

Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision

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The spatial focus of attention has traditionally been envisioned as a simple spatial gradient of enhanced activity that falls off monotonically with increasing distance. Here, we show with high-density magnetoencephalographic recordings in human observers that the focus of attention is not a simple monotonic gradient but instead contains an excitatory peak surrounded by a narrow inhibitory region. To demonstrate this center-surround profile, we asked subjects to focus attention onto a color pop-out target and then presented probe stimuli at various distances from the target. We observed that the electromagnetic response to the probe was enhanced when the probe was presented at the location of the target, but the probe response was suppressed in a narrow zone surrounding the target and then recovered at more distant locations. Withdrawing attention from the pop-out target by engaging observers in a demanding foveal task eliminated this pattern, confirming a truly attention-driven effect. These results indicate that neural enhancement and suppression coexist in a spatially structured manner that is optimal to attenuate the most deleterious noise during visual object identification.

attention | magnetoencephalography | visual

It is a common experience that one is able to focus on relevant parts of a visual scene even when irrelevant parts of the scene are more salient. It has been suggested that this voluntary focusing is mediated by a biasing of competitive stimulus interactions in the visual cortex, which promotes preferential processing of relevant over irrelevant input (1–3). This competitive advantage can be achieved by enhancing the processing of relevant inputs or by attenuating the processing of irrelevant inputs. Evidence has accumulated that attention operates by means of both neural enhancement (4–7) and neural suppression (8–13). More recent data from functional MRI in humans indicate that enhancement and suppression may cooperate across the visual scene (14, 15), leading to an increase in selectivity in a push-pull-like manner (15). That is, a spatially organized combination of enhancement and suppression may effectively sharpen the demarcation of relevant from irrelevant inputs, particularly in cluttered visual scenes in which neural representations of relevant and irrelevant information may become mixed together (16, 17).

Many behavioral and electrophysiological studies of attention have indicated that attending to a location produces a monotonic gradient of processing efficiency around the attended location (18–22). In contrast, computational models motivated by the known anatomy and physiology of the primate visual system have predicted that the spatial distribution of cortical activity around the focus of attention may be more complex than a simple gradient. In particular, the selective tuning model (ST) of Tsotsos *et al.* (23, 24) proposes an architecture of attentional selection that explicitly predicts a suppressive zone surrounding the focus of attention. In short, ST provides an account of attentional selection in the visual cortex based on hierarchical

winner-take-all (WTA) processes that propagate in top-down directions through visual cortex. Connections representing input from irrelevant locations are pruned away from level to level, causing a pass zone of enhanced activity for connections representing the attended input. Connections immediately surrounding the pass zone become suppressed, leading to a profile of cortical responsiveness with an excitatory center and an inhibitory surround.

The prediction by ST of a center-surround profile has received support from a number of behavioral observations. For example, probe detection at distractor locations close to a search target is slowed relative to distractor locations farther away from the target (25). Similarly, probe discrimination performance close to an attention-capturing feature singleton is reduced in comparison with probe locations at or farther away from the singleton (26, 27). In addition, shape matching between a cued and an uncued color singleton becomes degraded when the distance between them is reduced (28). Furthermore, single-cell recordings in monkeys (8, 10, 29) and event-related potential and functional MRI studies in humans (14, 30, 31) hint at the possibility that neural enhancement in the focus of attention may be accompanied by neural suppression of the immediate surround.

In contrast, other behavioral and electrophysiological studies have found simple monotonic gradients of attention (18–22). However, these monotonic gradients may reflect an insufficiently dense sampling of the attentional gradient or the use of measures that conflate perceptual and postperceptual mechanisms of attention. In addition, the inhibitory effects may dissipate once the attended object is removed, and many previous studies assessed the gradient of attention in the absence of an attended object (27). Thus, prior studies have not provided a direct and precise test of the hypothesis that the attended object is surrounded by a narrow ring of inhibition in visual cortex.

Here, we provide direct neurophysiological evidence from high-density magnetoencephalographic recordings for the existence of a suppressive attentional surround. By probing cortical responsiveness with a probe stimulus at varying distances from a target, we were able to observe the center-surround pattern predicted by ST (Exp. 1). A control experiment demonstrated that this pattern could be eliminated by using a demanding foveal task to divert attention away from the target (Exp. 2).

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Abbreviations: ERMF, event-related magnetic field; RSVP, rapid serial visual presentation; SDE, source density estimate; ST, selective tuning; WTA, winner-take-all; PD, probe distance; FO, frame-only; FP, frame-plus-probe; RT, response time.

