Mechanisms of Feature- and Space-Based Attention: Response Modulation and Baseline Increases

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McMains SA, Fehd HM, Emmanouil T-A, Kastner S. Mechanisms of feature- and space-based attention: response modulation and baseline increases. J Neurophysiol 98: 2110–2121, 2007. First published August 1, 2007; doi:10.1152/jn.00538.2007. Selective attention modulates neural activity in the visual system both in the presence and in the absence of visual stimuli. When subjects direct attention to a particular location in a visual scene in anticipation of the stimulus onset, there is an increase in baseline activity. How do such baseline increases relate to the attentional modulation of stimulus-driven activity? Using functional magnetic resonance imaging, we demonstrate that baseline increases related to the expectation of motion or color stimuli at a peripheral target location do not predict the modulation of neural responses evoked by these stimuli when attended. In areas such as MT and TEO that were more effectively activated by one stimulus type than the other, attentional modulation of visually evoked activity depended on the stimulus preference of a visual area and was stronger for the effective than for the noneffective stimulus. In contrast, baseline increases did not reflect the stimulus preference of a visual area. Rather, these signals were shown to be spatially specific and appeared to be dominated by the location information and not by the feature information of the cue with the experimental paradigms under study. These findings provide evidence that baseline increases in visual cortex during cue periods do not reflect the activation of a memory template that includes particular stimulus properties of the expected target, but rather carry information about the location of an expected target stimulus. In addition, when the stimulus contained both color and motion, an object-based attention effect was observed, with significant attentional modulation in the area that responded preferentially to the unattended feature.

INTRODUCTION

Evidence from functional brain mapping and single-cell physiology indicates that selective attention modulates neural activity in the visual system both in the presence and in the absence of visual stimulation. Neural responses to visual stimuli are typically enhanced when attended compared with when the same stimuli are ignored (attentional response modulation; Desimone and Duncan 1995; Kastner and Ungerleider 2000; Reynolds and Chelazzi 2004). Directing attention to a location in the absence of visual stimulation, in anticipation of the stimulus onset, increases neural baseline activity (attention-related baseline increases; Kastner et al. 1999; Luck et al. 1997). These attention effects have been found throughout the visual system, including the lateral geniculate nucleus and both striate and extrastriate cortices (Cook and Maunsell 2002; Martinez et al. 1999; Mehta et al. 2000; Motter 1994; O’Connor et al. 2002; Reynolds et al. 1999; Treue and Maunsell 1996), and appear to be controlled by a distributed network of higher-order areas in frontal and parietal cortex, which generates top-down signals that are transmitted by feedback connections to the visual system (Corbetta et al. 2002; Hopfinger et al. 2000; Kanwisher and Wojciulik 2000; Kastner et al. 1999).

The magnitude of attentional response modulation has been shown to depend on a number of variables. First, attentional enhancement effects increase with the task difficulty or attentional load required for selecting the behaviorally relevant information (Pinsk et al. 2004; Spitzer and Richmond 1991; Spitzer et al. 1988). Second, the effects depend on the presence of nearby distracter stimuli. Selective attention has been shown to operate by counteracting competitive influences of nearby distracters on target stimuli, thereby biasing neural responses in favor of the attended stimulus (Kastner et al. 1998; Moran and Desimone 1985; Recanzone and Wurtz 2000; Reynolds et al. 1999). Finally, attention to a particular stimulus attribute (e.g., color) that is selected among other stimulus attributes of an object (e.g., shape, motion) selectively activates neurons that preferentially process the attended attribute (Beauchamp et al. 1997; Clark et al. 1997; Corbetta et al. 1991; Ferrera et al. 1994; Haenny et al. 1988; Motter 1994; O’Craven et al. 1997; Saenz et al. 2002; Wojciulik et al. 1998). Similar to response modulation, the magnitude of increases in baseline activity depends on some of the same variables, including expectations about task difficulty (Ress et al. 2000), or the presence or absence of distracter stimuli (Serences et al. 2004). For example, baseline increases in primary visual cortex (V1) were shown to be larger when subjects expected a visual pattern that was difficult to discriminate compared with a pattern that was easy to discriminate (Ress et al. 2000). Baseline increases have also been implicated in reflecting the stimulus preference of neurons in a given visual area (Chawla et al. 1999). However, it is not clear how these baseline signals relate to the subsequent attentional modulation. Given that both signals appear to have very similar characteristics, one hypothesis is that attentional response modulation results from a summation of sustained baseline increases and visually evoked activity during attentional selection. Such a model of attentional modulation is supported by recent findings of additive modulatory effects on the contrast response function across visual cortex (Buracas and Boynton 2007; Williford and Maunsell 2006). Alternatively, it is possible that baseline and attentional modulation signals are independent of each other. This hypothesis is supported by functional magnetic resonance imaging (fMRI)

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findings demonstrating significant baseline increases in primary visual cortex without subsequent attentional modulation (Kastner et al. 1999).

Using fMRI we studied attentional modulation of responses evoked by color and motion stimuli and baseline increases related to the expectation of these stimuli across the human visual cortex. Our main question of interest was how baseline increases are related to modulation of stimulus-driven activity. In previous studies (Kastner et al. 1999), baseline increases and their relation to subsequent attentional modulation have been investigated while subjects were cued to a spatial location. To explore the relationship between baseline increases and attentional modulation more thoroughly, our paradigm required subjects to attend not only to a spatial location, but also to a particular feature, either color or motion. A secondary question that we investigated was whether baseline increases show feature specificity. If so, these signals may be closely related to sustained activity obtained in working-memory tasks that activate a memory template. To investigate these issues we conducted two experiments. The first experiment was designed to investigate attentional modulation and baseline increases while subjects were maximally biased toward a single feature dimension. In this study, referred to as the feature selectivity experiment, stimuli contained a single feature, either color or motion. This design also allowed us to determine the preference of certain visual areas, such as MT and TEO, for each feature dimension. The second study, referred to as the feature competition experiment, was designed to investigate attentional modulation and baseline increases when there was maximal competition between the two feature dimensions. In this experiment, stimuli always contained both features, color and motion. This paradigm also allowed us to investigate whether attentional selection of one stimulus feature leads to the attentional enhancement of an unattended feature belonging to the same object.

