A physiological correlate of the 'spotlight' of visual attention

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Here we identify a neural correlate of the ability to precisely direct visual attention to locations other than the center of gaze. Human subjects performed a task requiring shifts of visual attention (but not of gaze) from one location to the next within a dense array of targets and distracters while functional MRI was used to map corresponding displacements of neural activation within visual cortex. The cortical topography of the purely attention-driven activity precisely matched the topography of activity evoked by the cued targets when presented in isolation. Such retinotopic mapping of attention-related activation was found in primary visual cortex, as well as in dorsomedial and ventral occipital visual areas previously implicated in processing the attended target features. These results identify a physiological basis for the effects of spatially directed visual attention.

Helmholtz[1] and William James[2] each noted the potential dissociation between the point of gaze fixation and the focus of attention within the field of view. More recently, this phenomenon has been compared to a 'spotlight' that evokes attentional enhancement of visual information within a circumscribed region of visual space or within the confines of a target object[3–5]. Information inside the spotlight is processed more quickly or more efficiently, whereas outside the spotlight, information is processed "less, or differently, or not at all"[6–8]. However, the physiological basis of this spatially restricted attentional effect has remained obscure. Both neuroimaging and single-neuron studies have shown that visual attention can modulate responses in a number of visual areas[9–17]. It still remains controversial whether true attentional modulation occurs at the earliest stages of cortical processing such as primary visual cortex[18]. Although attention-related shifts of cortical activation have been observed previously[19–21], there has not been a convincing demonstration that such shifts have a precise spatial metric concordant with a subject's ability to accurately move the focus of attention. Here, we report experiments in which we used fMRI with human subjects to demonstrate focal enhancement of cortical activity that moves in precise register with covert shifts in the focus of attention. We show that these shifts are metrically accurate within the cortical representations of the visual field found in occipitotemporal visual cortex. (An animation of the cortical progression of attentional enhancement can be viewed at http://www.mcw.edu/cellbio/visionlab.)

Results

To study visuospatial attention, we used a task in which the subject's gaze remained fixated on a central marker while spatial attention was directed to a cued location (target segment) within an array of segments (Fig. 1). Subjects detected specific color/orientation conjunctions (for example, blue-horizontal) within the cued segment while ignoring other uncued segments. On average, subjects responded correctly on 85% of the trials. Over a period of 40 seconds, the cued segment was shifted to successively greater eccentricities (Fig. 1). The complete sequence of shifts was repeated 5 times within each 200-second fMRI scan run.

Repeated shifts of attention to targets at greater eccentricities in the right visual field produced cyclic cortical enhancement that was spatially mapped in both striate (V1) and extrastriate cortex of the left occipital lobe (Fig. 1). As attention shifted from the perifovea to the periphery, the locus of cortical enhancement shifted anteriorly away from the occipital pole. Although the amplitude of response varied from position to position, the progression was reminiscent of the retinotopic mapping of visual field eccentricity observed previously in human visual cortex[22–25]. Such spatially mapped attentional modulation was observed in all five subjects.

The region of attentional modulation extended throughout medial occipital cortex as well as ventrally into, and surrounding, the collateral sulcus. Based on previous retinotopic mapping[24], this swath traversed portions of V1 and proposed extrastriate visual areas V2, V3, VP, V4v and sometimes cortex anterior to V4v. Attentional modulation was also seen deep within the left calcarine fissure (Fig. 3e), verifying that V1 as well as extrastriate cortex was modulated by the shifting focus of attention. Mean Talairach coordinates[26] for the anterior–posterior extremes of the swath of enhancement in medial cortex (V1/V2) were (+*x* is left, +*y* is posterior, +*z* is superior) 15.4, 75.0, 10.0 mm and 20.4, 96.8, –4.2 mm, respectively. For ventral cortex, the swath of enhancement extended from 19.8, 62.8, –8.0 mm to 24.6, 89.0, –16.8 mm. (In the following analysis, we have simply compared responses in medial occipital cortex versus ventral occipitotemporal cortex, and have used the terms medial and ventral cortex to refer to these composite regions.)

