

Functional MRI reveals spatially specific attentional modulation in human primary visual cortex

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ABSTRACT Selective visual attention can strongly influence perceptual processing, even for apparently low-level visual stimuli. Although it is largely accepted that attention modulates neural activity in extrastriate visual cortex, the extent to which attention operates in the first cortical stage, striate visual cortex (area V1), remains controversial. Here, functional MRI was used at high field strength (3 T) to study humans during attentionally demanding visual discriminations. Similar, robust attentional modulations were observed in both striate and extrastriate cortical areas. Functional mapping of cortical retinotopy demonstrates that attentional modulations were spatially specific, enhancing responses to attended stimuli and suppressing responses when attention was directed elsewhere. The spatial pattern of modulation reveals a complex attentional window that is consistent with object-based attention but is inconsistent with a simple attentional spotlight. These data suggest that neural processing in V1 is not governed simply by sensory stimulation, but, like extrastriate regions, V1 can be strongly and specifically influenced by attention.

It has long been appreciated that selective attention can dramatically affect high-level visual perception (1). More recently, attention has been shown to influence low-level visual phenomena such as luminance detection (2, 3), motion perception (4, 5), orientation discrimination (6), contour detection (7), hyperacuity (6), and even “preattentive” visual search (8). These modulations of perception appear to result from selective spatial attention, because they depend on the location of directed attention. These studies exploited the fact that attention and eye position need not be directed to the same location; that is, attention may be covert (2). Under the same fixation conditions attention may be either directed toward a test stimulus, directed elsewhere, or not directed. Striking differences have been revealed when performance under directed attention is compared with performance when attention is engaged in a highly distracting task, such as identifying letters in a rapid serial visual presentation (RSVP) stream (5, 8, 9).

These phenomena indicate that attention operates at low levels of visual processing, but they do not identify the specific cortical areas in which processing is influenced by attention. This question of the locus of selection is fundamental to the cognitive neuroscience of attention. Theories suggest that processing of the attended representation is enhanced and/or that processing of unattended representations is suppressed. Enhancement and suppression may act directly on cells in the lower tiers of visual cortex that code retinotopic location or may act at higher cortical areas (10). One long-held theory, the spotlight model of spatial selection (2, 11), suggests that

attention is directed to a connected visual field region that contains no topological holes. A competing theory, object-based selection (12), suggests that attention is directed to objects rather than to specific visual locations.

It is now well established that attention modulates neural activity in extrastriate visual areas such as V2, V4, and MT (13–27). However, many of these same studies found little or no attentional modulation in V1 (13, 18–20, 25–27). One study (23) found some response elevation in V1 during reward stimulus presentation; however, such an effect may result from general arousal. Also, V1 cells did not exhibit the sharpening of orientation tuning with attention that was observed for V4 cells. Recently, a rather modest modulation was observed in human V1 by functional MRI (28); however, this report is also consistent with general arousal effects. More compelling is the 1993 macaque study of Motter (22), which found elevated V1 responses when attention was directed to the stimulus within the receptive field of recorded neurons, compared with when attention was directed elsewhere. Despite the apparent soundness of this study, the weight of negative evidence has left the issue of attentional effects in V1 quite controversial with several current authors arguing attention does not affect V1 (18, 19, 26, 29). The present study used functional MRI to reveal robust attentional effects in striate and extrastriate cortex.

METHODS

MRI and Analysis. Experimental details are similar to those described (30, 31). Seven normal human volunteers were scanned by using a 3-T General Electric Signa magnetic resonance imager. A custom-built, bilateral quadrature transmit-receive surface coil, placed at the back of the skull, covered all of the occipital lobe and the posterior portions of parietal and temporal lobes with high sensitivity. All subjects used custom-fitted bite bars to restrict head movement. Informed consent was obtained from each subject in writing before each scan (Massachusetts General Hospital Human Studies Protocol 96–7464).

Each subject participated in three or more scan sessions. In an initial session, high-resolution (1.0 × 1.0 × 1.3 mm) structural images were obtained for the purpose of three-dimensional reconstruction (32–34). Computer representations of each cortical hemispheric surface were unfolded and flattened (Fig. 1, ref. 30). These structural images were collected on either a 2-T Siemens MR scanner by using MP-RAGE or on a 1.5-T GE MR scanner by using SPGR [echo time (TE) = 3.3 msec; repetition time (TR) = 30 msec; flip

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This paper was submitted directly (Track II) to the *Proceedings* office. Abbreviations: RSVP, rapid serial visual presentation; ROI, region of interest.