METHODS

Subjects, visual stimuli, and tasks

Eight subjects (three males; age: 23–34 yr) participated in the study, which was approved by the Institutional Review Panel of Princeton University. All subjects were in good health with no past history of psychiatric or neurological diseases and gave their informed written consent. Subjects had normal or corrected-to-normal visual acuity.

In the first study, the feature selectivity experiment, moving achromatic or stationary chromatic dot patterns were used as visual stimuli. The patterns consisted of 100 dots randomly placed within a square-shaped aperture (2.8 × 2.8° in size) that was presented at 10.8° eccentricity from fixation in the upper right visual quadrant (Fig. 1). For motion patterns, the dots were achromatic and moved at a rate of 7/s in one of four directions (up, down, right, left; see arrows in Fig. 1A). For color patterns, the dots were stationary and were presented in one of four colors (green, blue, yellow, magenta). To minimize adaptation, the location of each dot was randomly chosen when each new color or motion stimulus was drawn. Luminance of chromatic and achromatic stimuli ranged from 60 to 100 cd/m² and was approximately matched for the two stimulus types. Stimuli were presented sequentially and in random order for 500 ms and at 2 Hz in blocks of 18 s; only one type of stimulus, either color or motion, was presented within a given block. In the second study, the feature competition experiment, the moving dot patterns were rendered in color and the two feature dimensions were always shown simultaneously. Stimuli were presented sequentially and in random order for 350 ms in blocks of 18 s. All other stimulus parameters were identical to the feature selectivity experiment.

In both the feature selectivity and feature competition experiments (Fig. 1, B and C), the two types of stimuli were probed under two conditions: unattended and attended. In the unattended condition, subjects were instructed to maintain fixation at a central fixation cross and to count brief luminance changes of the cross. The fixation task ensured proper fixation and prevented subjects from covertly attending to the peripheral stimuli (Beck and Kastner 2005; Kastner et al. 1998). In the attended condition, subjects covertly directed attention to the peripheral target location and counted the occurrences of a target stimulus (e.g., leftward motion, Att Mot in A). B in the feature selectivity experiment, only stimuli of one feature dimension were shown during a single run. An example for a motion sequence is shown. Feature dimensions changed from run to run. C: in the feature competition experiment, each stimulus contained both motion and color. Location of stimulus presentations was kept constant across all conditions.

FIG. 1. Experimental design. A: stimuli were presented sequentially in a square-shaped aperture at 10.8° eccentricity from a fixation cross in blocks of 18 s interleaved with blank periods. An example for a motion block in the feature selectivity experiment is shown. Arrows indicate direction of dot motion. At the beginning of each attended presentation block, a letter cue (“M” for motion trials; “C” for color trials) was shown, which indicated the feature dimension and the location of the to-be-attended stimuli. Presentations were delayed by 6 s, during which subjects directed attention to the target location in expectation of a motion or color stimulus (expectation period [exp], schematically indicated by the attentional spotlight). Two attentional conditions were tested: an unattended (dotted outlines in B and C), during which subjects detected luminance changes at fixation, thereby ignoring the peripheral presentations (not shown), and an attended (solid outlines in B and C), during which subjects covertly directed attention to the peripheral stimulus location and detected the occurrences of a target stimulus (e.g., leftward motion, Att Mot in A). B: in the feature selectivity experiment, only stimuli of one feature dimension were shown during a single run. An example for a motion sequence is shown. Feature dimensions changed from run to run. C: in the feature competition experiment, each stimulus contained both motion and color. Location of stimulus presentations was kept constant across all conditions.
presence of visual stimulation could be tested. Within a run, four blocks of attended and unattended presentations were interleaved with fixation task blocks, with the sequence of presentations and tasks counterbalanced across runs. Each run started with a blank period of 6 s and ended with a blank period of 24 s. During a scan session subjects completed 10 to 12 runs.

In the feature selectivity experiment, only one feature dimension was tested in a given run to bias subjects maximally toward that feature dimension (see Fig. 1B for a sample motion sequence). In addition, we were able to determine the preference of an area for a given feature. Feature dimensions changed from run to run, with subjects performing five to six runs of each feature dimension during a scanning session.

In the feature competition experiment, the two stimulus features were always presented simultaneously (Fig. 1C). This experiment further ensured that subjects were using the letter cue by providing competition between the color and motion feature dimensions. The first stimulus in a cued block no longer provided information about what type of attended block it was, color or motion; only the cue carried that information.

Subjects were extensively trained on all tasks in several behavioral testing sessions, during which performance measures (accuracy, reaction times) were taken. Procedures during behavioral testing were similar to those during scanning sessions except that subjects always responded by pressing a button. The efficacy of the fixation task in precluding subjects from covertly attending to the peripheral stimuli in the unattended condition was tested by measuring accuracy and reaction times to luminance changes during blank, motion, and color presentations. Performance did not differ during color and motion presentations and was also not different from that obtained during blank trials, suggesting that the peripheral stimulus presentations did not interfere with performing the luminance-detection task and indicating that this task provided sufficient attentional demands to preclude exogenous attentional cuing.