To determine conclusively if the pattern of attentional enhancement followed the cortical retinotopy of single cued segments, we repeated the experiment but with only one cued segment present at a time (Fig. 1). On this task, subjects responded correctly on 88% of the trials. The resulting spatial pattern of activation closely matched the pattern produced when only attention was shifted from segment to segment (Fig. 1, compare left

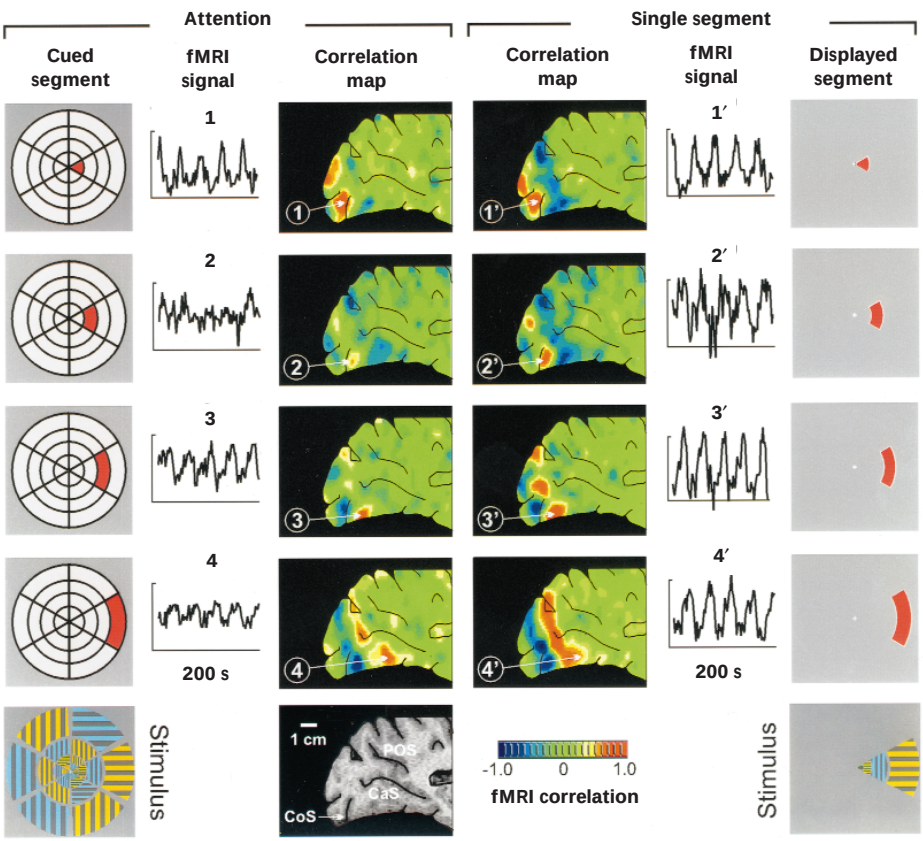

Fig. 1. Retinotopic attentional modulation compared to activation evoked by cued targets alone. Cued segment (left column) shows schematic sequence of target segments cued for attentional scrutiny. Stimulus (bottom left) is actual target array. FMRI signal (left) shows signal modulation of individual voxels at sites indicated on adjacent correlation maps. Temporal phase shift of the signal at each site identifies the corresponding locus of attention. Correlation maps show sites where timing of modulation was positively correlated (red) or anti-correlated (blue) with the timing of attentional shifts. Displayed segment (right column) shows schematic sequence of single segments presented during otherwise identical control experiment. Composite of single segments shown in stimulus bottom right. FMRI Signal and correlation map on right show results of control experiment. Structural MRI (bottom) is a parasagittal section (13.6 mm left of midline) through occipital lobe in same plane as correlation maps. Sulcal landmarks; CaS, calcarine sulcus; CoS, collateral sulcus; POS, parieto-occipital sulcus.

to right). To provide a quantitative measure of the match between the two data sets, we compared the response phase (representing eccentricity) for individual voxels pooled across all subjects. Temporal phases were highly correlated for attention-only versus single-segment responses in both medial and ventral cortex (Fig. 2). The correlation coefficient (r) was 0.94 for medial cortex and 0.96 for ventral cortex, thereby indicating a very close match between the locus of attentional enhancement and the retinotopy (visual field topography) of the individual segments presented in isolation. Together, these data show that the attentional mapping can be readily observed in individual subjects, but is also consistent across all subjects.

