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NeuroImage

NeuroImage 19 (2003) 1602–1611

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## Attentional inhibition of visual processing in human striate and extrastriate cortex

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Received 17 December 2002; revised 18 February 2003; accepted 18 March 2003

### Abstract

Allocating attention to a spatial location in the visual field is associated with an increase in the cortical response evoked by a stimulus at that location, compared to when the same stimulus is unattended. We used event-related functional magnetic resonance imaging to investigate attentional modulation of the cortical response to a stimulus probe at an attended location and to multiple probes at unattended locations. A localizer task and retinotopic mapping were used to precisely identify the cortical representations of each probe within striate (V1) and extrastriate cortex (V2, VP, V3, V4v, and V3A). The magnitude and polarity of attentional modulation were assessed through analysis of event-related activity time-locked to shifts in spatial attention. Attentional facilitation at the attended location was observed in striate and extrastriate cortex, corroborating earlier findings. Attentional inhibition of visual stimuli near the attended location was observed in striate cortex, and attentional inhibition of more distant stimuli occurred in both striate and extrastriate cortex. These findings indicate that visual attention operates both through facilitation of visual processing at the attended location and through inhibition of unattended stimulus representations in striate and extrastriate cortex.

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### Introduction

A large body of evidence has revealed that the deployment of attention to a location in space enhances the neural representation of a visual stimulus presented at that location. Both single-cell recording in monkey (e.g., Moran and Desimone, 1985; Motter, 1993, 1994; Connor et al., 1997; Vidyasagar, 1998) and event-related potential (ERP) recording and functional magnetic resonance imaging (fMRI) in human (e.g., Mangun and Hillyard, 1988; Heinze et al., 1994; Gomez Gonzalez et al., 1994; Clark and Hillyard, 1996; Tootell et al., 1998; Watanabe et al., 1998; Brefczynski and DeYoe, 1999; Martinez et al., 1999; Somers et al., 1999; Hopfinger et al., 2000, 2001; Martinez et al., 2001; Woldorff et al., 2002; Seiple et al., 2002; Slotnick et al.,

2002a; Yantis et al., 2002) have shown an increase in the magnitude of the neural response in both striate (V1) and extrastriate cortex when a visual stimulus is attended, compared to the response evoked by the same stimulus when it is unattended. This attentional facilitation occurs in early visual areas contralateral to the spatial location of the stimulus (i.e., attention to right visual field stimuli elicits left hemisphere attention effects and vice versa) and more specifically maps onto the retinotopic representations of the stimulus (Tootell et al., 1998; Brefczynski and DeYoe, 1999; Martinez et al., 2001).

Recent behavioral evidence has revealed regions of attentional inhibition surrounding a region of attentional facilitation, suggesting that a purely facilitative model of attention may be incomplete (Cepeda et al., 1998; Bahcall and Kowler, 1999; Mounts, 2000a, 2000b). These behavioral findings compliment previous ERP results, where it has been suggested that the ERP N1 component reflects attentional enhancement at the attended location and the P1 component reflects attentional suppression at unattended

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locations (Luck, 1995). A model of attention that includes both facilitation of the attended stimulus and inhibition of distracting stimuli is appealing because such inhibition would increase the perceived contrast of an attended object (relative to a facilitatory process alone), thus allowing for more effective visual scene segmentation. In contrast to the growing body of evidence concerning attentional facilitation effects in early visual areas, little is known regarding the neural substrates of attentional inhibition.

Using ERP cortical source localization, Slotnick et al. (2002a) reported evidence for both attentional facilitation at the attended location and attentional inhibition of surrounding stimulus probes. In that study, because the cortical sources were organized in accordance with the known retinotopic pattern and cortical magnification of V1 (Slotnick et al., 1999, 2001), it was argued that facilitatory and inhibitory attention effects occurred in this visual area. The purpose of the present investigation was to replicate the attentional inhibition effect in V1 using fMRI (to confirm the cortical basis of the effect), to determine whether attentional inhibition also extends to extrastriate areas, and if so, to determine the spatial distribution of both facilitatory and inhibitory attention effects in these visual areas.

The attention analysis employed in the present study focused on transient changes in event-related activity associated with contralateral and ipsilateral shifts in spatial attention. As shown previously (Müller et al., 1998; Yantis et al., 2002), a shift of attention from ipsilateral to contralateral space yields an increase in event-related activity within early visual areas and a shift of attention from contralateral to ipsilateral space yields a decrease in event-related activity within early visual areas. For example, in the stimulus array used in the present study (Fig. 1), consider the predicted attentional modulation within the left ventral cortical representation of the middle probe in the upper right quadrant. If a participant shifted attention from the middle probe in the upper left quadrant to the middle probe in the upper right quadrant (i.e., an ipsilateral to contralateral shift), an increase in event-related activity would be expected, while a shift back to the middle probe in the upper left quadrant (i.e., a contralateral to ipsilateral shift) would result in a decrease in event-related activity.

The opposite pattern of activity would be expected under conditions of attentional inhibition. For example, if attention to the middle probe in a quadrant inhibits the cortical representation of the outer probe in that quadrant, we would predict the representation of the outer probe to exhibit a decrease in event-related activity time-locked to contralateral shifts of attention, and an increase in activity following ipsilateral shifts of attention, the latter effect being driven by a release of inhibition.