Data acquisition and analysis

General scanning and data analysis procedures were identical in both experiments. Images were acquired with a 3-Tesla head scanner (Allegra, Siemens, Erlangen, Germany) using a standard head coil. Six subjects were tested in one scanning session (three subjects each for the feature selectivity and feature competition experiments), and two in two separate scanning sessions (one for the feature specificity and one for the feature competition experiment), each lasting about 2 h. In addition, retinotopic mapping was performed for all subjects in a separate scan session. Functional images were taken with a gradient echo, echo planar sequence (TR = 1.2 s, TE = 30 ms, flip angle = 90°, 64 × 64 matrix). Sixteen contiguous, coronal slices (thickness = 3 mm, gap = 1 mm, in-plane resolution: 3 × 3 mm) were acquired in 10–12 runs of 130–150 images each, covering areas in occipital, posterior temporal, and parietal cortex. Echo-planar images were compared with a co-aligned high-resolution anatomical scan of each subject’s brain taken in the same session (FLASH, TR = 150 ms, TE = 4.6 ms, flip angle = 90°, 256 × 256 matrix). Another high-resolution anatomical scan of the whole brain (MPRAGE sequence; TR = 11.1 ms; TE = 4.3 ms; flip angle = 8°; 256 × 256 matrix; three-dimensional resolution = 1 mm³) was taken to perform spatial normalization and to create cortical surface reconstructions using BrainVoyager software (Brain Innovation, Maastricht, The Netherlands).

Visual stimuli were projected with an Epson LCD projector onto a translucent screen located at the back of the scanner bore at a distance of 60 cm from the subjects’ eyes. Stimuli were viewed from inside the bore of the magnet by a mirror system attached to the head coil, providing a maximal visual angle of 28 × 36°.

Between-scan head movements were corrected by aligning each image to a reference image obtained in the middle of the session using Automatic Image Registration (AIR) software (Woods et al. 1993). Images were spatially smoothed in-plane with a small Gaussian filter (full width at half-maximum of 1.2 voxel lengths). Statistical analyses were restricted to brain voxels with adequate signal intensity (average intensity of >20% of the maximum value across voxels). The first five images of each scan were excluded from analysis. Statistical analyses were performed using multiple regression in the framework of the general linear model (Friston et al. 1995) with National Institutes of Health functional imaging data analysis program (FIDAP) software. Square-wave functions matching the time course of the experimental design were as designed as effects of interest in the multiple regression model. The square-wave functions contrasted J blocks of attended and unattended visual presentations versus blank periods, 2 blocks of attended versus unattended visual presentations, and J epochs of expectation with directed attention in the absence of visual stimulation, preceding the attended presentations, versus control epochs with blank presentations preceding the respective unattended visual presentations. The latter activity was defined as baseline, relative to which increases were measured. For each effect of interest, square-wave functions were convolved with a Gaussian model of the hemodynamic response (lag, 4.8 s; dispersion, 1.8 s) to generate idealized response functions, which were used as regressors in the multiple regression model. Additional regressors were used to factor out variance due to between-run changes in mean intensity and within-run linear changes. Statistical maps were thresholded at a Z score of 2.33 (P < 0.01, corrected for multiple comparisons) and overlaid on structural T1-weighted scans taken in the same session and in the same plane. Activity in visual cortex was assigned to retinotopically organized areas. Due to our statistical model the analysis was restricted to voxels activated by the peripheral stimuli and excluded foveal stimulus representations including the letter cue.

Time series of fMRI intensities were extracted for each subject from all voxels activated by contrast (1) in a given visual area (subsequently defined), normalized to the mean intensity obtained during the control condition and collapsed across the different sequences of unattended or attended presentations and expectation periods. Mean signals were computed by averaging across all intensity values obtained in a given condition and are given as percentage signal change. These values were further quantified by defining several indexes: a stimulus efficacy index (SEI), an attentional modulation index (AMI), and a baseline modulation index (BMI). The SEI indicates the efficacy of color or motion stimuli in driving activity in a given area and was calculated only for the feature selectivity experiment, where SEI = [(CRAtt + CRUnatt)/2 − (MRAtt + MRUnatt)/2] [(CRAtt + CRUnatt)/2 + (MRAtt + MRUnatt)/2] (R, mean response; C, color; M, motion; Att, attended presentations; Unatt, unattended presentations). Positive values indicate stronger activation by color stimuli, negative values indicate stronger activation by motion stimuli, and values around 0 indicate no difference in activity evoked by the two stimulus types. The AMI quantifies attention effects obtained during color and motion presentations. For the feature selectivity experiment, the AMI was computed as follows: AMIC = [CRAtt − (CRUnatt + MRUnatt)/2] [(CRAtt + CRUnatt)/2 + (MRAtt + MRUnatt)/2] and AMIM = [MRAtt − (CRUnatt + MRUnatt)/2] [(CRAtt + CRUnatt)/2 + (MRAtt + MRUnatt)/2]. For the feature competition experiment, the AMI was defined as: AMIC = [RAttCol − RUnatt]/[RUnatt] and AMIM = [RAttMot − RUnatt]/[RUnatt]. To compare the attention effects obtained for the two feature dimensions in the feature selectivity experiment the AMI was defined using a common normalization value, the averaged activity evoked during unattended color and motion presentations. It should be noted that this index definition leads to a slight distortion of the attention effects in areas with high preference for one feature dimension over the other (e.g., MT, TEO). In these areas, the AMI in this definition tends to overestimate the attention effects on the more efficient stimulus and tends to underestimate those on the less efficient stimulus. The BMI estimates the increase in baseline activity during expectation of color and motion stimuli and allows for a quantitative comparison of
baseline increases across the visual system (Kastner et al. 1999; O’Connor et al. 2002). For the feature selectivity experiment, the BMI was defined as: $\text{BML} = \text{EXP} - \frac{1}{2} (\text{CR}_{\text{Unatt}} + \text{MR}_{\text{Unatt}})$ and $\text{BML} = \text{EXP} - \frac{1}{2} (\text{CR}_{\text{Unatt}} + \text{MR}_{\text{Unatt}})$, whereas in the feature competition experiment, the BMI was computed as $\text{BMI} = \text{EXP} - \frac{1}{2} (\text{CR}_{\text{Unatt}} + \text{MR}_{\text{Unatt}})$, where EXP is the mean response during expectation of visual stimuli. To compare the magnitude of AMIs and BMIs across all activated visual areas in both experiments, the BMI used the same normalization value as the AMI, that is, mean signals evoked by unattended color and motion presentations. Larger index values indicate stronger baseline attention effects. Statistical significance of time series data was determined by a random-effects analysis using one-sample, two-tailed t-test. ANOVAs and t-test were calculated to assess significance for index values and behavioral data. Correlations for BMIs were compared by using a z-test statistic using Fisher transforms of the correlations. For each subject, statistical maps and structural images were transformed into Talairach space (Talairach and Tournoux 1988) using BrainVoyager software.