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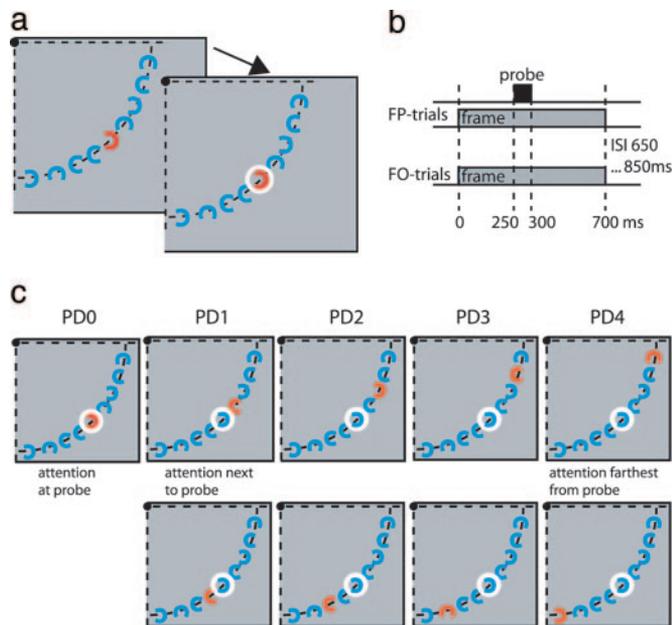


Fig. 1. Illustration of the search frame and the timing of the probe presentation. (a) Nine randomly oriented Cs were presented at an isoecentric distance from fixation (black dashed line) in the lower right visual field. The target item, a red C, appeared randomly at one of the nine locations (here at the center position), and observers had to discriminate its gap position (left, right). (b) On 50% of the trials, a probe stimulus (white circle) was flashed (duration = 50 ms) around the center position 250 ms after search frame onset (FP trials). On the remaining trials, no probe appeared (FO trials). (c) Illustrates all possible target-to-probe distance conditions, with attention at probe (PD0) through attention four items away (PD4).

Results

Exp. 1. While fixating the center of the screen, observers searched for a red target C among eight blue distractor Cs presented at a constant distance from fixation in the lower right quadrant (Fig. 1a). The target C appeared randomly at one of the nine possible stimulus locations (Fig. 1c), thus, forcing subjects to change the spatial focus of attention from trial to trial. On half of the trials, a white ring (the probe stimulus) was flashed around the center C 250 ms after the search frame onset (see *Materials and Methods* for details). In the other half of the trials, no probe was presented. Because the probe position was constant and the target position varied, there were five target-to-probe distances, ranging from probe distance 0 (PD0; target at probed location) through probe-distance 4 (PD4; target four items away from probe; see Fig. 1c).

To isolate event-related magnetic field (ERMF) response elicited by the probe from ERMF activity reflecting target processing, the ERMF response triggered by trials with a search frame but no probe stimulus (frame-only or FO trials) was subtracted from the ERMF response triggered by trials with a search frame followed by a probe (frame-plus-probe or FP trials). Previous studies have validated this approach (32–34). Fig. 2a shows the ERMF distributions of the resulting difference waves between 130–150 ms for each of the nine target locations, averaged across observers. The FP-minus-FO difference waveforms are shown for each target-to-probe distance in Fig. 2b (collapsed across mirror-symmetrical positions). Both the distributions and the waveforms show that the initial response was largest when the target location was probed (PD0, position 5), smallest when the location adjacent to the target was probed (PD1, positions 4 and 6), and intermediate for larger target-to-probe distances (PD2–PD4, positions 1–3 and 7–9). Thus, we