## Materials and methods

### Participants

Six adults (4 women) participated in the study. All participants had normal or corrected-to-normal visual acuity and were between 22 and 35 years old. The experimental protocol was approved by the Johns Hopkins University institutional review board, and informed consent was obtained from each participant.

### Attention task and event-related time course analysis

The stimulus consisted of checkerboard probes scaled according to the human cortical magnification factor, assuming  $E_2 = 0.50$  and  $A = 22$  (Slotnick et al., 2001). Probe sizes were selected to balance the robustness of the cortical response they would elicit while maintaining spatially separable cortical representations, with an interprobe cortical distance of 7 mm resulting in inner, middle, and outer probes measuring  $0.61^\circ$ ,  $0.96^\circ$ , and  $1.9^\circ$  visual angle along each edge and centered at  $2.3^\circ$ ,  $4.2^\circ$ , and  $7.2^\circ$  visual angle from fixation within each quadrant (Fig. 1). All probes were simultaneously and continuously present, and reversed in contrast 5 times/s. Participants were instructed to maintain central fixation and to switch attention between the middle probes in the upper right and upper left visual field following instructional cues.

Every 3–7 s, a randomly selected element within each probe flashed either red or green. Participants had been trained outside the scanner to interpret a red element within the attended probe as a cue to shift attention to the corresponding probe in the opposite hemifield and a green element as a cue to maintain attention at the currently attended location. Shift and hold cues were equally probable, with the constraint that no more than two hold cues occurred sequentially in an attended probe, to eliminate long periods of sustained attention. Participants indicated which probe was currently attended by continuously holding down either the left or right response button with the thumb of their preferred hand (the nonpreferred hand was at rest). All participants completed two 4-min 48-s attention runs, each with a trailing 14-s period of fixation.

Before fMRI preprocessing (described below), the first 5 time points of each attention run were deleted to remove stimulus onset-related activity; the two attention runs were then concatenated. Although the canonical hemodynamic response model has been shown to be accurate in modeling sustained sensory events with long intertrial intervals (Boynton et al., 1996; Cohen, 1997; Miezin et al., 2000), both theoretical and empirical results have shown that this hemodynamic response model may be less accurate in its description of rapid event-related protocols (e.g., Dale and Buckner, 1997; Burock et al., 1998; Clark et al., 1998; Buckner et al., 1998; Kourtzi and Kanwisher, 2001). To circumvent this potential limitation, a general linear model

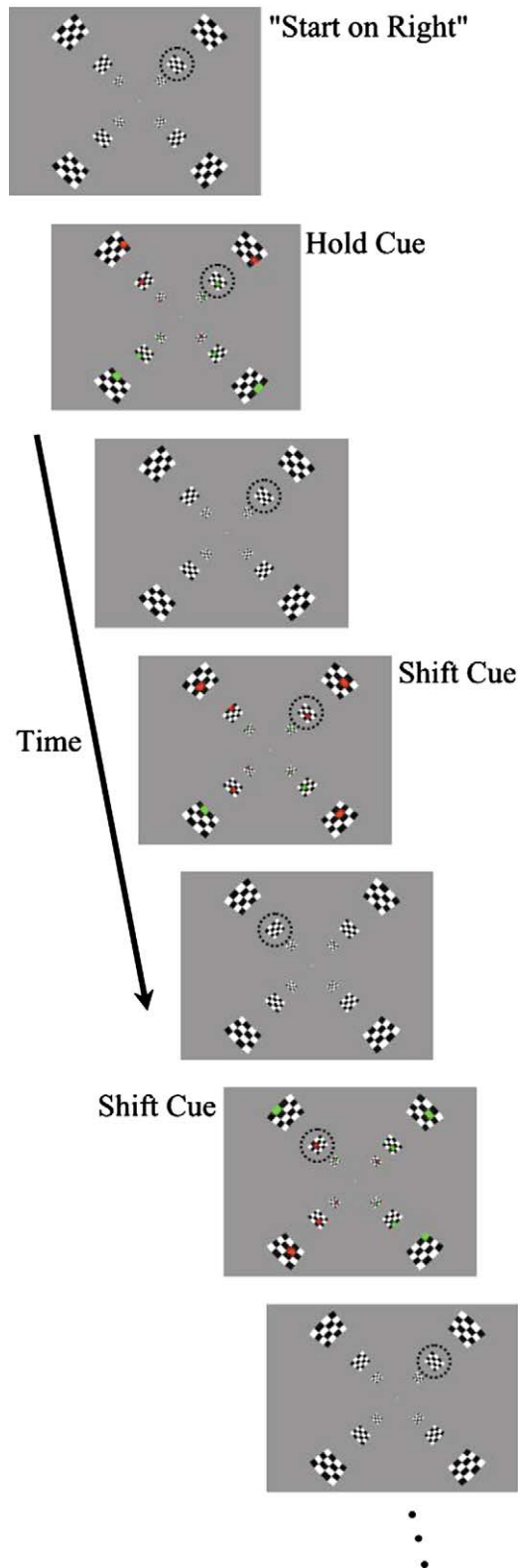


Fig. 1. Contrast reversing checkerboard stimulus used during the attention task. A dotted circle (not shown during the experiment) surrounds the attended probe. The top panel illustrates prerun verbal instruction orienting a participant to attend to the stimulus probe in the middle of the upper right quadrant. Within the attended probe, a red element cued participants to shift attention to the middle probe in the opposite upper quadrant, while a green element cued maintenance of attention to the same location.