Mapping visual areas

Retinotopic mapping was performed for each subject in a separate scanning session using procedures similar to those established by Sereno et al. (1995) and described in detail in Kastner et al. (2001). Briefly, areas V1, V2, and ventral V3 (referred to as VP) were identified by the alternating representations of the vertical and horizontal meridians, which form the borders of these areas (DeYoe et al. 1996; Engel et al. 1997; Sereno et al. 1995). Areas V4 and TEO were identified by their characteristic upper (UVF) and lower (LVF) visual field topography (Kastner et al. 1998, 2001). The UVF and LVF are separated in V4 and located medially and laterally on the fusiform gyrus, whereas this separation is not seen in the region anterior to V4, which we term TEO. Area V4 in this study likely corresponds to area V4 of McKeefry and Zeki (1997) and Wade et al. (2002) and appears to overlap with V4v and V8 described by Hadjikhani et al. (1998). Area TEO likely corresponds to area CoS described by Malach et al. (2002) and VO 1/2 described by Brewer et al. (2005). Activations in area MT were identified based on the characteristic anatomical location of this area (Dumoulin et al. 2000; Tootell et al. 1995; Watson et al. 1993) and confirmed in four subjects with a standard functional motion localizer (radially moving dots vs. stationary dots). Area IPS is located in the depth of the intraparietal sulcus, just anterior to V3A (Kastner et al. 1999), which most likely corresponds to V7 (Tootell et al. 1998). After each region was identified, ROIs were created by taking the voxels activated by the contrast attended and unattended blocks versus fixation for each region.

RESULTS

Results for both the feature selectivity and feature competition experiments will be presented together. In both experiments, five subjects were tested in a block design, in which epochs of visual presentations alternated with blank presentations while the subjects maintained fixation at a central fixation point. The only difference between the two experiments was whether the peripheral stimulus contained a single feature (feature selectivity) or both features simultaneously (feature competition). In the feature selectivity experiment, moving or colored dot patterns placed within a square-shaped aperture were presented to the periphery of the upper right quadrant. During motion blocks (Fig. 1A), the dot patterns consisted of achromatic dots moving in one of four directions. During color blocks, the dot patterns consisted of stationary chromatic dots (green, blue, yellow, or magenta). In the feature competition experiment, the stimulus always contained color and motion. In both experiments two attentional conditions were tested: an unattended condition, during which subjects maintained fixation and were engaged in a luminance change detection task at fixation, and an attended condition, during which subjects covertly directed attention to the peripheral stimulus location and counted the occurrences of a target stimulus (e.g., leftward motion of dots, Fig. 1A). The attended presentations were designated by a letter marker presented close to fixation that indicated both the target location and the to-be-expected feature dimension (the letter C for color, or M for motion; see Fig. 1A). The subjects’ task was to covertly direct attention to the target location as soon as the marker was shown and to expect the onset of the cued stimulus presentations, either color or motion. The spatial location of the target stimulus remained the same in all experiments. Therefore any response differences related to the expectations or presentations of color or motion stimuli were due to differences in feature properties, not spatial location. Subjects’ performance in the peripheral motion and color detection task was high [feature selectivity: 99% correct on motion trials, 93% correct on color trials; feature competition: 97% correct, reaction time (RT) = 497 ± 11 (SE) ms on motion trials, 99% correct; RT = 473 ± 11 (SE) ms on color trials, the differences of which were not significant].

Responses to color and motion stimuli in visual cortex

Motion and color stimuli, presented separately or in competition, evoked significant activity during unattended and attended presentations relative to blank presentations in early visual areas V1, V2, and VP, ventral extrastriate areas V4 and TEO, dorsal extrastriate area MT, and an area in the posterior intraparietal sulcus (IPS) in all subjects in both experiments. Because the border between V2 and VP could not be distinguished unequivocally in some of the subjects, activations in the combined region (hereafter referred to as V2) were used for further analyses.

The feature selectivity experiment in which the stimulus contained only a single feature allowed us to investigate the preference of a given area for a particular feature, either color or motion. The activity evoked by motion and color presentations averaged across unattended and attended conditions was used to estimate the efficacy of the two types of stimuli in driving a visual area. An analysis of the time series of fMRI signals (Fig. 2A) and the mean signal changes (Fig. 3A) averaged across subjects showed that there were no differences in responses evoked by motion and color stimuli in areas V1, V2/VP, and IPS (Fig. 3A; main effect of stimulus type: n.s.). Ventral extrastriate areas V4 and TEO (Fig. 3A) were significantly more activated by color stimuli compared with motion stimuli (main effect of stimulus type: $P < 0.05$ for V4; $P < 0.01$ for TEO). Dorsal extrastriate area MT showed the reverse response pattern with a significantly stronger response to motion stimuli compared with color stimuli (main effect of stimulus type: $P < 0.001$). The double dissociation of response patterns evoked by motion and color stimuli in ventral and dorsal extrastriate areas is also reflected in the stimulus efficacy index (SEI) shown in Fig. 4. Positive values indicate that color stimuli were more effective than motion stimuli in activating an area, negative values indicate that motion stimuli were more effective than color stimuli, and values around zero indicate no response differences evoked by the two types of stimuli (Fig. 4;
Attentional response modulation in visual cortex