To test these results further, three subjects performed a task in which the attentional sequence was directed into the opposite visual field. A comparison between rightward and leftward attentional sequences (Fig. 3a and b) shows that the regular pattern of phase mapping switched accordingly from the left to the right hemisphere. If instead, attention remained directed toward the fixation point throughout the scan, no consistent cyclic activation was detected (Fig. 3c). In the leftward and rightward sequences, we noted that activation was sometimes apparent at the homotopic location in the opposite hemisphere, though this was weaker and poorly phase mapped. This may reflect a mild suppressive effect at the mirror-imaged attentional focus.

To explicitly identify stimulus-related activation rather than attentional modulation, we presented the whole stimulus array for 20-second blocks alternated with comparable blocks consisting of the fixation point alone on an isoluminant gray field. This evoked strong activation uniformly throughout occipital

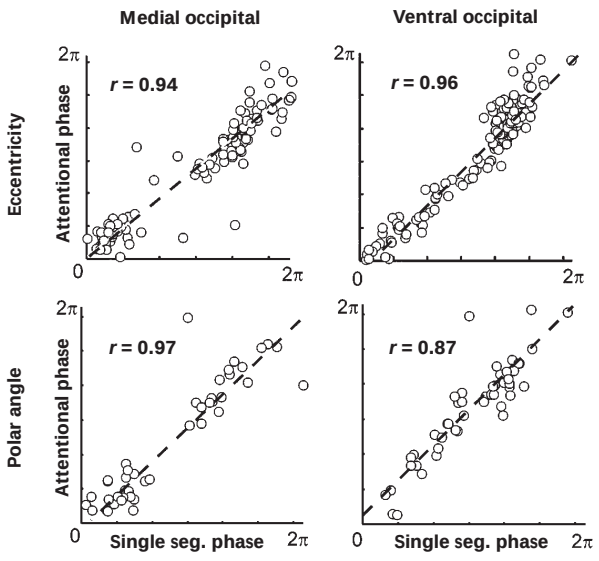

Fig. 2. Comparison of visual field topography (coded by temporal phase of fMRI response) for attentional foci (y-axis) versus single segments (x-axis). Each circle represents a single responsive voxel. Data are pooled across subjects. Left column, medial occipital cortex consisting primarily of V1 and V2. Right column, ventral occipitotemporal cortex within and surrounding the collateral sulcus. Top row, shifts in eccentricity. Bottom row, shifts in polar angle.

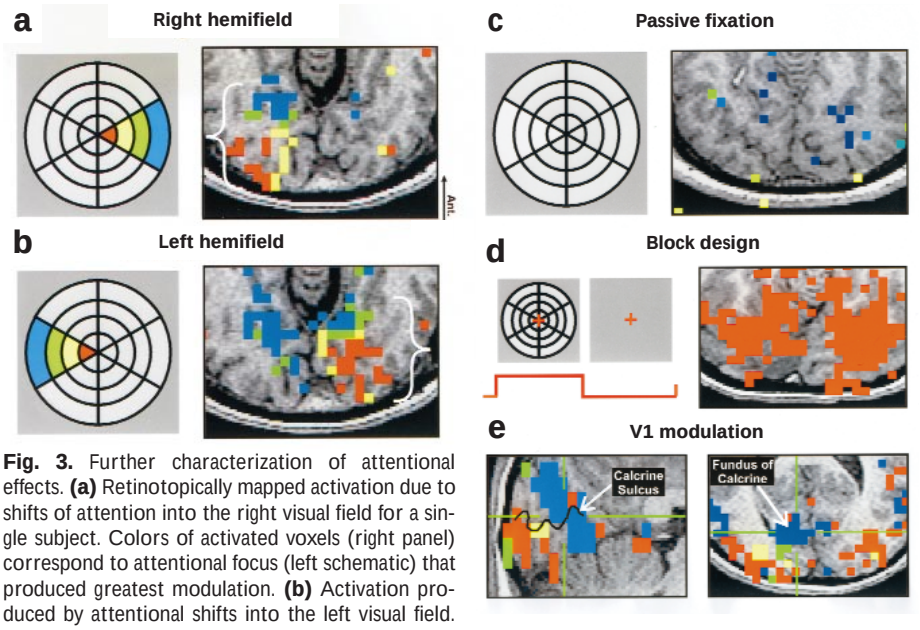

Fig. 3. Further characterization of attentional effects. **(a)** Retinotopically mapped activation due to shifts of attention into the right visual field for a single subject. Colors of activated voxels (right panel) correspond to attentional focus (left schematic) that produced greatest modulation. **(b)** Activation produced by attentional shifts into the left visual field. **(c)** Activation produced by attention maintained at fixation point. **(d)** Activation produced by presentation of whole target array alternated every 20 seconds with fixation point alone. Note diffuse activation in both hemispheres that contrasts with focal, retinotopic activation produced in **(a)** and **(b)** (denoted by white brackets). **(e)** Example of attentional modulation within the depths of the calcarine sulcus, unequivocally associated with V1.

