Darkness beyond the light: attentional inhibition surrounding the classic spotlight

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The aim of the present investigation was to determine the nature and spatial distribution of selective visual attention. Using cortical source localization of ERP data corresponding to 60 task-irrelevant stimuli across the visual field, we assessed attention effects on visual processing. Consistent with previous findings, visual processing was enhanced at the attended spatial location. In addition, this facilitation of processing extended from the attended location to the point of fixation resulting in a region of facilitation. Furthermore, a large region of inhibition was found surrounding this region of facilitation. The latter result is inconsistent with a simple facilitative spotlight model of attention and indicates that attention effects can be both facilitatory and inhibitory. *NeuroReport* 13:773–778 © 2002 Lippincott Williams & Wilkins.

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INTRODUCTION

The allocation of attention to a spatial location has been likened to a spotlight of enhanced processing centered at the locus of attention. Estimates of the spotlight's spatial extent have varied dramatically, ranging from 1 to 20° of visual angle [1,2]. It has also been argued that the spatial distribution of attention may be better construed using a zoom lens model [3] wherein spatial extent varies depending on the task [4]. However, a simple facilitatory model of attention may be incomplete.

Recent behavioral studies have provided evidence that the enhancement of stimulus processing within the attentional spotlight is accompanied by an inhibition of stimulus processing at surrounding spatial locations [5–10]. However, the locus within the brain at which this type of inhibition acts remains unknown.

In the present study, ERP cortical source localization was conducted on numerous visual field probes with two aims: to assess the nature and extent of attention effects on visual processing and to determine whether behavioral inhibition has its basis in early visual cortex.

MATERIALS AND METHODS

Participants: Three female participants between the ages of 28 and 41 years participated in the study. Informed consent was obtained in accordance with the University of California, Berkeley protocol review board.

Multi-electrode recording: Forty-seven posterior scalp electrodes (49 electrodes in one participant) spaced 2.5 cm apart were used to record voltage responses (Fig. 1c). Impedances were maintained $< 5\,k\Omega$ and electrode czp was used as a reference [11]. Voltages were amplified 100 000 times, bandpass filtered between 0.5 and 100 Hz, and sampled every 1.67 ms.

Multi-stimulus array: Sixty 4×4 checkerboard probes spanning the central 15.6° of the visual field with mean luminance of $35\,cd/m^2$ were used to elicit cortical responses (Fig. 1a,b). Probes were scaled by the human cortical magnification factor (i.e. a decrease in cortical response area elicited with an increase in stimulus eccentricity) to activate an equivalent area of cortex at all stimulated eccentricities [12]. Each probe reversed in contrast according to an orthogonal binary m-sequence at a mean rate of 37.5 Hz (75 Hz refresh rate). The voltage response at one electrode elicited by the contrast reversal of one probe was obtained by cross-correlating that electrode's response with that probe's m-sequence as described previously [11–13].

Behavioral task: Participants completed sixteen 54 s segments for each of three experimental conditions: attend center, attend right, and attend left. In the attend center condition, participants fixated a centrally placed red circle, 0.1° in diameter (i.e. the attended circle). During each segment, the circle alternated in color between red and green at randomly selected time intervals ranging from 1 to

10 s. Participants were instructed to silently count the number of color reversals during each segment and then report this number verbally at the end of each segment.

The attend right condition was identical to the attend center condition, except the attended circle was centered on a probe 2.6° from fixation in the right visual field, adjacent to the horizontal meridian (Fig. 1a,b). Of the two probes fitting this description (one above the horizontal meridian, one below), the probe eliciting the maximal response was selected based on an on-line analysis conducted immediately after the attend center condition. This procedure was performed to ensure that the probe at the attended location elicted a robust ERP; given the variability of gyral anatomy, certain probe locations do not elicit a significant response [11]. For one participant, the attended locations were in the lower visual field; therefore, her data were flipped over the horizontal meridian to align attended locations. The attend left condition was identical to the attend right condition except the attended circle was centered on the analogous probe in the left hemifield.

Dipole source localization: Numerous ERP studies have shown that scalp voltage responses are larger when a visual stimulus is attended relative to when it is unattended [14,15]. Dipole source localization is a complementary method of analysis that has proven quite useful in identifying the cortical loci of attention effects [16,17].