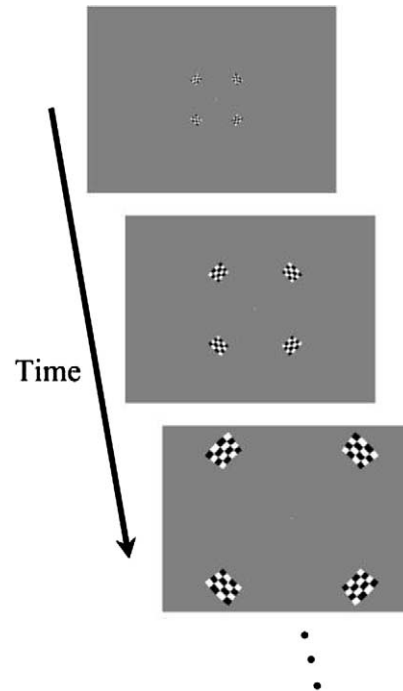


Fig. 2. Contrast reversing checkerboard stimulus used to localize probes in early visual areas. Each display was presented for 12 s and then the cycle repeated. Participants responded when a red element flashed within any stimulus probe (not shown).

was not used in the attention analysis. Rather, event-related activity time courses were retrieved from each stimulus probe representation on the cortical surface as identified from the localizer analysis (see below). Analysis of event-related activity associated with shifts of attention was restricted to trials in which participants correctly shifted attention following a shift cue, as indicated by their behavioral responses.

To ensure increases and decreases in event-related activ-

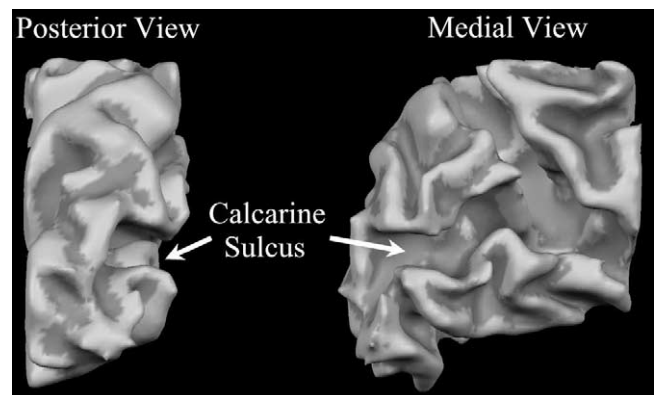


Fig. 3. Left hemisphere cortical surface region-of-interest (ROI) for one participant. Gyri are colored light gray; sulci are colored dark gray. This ROI included early visual areas, as determined by retinotopic mapping, and was used to calculate the total number of voxels used in Bonferroni correction for multiple comparisons.