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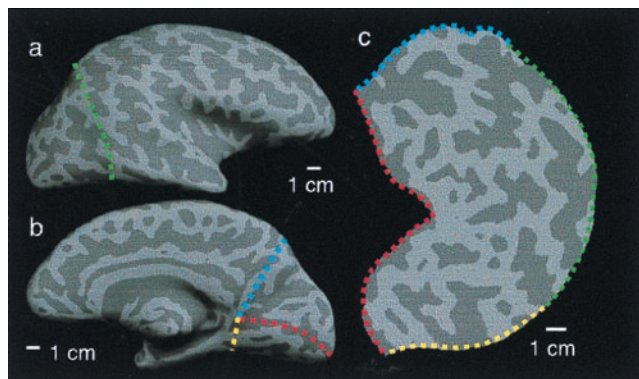


FIG. 1. Cortical reconstruction and flattening. (a) Lateral and (b) medial views of a mathematically inflated cortical surface reveal buried sulci (gyri, light gray; sulci, dark gray). The posterior portion is cut off (green, yellow, and blue lines) and cut along the fundus of the calcarine sulcus (red line in b). (c) The resulting cortical patch is unfurled and laid flat for data visualization.

angle = 40°]. To register functional data to the three-dimensional reconstructions, a set of high-resolution (1.5 × 1.5 mm in-plane) inversion time (T1)-weighted echo planar images [TE = 56 msec; TI = 1200 msec; TR = 22 sec; number of excitations (NEX) = 4] was acquired in each functional session using the same slice prescription used in the functional scans.

In a second session, visual cortical retinotopic representations and areal boundaries were functionally mapped, as described (30). T2*-weighted gradient-echo, echo-planar images were collected from 16 slices (4 mm thick with no gap) oriented approximately perpendicular to the calcarine sulcus (TE = 50 msec; TR = 4 sec; matrix = 128 × 64; in-plane resolution, 3.1 × 3.1 mm; 128 image/slice; scan duration, 8 min, 32 sec). Functional scans measured changes in the intrinsic blood oxygenation level dependent (BOLD) contrast (35, 36). Cortical representations of eccentricity and polar angle were mapped in separate runs (see refs. 30 and 31). These data were used to identify eight retinotopic visual cortical regions (V1- V1+, V2- V2+, V3-, VP+, V3A, V4v+; Fig. 2c and d). Area V1 (also V2) was subdivided into upper (+) and lower (-) visual field representations to provide an extra control on V1 activation. These areas have been described (30, 31, 37, 38). Eccentricity data also were used to subdivide regions into foveal and extrafoveal representations (Fig. 2c). Regions of interest (ROIs) for extrafoveal regions of each area were functionally defined by these data and used in the analysis of attentional data. Because of technical difficulties in identifying cortical area boundaries at the fovea, the foveal confluence was defined as a single ROI for each hemisphere.

Third and subsequent scan sessions collected functional images for the attentional and control studies. Imaging parameters were the same as in the retinotopic studies except that TR was 2 sec and scan duration was 4 min, 16 sec. Subjects were run in 2-4 scans of each condition in a single session and signal averaging was performed. Overall, the results from 108 functional scans (221,184 images) are presented here. Single subject data were analyzed voxel by voxel by selective averaging of epoch time points corresponding to the two compared attentional states. A *t* test was performed on each voxel to test the hypothesis that greater activation occurred during one condition. Significance (*P*) values were projected onto flattened cortical hemispheric representations. In addition, time course data for all voxels within a functionally defined ROI were averaged for each hemisphere. These data were normalized for each subject as percent signal change from the mean activation of the initial fixation epoch (see below). Normalized time