In the present study, when a single probe reversed in contrast, voltages were elicited on the scalp reflecting cortical activity. At any moment in time, cortical activity was modeled using a single dipole with location, orientation, and magnitude. Over time, the dipole was assumed fixed in location and orientation (across attend right and attend left conditions), but variable in magnitude. By assuming probes at the same eccentricity in the stimulus array produced dipoles with the same temporal response and normalizing that temporal response to unity, a time invariant value of dipole magnitude was obtained [11]. Using this overall method, dipole magnitude has been shown to reasonably estimate cortical activity [18].

For the main analysis, dipole modeling was conducted on voltage responses in the 50–110 ms epoch following stimulus onset, which includes the dominant ERP response using the described stimulus methodology [11]. In addition, to test for differences in attentional modulation over time, analyses were conducted after splitting the data equally into 50–80 ms and 80–110 ms epochs (i.e. early and late epochs).

Measuring attention effects: To measure attentional modulation, the dipole magnitude corresponding to a particular probe with attention can be compared to the magnitude of the same dipole without attention. For example, Fig. 1c shows the dipole magnitude corresponding to probe 1 (Fig. 1b) when at the locus of attention and that dipole's magnitude without attention. The difference of magnitude (DOM) is a measure of the effect of attention on the cortical response, where a positive DOM indicates attentionally mediated facilitation and a negative DOM indicates attentionally mediated inhibition (Fig. 1b–d). Note that attentionally mediated effects as measured using DOM values are relative to baseline dipole magnitudes and thus do not necessarily reflect classical neuronal facilitation or inhibition (see Discussion). In all participants, the DOM was determined for all probes. For right visual field probes, the attend left condition served as baseline and *vice versa*.

Determining spatial extent: The size of the attentional window is task dependent [1–4]; thus, *a priori* predictions of spatial extent are somewhat speculative. However, *post hoc* measurements of spatial extent suffer, though arguably less so, in that they are defined by the data under scrutiny. We used both approaches to obtain complementary evidence.

Our *a priori* model of facilitatory and inhibitory regions was borrowed from two recent behavioral studies [7,9]. Both studies tested attentional modulation using multiple stimuli at an eccentricity of ~4° and showed a facilitatory region extending ~1° from the locus of attention and a surrounding inhibitory region extending ~2° from the locus of attention. Applying these values to the multi-stimulus array used in the present study, facilitation was expected at the probe underlying the attended circle and inhibition was expected at the probes immediately surrounding that probe. This model was refined based on additional behavioral evidence indicating facilitation extends from the locus of attention toward fixation [19]; therefore, the surrounding probe toward fixation was not included in the *a priori* inhibitory region resulting in a horseshoe shaped region (Fig. 2a).

Our *post hoc* model assumed that attention effects were spatially contiguous [7,9]. A facilitative elliptical region was determined as follows. First, beginning with the probe underlying the attended circle, the group of contiguous facilitated probes (i.e. DOM > 0) were selected where contiguity was defined by at least one of a probe's edges abutting another facilitated probe. Then, for each probe defining the outer extent of the selected region, a point was placed at the center of each edge abutting a non-facilitated position (see magenta asterisks in Fig. 2a). The best fit five-parameter ellipse with center x, y, spatial extent a, b, and rotation parameter θ was fit to these points using the Marquardt least squares algorithm. A similar elliptical fitting procedure was used to determine the spatial extent of the inhibitory region. For analysis purposes, a probe was included in a region if its center was within that region. To assert statistical independence, the *post hoc* facilitatory region did not include the probe at the attended location.

Statistical analyses: In each selected stimulus region, a within-hemisphere ANOVA was conducted to maximize sensitivity. The main analysis tested condition where, for each probe, dipole magnitudes with and without attention were compared. When the condition × time interaction was tested, a hierarchical approach was taken whereby simple effects were restricted to significant interactions.

Eye movements: In one participant, eye movements were monitored using a custom built video monitoring system to within 0.5° of fixation. Eye movements were not monitored in the other participants.

