject. Each regressor consisted of a boxcar model of each respective stimulation epoch convolved with a gamma function (delta = 2.5 s, tau = 1.25 s; Boynton et al. 1996). The resultant regression vector was cross-correlated with the blood oxygenation level-dependent (BOLD) time series, yielding scalar beta weights corresponding to the relative changes in signal strength associated with that particular set of stimulus locations. A single voxel statistical threshold of $t(172) = 4.0$, $P < 0.0001$ was used. Regions of interest (ROIs) responding more strongly to a particular set of locations were defined by contrasting the beta weights for each pair of locations, and identifying clusters of voxels within the occipital cortex (e.g., Fig. 2, A and B). The

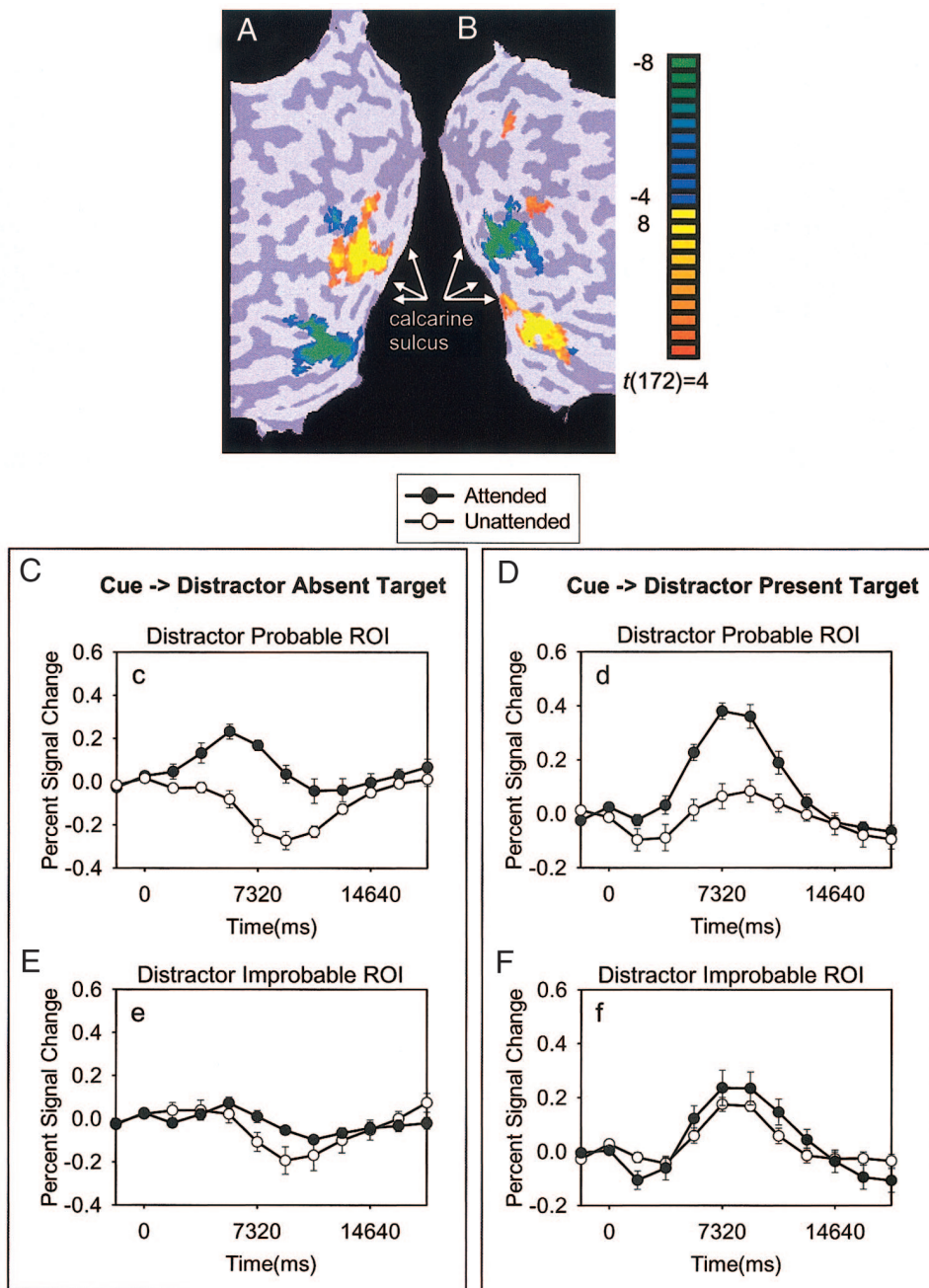


FIG. 2. A and B: statistical maps showing the regions of interest (ROIs) corresponding to distractor-probable and distractor-improbable cue locations for a single subject. Activations are projected onto a computationally flattened cortical surface. A: left hemisphere visual cortex showing the ROIs activated by the top right target (blue-green in left ventral occipital cortex) and the bottom right target (red-yellow in left dorsal occipital cortex). B: right hemisphere visual cortex showing the ROIs activated by the bottom left target (blue-green in right dorsal occipital cortex) and the top left target (red-yellow in right ventral occipital cortex). C-F: group average cue-evoked blood oxygenation level-dependent (BOLD) time course from ROIs corresponding to distractor-probable and distractor-improbable cues as a function of whether distractors appeared in the ensuing target display. C and D: BOLD responses evoked by distractor-probable cues when the cue was followed by distractor-present (C) and distractor-absent target displays (D). E and F: BOLD responses evoked by distractor-improbable cues when the cue was followed by distractor-present (E) and distractor-absent target displays (F). Note that an error bar is plotted for every point; some are smaller than their symbol.

ROIs were restricted to the regions of occipital cortex that were contralateral and inverted relative to the target location, in accordance with the known retinotopic anatomy of early visual cortical regions.

Data from the attention task were collected in 10 runs, with 40 trials and 200 time points in each run. Event-related averaging of the BOLD time series data from each functional ROI was carried out by defining a temporal window extending from 1 TR (1,830 ms) before cue display onset to 10 TRs (18,300 ms) after the cue onset. The BOLD signal was then averaged within this temporal window for each of the different cueing conditions. The 0% baseline for