

The Effects of Feature Attention on Prestimulus Cortical Activity in the Human Visual System

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Covert attention affects prestimulus activity in the visual cortex. Although most studies investigating neural mechanisms of attention have focused on the effects of spatial attention, attention can also be directed to particular features. To investigate the spatiotemporal nature of feature attention, we measured subjects' brain activity using magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI) while subjects attended to color or motion of a stimulus based on a visual cue, which was presented 1 s before the stimulus onset. We used the hierarchical Bayesian method that allows us to estimate cortical currents with MEG and fMRI data in the order of millimeters and milliseconds. When subjects attended to color, activity within the color-sensitive area (fusiform gyrus) was selectively enhanced within the prestimulus period. By contrast, when subjects attended to motion, activity within the motion-sensitive area (middle temporal gyrus) was selectively enhanced during this period. This effect was not seen in frontal, parietal, and lower visual areas. Additionally, this effect was transient rather than sustained, suggesting that it differs from temporal aspects of spatial attention. These results suggest that, although both spatial and feature attention modulate prestimulus activity within specific visual areas, neural mechanisms underlying these effects might be different.

Keywords: color, feature attention, hierarchical Bayesian estimation, MEG, motion, preparatory activity

Introduction

Visual attention enables us to extract behaviorally significant information from a cluttered environment. Single-unit studies for nonhuman primates and neuroimaging studies over the past 15 years have provided substantial insight into the neural basis of information selection by visual attention. Spatial attention modulates the response gain of neurons in the visual cortex in a retinotopic fashion (Luck et al. 1997, 2000; Hillyard and Anllo-Vento 1998; Hopfinger et al. 2000), whereas feature attention modulates a response gain of neurons within feature-sensitive visual areas such as V4 in the ventral pathway and middle temporal (MT) visual area in the dorsal pathway (Motter 1994; Chawla, Ress and Friston 1999; Treue and Martinez Trujillo 1999; Maunsell and Treue 2006; Schoenfeld et al. 2007). Combining these insights from spatial and feature attention, it is possible to infer that common neural mechanisms are involved in both spatial and feature attention (Maunsell and Treue 2006). On the other hand, recent psychophysical (Kanai et al. 2006) and

physiological studies (McAdams and Maunsell 2000; Hayden and Gallant 2005) have suggested that spatial attention and feature attention are based on distinct neural substrates.

Neural activity in the visual cortex is affected by covert attention even before a stimulus onset (Luck et al. 1997; Chawla, Ress and Friston 1999; Kastner et al. 1999; Hopfinger et al. 2000; Fries et al. 2001; Wylie et al. 2006; Silver et al. 2007). It has been claimed that this neural modulation may play a causal role in the attentional effects on sensory activity for a subsequently presented stimulus (Driver and Frith 2000). For spatial attention, this effect is observed in a retinotopic fashion and sustained while subjects keep attending to the corresponding visual field (Luck et al. 1997; Worden et al. 2000; Thut et al. 2006; Silver et al. 2007). For feature attention, functional magnetic resonance imaging (fMRI) studies have described a detailed picture of the anatomical regions related to this effect and identified feature-sensitive visual areas such as V4 and MT (Chawla, Ress and Friston 1999; Wylie et al. 2006). However, little is known about the temporal nature of neural activity associated with feature attention before the stimulus onset.

In the present study, we examined the effects of feature attention on neural activity, particularly within feature-sensitive visual areas before the stimulus onset, using magnetoencephalography (MEG) in combination with fMRI. Subjects attended to color (color condition) or motion (motion condition) of the stimulus and discriminated the attribute of the attended feature of the stimulus. The stimulus consisted of 1000 dots whose color and motion changed with the stimulus onset. To observe the effects of feature attention before and after the stimulus onset separately, a visual cue indicating the feature to be attended was presented to subjects 1 s before the stimulus onset. As it has been suggested that color and motion flow into different visual pathways and activate different areas (Zeki et al. 1991; Tootell et al. 1995; Toyama et al. 1999; Kuriki et al. 2000, 2005), this experimental paradigm allows us to investigate the effects of attention to color and attention to motion within color-sensitive visual areas and motion-sensitive visual areas separately.