A follow-up eye movement control experiment was conducted on three age- and sex-matched participants at

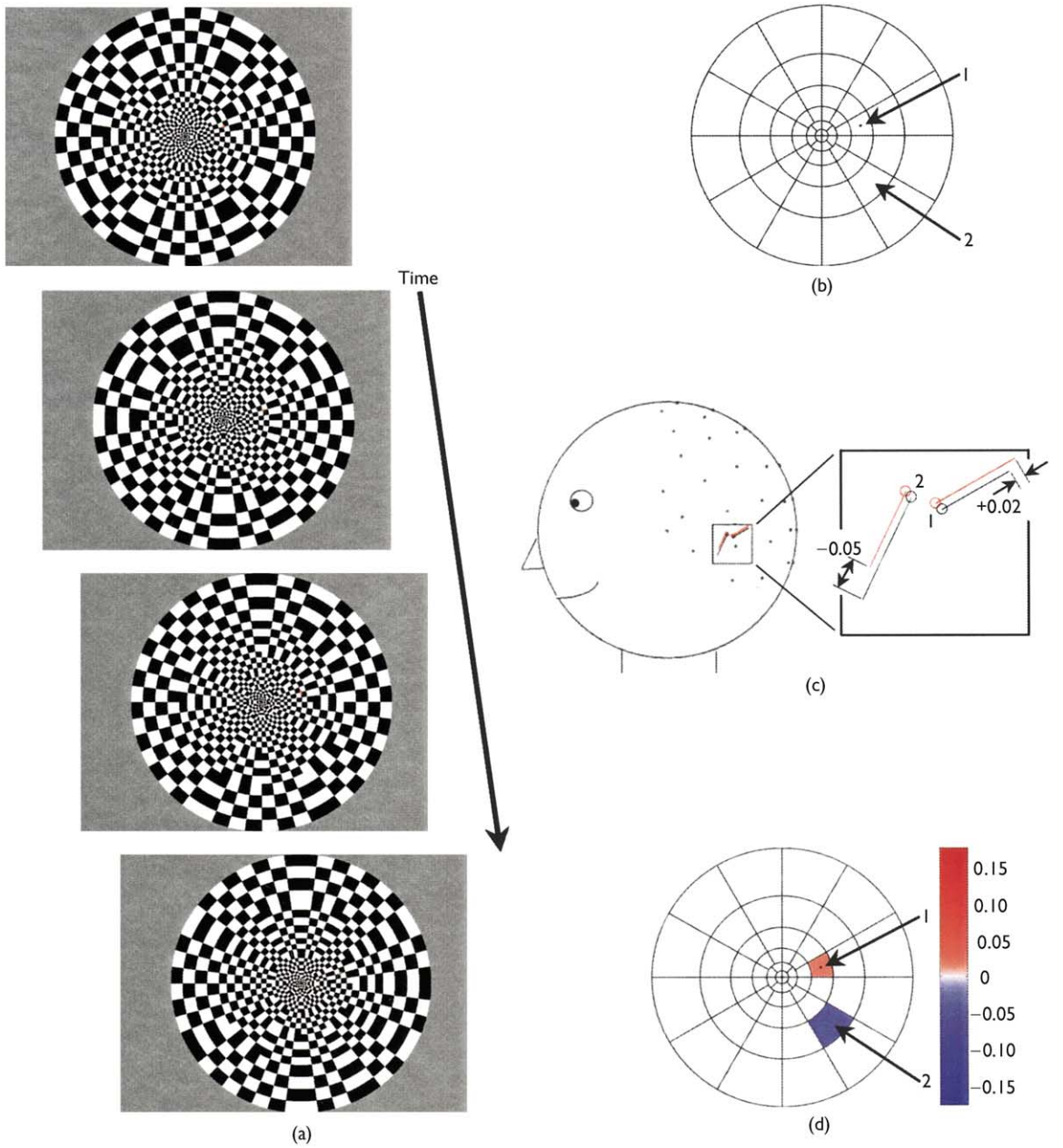

Fig. 1. (**a**) Snapshots of multi-stimulus array over time where each probe reversed in contrast on average every 27 ms. (**b**) Outline of all probes within the multi-stimulus array. On this and subsequent figures, attended circle shown as a small black dot. Two probes of interest, probe 1 at the attended location and probe 2 at an unattended location. (**c**) Left, profile of head model with electrodes. At posterior of head, dipole locations, orientations, and magnitudes corresponding to two selected probes. Magnitudes corresponding to attend right condition shown in red and magnitudes corresponding to attend left condition shown in black, with slight offsets for ease of magnitude comparison. Right, blowup of outlined region. Difference in dipole magnitudes in attend right *vs* attend left conditions was used to measure attentional modulation. A positive DOM indicates attentional facilitation and a negative DOM indicates attentional inhibition. (**d**) Color map illustrating DOM in attend right *vs* attend left conditions projected onto probes of interest. Red illustrates facilitation and blue inhibition.