visual cortex, illustrated in a ventral slice (Fig. 3d). This diffuse activation was in marked contrast to the focal, ordered pattern of activation caused by the shifts of visual attention. In sum, activation produced by pure attentional shifts (Fig. 3a and b) consisted of a modulation of the ongoing, stimulus-related activation (Fig. 3d).

We were concerned that uncontrolled eye movements, especially toward the cued segment, might produce an artifactual response modulation that could be mistaken for attentional retinotopy. To test this, we used an infrared eye tracker to monitor subjects' eye movements during performance of the attentional task outside the scanner. There was no detectable pattern of eye movements that correlated with the sequence of attentional shifts. Although tiny eye movements below the resolution of our eye tracker could not be ruled out, such instabilities could not produce the large-scale retinotopic organization observed here.

We next compared the strength of attentional modulation to the magnitude of response for the isolated single segments. The attentional enhancement was modestly but significantly stronger in ventral cortex compared to medial cortex (Fig. 4a). We averaged the mean fMRI signals across comparable regions-of-interest in five subjects (Fig. 4b). Although the mean attentional modulation for all active voxels was less than half the single-segment response, the amplitude in select voxels of ventral cortex could be as large as the response evoked by the isolated single segments (for example, site 1, 1′ in Fig. 1). This was not the case for medial cortex. This suggests that, in some restricted brain locations, the attentional effects may be comparable to the stimulus effects themselves.

Finally, we repeated the attentional-shift experiment using a circumferential cue pattern that required the subject to shift attention to segments at successive polar angles. The observed pattern of activation (Fig. 5a) matched the known cortical representation of polar angle in which the inferior quadrant is represented dorsally and the superior quadrant is represented ventrally in medial occipital cortex[24]. Again the topography of the attentional shifts closely matched the topography of the isolated cued segments (compare Fig. 5a and b). Accordingly, the temporal phase of the fMRI response (representing polar angle) for individual voxels was highly correlated in both medial and ventral occipital cortex (r = 0.91 and 0.86 respectively; Fig. 2).

Discussion

Our results show that attention directed to a specific target location in the visual field produced multiple foci of cortical enhancement in occipital visual cortex. The positions of these foci within