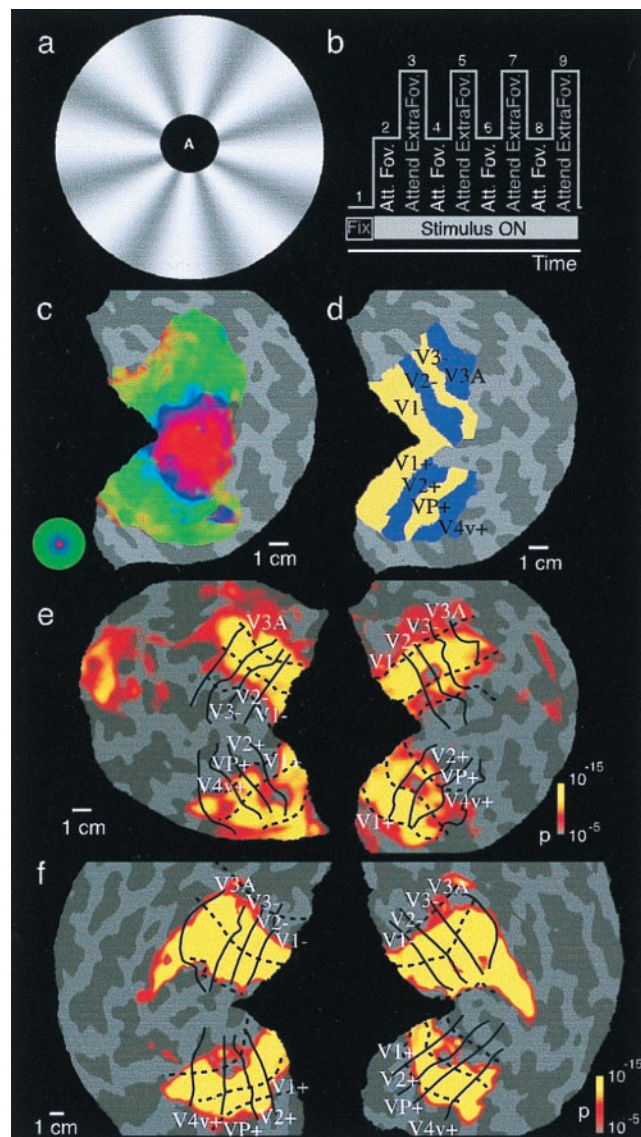


FIG. 2. Attentional modulation in mid-eccentricity regions of primary and higher visual cortex. (a) Visual stimuli were composed of an annulus and a central target. Radial wedge patterns were rotated in the annulus. Single letters or a fixation point appeared as the central target (see *Methods*). (b) Scans consisted of nine 28-sec epochs. A fixation target alone was passively viewed in the first epoch. Attention was alternately directed to foveal and extrafoveal regions of the stimulus (a) in subsequent epochs. (c) Functional mapping of visual eccentricity reveals a foveal representation (shown in red; see color key) in the center of the patch, with more peripheral eccentricities (up to 15°-20°) represented inferiorly (upper visual field) and superiorly (lower visual field). (d) Functional labeling of retinotopic visual cortical areas identifies areas V1-, V2-, V3-, and V3A, superior to the calcarine sulcus, and areas V1+, V2+, VP+, and V4v+, inferior to the calcarine. Upper and lower visual field representations are indicated by + and -, respectively. (e and f) Patterns of statistically significant increased activation for attend extrafoveal motion vs. attend foveal letters for both hemispheres of two example subjects (color map shows *P* values). Mid-eccentricity regions (green in c) of all four visual field quadrants of V1 and higher visual cortical areas exhibit highly significant increases in activation. Dashed lines mark iso-eccentricity contours. Solid lines mark boundaries between neighboring cortical areas.

course data were averaged across subjects. Finally, normalized ROI data were selectively averaged by epochs (with 4-sec delay for hemodynamics) to obtain average attentional modulation values for each subject and condition. *t* test statistics were performed on these data to test a random effects model.

Visual Stimulation. Visual stimuli were projected into the patient chamber (NEC MT-850 LCD color projector) onto a rear projection screen (Da-Plex, Da-Lite Screen Co., Cincinnati, OH) and viewed via an adjustable mirror angled at $\approx 45^\circ$ to the subject's normal line of sight. Stimuli were driven on a Macintosh 7600 (Apple Computer) by using the Vision Shell environment (Micro ML, Saint-Hyacinthe, Quebec, Canada).