Johns Hopkins University. Following informed consent, which had been approved by the protocol review board, a SensoMotoric Instruments Eyelink System (Teltow, Germany) eye tracker was calibrated to within 0.5° visual angle and then validated within the central 16 degrees of the visual field. After one practice segment, each participant completed two attend left and two attend right segments. Analysis was conducted using custom software written in MATLAB (The MathWorks, Inc., Natick, MA, USA).

RESULTS

In line with the *a priori* model of the facilitatory region, a significantly positive DOM was found at the attended

location replicating a large body of evidence showing cortical facilitation at an attended location [14,15,17] (Fig. 2; mean DOM = 0.040, $F(1,5) = 54.52$, $MS_{error} = 7.3 \times 10^{-5}$, $p < 0.001$). Although the DOMs corresponding to the *a priori* model of the inhibitory region were consistently negative (Fig. 2a), this trend was only marginally significant (mean DOM = −0.099, $F(1,5) = 4.64$, $MS_{error} = 0.0063$, $p < 0.1$).

The regions used in the *post hoc* analysis were defined by two ellipses with facilitatory center x = 1.57° and y = −0.46°, extent a = 1.68° and b = 2.03°, and rotation θ = −8.53° and inhibitory center x = 3.14° and y = −0.69°, extent a = 3.93° and b = 5.00°, and rotation θ = −7.97° (Fig. 2a). DOMs within the *post hoc* facilitatory region were significantly increased (Fig. 2; mean DOM = 0.21, $F(1,5) = 17.30$, $MS_{error} = 0.0079$, $p < 0.01$) while DOMs within the *post hoc* inhibitory region were significantly decreased (Fig. 2; mean DOM = −0.20, $F(1,5) = 7.81$, $MS_{error} = 0.015$, $p < 0.05$). DOM outside the *post hoc* model of inhibitory processing were not effected by condition (Fig. 2b; mean DOM = 0.012, $F(1,5) < 1$).

To maximize power, the subsequent analyses only included the *post hoc* inhibitory region. Neither the DOM of the probe at the attended location nor the DOMs corresponding to the inhibitory region showed a significant interaction over time (attended location, $F(1,5) < 1$; inhibitory region, $F(1,5) = 1.40$, $MS_{error} = 0.049$, $p = 0.29$). In contrast, the facilitatory region did show a significant interaction over time ($F = 13.36$, $MS_{error} = 0.0089$, $p < 0.05$). Simple comparisons within the facilitatory region showed no significant modulation within the 50–80 ms epoch (mean DOM = −0.064, $F(1,5) = 1.93$, $MS_{error} = 0.0064$, $p = 0.22$) but a significant modulation within the 80–110 ms epoch (mean DOM = 0.22, $F(1,5) = 12.57$, $MS_{error} = 0.0113$, $p < 0.05$). Thus, attention effects at the attended location and in the inhibitory region were sustained throughout the early and late epochs while attention effects in the facilitatory region did not reach significance until the late epoch.

No eye movements >0.5° occurred using the video monitoring system. Results from one representative participant in the eye-movement control study are shown in Fig. 3b,c (Fig. 3a addresses precision). Changes in the attended circle's color did not result in eye movements toward the attended circle indicating the present results