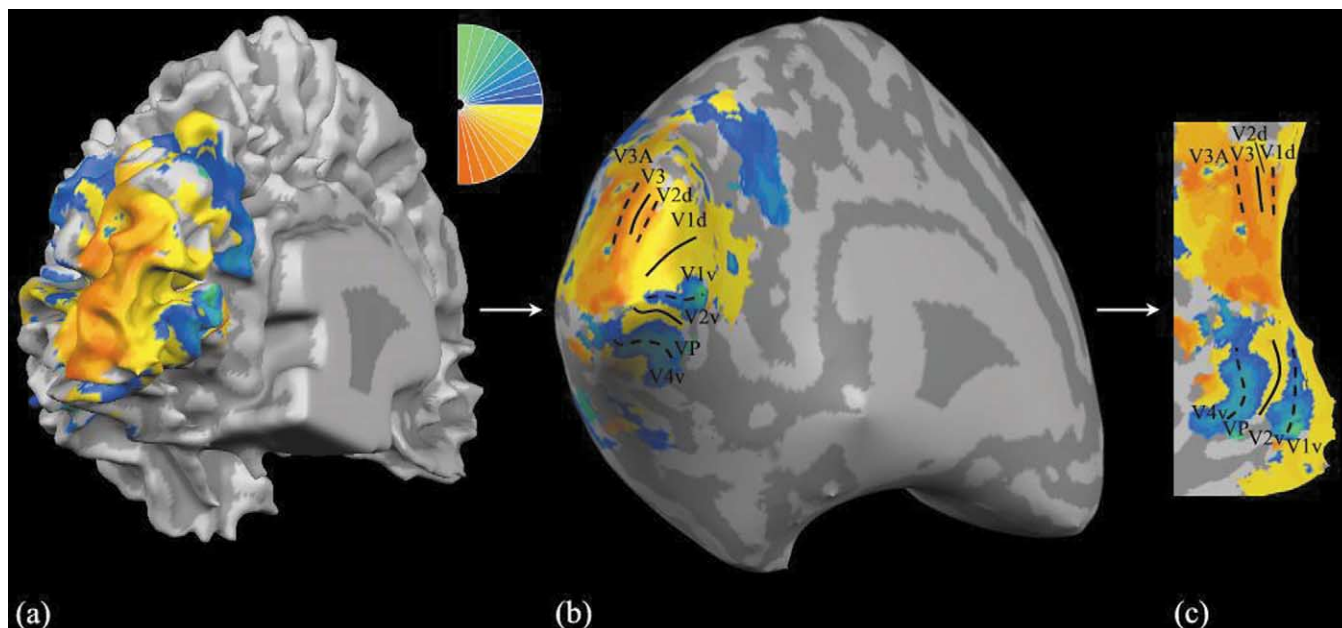


Fig. 4. (a) Left hemisphere cortical surface reconstruction of one participant, with retinotopic map of the right visual field. Colors represent unique stimulus positions in the right visual field (see color wheel). Note that the lower visual field quadrant maps onto dorsal visual areas and the upper visual field quadrant maps onto ventral visual areas. (b) Inflation of the same surface and retinotopic map with borders between visual areas and early visual areas identified. Solid black lines demarcate multiple representations of the right hemifield horizontal meridian and dotted lines demarcate vertical meridians. (c) Flattened cortical region consisting of early visual areas. The rightmost edge of the surface is the base of the calcarine sulcus and demarcates the V1 horizontal meridian.

ity were not influenced by preceding events, and given that measurable event-related activity is known to lag event onset by approximately 2 s, event-related activity time courses were set to 0% signal change at 2 s following stimulus onset (i.e., time point 1, the moment when event-related changes were expected to begin). In this way, the analysis was refined by focusing on the transient increases and decreases in event-related activity associated with shifts in attention. Additionally, as the hemodynamic response was expected to reach its maximum amplitude by 6 s following stimulus onset (Boynton et al., 1996; Cohen et al., 1997; Miezen et al., 2000), statistical assessment of differences between contralateral shift-related and ipsilateral shift-related activity was restricted a priori to time point 3 (6–8 s after shift onset) using a paired *t* test. Specifically, a positive difference-of-magnitude between contralateral shift-related activity and ipsilateral shift-related activity was diagnostic of attentional facilitation, and a negative difference-of-magnitude was diagnostic of attentional inhibition.

To monitor eye movements, three of the participants also underwent eye tracking using a SensoMotoric Instruments Eyelink System (Teltow, Germany) outside the scanner while performing the same attention task as that used in the scanner.

#### Localizer task and general linear model analysis

A localizer task was used to identify the cortical representations of each probe used in the attention task. During

the localizer runs, inner, middle, and outer probes were sequentially presented for 12 s within each 36-s cycle (Fig. 2). All participants completed two 4-min 48-s localizer runs (8 cycles), each with a trailing 14-s period of fixation. Participants were instructed to maintain fixation and were instructed to press the response button if one element within any of the checkerboard probes flashed red (a task designed to maintain vigilance). Such targets appeared on average once every 15 s, with random temporal jitter.

Before fMRI preprocessing, the two localizer runs were concatenated. Three hemodynamic response models corresponding to inner probe stimulation, middle probe stimulation, and outer probe stimulation were constructed by convolving each 16-cycle protocol with a canonical hemodynamic impulse response function, where  $\delta = 2.5$  and  $\tau = 1.25$  (see Boynton et al., 1996; Cohen, 1997; Miezin et al., 2000). For each voxel, a general linear model was used in which the three hemodynamic response models were fit to the activation time course using the Marquardt least-squares algorithm (Press et al., 1992) to yield model amplitudes (i.e., beta values).

Because the probes were scaled to be separable on cortex, voxels representing inner probe locations were assumed to correlate exclusively with inner probe stimulation. To identify such voxels, a weighted *t* test between the inner probe beta value and the middle and outer probe beta values was used. Voxels correlated with middle and outer probe stimulation were similarly identified. The threshold for significant activation was set a priori to  $P = 0.05$ , Bonferroni

corrected for multiple comparisons. To determine the number of comparisons for use in this statistic, the cortical surface associated with early visual areas, as revealed by retinotopic mapping, was computationally sectioned by using custom software written in MATLAB (The MathWorks, Inc., Natick, MA, USA). Fig. 3 illustrates the left hemisphere region-of-interest (ROI) for one participant (the ROI for all participants was bounded by Talairach coordinates  $x = -29$  to  $+27$ ,  $y = -48$  to  $-102$ , and  $z = +34$  to  $-30$ ). For each hemisphere, the total number of voxels used to determine the corrected significance level included those within 2 mm of the surface ROI (see below). Significant localizer activity (i.e., the cortical representations of each stimulus probe) was projected onto the flattened cortical surface and color-coded yellow, green, and blue, corresponding to the inner, middle, and outer probes, respectively. It is important to note that all probe representations that could unambiguously be identified within early visual areas (i.e., V1v, V2v, VP, V4v, V1d, V2d, V3, and V3A) were subsequently used to assess the effects of attention.