Directing attention to the peripheral stimuli significantly modulated visually evoked signals in all visual areas except V1 in both experiments (feature selectivity: Figs. 2A and 3A; main effect of attention: $P < 0.05$ in V2, MT, TEO; $P < 0.01$ in V4, IPS; feature competition: Figs. 2B and 3B; main effect of attention: $P < 0.05$ in V2, $P < 0.01$ in V4, MT, TEO, IPS). In visual areas that did not show any differences in responses evoked by the two stimulus types, or no feature preference, mean fMRI signals evoked by motion and color stimuli were enhanced to a similar degree when attended. This included areas V2 and IPS in the feature selectivity study and areas V2, V4, and IPS in the feature competition study (Fig. 3). In visual areas that were more effectively activated by one stimulus type over the other, attentional modulation of activity evoked by the more effective stimulus tended to be stronger than that evoked by the less effective stimulus. This is most clearly demonstrated by areas TEO and MT in the feature selectivity experiment, in which a significant interaction of stimulus type and attention was found (TEO: $P = 0.05$; MT: $P < 0.05$). This reflects the fact that neither area showed a significant effect of attention when only the nonpreferred feature was present. In area V4, activity evoked by the more effective color stimuli tended to be modulated more strongly than that evoked by the less effective motion stimuli in the feature selectivity experiment, although the interaction of stimulus type and attention did not reach significance. This reflects the fact that V4 had

main effect of area: $P < 0.001$; V4, TEO vs. MT: $P < 0.01$; V4 vs. TEO: $P = 0.08$.

**FIG. 2.** Time series of functional magnetic resonance imaging (fMRI) signals in visual cortex. Time series of fMRI signals in the extrastriate visual cortical areas V2/VP and V4, the middle temporal visual area (MT), and the region anterior to V4, which we term TEO, averaged over all subjects ($n = 5$). Gray shades indicate presentation periods; the beginning of the expectation period is indicated by the dotted vertical line. In all areas, activity increased when subjects directed attention to the target location in expectation of a color or motion stimulus, but these increases were independent of the expected feature dimension. A: feature selectivity experiment. In the unattended condition (dashed curves), motion stimuli evoked more activity in MT, whereas color stimuli tended to evoke more activity in areas V4 and TEO. In the attended condition, stronger response modulation was found with motion relative to color stimuli in area MT. The opposite response pattern was found in area TEO. B: feature competition experiment. Greater attentional enhancement was found in TEO when color was the attended feature, whereas greater enhancement was observed in MT when motion was attended. Remarkably, activity was significantly increased by the unattended feature in these areas.

**FIG. 3.** Mean signal changes in areas V1, V2/VP, V4, TEO, MT, and intraparietal sulcus (IPS), averaged across subjects for the feature selectivity (A) and feature competition (B) experiments. For each subject, the peak intensities of the fMRI signal obtained during attended and unattended color and motion trials were averaged. Except for V1, a main effect of attention was found in all areas. In areas TEO and MT, responses evoked by the more effective stimulus were more strongly modulated than those evoked by the less effective stimulus.
significant attentional modulation for both features (attention effect on color: \( P < 0.05 \); attention effect on motion: \( P < 0.01 \)) and suggests that, although area V4 might have some preference for processing color stimuli, it is recruited in a top-down manner for the processing of both color and motion. This notion is further supported by the finding that area V4 did not show a feature preference when the stimulus always contained both color and motion, as in the feature competition experiment (Fig. 3B, attend color vs. attend motion: \( P = \text{n.s.} \)). On the other hand, the strong feature preference of areas TEO and MT was still evident even when the stimulus contained both features. Greater attentional modulation was observed when attention was directed toward the preferred stimulus (attend color vs. attend motion: \( \text{TEO: } P < 0.05, \text{MT: } P < 0.05 \)). It is important to note, however, that unlike in the feature selectivity experiment, there was significant attentional modulation in these regions when subjects directed attention to the nonpreferred feature dimension (Fig: 3B, attend nonpreferred vs. unattended, TEO: \( P < 0.05, \text{MT: } P < 0.05 \)), suggesting an object-based spread of attention.

The differential pattern of attentional response modulation on color and motion stimuli in visual cortex is also reflected in the attentional modulation index (AMI) shown in Fig. 5. The AMI estimates the attentional response enhancement of visually evoked activity by normalizing the increase in responses to the attended relative to the unattended stimulus presentations. AMIs were calculated separately for color (AMI_c) and motion (AMI_m) trials. For the feature selectivity experiment, they were normalized to the mean signals averaged across unattended color and motion stimulus presentations. For the feature competition experiment, they were normalized to the mean signals for the unattended condition (which contained both features). The common normalization value allowed for a direct comparison of the magnitude of the attention effects on the different stimulus types across all visual areas. Again, across both experiments areas TEO and MT stand out in exhibiting significantly greater attention effects for their preferred stimuli (AMI_c vs. AMI_m: feature selectivity: TEO: \( P < 0.05, \text{MT, } P < 0.05, \text{V4, } P = 0.05; \) feature competition: TEO: \( P = 0.05, \text{MT, } P < 0.05, \text{V1, } P < 0.05 \)).

**Baseline increases in visual cortex**

When subjects were covertly directing attention to the peripheral target location in expectation of a color or motion stimulus, fMRI signals increased for both experiments in all attentionally modulated regions relative to the preceding blank period in which subjects were fixating but not directing attention to the periphery, as can be seen from the time series of signals (Fig. 2) and the mean signal changes (Fig. 6) averaged across subjects. The baseline increases observed appear to be related to directed attention and not the result of bottom-up stimulation. First, the visual input, a blank screen, was identical in both conditions. Second, the analysis was restricted to voxels activated by the peripheral stimuli, excluding foveal representations, and therefore the increase in baseline activity was not evoked by the presentation of the cue, which was shown close to fixation. The increase in activity during the expectation period was significant in all visual areas for the feature selectivity experiment (V1: \( P = 0.14 \); V2, V4, MT, IPS: \( P < 0.01 \); TEO: \( P < 0.05 \)) and was followed by a further increase of activity after the onset of the visual stimuli (Fig. 2). Importantly, there were no differences in baseline increases obtained during the expectation of color or motion stimuli in any of these areas, for either experiment (Fig. 6; feature selectivity: main effect of expectation, n.s.; feature competition: paired t-test, n.s.), suggesting that the baseline signals were dominated by the location information of the cue under these conditions. Even in areas showing greater preference for a particular stimulus type such as TEO and MT, no differences in baseline increases during the expectation of color versus motion stimuli were found (Fig. 6).