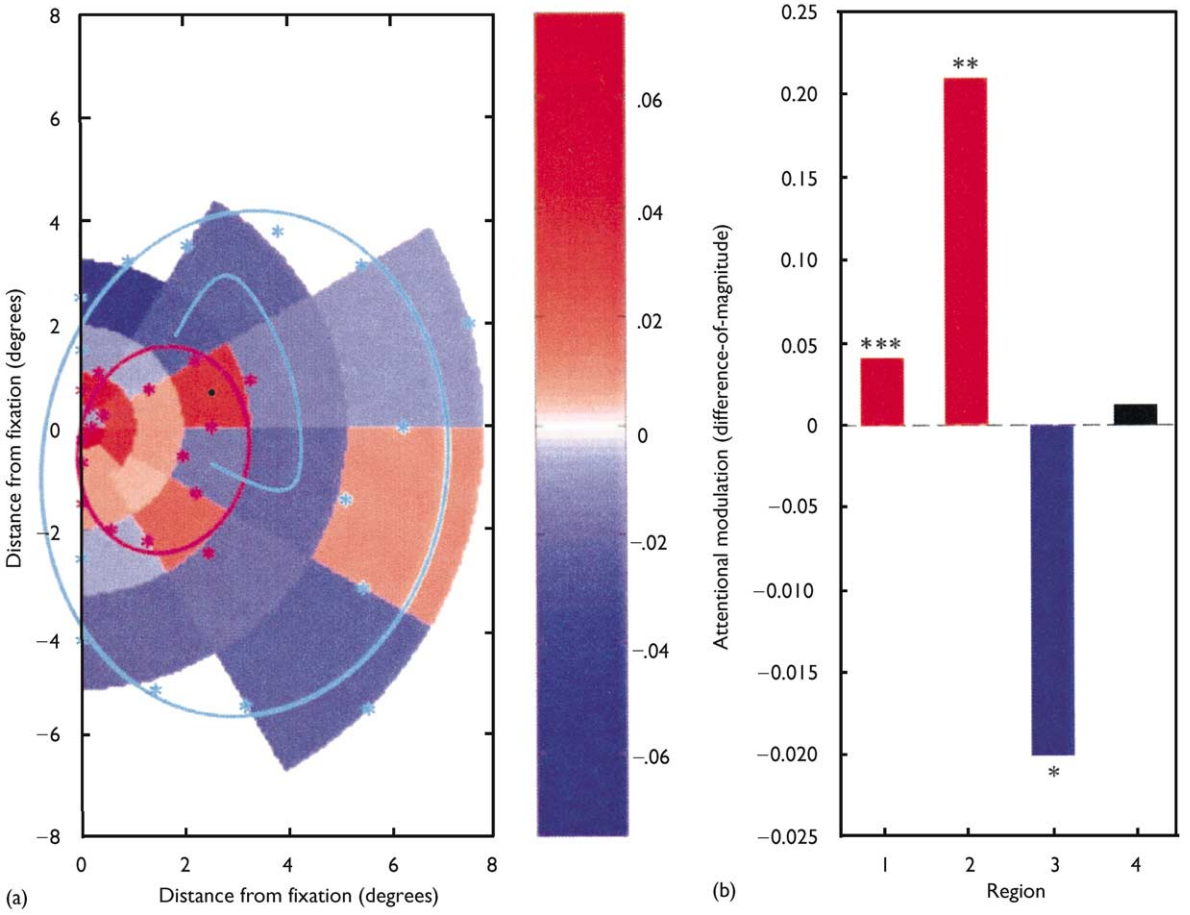

Fig. 2. (**a**) DOMs for all probe locations (left visual field data flipped over vertical meridian). Cyan horseshoe surrounding attended location illustrates *a priori* region of inhibition. Magenta and cyan asterisks demarcate boundary of *post hoc* facilitatory and inhibitory regions, respectively. Ellipses, shown in magenta and cyan, illustrate *post hoc* model of attentionally mediated facilitation and inhibition. For clarity, DOMs outside inhibitory region not shown. (**b**) Results corresponding to four selected regions: (1) probe at the attended location, (2) *post hoc* facilitatory region, (3) *post hoc* inhibitory region, (4) region outside *post hoc* inhibitory region. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