calculating percentage signal change was defined as the average BOLD signal during the 1 time point preceding each event type. Note that event-related averaging of the BOLD signal was used to quantify the BOLD response to the cueing elements in each of the corresponding localizer-defined ROIs, rather than modeling the cue-evoked BOLD responses using a general linear model (GLM) (e.g., Dale and Buckner 1997). We did not use a GLM to estimate the evoked BOLD response because this method assumes that the duration of the evoked BOLD response to a particular event type is fixed. However, in the present experiment, the duration of the cue-evoked response is likely to vary with the duration of the (variable) cue-target stimulus onset asynchrony (SOA), potentially leading to inaccurate estimates of the responses evoked by the cues and targets, respectively. By instead analyzing event-related averages of the BOLD signal from independently localized ROIs, we avoid the potential problems associated with a GLM estimate of the event-related time series in the present experimental design. However, because the cues and targets were separated by only 2,500–8,500 ms, the cue-evoked responses overlapped with the temporally adjacent target responses. We therefore analyzed the cue-evoked responses separately for distractor-absent and distractor-present target displays to examine the possible contribution of target-evoked responses.

RETINOTOPIC MAPPING. Retinotopic maps were obtained for a subset of the subjects ($n = 6$) using previously described procedures (Serenio et al. 1995; Slotnick and Yantis 2003). The boundaries between ventral visual areas V1, V2, VP, and V4v were identified and the time series within the target-selective ROIs were extracted separately for each of these visual areas. We focus selectively on ventral visual regions because of difficulty resolving the boundaries of dorsal visual areas in several of the subjects. The event-related BOLD time course was computed for an area encompassing about 25 cm² of each visual area on the flattened cortical sheet. To quantify the responses, the mean percentage signal change for time points 2–6 poststimulus was computed for the cue-evoked response in each visual area as a function of whether the ROI in question was cued (and therefore attended on that trial) or not cued. The mean response when each ROI was attended was then subtracted from the response when that ROI was unattended, yielding an index of the cue-evoked preparatory activity in each visual area. Because no interaction was observed in the group data between the size of attention effects and the type of target display that followed the cues, the time courses from each visual area were collapsed across target display type.