The spatial specificity of baseline increases was further investigated in the feature selectivity experiment by examining the statistical maps in individual subjects obtained by contrasting epochs with directed attention in the absence of visual stimulation (i.e., expectation periods) to control epochs during which subjects maintained fixation without directing attention to the peripheral target location. Activation maps, overlaid on
To quantify the attention effects on baseline activity we defined a baseline modulation index (BMI), which allows for a comparison of baseline increases across visual areas. The BMI estimates the increase in baseline activity during expectation relative to the unattended visual presentations (averaged across activity evoked by color and motion stimuli to provide a common normalization value) and was calculated separately for color and motion expectation periods. Positive values indicate increases in baseline activity, negative values indicate suppression of baseline activity, and values around 0 indicate no change in activity. BMIs obtained during expectation of color (BMI_C) or motion stimuli (BMI_M) are plotted in Fig. 8, A and B for each activated visual area. A strong correlation is apparent (feature selectivity: $r = 0.68$, $P < 0.001$; feature competition: $r = 0.84$, $P < 0.001$, no difference between correlations for the two experiments), such that BMI_C and BMI_M fall close to the unity slope line, indicating that baseline

anatomical scans, are shown in Fig. 7 for four subjects. In all subjects, activations obtained during the expectation period were restricted to peripheral representations of the ventral visual areas of the left hemisphere, thus representing the attended target location in the upper right quadrant (Fig. 7A, arrows). No activations in visual areas representing other parts of the visual field were found, including more foveal representations of the upper right visual quadrant. The dorsal activations shown in Fig. 7 were located in superior parietal cortex and will not be further discussed in the present study (see Kastner et al. 1999). In addition, we compared the time courses of fMRI signals in peripheral representations corresponding to the eccentricity of the stimulus in left and right V4 for the four subjects shown in Fig. 7A. Area V4 showed a strong increase in baseline activity during the expectation period (see Figs. 2 and 6) and receives, in contrast to TEO and MT, an exclusive input from the contralateral visual field. Therefore the spatial specificity of baseline increases can be ideally probed by a time course analysis of signals in this area. Signals evoked during color and motion trials were pooled in this analysis. In left V4, the time course of fMRI signals showed a baseline increase during the expectation period, which was followed by a further increase in activity during the attended presentations (Fig. 7B), confirming our earlier analysis. In right V4, the signal was not significantly modulated, either during the expectation period or during the attended (or unattended) presentations (Fig. 7B; main effect of expectation: n.s.). Together with the results of the statistical maps, the time course analysis confirms the spatial specificity of baseline increases (see also Kastner et al. 1999; Fig. 2B). In addition, these findings rule out the possibility that baseline increases were due to nonspecific task expectations or general arousal effects.

**FIG. 6.** Mean signal changes for the expectation period. Mean signal changes across visual cortex during the expectation of color or motion stimuli, averaged across subjects for the feature selectivity (A) and feature competition (B) experiments. For each subject, the peak intensities of the fMRI signal obtained during the expectation periods were averaged. Activity during the expectation of color or motion stimuli was not different in any of the visual areas. Vertical bars indicate SE.

**FIG. 7.** Spatial specificity of baseline increases. A: examples of activations obtained during epochs with directed attention to the target location in expectation of the onset of a motion or color stimulus compared with control epochs, overlaid on anatomical scans in 4 individual subjects (S1–S4) for the feature selectivity experiment. Activations in visual cortex were restricted to peripheral representations of the ventral visual areas of the left hemisphere, representing the attended location in the upper right quadrant (Fig. 7A, arrows). R, right. B: time series of fMRI signals in right and left area V4 averaged across the 4 subjects shown in A. Activity evoked during color and motion trials was collapsed. First vertical line indicates the beginning of the expectation period, and the second vertical line indicates the beginning of the unattended, or attended presentations. Baseline activity during directed attention in the absence of visual stimulation increased significantly only in left V4 ($\approx$ LV4), representing the attended location, but not in right V4 ($\approx$ RV4), representing the corresponding location in the contralateral (unattended) hemifield, demonstrating the spatial specificity of attention effects on baseline activity.

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increases evoked during the expectation of color and motion stimuli were similar.

Relation of baseline increases and response modulation

Our main question of interest is: How do increases of baseline activity during the expectation of visual stimuli relate to attentional modulation of responses evoked by visual stimuli? To investigate this, the AMI and BMI were compared for each experiment. It should be noted that because the AMI and the BMI were normalized to the same values, these measures allow for a direct comparison of the magnitude of the attentional effects on the baseline activity and on the visually evoked responses.

Under the assumption that attentional response modulation is an additive summation of sustained baseline increases and visually evoked responses, AMIs and BMIs should be similar and fall close to the equality line. As shown in Fig. 9, this was the case in some areas, but not in others. In V2 and V4, the BMIs were similar in magnitude to the AMIs for both color and motion trials. However, AMIs were significantly larger than BMIs in TEO and MT for the more effective stimulus (feature selectivity: $P < 0.05$; feature competition: MT, $P < 0.05$; TEO, $P = 0.09$). In addition, in the feature selectivity experiment where each stimulus contained a single feature AMIs were significantly smaller than BMIs in MT for the less effective stimulus and in IPS for both stimulus types ($P < 0.05$). Furthermore, significant modulations were observed in V1 during the expectation period as measured by the BMI ($P < 0.05$), whereas AMIs were not significantly different from zero ($P > 0.05$).