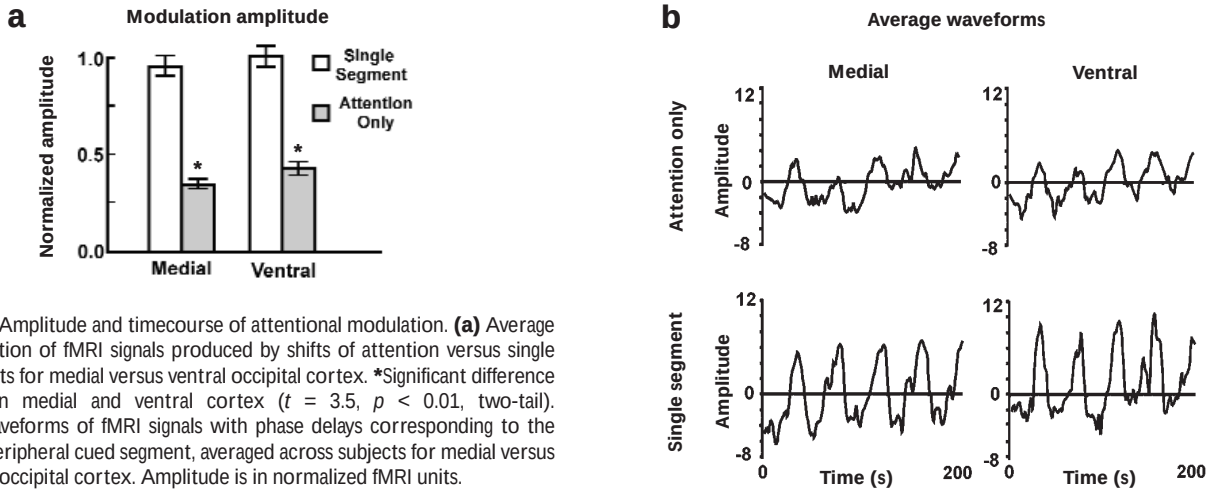

Fig. 4. Amplitude and timecourse of attentional modulation. **(a)** Average modulation of fMRI signals produced by shifts of attention versus single segments for medial versus ventral occipital cortex. *Significant difference between medial and ventral cortex (t = 3.5, p < 0.01, two-tail). **(b)** Waveforms of fMRI signals with phase delays corresponding to the most peripheral cued segment, averaged across subjects for medial versus ventral occipital cortex. Amplitude is in normalized fMRI units.

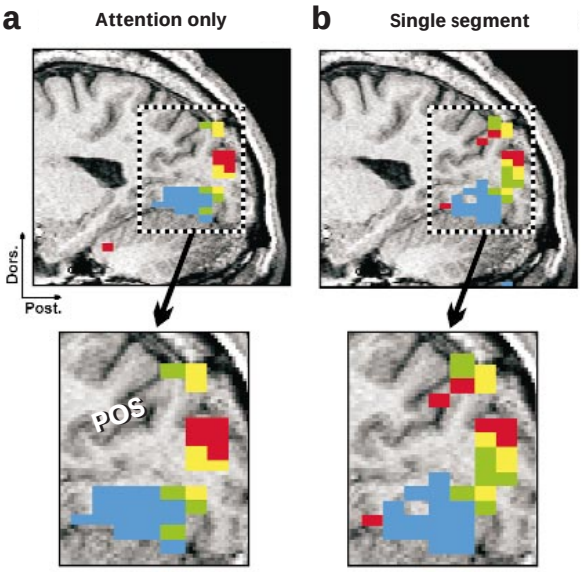

Fig. 5. Example of retinotopic mapping of cortical activation in an individual subject. **(a)** Activity produced by shifts of attention to cued targets increasing in polar angle or **(b)** by same targets presented in isolation. Anatomical slice is parasagittal, 17 mm left of midline. Conditions matched those for the eccentricity mapping experiment (**Fig. 1**) except that targets were cued in a circumferential sequence (within the third ring of segments) proceeding from inferior to superior within the left visual field. Resulting fMRI activation in the right hemisphere shifted sequentially from dorsal to ventral occipital cortex (red, target at 202.5°; yellow, target at 247.5°; green, target at 292.5°; blue, target at 337.5°; zero reference at superior vertical meridian). Quantitative comparison of retinotopy for attentional shifts versus single segments is illustrated in Fig. 2. POS, parieto-occipital sulcus.

the cortex corresponded precisely with the cortical representations of the attended target presented in isolation. When the focus of attention shifted, the cortical enhancement shifted in precise correspondence. Because this study used a dense array of visual targets filling the field of view, the resulting focal activation reflected the spatial characteristics of the attentional modulation itself, not a 'filtering' of the modulation through a pattern of spatially isolated stimulus features. In sum, these results not only demonstrated a physiological correlate of spatial attention, but also showed that it is accurately described using a retinotopic metric. In principle, it should be possible to use these results to determine the locus of attentional scrutiny from the pattern of brain activation alone.

Attentional enhancement was strongest for a small subset of voxels in ventral cortex encompassing a region that is active in processing the color and orientation attributes that are selected for attentional scrutiny[27–31]. However, retinotopically mapped attentional effects were also seen at the earliest stages of cortical processing in the medial occipital lobe, including V1. The experience of shifting one's focus of attention could therefore reflect neural events occurring at a variety of cortical sites, even primary visual cortex. (We did not examine the lateral geniculate nucleus.) However, recent psychophysical work indicates that the spatial resolution of focal attention is not as fine as the spatial resolution of cells in V1, at least for certain tasks[32]. This suggests that the attentional experience is more likely to be linked to neural events at cortical stages beyond V1. Indeed, our own observations showed that the largest attentional effects were found in a small subset of voxels in ventral occipitotemporal cortex. These conclusions are generally in accord with those of a recent report[33].