#### *Retinotopic mapping*

To determine the level in the visual cortical hierarchy at which attention effects occurred, retinotopic mapping was conducted for each subject to identify early visual area borders (see Engel et al., 1994, 1997; Sereno et al., 1994, 1995; DeYoe et al., 1996; Tootell et al., 1997; Slotnick et al., 2002b; Slotnick and Yantis, 2003). A new retinotopic mapping technique was used that involves simultaneous stimulation of the left and right hemifields, as this method has been shown to reduce acquisition time without compromising map quality (Slotnick and Yantis, 2003). Rotating checkerboard wedges were  $30^\circ$  in polar angle width, spanned  $0.30$  to  $6.8^\circ$  visual angle, and reversed in contrast 8.3 times/s. Each participant completed eight cycles (42 s per cycle) lasting 5 min 36 s, with an additional 15 s of fixation to allow the hemodynamic response to return to baseline. Retinotopic maps were projected onto cortical surface representations, where borders between visual areas were identified by reversals in phase map color, which were easily identifiable on inflated and flattened cortical representations (Fig. 4). See Slotnick and Yantis (2003) for additional details of the retinotopic mapping procedure.

#### *Image acquisition and preprocessing*

Whole brain T1-weighted anatomic images were acquired using an MPRAGE sequence and a receive-only Philips end-capped quadrature birdcage head coil (12-min 24-s acquisition time, TE 3.7 ms, flip angle  $8^\circ$ , TR 8.1 ms, NEX 1, coronal  $256 \times 256$  matrix, FOV  $256 \times 256$  mm, and  $256 \times 1$  mm slices, no gap, yielding 1-mm isotropic voxels). Occipital T2\*-weighted functional images were acquired by using an echo planar imaging (EPI) sequence with a circular Philips C3 surface coil centered on theinion

of each participant (TE 40 ms, flip angle  $90^\circ$ , foot-to-head phase encoding, coronal oblique  $64 \times 64$  matrix, FOV  $192 \times 192$  mm, and  $20 \times 3$  mm slices, no gap, yielding 3-mm isotropic voxels). Functional images were acquired in an oblique orientation perpendicular to the calcarine sulcus with the most posterior slice positioned to include the occipital pole. A TR of 3 s was used for retinotopic mapping and a TR of 2 s was used for localizer and attention runs; otherwise the EPI sequences were identical.

fMRI analyses were conducted using BrainVoyager (Brain Innovation, Maastricht, The Netherlands). Functional data were slice-time corrected and motion corrected. Retinotopic mapping data were spatially lowpass filtered at 16 cycles/image matrix and temporally bandpass filtered between 3 and 32 cycles/run length. Localizer and attention data were temporally highpass filtered at 5 cycles/run length, and were not spatially smoothed in an effort to maximize spatial resolution. All anatomic and functional data were transformed into Talairach space (Talairach and Tournoux, 1988).

#### *Cortical surface reconstruction*

Both hemispheres within each anatomic volume were individually segmented at the gray matter/white matter boundary, and then the surface of this boundary was reconstructed by using methods similar to those used by others (Sereno et al., 1995; Tootell et al., 1997; Van Essen and Drury, 1997; Dale et al., 1999). The surface of each hemisphere was then smoothed, inflated, cut on the medial surface (one cut was placed at the base of the calcarine sulcus), flattened, and then spatially corrected such that linear distortion was less than 15% (Fig. 4). Functional imaging activation within 2 mm of the smoothed surface was 'painted' onto the associated flattened surfaces for subsequent display and analyses.

## **Results**

#### *Behavioral results*

Mean accuracy (indexed by correctly shifting or maintaining the locus of attention following a given cue) was  $87.6 \pm 8.8\%$ . All three participants who underwent eye-movement tracking during the attention task maintained fixation to within  $0.5^\circ$  of visual angle.

#### *fMRI results*

Fig. 5 illustrates the effects of attention in the left hemisphere of one participant. The cortical representations of inner, middle, and outer probes in the right visual field were localized in accordance with the known retinotopic organization of early visual areas; inner probe representations were closer to the representation of the fovea, and middle

and outer probes representations were progressively more eccentric. Cortical representations of inner, middle, and outer probes are shown in yellow, green, and blue, respectively. As expected, ipsilateral to contralateral shifts of attention increased activity, and contralateral to ipsilateral shifts of attention decreased activity, in extrastriate representations of the upper middle probe. This is illustrated in visual area V2v (within green areas of ventral cortex marked with asterisks) where there was a relative increase in shift contralateral-related activity, shown in red, compared to shift ipsilateral-related activity, shown in black. Attentional facilitation also extended to other stimulus probe representations in ventral cortex, as shown in visual area VP. Inhibitory effects were also evident. Consistent with previous findings (Slotnick et al., 2002a), the inhibitory pattern was revealed in the outer probe representation in ventral visual area V1v. In addition, attentional inhibition dominated many of the lower visual field probe representations in dorsal visual areas, as indicated by the activity profiles in V1d, V2d, and V3. The group average event-related activity associated with the visual areas just described exhibited the same pattern of attentional modulation (Fig. 6).

Group results for all visual areas in which attentional effects were assessed are illustrated in Fig. 7. Note that ventral areas represent the upper visual field (i.e., the quadrants within which attention was directed in this task), while dorsal visual areas represent the lower visual field (where attention was never directed in this task). Therefore, both facilitation and inhibition might be expected in ventral visual areas. In contrast, although we expected to see inhibition in dorsal visual areas (reflecting attentional inhibition in the unattended quadrant of the attended hemifield), we expected little or no attentional facilitation in dorsal visual areas.