Taken together, these results do not support a hypothesis that assumes attentional response modulation to be an additive summation of sustained baseline increases and visually evoked responses during stimulus selection. Feature-selective regions showed greater attentional modulation when their preferred feature was selected, but did not show such bias during the
expectation periods. This suggests that baseline increases in visual cortex carry information about the spatial location of an expected target stimulus, but not about its feature characteristics under the conditions that were tested in the present studies.

**DISCUSSION**

We studied effects of selective attention on baseline activity in the absence of visual stimulation during the expectation of color and motion stimuli and on neural responses evoked by color and motion stimuli. Attentional modulation of stimulus-driven activity was stronger on effective than on noneffective stimuli in areas TEO and MT. However, directing attention to a target location in expectation of color or motion stimuli induced similar increases in baseline activity. These baseline increases occurred only in visual representations of the attended location. Together, these findings suggest that the baseline signals were not dominated by the feature information of the cue, which was different from run to run in the feature selectivity experiment and from block to block in the feature competition experiment, but rather by the spatial information of the cue that remained constant over the course of the experiments. Importantly, an additive summation of sustained baseline increases and visually evoked activity proved to be a poor predictor of attentional response modulation in visual areas V1, MT, TEO, and IPS. Therefore our findings do not support a model that assumes attentional response modulation to be simply an addition of sustained baseline increases on visually evoked responses during the attentional selection process.

The modulation of both baseline (Ress et al. 2000) and stimulus-driven activity (Pinsk et al. 2004; Spitzer and Richmond 1991; Spitzer et al. 1988) has been shown to depend on the difficulty of an expected or given task. It is important to note that neither our findings of baseline increases, nor the attentional modulation of stimulus-driven activity can be easily explained by task difficulty associated with detecting the two types of stimuli. An account of task difficulty differences would predict a stronger modulatory effect associated with one stimulus type compared with the other across visual cortical areas. Instead, when subjects attended to the different types of stimuli, we found a double dissociation of neural response patterns evoked by the two types of stimuli in some areas and modulatory effects of similar magnitude in other areas. Finally, our behavioral results did not indicate significant differences in detection accuracy of the two types of stimuli. Together, these findings support the idea that the two types of stimuli were well matched in terms of task difficulty, which therefore is not a likely source of modulatory influence and cannot explain our results.

In the feature selectivity experiment, we studied attentional effects on stimulus features using nonidentical stimuli that were more effectively processed in some visual areas, but not in others. The stationary colored dot stimuli activated ventral extrastriate areas V4 and TEO more effectively than achromatic moving dot stimuli; the reverse was true in area MT. It should be noted that our study was not designed to determine color or motion selectivity in these areas, although our results are in agreement with other studies that have more rigorously attempted to probe their feature selectivity (Bartels and Zeki 2000; Hadjikhani et al. 1998; Zeki et al. 1991). This approach is similar to that taken in single-cell physiology studies investigating the effects of selective attention on effective and noneffective stimuli in the same neurons and showing that attention effects were larger when attention was directed to the effective stimulus than when directed to the ineffective stimulus (Luck et al. 1997; Moran and Desimone 1985; Reynolds et al. 1999). In agreement with these results from physiology, we found that attentional response enhancement was significantly larger on the more effective stimulus in areas TEO and MT. In area V4, which showed a small, but significant stimulus preference for the color stimuli, significant attention effects on both motion and color stimuli were found. This pattern of neural responses in V4 is not surprising given that this area has been reported in the macaque to contain about 44% of color-selective neurons and ≤30% of neurons that are responsive to motion stimuli and exhibit some degree of direction selectivity tuning (Desimone and Schein 1987; Ferrera et al. 1994; Schein and Desimone 1990; Tolias et al. 2001). In the feature competition experiment, we used an approach similar to single-cell physiology studies in monkeys and functional brain imaging studies in humans. These studies have typically used experimental paradigms in which neural activity evoked by identical stimuli was compared under conditions where different stimulus attributes were selectively attended (e.g., a colored oriented line stimulus; Beauchamp et al. 1997; Corbetta et al. 1991; Ferrera et al. 1994; Motter 1994; O’Craven et al. 1997). It was shown that neural responses matching the selected feature (e.g., the color of the line) were enhanced, whereas responses to stimuli that did not match the selected feature (e.g., the orientation of the line) were attenuated. In agreement with these studies, we observed increased attentional enhancement in TEO and MT when their preferred feature was selected. Taken together, the different approaches to the study of feature-based effects of attention converge in supporting the idea that selective attention to a particular stimulus attribute biases neural activity in those extrastriate areas that preferentially process the selected attribute.

Although attentional enhancement was observed in the feature competition experiment in TEO and MT when their preferred feature was selected, activity in these regions was also enhanced, but to a lesser degree, when their nonpreferred feature was selected. In contrast, during the feature selectivity experiment, when the stimulus contained only one feature, activity in these regions was enhanced only when their preferred feature was selected. This effect is consistent with an object-based spread of attention to the unattended feature during the feature competition experiment (Beauchamp et al. 1997; Duncan 1984; Melcher and Vidnyanszky 2006; O’Craven et al. 1999; Schoenfeld et al. 2003). Alternatively, one could argue for a space-based mechanism where all features at an attended location are enhanced. However, there are several instances in the literature that suggest that not all features or objects at an attended location are selected (Beauchamp et al. 1997; Clark et al. 1997; Corbetta et al. 1991; Motter 1994; O’Craven et al. 1997; Saenz et al. 2002; Schoenfeld et al. 2003; Wojciulik et al. 1998). In these studies, the critical issue that determines which features are selected is whether they are grouped together by sharing a common feature or being part of the same object. Therefore the current results can best be explained by an object-based spread of attention. O’Craven et al. found a similar object-based spread.
of attention effect in an fMRI study using stimuli that consisted of houses, faces, and motion. In their study, unattended features of attended objects were enhanced relative to features of unattended objects. However, the bottom-up stimulus drive was not measured, making it impossible to distinguish whether the unattended features of the attended object were truly enhanced, or just less suppressed compared with features of unattended objects. It is important to note that in the current experiment, activity evoked by the unattended feature in these feature-selective regions was greater than the activity evoked by the stimulus when attention was drawn away from it, suggesting true attentional enhancement of the unattended feature on the attended object.