Visual stimuli were composed of a central target ($\approx 1^\circ$ radius) and a surrounding annulus (inner radius $\approx 3^\circ$; outer radius $\approx 12^\circ$) with a gap between them (Fig. 2*a*). Subjects were required to maintain central fixation throughout each scan, but required to attend foveally, attend extrafoveally, or view passively. The primary focus of this study was a set of functional MR scans designed to alternately direct visual attention toward and away from an extrafoveal moving stimulus. The central stimulus component was a series of five letters displayed at the point of fixation in RSVP (200–500 msec letter duration), followed by a bulls-eye target that persisted for the remainder of the trial duration. Trials lasted 1.5–3 sec. The surround annulus contained a radial wedge pattern that rotated in one direction (clockwise or counter-clockwise) and then stopped on each trial. Rotation started and stopped synchronously with the beginning and end of the RSVP letter stream. This design was inspired by psychophysical studies showing that low-level visual processing can be dramatically impaired when subjects are required to perform attentionally demanding RSVP discriminations elsewhere in the visual field (5, 8).

Scans lasted 256 sec, which were divided into nine 28-sec epochs plus a final 4 sec for hemodynamic delay. The first epoch was intended to establish baseline activation. The annulus was uniformly gray, the foveal target was a bulls-eye, and the subjects were required to maintain fixation. In the remaining eight epochs, the stimulus came on (Fig. 2*a*) and subjects alternated between foveal and extrafoveal attentional tasks (Fig. 2*b*). Epoch order was counterbalanced across subjects.

When attending to the extrafoveal stimulus, subjects were required to report whether the direction of rotation was the same as or different from that of the preceding trial. In the attend-fovea condition, subjects were required to report whether the letters were the same as or different from those on the previous trial. On consecutive trials, either the same five letters appeared in the same order or one letter changed. Behavioral data were collected via a button press box connected to the stimulus-driving computer. Motion contrast (typically $\approx 3\%$) and RSVP timing parameters were manipulated to create high attentional demand while permitting subjects to perform well in all epochs (5–20% error rates). Subjects were trained on the tasks before scanning.

Two additional experiments used the same stimuli but replaced either the attend-fovea or attend-extrafovea conditions with passive viewing of the stimuli. To maintain alertness, subjects were required to press a button at the onset of each trial during passive viewing. Two task-control experiments also were performed. In the motion-vs.-motion experiment, the RSVP letter stream was replaced by a disk containing a rotating radial pattern. On each trial, disk and annulus movement directions were independent. In the second control (letters vs. blank) experiment, central RSVP letters were combined with a blank surround annulus.

The first experiments (letters vs. motion) initially were intended as part of a two-by-two design to investigate the effects of attention on the processing of both luminance-defined (first-order) and texture-defined (second-order) motion. In half of the epochs of both attentional conditions, the spatial pattern of wedges (Fig. 2*a*) was defined by luminance differences (3% contrast). In the other half of the epochs, the spatial pattern was defined by variation in the contrast (from 0% to 8–12%) of a high spatial frequency texture made up of

concentric rings (0.2° wide at 3° eccentricity). Movement of the spatial pattern was identical for both pattern types. This motion-attention paradigm was inspired by a report of performance differences between first- and second-order motion discrimination as attentional load was varied (5). Here, attentional modulations were not significantly different for the two types of motion. Therefore, the motion condition data were combined for presentation here. The motion manipulation will be addressed at length elsewhere. In the subsequent control experiments presented, only luminance-defined motion was used.

Subject performance (95% correct) on second-order motion trials in the primary experiment demonstrates that subjects necessarily processed both high and low spatial frequencies. Visibility of second-order motion depends on visibility of the high spatial frequency carrier; if vision is blurred or high spatial frequencies are lost, the stimulus disappears to a uniform gray annulus and motion is not seen. Because results for first-order and second-order stimuli were not different, it is unlikely that selective spatial frequency channel processing contributed significantly to the results.

Eye Tracking. Eye position was monitored (250-Hz sample rate) in the scanner for three subjects by using MR-compatible eye-tracking goggles (Ober2, Permobil Meditech AB, Timre, Sweden). Calibration was performed for each subject. To remove eye blink artifacts from raw eye position data, median filtering (1.6-sec window) was performed for all traces. Eye blink artifacts in the eye position records were easily distinguished by large and transient downward Y-deflections.