Across participants, significant attentional facilitation was observed in all ventral visual areas (V1v, V2v, VP, and V4v). Although significant facilitation was restricted to the representation of the attended probe in V1v, it included both the attended probe and outer probe in V2v, spread to all probes in VP, and was restricted to one probe in V4v. Significant attentional inhibition occurred in ventral visual area V1v, and dorsal visual areas V1d, V2d, and V3. All probe representations were significantly inhibited in V1d while two probes in each of V2d and V3 were significantly inhibited. There were no significant facilitatory effects in dorsal visual areas.

## Discussion

The present results provide evidence for attentionally mediated inhibition in both striate and extrastriate cortex. The attentional inhibition effects in V1 corroborate those reported previously (Slotnick et al., 2002a). In both the Slotnick et al. (2002a) study and the present study, the

inhibitory region included stimuli that were more eccentric than the attended location within the attended quadrant, and extended broadly to stimuli in the unattended quadrant within the attended hemifield. Slotnick et al. (2002a) also reported attentionally mediated facilitation at the attended location that extended toward fixation, a finding that has been reported by others (Collie et al., 2000; Seiple et al., 2002). Although the present results did replicate the V1 facilitatory effect at the attended location (V1v/M), this facilitation did not extend to the probe between the attended location and fixation (V1v/I). However, given that the attention effect in this probe was in the expected facilitative direction, this null finding may have been due to insufficient statistical power.

In contrast to the V1 inhibitory effect within the attended quadrant, there was no evidence for attentional inhibition in extrastriate visual areas within this quadrant. Rather, all extrastriate visual areas within the attended quadrant exhibited only attentional facilitation. The broader facilitation in extrastriate visual areas, coupled with the within-quadrant inhibition in V1, indicate that more spatially restrictive attentional processing may recruit inhibitory mechanisms that operate exclusively at the level of V1, at least within the attended quadrant. In contrast to the absence of extrastriate inhibition within the attended quadrant, attentionally mediated inhibition in the unattended quadrant of the attended hemifield was observed in V1, V2 and V3.

This overall pattern of attentional inhibition may be due to receptive field size differences across early visual areas. In a recent fMRI study, the estimated diameter of human receptive fields at an eccentricity of  $5.5^\circ$  was found to be less than  $2^\circ$  in V1, between  $2^\circ$  and  $4^\circ$  in V2, and between  $4^\circ$  and  $6^\circ$  in V4; in addition, receptive fields in these areas were confined to each quadrant (Kastner et al., 2001). In the present study, only V1 receptive fields were small enough to consistently encompass a single probe, while extrastriate receptive fields frequently encompassed both the attended probe and adjacent probe(s) within the attended quadrant. Stimulus-specific inhibition within the attended quadrant may have been restricted to V1 to avoid concomitant inhibition of the attended probe had extrastriate representations of unattended probes been inhibited. Similar arguments can be used to explain the findings in the unattended quadrant within the attended hemifield. Here, the absence of the attended probe's representation in extrastriate cortex allowed for attentional inhibition of probe representations in both striate and extrastriate cortex. Therefore, one way to attend to a specific stimulus within a crowded visual scene appears to be through selection at the earliest level of the cortical visual hierarchy.

The present results provide a possible neural basis for previous behavioral reports of attentionally mediated inhibition of visual stimuli (Cepeda et al., 1998; Bahcall and Kowler, 1999; Mounts, 2000a). In these studies, attentional facilitation extended approximately  $1^\circ$  from the locus of attention, while attentional inhibition was most pronounced