It has proved difficult to estimate distributed sources of electrical activity within cortical areas from MEG data as the estimation of cortical activity based on MEG data is fundamentally ill posed due to the essential difficulty of the inverse problem. Recently, to overcome this difficulty, Sato et al. (2004) proposed a hierarchical Bayesian method for source-current estimation with MEG data. By constraining cortical regions based

on fMRI information, this technique enables us to estimate the source currents on the cortical surface in the order of milliseconds and millimeters. We used this method to investigate the spatiotemporal nature of feature attention in the brain.

We conducted 3 experiments. In the first experiment, we measured subjects' cortical activity using MEG while they attended to the color or motion of the stimulus (selective attention MEG experiment). In the second experiment, the subjects' blood oxygen level-dependent (BOLD) signals were measured during the same task (selective attention fMRI experiment). In the last experiment, to determine color- and motion-sensitive areas for each subject, we conducted a separate control experiment (visual area specification fMRI experiment). Cortical currents were estimated by combining the results of the first and second experiments. Then, we compared the effects of attention to color and motion in frontal, parietal, and visual areas. We found no significant difference within frontal, parietal, and lower visual areas. On the other hand, during the 1-s prestimulus period, activity within the color-sensitive area and within the motion-sensitive area was selectively increased by attention to color and attention to motion, respectively. In addition, we found that this effect is transient rather than sustained. This result supports the idea that the neural mechanism underlying feature attention is different from that underlying spatial attention.

Materials and Methods

Subjects

Six healthy subjects (aged 23–27 years) participated in the experiments, which were approved by the ATR Human Subjects Review Committee. All subjects gave informed consent and had normal or corrected-to-normal visual acuity and normal color vision.

Stimuli

The stimulus consisted of 1000 colored moving dots, which were arranged randomly in a circular area with a 5° radius from the center of the screen on a white background (Commission Internationale de l'Éclairage [CIE] coordinates $x = 0.28$, $y = 0.33$). The mean luminance of the background and stimulus was the same (70 cd/m²). The size of each dot was 0.06° square. Twenty percent of the dots moved toward a target direction, whereas the others moved in random directions at a speed of 10°/s. The target direction was from the center to the outside (expansion) or from the outside to the center (contraction). Each dot was vanished within 2 frames (33 ms) and rearranged randomly within the same circular area. Separately, 20% of the dots were colored in a target color, whereas the others were colored randomly in the 1 of 16 alternative colors. The target color was red (CIE coordinates $x = 0.30$, $y = 0.32$) or green (CIE coordinates $x = 0.26$, $y = 0.34$). Results from pretesting determined that the percentage of dots with the target color or motion equalizes the subjects' task performance (percent correct) between the 2 conditions. The stimulus was generated using a VSG2/5 graphics board from Cambridge Research Systems (Rochester, UK).

Selective Attention MEG Experiment

Procedure

The task procedure is depicted schematically in Figure 1. Subjects were instructed to discriminate an attribute of an attended feature of the stimulus and were asked to respond as soon as possible but accurately. There were 2 attention conditions: attention to color (color condition) and attention to motion (motion condition). Subjects were asked to maintain fixation on the center of the screen throughout the entire experiment, and 1000 white stationary dots were presented around the central fixation point. One second before the stimulus onset, subjects directed their attention to 1 of the 2 features of the stimulus,

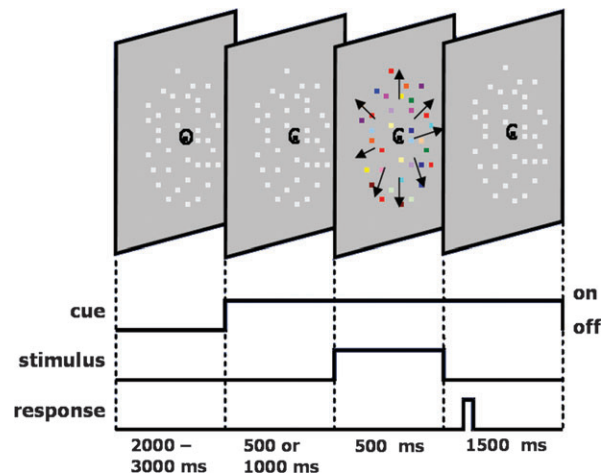


Figure 1. Schematic illustration of a trial sequence. Subjects covertly attended to either color or motion depending on a visual cue (for color: C, for motion: M) and discriminated an attribute of the attended feature of the following stimulus as quickly and accurately as possible.