RESULTS

In alternating epochs, seven subjects attended to foveal (letters) or extrafoveal (motion) components of the same stimulus configuration (see *Methods*; Fig. 2*a* and *b*). Subjects were required to maintain central fixation throughout, while performing same-different discriminations at the attended location. Subjects were well trained and performed well on the tasks, with the exception of one subject who performed poorly in the attend-extrafoveal-motion condition. This subject was excluded from subsequent group analysis (even though the subject exhibited V1 attentional modulation). The remaining six subjects performed significantly better ($P < 0.02$, *t* test) on the extrafoveal-motion task (95.7% correct \pm 1.6% SEM) than on the foveal-letters task (88.5% \pm 1.9 SEM). Subjects reported that each task was very attentionally demanding, and they were generally unaware of the nonattended discrimination.

Comparison of functional MRI BOLD signal activation during attend-extrafoveal-motion to that during attend-foveal-letters epochs revealed robust activation modulations in all subjects. Two aspects of the modulation are remarkable: (i) robust modulations were observed in primary visual cortex and (ii) the modulations were spatially specific to the retinotopic representations of the attended target. In all subjects, subtracting attend-foveal-letters from attend-extrafoveal-motion conditions revealed significantly ($P < 10^{-5}$) increased activation in sets of voxels corresponding to the mid-eccentricity regions of visual cortical areas V1–, V1+, V2–, V2+, V3–, VP+, V3A, and V4v+. This activation pattern can be seen in flattened cortical hemispheric representations for two subjects in Fig. 2*e* and *f*. The increased activation was specific to the retinotopic cortical representations of the attended annulus and did not include the unattended fovea (Fig. 2*c* and *d*).

Visual cortical areas V1–, V1+, V2–, V2+, V3–, VP+, and V4v+ each represent a quadrant of the visual field (V3A represents the contralateral hemifield). The – and the + labels indicate cortical representations of lower and upper contralateral quadrants, respectively. In five of seven subjects, the mid-eccentricity regions of all four quadrants of primary visual

cortex exhibited significantly increased modulation for the attend-extrafoveal-motion condition (Fig. 2*e* and *f*). In all, 25 of 28 V1 quadrants exhibited significant modulation at the mid-eccentricities.

Although these experiments primarily were designed to reveal attentional modulations away from the fovea, the reverse subtraction (attend foveal letters and attend extrafoveal motion) revealed increased activation specifically in voxels that represent the fovea and thus correspond to the position of the attended letters (Fig. 3*i*). Thus activation at retinotopic representations of a stimulus, whether foveal or extrafoveal, is significantly greater when attention is directed to that target than when attention is directed away. This dissociation between foveal and extrafoveal modulations also provides an important control against nonspecific arousal effects.

Across-subject average time courses ($n = 12$ hemispheres of six subjects) for the mid-eccentricity ROIs of cortical areas V1⁻, V1⁺, V2⁻, V2⁺, V3⁻, VP⁺, V3A, and V4v⁺ exhibit an approximately square wave shape time-locked to the epoch blocks (Fig. 3*a-h*). The average attention-related modulation (measured as % signal change from baseline) across subject hemispheres ($n = 12$) in V1⁻ was $0.82\% \pm 0.14\%$ SEM ($P < 10^{-5}$), and in V1⁺ was $0.49\% \pm 0.14\%$ ($P < 0.01$). Average modulations in other ROIs were as follows: V2⁻, $0.87\% \pm$