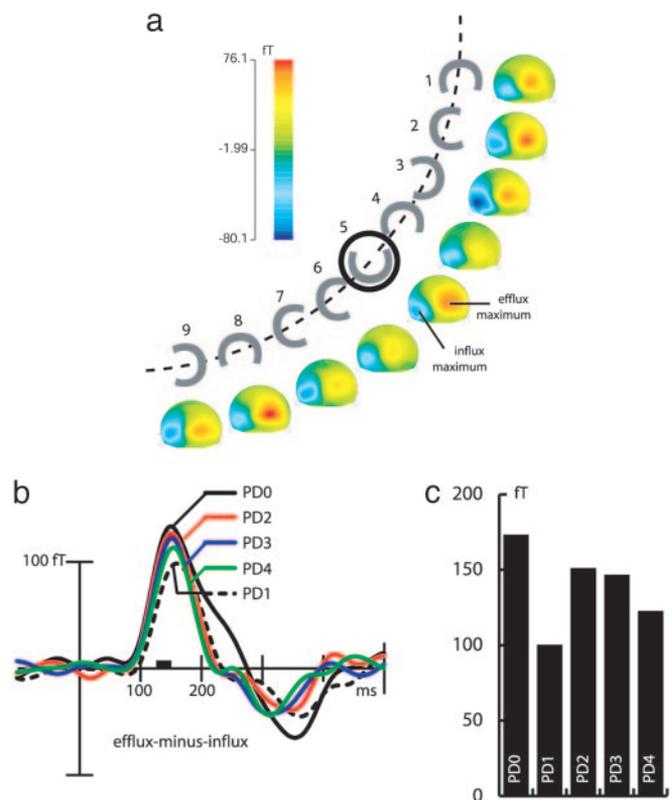


Fig. 2. ERMF distribution and time course of the probe-related response. (a) Mean ERMF distribution of the probe-related response (FP-minus-FO difference from 130–150 ms, averaged across observers) for all probe-distance conditions of Exp. 1. Attending to the C next to the probe (positions 4 and 6) reveals a reduced response magnitude in comparison with both the at-probe position (5) as well as the positions farther away from the probe (1–3, 7–9). (b) Time course of the probe-related ERMF response (FP-minus-FO) for each probe distance collapsed across corresponding conditions toward the horizontal and vertical meridian (4 and 6, 3 and 7, etc.). Shown is the time course of the ERMF difference between corresponding efflux- and influx-field maxima (efflux-minus-influx; see a). (c) Mean size of the probe-related response between 130–150 ms, collapsed across corresponding probe-distance conditions. The size of the effect represents the average of the ERMF difference between the observers' individual field maxima and minima.

observed an enhancement at the target location and a suppression at the adjacent location compared with the more distant locations, demonstrating that a narrow zone of attenuated cortical responsiveness surrounds the attended item. When inspecting the waveforms in Fig. 2b, it seems that there is also a small delay in latency for PD1 relative to PD0 and the other probe-distance conditions. However, a statistical comparison of the peak-latency for the PD0 and the PD1 conditions indicated that this difference was not statistically significant ($F_{1,11} = 2.5$, $P = 0.14$).

The bar graph in Fig. 2c summarizes the magnitude of the average ERMF effect, using the difference between each observer's individual efflux and influx maxima to measure the size of the effect. Again, attending to the location adjacent to the probe's location led to a smaller probe response than attending to the probe's location or attending one location farther from the probe. For statistical validation of this activity profile, the magnitude of the magnetic field from 130–150 ms was subjected to an overall one-way repeated measures ANOVA (RANOVA) with a factor of target-to-probe distance (five levels: PD0–PD4). This analysis revealed a significant effect of target-to-probe distance ($F_{4,8} = 4.08$, $P < 0.05$). Planned follow-up RANOVAs showed that the probe response was significantly smaller when

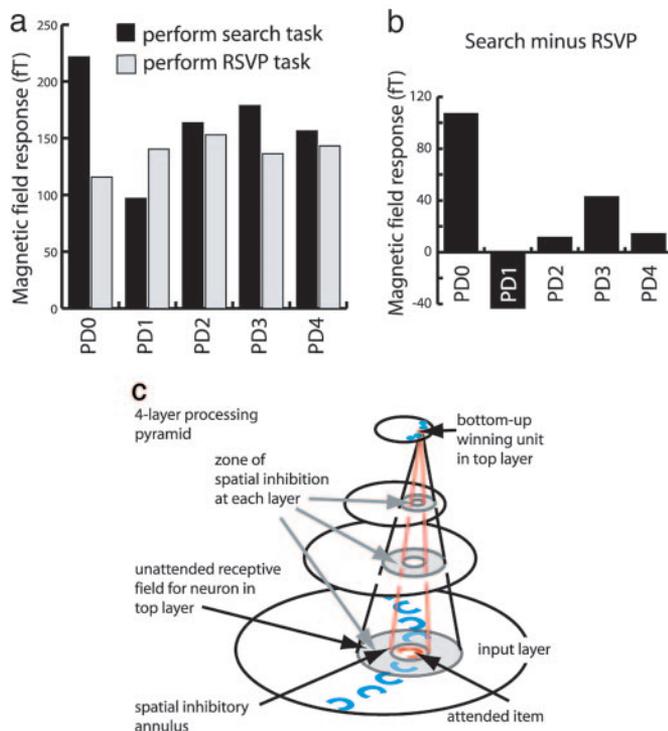


Fig. 4. Results of Exp. 2. (a) Shown is the mean size (average between 130 and 150 ms) of the probe-related response (FP-minus-FO, collapsed across corresponding probe distance conditions, analogous to Fig. 2c) when observers performed the search task (black) or when the observers' attention was withdrawn from the search items with a demanding RSVP task at fixation (gray). The center-surround profile is observed for the search task but not for the RSVP task, indicating a truly attention driven effect. (b) Differences between the probe-related response in the search and RSVP tasks at each target-probe distance. Note that a significant enhancement was present at PD0 and a significant suppression was present at PD1. (c) Top-down selection pyramid as proposed by the ST (23). The inhibitory zone surrounding the attended item results from top-down propagation of a WTA mechanism that attenuates irrelevant upstream connections iteratively from one hierarchical level down to the next.

demanding foveal task, which provides a very conservative baseline.