Results and discussion

BEHAVIORAL DATA. Performance on distractor-present trials was significantly better when distractors were likely than when they were unlikely [$t(11) = 5.95$, $P < 0.001$]. However, on distractor-absent trials, the probability of distractors had no effect [$t(11) = 1.8$, ns], yielding a significant interaction between display type and distractor probability [Fig. 1C, $F(1,11) = 32.9$, $P < 0.0005$]. If a high probability of distractors led to an increase in signal enhancement, then performance in both distractor-present and distractor-absent trials should have exhibited better performance when distractors were probable than when they were improbable, given that amplified sensory signals should be beneficial whether or not the display contains interference (and the staircase exposure duration procedure ensured that difficulty was matched in the distractor-absent and distractor-present trials). In addition, previous studies using variants of this paradigm have shown that it is sensitive to spatial cueing effects (valid – invalid target discrimination accuracy) on distractor-absent trials (Awh et al. 2003). Although we were not able to assess spatial cueing effects directly in the present study because we used 100% valid spatial cues, it is likely that signal enhancement was operating to some extent in all conditions of the present experiment as well. However, the psychophysical data show that the probability manipulation caused changes in distractor suppression and not signal enhancement. Therefore by enabling a direct comparison between conditions that vary only in terms of the degree of suppression, this paradigm allows a direct assessment of the relationship between endogenous distractor suppression and preparatory activity in visual cortex.

FMRI DATA. A visual stimulation procedure was used to define ROIs specifying the areas of visual cortex that processed the cue/target locations. Separate ROIs were determined for the distractor-probable and distractor-improbable locations (see METHODS and Fig. 2, A and B). To characterize preparatory activity in visual cortex, all further analyses focused on the cue-evoked changes in the BOLD signal from these ROIs during the attention experiment.

We introduced temporal jitter to minimize contamination of the cue-evoked BOLD responses by subsequent target-evoked responses. However, cue type and target type were yoked in this experiment: distractor-probable cues were followed 80% of the time by distractor-present displays and distractor-improbable cues were followed 80% of the time by distractor-absent displays. Thus any difference in the cue-evoked response in these 2 conditions could be attributable to larger target-evoked responses in the distractor-probable condition than in the distractor-improbable condition. Thus in the analysis that follows, we present the cue-evoked response separately for cues followed by distractor-present displays and cues followed by distractor-absent displays. All analyses were carried out on time courses computed by defining a temporal window extending from 1,830 ms before event onset to 18,300 ms after event onset and averaging all evoked BOLD responses to a given cue type over this temporal window. The baseline, or 0% signal change, is the average BOLD signal level during the time point preceding the event onset.

Figure 2, C–F depict the cue-evoked responses from the ROIs for the distractor-probable and distractor-improbable cue locations. A 3-way ANOVA (ROI \times locus of attention \times

display type, collapsing across time points 1–10 poststimulus) was performed to evaluate the cue-evoked preparatory responses in distractor-probable and distractor-improbable ROIs. Overall, attended cues (closed symbols) evoked a larger response than unattended cues [open symbols; $F(1,11) = 8.8$, $P < 0.05$]. However, this attention effect was primarily driven by cue-evoked responses in the distractor-probable ROIs (Fig. 2, *C* and *D*), yielding a significant interaction between ROI and the locus of attention [$F(1,11) = 41.2$, $P < 0.001$]. Therefore preparatory attention effects were significantly larger in the condition where the psychophysical data indicate higher levels of distractor suppression. Recall that a staircase timing procedure was used to equate accuracy across distractor-absent and distractor-present displays, ruling out differences in difficulty as a potential explanation for the enhanced responses to distractor-probable cues.

As expected, cues followed by distractor-present displays evoked a larger overall response than cues followed by distractor-absent displays [compare Fig. 2, *D* and *F* with Fig. 2, *C* and *E*; $F(1,11) = 5.9$, $P < 0.05$], presumably because of differences in the sensory response to distractor-present displays. However, a 2-way ANOVA comparing the size of attention effects in distractor-probable ROIs revealed that the target display type (distractor-present vs. distractor-absent) did not interact with the magnitude of the attention effects [$F(1,11) = 0.67$, ns]. This disconfirms the alternative hypothesis that the heightened attention effect in the distractor-probable ROI was caused by the sensory response to distractor-present target displays (which were more likely after distractor-probable cues). Furthermore, a 2-way ANOVA examining attention effects over time points 1 and 2 postcue revealed that the attention effect in distractor-probable ROIs was already significant at 3,660 ms after cue onset, just 1,160 ms after the earliest possible target display [$F(1,11) = 7.7$, $P < 0.05$]. Any effect driven by the target display should not appear until 2–3 s after its onset because of the temporal delay typically observed with an evoked BOLD response in visual cortex (Boynton et al. 1996).