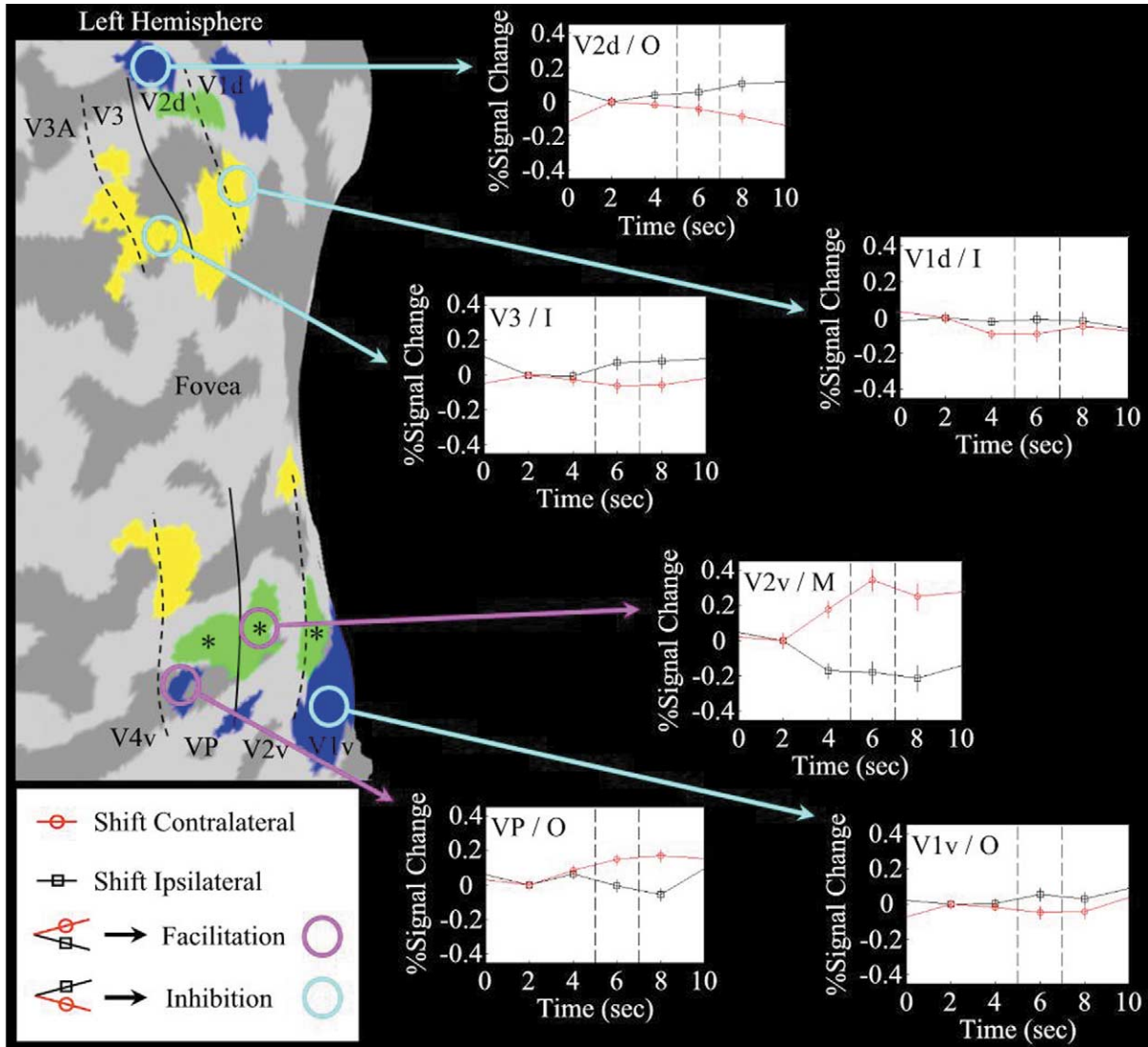


Fig. 5. Attentional modulation in the left hemisphere of one participant. The rightmost edge of the cortical surface demarcates the V1 horizontal meridian. The representation of the fovea is near the center of the surface. Dorsal visual areas are located on the upper half of the surface and ventral visual areas are located on the lower half of the surface. Solid lines represent the right horizontal meridian and dashed lines represent vertical meridians; adjacent meridians bound early visual areas. Significant inner (I), middle (M), and outer (O) probe activity, obtained using the localizer analysis, are shown in yellow, green, and blue, respectively. The cortical representation of the attended probe (middle position in the upper visual field) is shown ventrally in green, and is marked with asterisks. Event-related activity from circled probe representations is shown to the right (one standard error of the mean reported, computed using between trial variance). Visual area and probe type are shown in the upper left of each timecourse plot. Attentional facilitation is indicated by an increase in activity following a contralateral attentional shift and a decrease in activity following an ipsilateral attentional shift, while attentional inhibition is indicated by the reverse pattern of activity (see key to lower left). Time points 6 s following event onset, flanked by dotted lines, were used for statistical assessment of attention effects.

at 1.5°, gradually decreasing to zero by either 3° (Bahcall and Kowler, 1999), 5° (Mounts, 2000a), or by at least 8° (Cepeda et al., 1998) from the attentional locus. In the present study, the distance at which attentional inhibition occurred was up to 8.3° from the locus of attention (i.e., the within-hemifield distance between the upper quadrant-middle probe and the lower quadrant-outer probe), which is similar to the extent of attentional inhibition measured behaviorally. These results suggest that the spatial extent of attentional inhibition may be particularly sensitive to details

of the stimulus and task, as has been shown with attentional facilitation (Eriksen and St. James, 1986; Downing, 1988).

Perceptual load may be an important factor in dictating the spatial extent of attentional inhibition. ERP P1 and N1 components evoked by an attended stimulus (used to quantify attention effects) have been reported to be greater in magnitude under conditions of high perceptual load, compared to low perceptual load (Handy and Mangun, 2000). Moreover, the P1 component elicited by an unattended probe has been shown to be smaller in magnitude under