Discussion

In this study we investigated the spatial profile of cortical activity surrounding the focus of attention in an array containing a target surrounded by distractors. Cortical responsiveness was probed with a task-irrelevant luminance increment at a fixed spatial position while the distance of the focus of attention was varied relative to the probe. Instead of a simple monotonic gradient, the observed activity profile was found to be shaped like a “Mexican hat,” with an enhanced probe response at the focus of attention, a suppressed response in a narrow zone surrounding the attended location, and a rebound at more distant location. A current source density analysis indicated that this center-surround profile is present in early-to-intermediate areas of visual cortex. Because we probed only along a single dimension, we did not show suppression around a complete ring. However, there is no reason to believe that attention-related suppression would be present above and below a target but not to the left and right of the target, and a ring-shaped region of inhibition is therefore the most likely explanation for the observed results.

Previous single-unit, event-related potential (event-related potential) and ERMF studies have shown that occipito-temporal attention mechanisms are focused onto a pop-out target within

200 ms of the onset of the search array (17, 38–41), and previous event-related potential studies have shown that probes presented at 250 ms elicit enhanced occipito-temporal responses when presented at the target location compared with a location in the opposite visual field (32, 33). Prior behavioral and physiological studies of the spatial distribution of attention, however, have provided mixed results, either in favor of a simple spatial gradient (18–22), or consistent with an inhibitory zone (25–31, 42–44). The present study demonstrates unequivocally that attending to an object leads to a ring of inhibition. Previous failures to observe this pattern may reflect an inadequate spatial sampling or the use of experimental paradigms in which the target and distractors were not present simultaneously.

In addition, electrophysiological evidence for an inhibitory zone surrounding the focus of attention has been limited with respect to the timing of this effect. Slotnick *et al.* (30) report data from a probe paradigm in which subjects were asked to constantly focus onto a target location for ≈ 50 s while the probe's location varied relative to the target. Based on inverse dipole modeling of the event-related potential data, an inhibitory region surrounding the attended location was inferred under these conditions. However, these data do not indicate whether this inhibitory zone arises rapidly enough to represent a correlate of fast and flexible focusing, or instead, evolves gradually over several seconds. Related functional MRI studies addressing this issue were limited in an analogous way (14, 31), aside from the low temporal resolution inherent in this method. The present data now demonstrate that the Mexican hat profile builds up rapidly under conditions of fast and flexible attentional focusing, as required in visual search. The occurrence of the effect within 250 ms after search frame onset is therefore consistent with the time course of attention-based suppression effects observed at the cellular level in monkeys performing visual search (9), as well as with behavioral estimates of the attentional dwell time in visual search in humans (45, 46).

In view of recent evidence demonstrating retinotopically specific suppression effects during the anticipation of distractors (13), it is important to consider whether the use of a predictable probe location may have led subjects to develop a sustained inhibition at the probe's location (PD0), irrespective of the location of the target on a given trial. Indeed, RTs were slowed when the target appeared at the location where the probes were presented, even on probe-absent trials. However, this sustained inhibition would have had the same impact on the probe response irrespective of the location of the target, and it cannot therefore explain the observed variations in probe amplitude as a function of target-probe distance. It is also possible, although unlikely, that subjects specifically suppressed the PD0 location when they noticed that the target appeared at the PD1 location, anticipating that a probe might occur at the adjacent location. This seems like an implausible strategy, because the simultaneously presented distractors at the adjacent locations presumably interfered with perception of the target much more than the probe, which was presented 250 ms later. Indeed, the presence of a probe caused only a 4-ms slowing of RTs, and this slowing was independent of target-probe distance. Moreover, a ring of inhibition has been observed behaviorally even when distractor locations were unpredictable (28). Thus, the observed effects almost certainly reflect a temporary suppression that was triggered around the location of the target shortly after the appearance of the target.

The present results are consistent with the biased competition theory of attention of Desimone and Duncan (47). According to this theory, attention operates when multiple stimuli compete for access to neural representation, and this competition occurs when multiple stimuli fall within a neuron's receptive field. As a result, distractors within a receptive field are suppressed while attended stimuli are enhanced. How this mechanism operates within a hierarchical network of neurons is unspecified, but the general idea is consistent with our results.

TX). Computations were performed on the basis of realistic anatomical constraints derived from 3D-surface segmentations of the cortical surface (source compartment) and the cerebrospinal fluid space (volume conductor) of the standard Montreal Neurological Institute (MNI) brain (see ref. 39 for details). To maximize signal-to-noise ratio, the localization was performed by using data averaged across all observers. This averaging may blur the SDE distribution somewhat, but the goal of the localization was to estimate the general location of the activity, not to make fine discriminations between nearby brain regions.

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