Because the behavioral data show that the distractor-probable cues elicited increased levels of distractor suppression without changes in the degree of signal enhancement, we conclude that the cue-evoked responses reflect preparatory increases in neural activity related to distractor suppression. Although it may be counterintuitive that an increased BOLD signal corresponds to increases in the level of distractor suppression, the BOLD response is known to be modulated by both excitatory and inhibitory neural activity (Caesar et al. 2003; Logothetis et al. 2001; Smith et al. 2002). Thus these preparatory responses may reflect inhibitory interactions among regions of cortex representing target and distractor locations that occur before the onset of the stimulus array.

To further characterize the BOLD response in the ROIs defined in occipital cortex, retinotopic maps were acquired for 6 of the original subjects (Sereno et al. 1995; Slotnick and Yantis 2003). The retinotopic maps were used to divide the functional ROIs into ventral visual areas V1, V2, VP, and V4v. Because target display type did not interact with the size of attention effects, cue-evoked responses from each visual area were collapsed across target display type for clarity. A 2-way ANOVA (visual area \times ROI) revealed that cue-evoked preparatory effects were larger in distractor-probable ROIs com-

pared with distractor-improbable ROIs [$F(1,5) = 20.4$, $P < 0.01$], consistent with the group data above (Fig. 3). In addition, the size of the preparatory attention effects increased across visual area [$F(3,15) = 3.6$, $P < 0.05$], but this increased attention effect did not vary as a function of distractor probability [i.e., the interaction between visual area and ROI, $F(3,15) = 0.36$, was not significant].

The BOLD responses evoked by distractor-probable cues were greater than those evoked by distractor-improbable cues, and we argue that this is a manifestation of endogenous distractor suppression during the preparatory interval. However, the close temporal proximity of the cues and targets in *experiment 1* does not permit a full assessment of the time course of the cue-evoked preparatory activity because the cue-evoked responses overlapped substantially with the target responses. To address this issue, we performed a second experiment that used a 12-s cue-target SOA, permitting a clear separation of the cue-evoked and target-evoked responses. Furthermore, we minimized the cortical sensory responses to the cuing elements by using hollow, rather than filled, cue symbols.

EXPERIMENT 2

Methods

All methods in *experiment 2* replicated those in *experiment 1* except where noted.

SUBJECTS. Twelve neurologically intact young adults (5 females), age 18–30 yr, gave written informed consent to participate in the study, which was approved by the University of Oregon institutional review board. None of the subjects run in *experiment 1* participated in *experiment 2*.

BEHAVIORAL TASK. The behavioral protocol followed that of *experiment 1*, except that the cue-target SOA was either 6 s (± 1 s) or 12 s (± 1 s), equally represented and randomly interleaved in each run. The intertrial interval (ITI) after target presentation varied randomly from 2,750 to 7,750 ms (equally represented). On those trials with a short SOA, an additional 6 s was added to the ITI (making all “trials” an average of 12 s in duration).

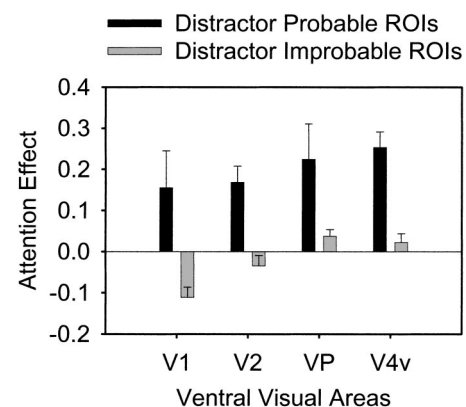


FIG. 3. Difference in cue-evoked responses for attended vs. unattended cues (attention effect) plotted separately for distractor-probable and distractor-improbable ROIs in ventral visual areas V1, V2, VP, and V4v. Data are from a subset of the subjects ($n = 6$) that participated in *experiment 1*. Error bars: ± 1 SE.