The present findings do not necessarily imply that the perceived attentional spotlight must be two-dimensional, or that it corresponds to an undifferentiated region of space. Within a given retinotopic zone of cortex, distinct populations of cells representing different distances, objects, features or surfaces may be selectively modulated depending on the attentional task. Thus, it is possible for attentional effects to be both retinotopic and 'object-based'[5], especially for two-dimensional displays such as those used in this study. Under other circumstances, the perceived window of attention, as well as the properties of the cortical activation, could depart significantly from the analogy of an attentional spotlight.

Methods

Subjects, stimulus and task. Seven subjects (four male and three female) drawn from the Medical College of Wisconsin faculty and students participated in this study. (Not all subjects participated in all tests.) Informed consent was obtained from all subjects in accordance with procedures and protocols approved by the Medical College of Wisconsin internal review committee.

Subjects used a custom-designed optical system[34] to view a computer graphics stimulus array generated with a Cambridge Instruments VSG video board driving a modified Sharp XG-2000U video projector. The stimulus array depicted in Fig. 1 consisted of either 6 (eccentricity mapping) or 8 (polar angle mapping) sectors, each containing 4 target segments, altogether subtending 56° of visual angle. The sizes and stripe periods of the segments were varied to compensate for corresponding changes in cortical magnification factor and spatial acuity at increasing eccentricities from the center of gaze. Color differences (blue versus orange) were clearly evident even at the largest eccentricities. Every two seconds, the color and/or stripe orientation of each segment could change randomly. The subject's task was to fixate the central white cross but monitor the color/orientation pattern of a segment designated by a prearranged audio cue ("one", "two", "three" or "four") presented every ten seconds via custom electrostatic headphones (Koss Inc.). No visual aspect of the stimulus array could be used to identify the cued segments. The subject pressed one of two buttons to indicate the observed conjunction (blue-horizontal or orange-vertical versus blue-vertical or orange-horizontal). This feature-conjunction task ensured that focal attention was engaged and directed toward the cued segment[35].

To map the effects of shifting focal attention, the target segment was cued in one of two sequential patterns, either along the horizontal meridian at successively increasing eccentricities or along a circumference at successive counterclockwise positions. At each cued location, the subject made five successive judgments (one every two seconds). The complete sequence of four cued locations was then repeated five times within each 200-second fMRI scan.

Imaging and data analysis. Gradient-recalled, echo-planar, functional imaging was done with a General Electric (Milwaukee, Wisconsin) Signa 1.5-tesla MRI scanner equipped with a custom RF/gradient head coil acquiring 102 gradient-recalled (TE = 40 ms,TR = 2 s, FA = 90°) echo-planar images with $3.75 \times 3.75 \times 6.0$ mm resolution. Twelve slices spanning occipitotemporal cortex were collected in the axial plane. (Two of the polar angle experiments were collected in the coronal plane with identical slice thickness.) Anatomical images were obtained using a T1-weighted spoiled GRASS (gradient recalled at steady state) pulse sequence at a resolution of $256 \times 192 \times 1.0$–$1.2$ mm depending on subject brain size.

After coregistering successive fMRI images to reduce motion artifacts, activated voxels were identified by cross-correlation with an idealized response waveform[36] based on a smoothed and delayed version of the cue timing sequence. The temporal phase of the fMRI response was determined using a custom algorithm based on the Hilbert transform[37]. Response amplitude for each voxel was estimated as the covariance of the fMRI response with the idealized response waveform. Phase maps were constructed in one of two ways. For Fig. 1, voxels were pseudo-col-

ored using a color scale representing the magnitude and sign of the correlation coefficient and then subsampled, smoothed and interpolated using a gaussian filter of half-width equal to the original voxel size. An outline drawing of the primary sulcal landmarks in the section of interest was then overlaid on the resulting correlation map. Such maps are advantageous in that no arbitrary thresholding is applied to the data, thereby retaining maximum sensitivity. However, responses for only one temporal phase can be shown on each map. In Figs. 3 and 5, different colors were used to code different temporal phase ranges for voxels whose correlation exceeded a minimum threshold ($r > 0.35$). This allowed construction of composite figures showing responses to different phases on the same map.

It is important to note that the phase-mapping technique used here to identify retinotopic organization does not distinguish cyclic enhancement (increased activation) from cyclic suppression (decreased activation) or from alternating enhancement and suppression. However, direct inspection of typical response waveforms indicated that the primary attentional effect was enhancement.

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