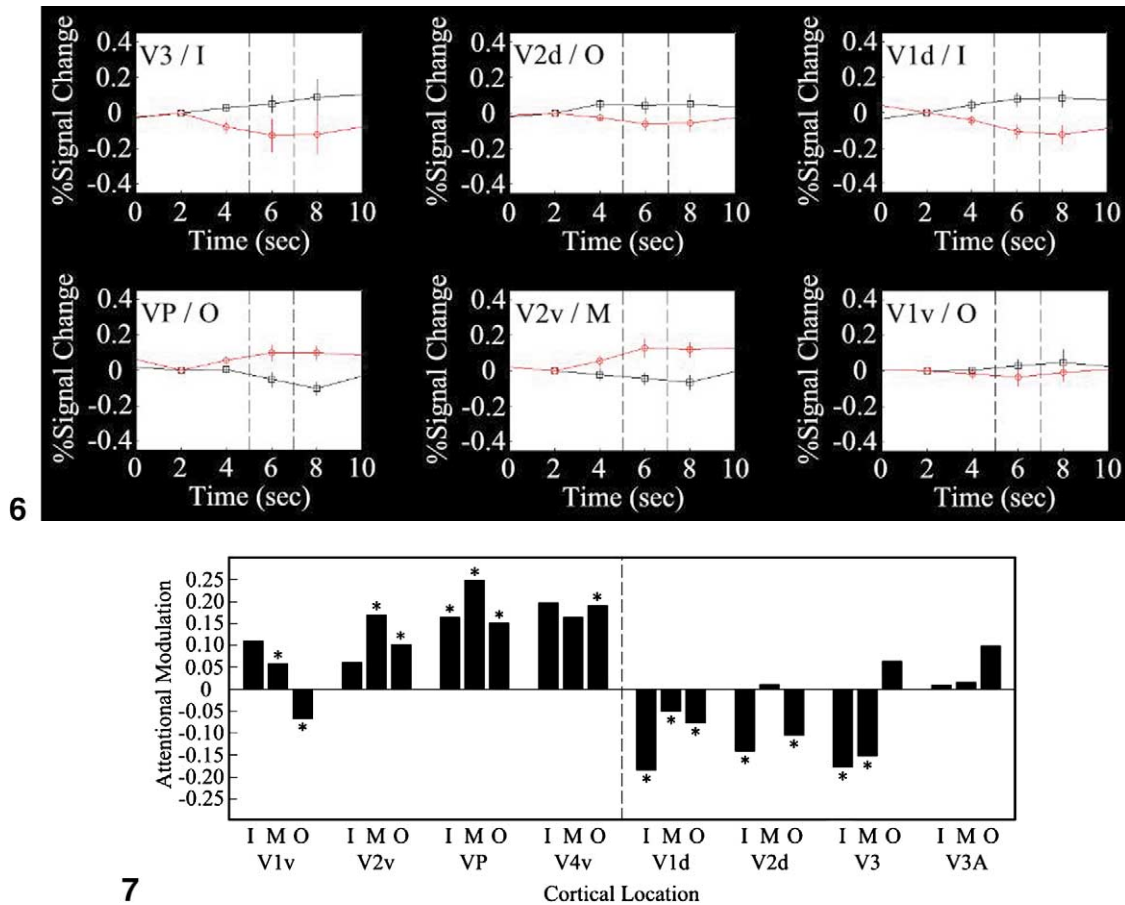


Fig. 6. Group average event-related activity corresponding to the same probe representations evaluated in Fig. 5 (one standard error of the mean reported, computed using between-hemisphere variance).

Fig. 7. Group attention effects in early visual areas. Attentional modulation is defined as the mean difference-of-magnitude 6 s following a contralateral shift compared to an ipsilateral shift. A positive difference-of-magnitude is indicative of attentional facilitation and a negative difference-of-magnitude is indicative of attentional inhibition. Ventral visual areas are separated from dorsal visual areas by a dashed line. Significant attentional modulation is indicated with an asterisk.

conditions of high perceptual load, relative to low perceptual load (Handy et al., 2001). Given that the P1 response has been localized to extrastriate cortex (Heinze et al., 1994; Clark and Hillyard, 1996; Mangun et al., 1997), the latter reduction in P1 magnitude under conditions of high perceptual load may reflect attentional inhibition of the unattended probe's extrastriate representation. Such variability in the magnitude of the P1 component suggests that the spatial extent of attentional inhibition may be particularly sensitive to manipulations of perceptual load.

Two previous fMRI studies have reported attentionally mediated inhibitory effects in early visual areas (Somers et al., 1999; Smith et al., 2000). In both studies, inhibitory effects were assessed by subtracting activation levels during passive viewing from activation levels during active attention. It is possible, however, that at least some of the differences observed in these studies may have been due to the fact that "passive" or "baseline" tasks can elicit greater cortical activity than active tasks (Binder et al., 1999). The contralateral versus ipsilateral attention task used in the

present study required the maintenance of a consistent attentive state and therefore avoided this possibility. Furthermore, Smith et al. (2000) reported attentional inhibition corresponding to locations at which no stimulus was present, which is at odds with behavioral evidence that attentional inhibition is spatially restricted to stimulus locations (Cepeda et al., 1998). In comparison, the attentional inhibition effects of the present study were in line with the expected stimulus specificity.

The inhibitory effects of attention reported here depend upon the differences in activity associated with contralateral and ipsilateral shifts of attention. It is possible that these differences do not reflect attentionally mediated inhibition at distracting probe representations, but instead reflect greater attentional facilitation in stimulus locations following ipsilateral shifts of attention than following contralateral shifts. We believe the latter possibility is implausible, given that it is at odds with behavioral evidence showing little or no effect of attention on stimuli situated far from the locus of attention (Bahcall and Kowler, 1999; Mounts, 2000a).

Nevertheless, single-cell recording in monkey will be needed to definitively resolve this issue.

## Acknowledgments

We would like to thank Lauren Moo, Joe Hopfinger, John Serences, Joe Sala, and Stephen Monsell for valuable discussions and insightful comments on the manuscript. This research was supported by the Johns Hopkins University School of Medicine General Clinical Research Center, NIH/NCRR grant MO1 RR00052 and by NIH grant RO1 DA13165 (S. Yantis, PI).

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