The stimulus dimensions and display characteristics were identical to those used in *experiment 1* except that the fixation point and the cueing elements were rendered as hollow outlines; this was done to minimize the sensory response evoked by the cueing elements. Because of the long cue-target SOAs in *experiment 2*, only half as many event-related responses were collected as in *experiment 1* (20 trials per block). The staircase timing procedure (performed in the scanner) yielded mean exposure durations of 125 ms (SD: 24 ms) for targets with distractors and 66 ms (SD: 19 ms) for targets without distractors. Note that these exposure durations are somewhat smaller than those obtained in *experiment 1*. We speculate that this difference arose because the cuing elements in *experiment 2* were outlined circles and squares rather than solid shapes; this small display change was intended to mute forward masking of the targets from the cues.

FMRI SCANNING. MRI scanning was performed on a Siemens Allegra 3T scanner at the Lewis Center for Neuroimaging, University of Oregon. Anatomical images were acquired using an MP-RAGE T1-weighted sequence that yielded images with a 1-mm isovoxel resolution (TR = 2,500 ms, TE = 4.38 ms, flip angle = 8°, inversion time = 1,100 ms). Whole brain EPIs were acquired in 32 transverse slices (TR = 2,000 ms, TE = 30 ms, flip angle = 80°, matrix = 64 × 64, FOV = 220 mm, slice thickness = 4 mm, no gap). The same EPI parameters were used for the functional localizer scans. Localizer data were collected in 2 runs (88 time points/run); data from the attention task were acquired in 10 runs (180 time points/run).

DATA ANALYSIS. As in *experiment 1*, ROIs were defined in visual cortex corresponding to the spatial location of the 4 cueing elements; event-related averages were then used to evaluate the BOLD signal within these ROIs during the attention task. Just as in *experiment 1*, separate ROIs were defined for the distractor-probable and distractor-improbable positions. The mean cue-evoked event-related average BOLD time course during the attention task was computed based on a temporal window extending from 1 time point (2 s) before cue onset to 14 time points (28 s) after cue onset. The increased width of the temporal window (28 s compared with 18.3 s in *experiment 1*) was adopted to account for the increased duration of the cue-target SOA. The baseline (0% signal change) for the event-related averages was determined as the average activation level during the 2 s before cue onset. Because the cues and targets were separated by a sufficient amount of time in *experiment 2*, we did not bin cue responses according to target type (as was done in *experiment 1*). Instead, we restricted our analysis to the temporal interval consisting of the 2 time points immediately before target onset, collapsed across SOA. By focusing on this temporal interval, we could be sure that any cue-related attentional modulations were not caused by sensory differences (i.e., distractors present or absent) in the target displays.

Results and discussion

BEHAVIORAL DATA. The behavioral data were collapsed across the short and long SOA conditions and are presented in Fig. 4. A paired 2-tailed *t*-test revealed that the effect of distractor probability was significant when distractors were present [$t(11) = 3.65, P < 0.01$] and not when distractors were absent

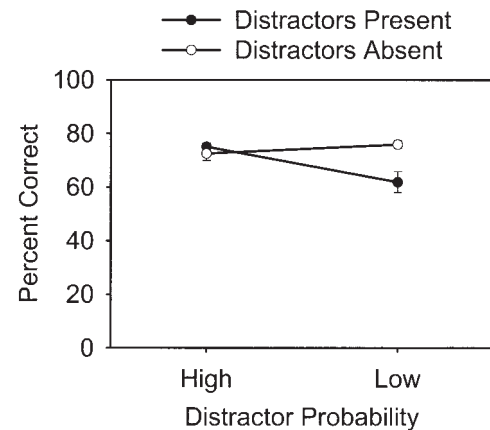


FIG. 4. Accuracy on the behavioral task (data collected in the scanner) for *experiment 2*, collapsed across short and long stimulus onset asynchrony (SOA) conditions.

[$t(11) = -0.98, ns$], yielding a significant interaction between display type and distractor probability [$F(1,11) = 13.3, P < 0.005$]. These data mirror the results of *experiment 1* showing that a high probability of distractors improved performance by suppressing the effects of distractors (which could occur only when distractors were present) and not by increasing signal enhancement (which, if present, would have been seen in both distractor-present and distractor-absent conditions).