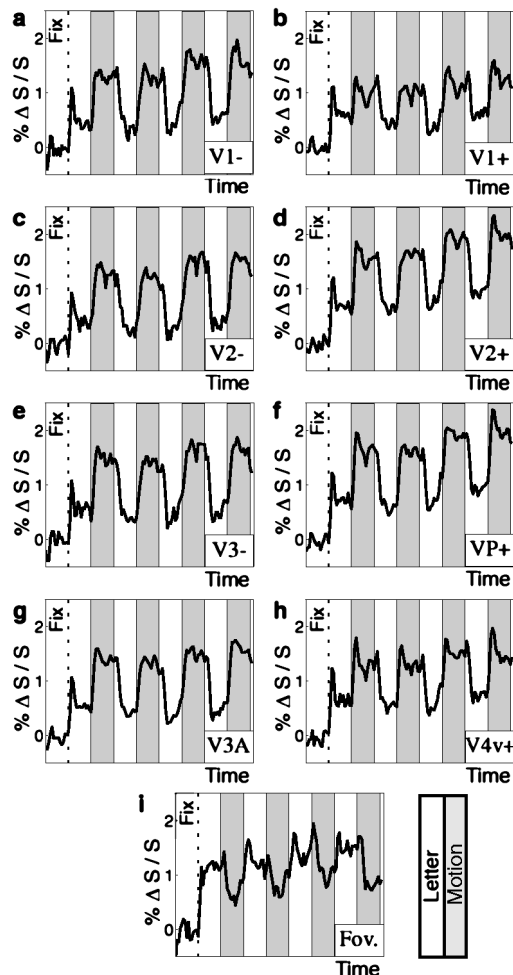


FIG. 3. Time course data by cortical area, averaged across subjects ($n = 12$ hemispheres) for attend foveal letters vs. attend extrafoveal motion. (*a-h*) Mid-eccentricity ROIs in V1⁻, V1⁺, V2⁻, V2⁺, V3⁻, VP⁺, V3A, and V4v⁺ exhibited greater activation during attend-extrafoveal-motion epochs. (*i*) Confluent foveal representation (e.g., red region of Fig. 2*b*) exhibited greater activation during attend-foveal-letters epochs.

0.15%; V2⁺, $0.87\% \pm 0.19\%$; V3⁻, $0.91\% \pm 0.17\%$; VP⁺, $0.92\% \pm 0.19\%$; V3A, $0.86\% \pm 0.13\%$; and V4v⁺, $0.66\% \pm 0.11\%$ (also see Fig. 4). Each of these attention-related modulations is highly significant ($P < 0.001$, random effects model; t test). Remarkably, the amplitude of attentional modulation is roughly half of stimulus-plus-attention activation from baseline fixation (Fig. 3). Average time course data for the fovea (Fig. 3*i*) show modulation in the reverse direction with mean across-subject modulation amplitude for the foveal ROI of $0.34\% \pm 0.12\%$ SEM, which is significant for the $P < 0.01$ level.

Several control studies were performed. Eye position measurements made for three subjects show no systematic differences between attend-fovea and attend-extrafovea epochs (Fig. 5; *Methods*). The pattern of activation observed for extrafoveal attention, quadrant-symmetric activation of mid-eccentricities with foveal sparing, also indicates that subjects generally held central fixation well. Shifting of gaze would be expected to activate visual field quadrants asymmetrically and to alter foveal activation. Thus it is unlikely that eye movements contributed significantly to the observed modulations.

Because subjects performed relatively well on the tasks, it is important to demonstrate that performance of each task impaired processing of the other stimulus. Four subjects were trained (after all imaging sessions) to perform both tasks simultaneously. Subjects performed the dual task psychophysics with task parameters identical to those in their imaging sessions, except that the poststimulus response period was doubled. Subjects performed the dual tasks under three conditions: priority for foveal letters, priority for extrafoveal motion, and equal priority. Subjects also performed the two single conditions tasks. Mean performance in the dual tasks was 77.5% for foveal letters and 77.3% for extrafoveal motion. This finding compares with mean single task performance of 94.2% for foveal letters and 98.2% for extrafoveal motion. Both tasks were significantly impaired ($P < 0.01$) in the dual task. This control demonstrates behavioral changes with attentional allocation and thus supports the claim that the observed modulations result from spatially specific, selective attention.

One potential concern with these spatial attention experiments is that the tasks differed between foveal and extra-foveal locations. To rule out task specificity, two subjects were run again with a modified stimulus and task. The central letters were replaced by a disk with a moving radial pattern. Subjects performed same-different motion discriminations on either the foveal or extrafoveal components (rotation directions were independent). The observed pattern of activations was quali-