Baseline increases during directed attention to a cued location and in the absence of visual stimulation have been found in previous monkey physiology and human fMRI studies (Colby et al. 1996; Kastner et al. 1999; Luck et al. 1997; O’Connor et al. 2002; Ress et al. 2000). In single-cell physiology studies, it was found that the spontaneous (background) firing rate of neurons in extrastriate cortex increased significantly, when the monkey was cued to attend to a location within a neuron’s receptive field (RF) compared with when the monkey attended elsewhere in the visual field (Colby et al. 1996; Luck et al. 1997). In human fMRI studies, it was shown that baseline increases were on the order of 0.5–1.1% signal change and occurred across the visual system including areas that did not show any modulatory effects on stimulus-driven activity, such as V1 (Kastner et al. 1999; O’Connor et al. 2002). The present findings confirm these studies with respect to the magnitude of the baseline effects and extend previous findings by demonstrating that the expectation of different stimulus features did not differentially influence the baseline effect in multiple visual areas, even in those that showed stimulus preference. This finding suggests that the baseline signals were dominated by the spatial information of the cue, and not by the feature information, under the conditions tested in our studies.

Importantly, these results render the possibility unlikely that baseline increases reflect an activated memory template of particular target features and are closely related to signals obtained in visual working memory or imagery studies (Chelazzi et al. 1998; Goebel et al. 1998). According to such an account, one would predict that baseline increases would be stronger in visual areas exhibiting a stimulus preference when the preferred feature dimension was cued. Indeed, Chawla and colleagues (1999) found evidence for feature-specific increases in areas V4 (which most likely corresponds to area TEO of the current experiment) and MT for color and motion, respectively, using moving colored dot stimuli that were continuously present, but rendered stationary and achronatic during cue periods. Due to the continuous presentation of a stimulus similar to the cued one it is possible that the “baseline shift” that they obtained reflected mixed signals related to both baseline increases and attentional modulation of stimulus-driven activity. An alternative hypothesis is that the difference between the findings is due to the placement of the stimulus. In the Chawla et al. study, stimuli were presented foveally, whereas our stimuli were presented peripherally. With foveal stimulus presentation, baseline increases related to the spatial location of the stimulus might be reduced. Consistent with this hypothesis, differences between cue-related activity to color or location were found to be greatly reduced when stimuli were presented peripherally (Giesbrecht et al. 2003). Importantly, our finding of baseline increases that were similar in magnitude when expecting either an effective or a noneffective stimulus in areas TEO and MT is in agreement with results from single-cell physiology. Approximately equal increases in spontaneous activity of neurons in extrastriate cortex were found when monkeys expected a target stimulus that was either effective or ineffective in driving the sensory responses of the neurons (Luck et al. 1997). Taken together, these findings provide converging evidence that baseline increases during cue periods do not reflect the activation of a memory template that includes particular stimulus properties of the expected target, but simply carry information about the location of an expected target stimulus, at least under the experimental conditions that were used here (Kastner et al. 1999; Ress et al. 2000).

Attentional response enhancement of stimulus-driven activity has been found across the visual system in numerous studies using different techniques (Beauchamp et al. 1997; Chawla et al. 1999; Cook and Maunsell 2002; Kastner et al. 1998; O’Connor et al. 2002; O’Craven et al. 1997; Reynolds and Chelazzi 2004; Spitzer et al. 1988; Treue and Maunsell 1996). However, in most studies of visual attention it is not clear whether such enhancement was due to an increase in baseline activity that is sustained during stimulus selection, to an increased response evoked by the visual stimuli, or to both. Our finding that an additive summation of baseline increases and visually evoked activity was a poor predictor of the attentional response modulation that was actually obtained across visual cortex does not support the idea that attentional response enhancement is merely a result of sustained baseline increases during visual selection. Instead, attentional mechanisms that occur during a Posner-type cueing paradigm, as used here, may be described as a two-stage process. During the first stage, when subjects are cued to the peripheral target location, all neurons with RFs representing the attended location, receive a spatial bias signal that increases synaptic activity and spontaneous firing rates, as reflected in spatially specific but feature-nonspecific baseline increases across the visual system. It should be noted that this pool of neurons encompasses both those that will respond highly selectively to the features of the target stimulus and those that will respond nonspecifically to these features. During the second stage, when subjects attend to a series of target and nontarget stimuli, the response gain of those neurons that respond most selectively to the features of the target stimulus is enhanced. This enhancement results in a large feature-specific attentional response modulation on stimulus-driven activity that is mostly expressed in visual areas containing a large pool of neurons that respond selectively to the features of the target stimulus as indicated by the strong attentional response modulation found in areas TEO and MT. Whether baseline increases are sustained during the attentional selection process is an open question. Our results in area V1, which showed a significant baseline increase, but no attentional response modulation, raise the possibility that the spatial bias signals that occur during cueing periods are discontinued during the attentional selection process. The spatial bias may be replaced by a feature-specific attentional mechanism that operates in parallel across the entire visual field (Bichot et al. 2005; Muller et al. 2006; Saenz et al. 2002; Treue and Martinez Trujillo 1999). Current studies have only just begun to inves-
tigate how feature- and space-based attention interact (Hayden and Gallant 2005; McAdams and Maunsell 2000), and future studies will be needed to investigate the interaction and temporal dynamics of such spatial and feature-based attention mechanisms, including how each mechanism interacts with object-based attention.

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