FMRI DATA. Figure 5, A–D depict the cue-evoked responses from the localizer-defined ROIs during the attention task. Our analysis centers on the mean cue-evoked BOLD response during the 2 time points immediately before target presentation, collapsed across SOA. A 2-way ANOVA (ROI × locus of attention) revealed that attended cues evoked a larger response than unattended cues during the preparatory interval as reflected by a significant main effect of the locus of attention [$F(1,11) = 17.3, P < 0.005$]. However, this BOLD attention effect was larger in the distractor-probable than in the distractor-improbable ROIs, yielding a significant interaction between ROI and the locus of attention [$F(1, 11) = 6.9, P < 0.025$].

Experiment 2 replicated the key finding from *experiment 1*: preparatory activity before target onset was greater in the distractor-probable than in the distractor-improbable cortical regions. This result was obtained using an extended cuing interval that provided a measurement of cue-evoked responses uncontaminated by responses to target displays. Here again, the psychophysical and neuroimaging data suggest that this cue-evoked activity reflects endogenous distractor suppression in preparation for an upcoming display containing a dense array of distractors.

DISCUSSION

Previous reports have demonstrated that preparatory activity in visual cortex occurs even before the appearance of a visual target (Hopfinger et al. 2000; Kastner et al. 1999; Luck et al. 1997; Muller and Kleinschmidt 2003; Ress et al. 2000). The fMRI results from *experiment 1* showed that preparatory activity is more pronounced when interference from distractors is likely. *Experiment 2* replicated this finding and confirmed that the attentional modulations reported in *experiment 1* reflect sustained cue-related responses, and not target-evoked sensory or attention effects.

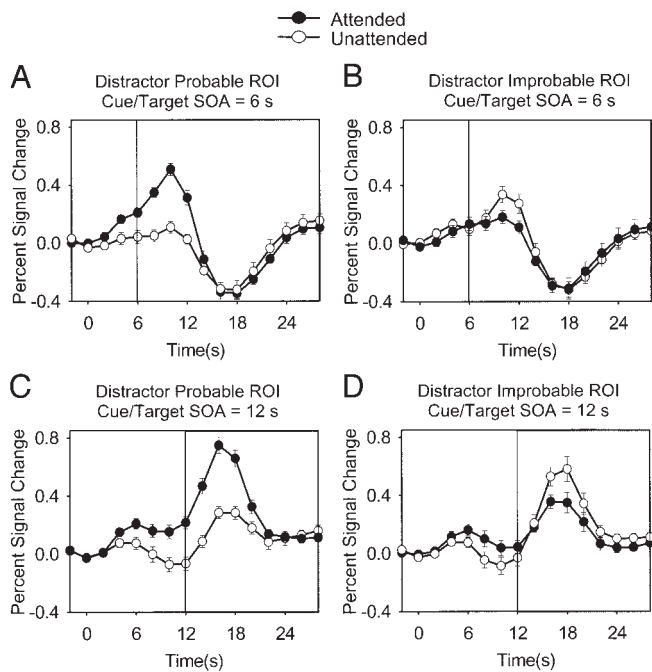


FIG. 5. *A–D*: group average cue-evoked BOLD time course from (*A*) distractor-probable and (*B*) distractor-improbable ROIs, respectively, in the 6-s SOA condition of *experiment 2*. *C* and *D*: corresponding time courses from the 12-s SOA condition. Cue appeared at *time 0* and the target was presented (on average) at time point 6 in the short SOA condition and at time point 12 in the long SOA condition. Shaded regions indicate data from the time points after target onset. Note that the target responses vary considerably in each panel; this occurred because the distractor-probable cues were followed 80% of the time by a distractor-present target display, which resulted in a relatively large target-evoked response. This association between display type and the cued locations is the reason that the target-evoked responses in the distractor-improbable condition were larger in the unattended condition; the unattended trials in this condition were associated with a greater incidence of distractor-present displays. Error bars: ± 1 SE. Note that an error bar is plotted for every point; some are smaller than their symbol.

One challenge for understanding the effects of spatial attention is that both signal enhancement and distractor suppression contribute to selective visual attention. The present studies isolated a distractor suppression component of selection, while holding constant the contributions from signal enhancement. The behavioral data show that the distractor probability manipulation had a selective influence on distractor-present trials; no effects of distractor probability were observed when distractors were absent. The null probability effect on distractor-absent trials suggests that the probability manipulation did not modulate signal enhancement processes because changes in signal enhancement should affect performance even in the absence of distractors.