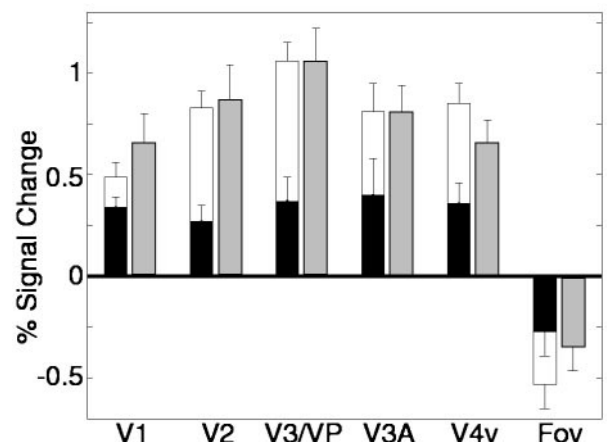


FIG. 4. Average attentional modulation amplitudes. Attend extrafoveal motion - passive viewing shown in black. Passive viewing - attend foveal letters shown in white stacked on top of black bars. Attend extrafoveal motion - attend foveal letters shown in gray.

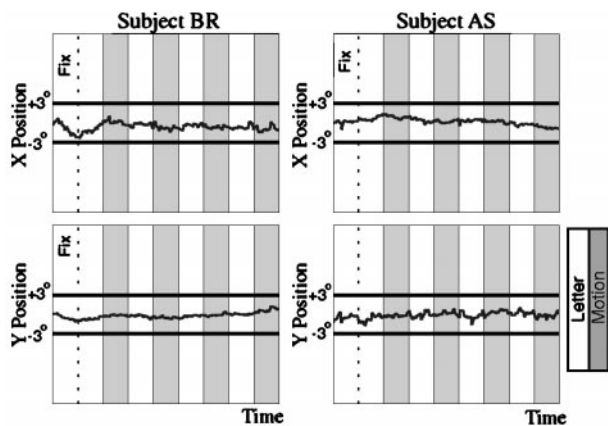


FIG. 5. Eye tracking control data. X and Y eye position traces are shown for two subjects monitored in the MR scanner (see *Methods*). Thick horizontal lines indicate location of the inner radius of the motion annulus (three degrees eccentric).

tatively similar to that of the first experiments. Average signal changes were 0.42% in V1-, 0.49% in V1+, 0.51% in V2-, 0.67% in V2+, 0.56% in V3-, 0.75% in VP+, 0.42% in V3A, and 0.28% in V4v+. The foveal modulation had the opposite phase with an average amplitude of 0.48%.

In an additional control test, three subjects alternated between attending to a blank annulus (no task) and performing the central letters task. Directing attention toward the blank surround proved demanding because of the exogenous attentional demands of the flashing RSVP letters. Average signal changes of 0.89% and 0.91% were observed in V1- and V1+, respectively. The other extrafoveal regions exhibited similar results with a combined average signal change of 1.1%. These data demonstrate that the attentional modulations were not task specific, but rather are consistent with spatially specific attentional effects.

Do the attend-to vs. attend-away modulations reflect increased activation under directed attention, decreased activation when attention is directed away, or a combination of both effects? Two additional experiments were run on each of four subjects to address this question. In one experiment, subjects alternated epochs of attending to foveal letters and epochs of passive viewing of the same stimulus (same fixation). In a second experiment, subjects alternated between attending to extrafoveal motion and passive viewing. The first experiment reveals attend-to modulations for the fovea and attend-away modulations for the extrafovea. In the second experiment, the logic is reversed.

Significant modulations were observed at both extrafoveal and foveal sites in both experiments (Fig. 4). Average modulations were computed for each visual field quadrant. Quadrant measurements for the four subjects were averaged together ($n = 16$) within V1, V2, and V3/VP. Similar upper/lower visual field pairings do not exist for V3A, V4v, or the combined foveal representation. In these areas, hemispheric measurements ($n = 8$) were averaged together. Attend extrafoveal motion—passive viewing comparison yielded across-subject average amplitudes in mid-eccentricity ROIs as follows: V1, 0.34% ($P < 10^{-5}$); V2, 0.27% ($P < 0.01$); V3/VP, 0.37% ($P < 0.01$); V3A, 0.40% ($P < 0.05$); and V4v+, 0.36% ($P < 0.01$). The across-subject average amplitudes of the passive viewing—attend foveal letters comparison in mid-eccentricity ROIs were as follows: V1, 0.15% ($P < 0.05$); V2, 0.56% ($P < 10^{-5}$); V3/VP, 0.69% ($P < 10^{-5}$); V3A, 0.41% ($P < 0.02$); and V4v+, 0.49% ($P < 0.01$). The sum of the signal changes observed in the two attend vs. passive experiments is similar to the net change observed in the attend-to vs. attend-away experiments (Fig. 4). In the foveal region, the attend