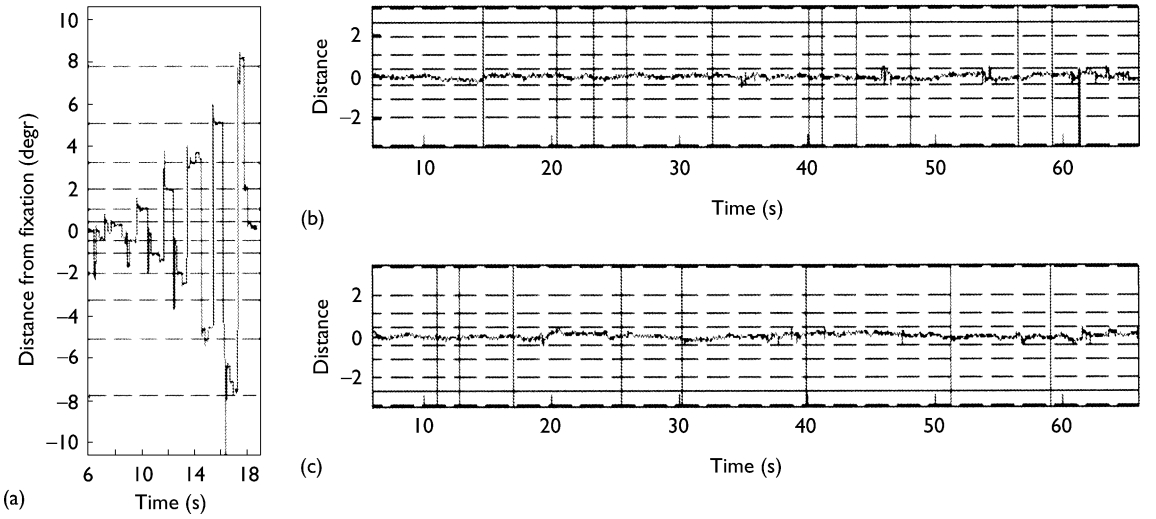

Fig. 3. (**a**) Eye movement calibration plot with horizontal distance from fixation on y-axis. A practiced participant made horizontal eye movements at 1 s intervals to progressively more eccentric annuli within the multi-stimulus array. Dotted lines indicate actual distances at which annuli intersect the horizontal meridian (right of fixation positive). The high correspondence between actual annulus distances and measured eye movement distances shows the eye tracker was precise. (**b**) Horizontal eye movements of one control participant during a segment of the attend right condition. Vertical lines demarcate a change in attended circle color and horizontal solid line demarcates the location of the attended circle. A 6 s fixation period preceded and trailed the 54 s segment such that multi-stimulus array offset occurred at 60 s. (**c**) A similar plot for the same participant during a segment of the attend left condition.

were not simply due to involuntary saccades toward the attended location. Also, participants did not maintain an eccentric point of fixation toward the attended stimulus as shown by the constancy in eye position before and after stimulus offset. All eye movement monitoring results indicated that participants maintained fixation during the task.

DISCUSSION

We have shown previously that the m-sequence multi-stimulus technique primarily activates V1 [11,18]; therefore, the present attention effects appear to be operative at the earliest level in the cortical visual hierarchy. Although the modulatory effects of attention were not originally found to effect V1 [15,20,21], recent evidence has shown that attention can modulate activity in primary visual cortex [17,22–25].

It has been argued that attentional modulation of V1 occurs via feedback processes, after the initial neuronal response to the stimulus [17,24]. In the present study, the later onset of attention effects in the *post hoc* facilitatory region fits well with such a feedback hypothesis. However, we also found an early onset and sustained highly significant facilitation at the attended location, which was small in magnitude relative to that of the broader facilitatory region (Fig. 2b). The small magnitude of this early onset facilitatory effect may explain why it has not been reported previously.

In addition to delineating the spatial extent and time course of attentional facilitation, we also found evidence for an early onset region of inhibition surrounding the region of facilitation. As all attention effects were computed relative to a baseline, the inhibitory effects reported here could have been due to a decrease in cortical activity with attention *vs* without attention or due to an increase in cortical activity without attention *vs* with attention. Although all evidence known to us supports the former possibility, and thus suggests a mechanism involving classic neural inhibition, single-cell recording in monkey will likely be needed to resolve this issue. However, this does not challenge the present finding of attentionally mediated inhibition but only illuminates its relativity to baseline.

Recently, it has been posited that a purely facilitative model of attention may correspond to top-down processes (e.g. voluntary selective attention) while surrounding inhibition may occur during bottom-up processes (e.g. attentional capture) [10]. The task in the present study was top-down in nature; however, the stimulus array was composed of flashing probes that the visual system may automatically have interpreted as relevant in the bottom-up sense. Our finding of inhibition in a top-down task suggests that stimulus factors play an important role during selective attention and should be considered in any theory of attention.

CONCLUSION

Using numerous probes spanning the visual field, we measured changes in cortical activity to delineate the nature and spatial distribution of attention. Not only was facilitation found at the attended location but this facilitation extended toward fixation. Moreover, in line with recent behavioral results, a region of attentionally mediated inhibition was found surrounding the region of facilitation. Such results suggest a general model of attention that includes both facilitation and inhibition.

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