Of course, this conclusion depends on the assumption that performance with the distractor-absent displays would have been affected by changes in the degree of signal enhancement. Two arguments suggest that the present procedure was in fact sensitive to potential changes in signal enhancement. First, the staircase timing procedure ensured that target discrimination difficulty was well matched with the distractor-absent and distractor-present displays. Thus accuracy with the distractor-absent displays was in the proper range for detecting changes in the degree of signal enhancement. More important, previous research using almost identical stimulus displays and staircase procedures (Awh et al. 2003) has demonstrated reliable spatial

cueing effects (i.e., better target discrimination at attended relative to unattended locations) with the distractor-absent displays, an effect that is most naturally explained in terms of increased signal enhancement at the attended locations. Thus the fact that performance with the distractor-absent displays was not affected by distractor probability suggests that the probability manipulation did not elicit changes in signal enhancement.

Previous demonstrations of baseline shifts have been reported in the absence of a peripheral cueing element marking the to-be-attended location (Kastner et al. 1999). In contrast, the preparatory activity reported here was evoked by the appearance of cueing elements in the 4 potential target locations. Thus the BOLD responses could have been affected by competition between the multiple cue stimuli. However, such putative interactions cannot account for the amplified preparatory activity that was observed in the distractor-probable trials because the number of cueing elements—and therefore the competition between these elements—was identical in the distractor-probable and the distractor-improbable conditions. Thus we conclude that the amplified preparatory activity in the distractor-probable trials was a product of changes in the observers' attentional control settings for distractor suppression, with increased preparatory activity when distractors were likely.

As shown in Figs. 2 and 5, increasing the probability of distractors leads to an increased BOLD response at attended locations. One might not have expected this pattern of BOLD response: distractor suppression most readily suggests an attenuated signal in the cortical regions representing the areas of space immediately surrounding the cue locations. However, the precise nature of the BOLD response is still under debate, and this complicates interpretation. Most current theories suggest that the BOLD signal reflects a combination of both excitatory and inhibitory activity (Caesar et al. 2003; Logothetis et al. 2001; Smith et al. 2002); several possible mechanisms are therefore consistent with the observed increase in the BOLD signal. For instance, the heightened BOLD response may be driven by the increased activity of inhibitory interneurons, reflecting mutually suppressive interactions between the cue-driven regions and surrounding areas of cortex. This explanation is consistent with findings from single-unit neurophysiology, which suggest that attention gates inhibitory input from neighboring neurons (Reynolds et al. 1999). However, given uncertainty about the relationship between excitatory and inhibitory neural activity and BOLD, specification of the neural mechanisms underlying the present data must await further study.

Although the present results show that preparatory attention effects are selectively enhanced when a high degree of distractor interference is likely, previous reports of preparatory activity are at least superficially consistent with signal-enhancement mechanisms. For example, Ress et al. (2000) showed that increased preparatory activity in V1 is positively correlated with performance on a difficult grating-detection task—with no visual distractors present in the visual field. However, the stimulus consisted of a textured ring extending from 3 to 6° in the periphery; the foveal aspect of the stimulus consisted of the steady-state background. Therefore when detecting a very faint gradient in the periphery, it would be advantageous to suppress those aspects of the visual scene that correspond to the back-

ground color (or visual “noise”; see, e.g., Shiu and Pashler 1994). The studies by Kastner et al. (1999) and Luck et al. (1997) involve instances where the stimuli are alternately presented with and without concurrent distractors—perhaps inducing subjects to engage in preparatory distractor-suppression processes. In all of these paradigms, including the present study, both signal-enhancement and distractor-suppression aspects of selection are likely to occur. However, because none of these previous experiments systematically varied the degree of distractor suppression, it was not possible to separate the neural responses that were associated with enhancement and suppression, respectively. The present paradigm directly manipulated the distractor-suppression component of selection and thereby provides direct evidence that distractor suppression can drive preparatory cortical activity.

To summarize, in 2 experiments we find that preparatory activity in visual cortex is driven by distractor suppression during visual selection. The psychophysical data demonstrate that changes in distractor probability induced changes in distractor suppression without concurrent changes in signal enhancement. The fMRI data reveal that the preparatory activity induced by attention is selectively enhanced when and where distractors must be suppressed. We conclude that this preparatory activity is directly linked to endogenous distractor suppression during covert spatial orienting.

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