extrafoveal motion—passive viewing comparison produced an average modulation of -0.27% ($P < 0.05$) and the passive viewing—attend foveal letters comparison produced an average modulation of -0.26% ($P < 0.05$). Thus attention increases activation in the cortical representations of the attended stimulus and decreases activation elsewhere. This push-pull attentional modulation was observed independently for both foveal and extrafoveal targets. These experiments also demonstrate that the hole in the cortical pattern of increased activation observed when attending to the motion annulus (Fig. 2 *e* and *f*) reflects, in part, decreased activation in the unattended fovea.

DISCUSSION

Strong attentional modulation was repeatedly observed in primary and other visual cortical areas. Visual fixation and stimulus conditions were equivalent in the compared attentional states, and control experiments rule out eye position differences and task-related differences as sources of the modulations. Dual-task psychophysics experiments demonstrate that allocation of attention significantly affects task performance. These controls strongly support the conclusion that the modulations result primarily from selective visual attention. To identify the loci of attentional modulation, retinotopic mapping was performed on each subject. These mappings clearly demonstrate that large regions of V1 were attentionally modulated.

Several aspects of V1 attentional modulation were demonstrated. First, the attentional modulations were robust. On average, attentional modulations in V1 were equal to half of the stimulus-plus-attention modulation from baseline fixation. In some subjects, the attentional modulation was approximately 1% of baseline signal. Second, modulations were spatially specific between attended and nonattended locations. Third, both spatially specific enhancement and spatially specific suppression (as compared with neutral passive viewing) were observed, suggesting that attention operates in a push-pull manner. Finally, these properties of V1 attentional modulation were qualitatively similar to those observed in higher retinotopic areas, suggesting that common spatially specific attentional mechanisms may operate across retinotopic visual cortical areas. The observation that visual attention operates at the lowest levels of the cortical hierarchy is consistent with the requirements of early-selection models of attention (2, 11, 39).

Although the observed attentional modulations were spatially specific, this specificity need not imply spatial selection, *per se*. The complex spatial window of attention that was observed in striate and extrastriate cortex is consistent with object-based selection (12). In five of seven subjects, attending to the moving annulus produced patterns of increased activation that closely correspond to the representation of the annulus—mid-eccentricities of all four visual field quadrants, while sparing the fovea. A sixth subject showed this pattern in extrastriate cortex and three striate cortex quadrants. In contrast, the hole in this attentional annulus appears inconsistent with the topological requirement of a simple attentional spotlight mechanism for spatial selection (2). Thus, our results demonstrate that the window of attention can be spatially complex. Further experiments will be required to determine whether this reflects object-based selection or a more complex form of spatial selection.

The present results in the human parallel many of Motter's findings (22) in the monkey. Motter reported that one-third of cells in V1, V2, and V4 exhibited modulated responses when comparing attend-to and attend-away trials with identical stimuli. Comparing responses to a baseline condition revealed that both the attend-to and attend-away states contributed to the observed modulations. Like Motter (22), the present study

found roughly equivalent attention effects across striate and extrastriate visual areas. Both facilitatory and suppressive components contributed to the modulation. To this degree, the present study can be viewed as confirming Motter's findings in the monkey, and extending them to human visual cortex. The present study is also consistent with a recent report of object-based attention in monkey V1 (40).

These findings, taken together with Motter's (22) and other very recent findings (41–43), make clear that attention can have strong and specific effects in V1. The overall view that emerges suggests that V1 is not simply a passive, image-processing front end, as is often assumed. More integrated models, in which responses depend on strong influences other than the bottom-up thalamic inputs, are required (e.g., ref. 44). The results of this study also help to bolster conjectures that perceptual learning occurs within V1 (e.g., refs. 45 and 46), as it has been argued that attention is required for perceptual learning (47). More generally, strong attentional modulations in V1 suggest that top-down, cognitive influences affect all levels of the cortical substrates of visual perception. This finding is consistent with studies of mental imagery (48). Despite extensive evidence for hierarchical neural processing, this and other evidence suggest that visual perception is a highly integrative process that incorporates not only inputs from V1, but also V1 cortical circuitry directly.

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