depending on a preceding visual cue presented on the center of the screen ("C" for color and "M" for motion). Then, the stimulus was presented for 500 ms. In the color condition, subjects reported whether the stimulus looked reddish or greenish, and in the motion condition, they reported whether the stimulus featured motion of expansion or contraction. A report was issued by the subjects pressing 1 of 2 buttons held in the left and right hand. The button assignment for target colors and motions varied across subjects. Subjects practiced the task extensively (more than 300 trials) before the main experiment.

Subjects underwent 2 color sessions in which all trials were under the color condition, and 2 motion sessions in which all trials were under the motion condition. One session contained 52 trials. The order of sessions varied across subjects. Four types of stimulus (2 target colors and 2 target motions) were presented in the same frequency and pseudorandom order. To help maximize retention of the subjects' attention, the stimulus was presented after an interstimulus interval (ISI) of either 1000 ms (44 trials in 1 session) or 500 ms (8 trials in 1 session). The 2 ISI conditions were mixed in a pseudorandom order in each session. The trials containing an ISI of 500 ms were not included in the analysis of MEG data. The intertrial interval (ITI) was randomly varied between 2000 and 3000 ms. The stimulus was projected (ELP-710 projector; Epson, Tokyo, Japan) from outside a magnetically shielded room (Tokin Corp., Sendai, Japan) onto a semitranslucent screen inside the dark room.

MEG Acquisition

Magnetic responses were recorded using a 201-channel, whole-head biomagnetic imaging system (Shimadzu, Kyoto, Japan). The responses were sampled at 1000 Hz for 2048 ms, beginning 300 ms before the visual cue onset. Simultaneous recording with an electrooculogram (EOG) was used to continually monitor eye movements, and a chin rest was used to minimize head movement. All MEG data were band-pass filtered at 1–100 Hz (a linear-phase Finite Impulse Response filter using the Parks-McClellan algorithm, 63 degree). Because of an artifact in the band-pass filter, signals recorded during the first 50 ms and the last 248 ms in each trial were discarded. Trials were rejected if 1) the EOG exceeded 100 μ V and 2) the max/median ratio of the MEG data exceeded 13. The max/median ratio was calculated using the maximum amplitude of each trial divided by the median amplitude of the trial.

Selective Attention fMRI Experiment

Procedure

The task procedure was the same as that in the selective attention MEG experiment except for a fixed ITI (2000 ms) and a fixed ISI (1000 ms). Therefore, the length of 1 trial in this experiment was 5 s.

There were 88 scans in 1 session (time repetition [TR] = 3 s). The data from the first 4 and last 4 scans were not included in the analysis. The remaining 80 scans were alternately divided into 4 task blocks and 4 fixation blocks. Each block contained 10 scans. In each task block, subjects performed the task 6 times. Four types of stimulus (2 target colors and 2 target motions) were presented in the same frequency and in a pseudorandom order. Two of the 4 task blocks were for the color condition; the other 2 were for the motion condition. The subjects were informed the order of task blocks before the experiment, and the order was varied between subjects. In each fixation block, 1000 white stationary dots were presented around a central fixation point, and subjects were asked to maintain central fixation during the block. Each session was repeated 5 times for each subject.

fMRI Acquisition

A 1.5-tesla scanner (Shimadzu-Marconi Magnex Eclipse) was used to acquire both structural T_1 -weighted images (TR = 20 ms, time echo [TE] = 2.3 ms, flip angle = 40° , matrix = 256×256 , field of view [FoV] = 256 mm, thickness = 1 mm, slice gap = 0 mm) and T_2^* -weighted echo planar images (TR = 3 s, TE = 49 ms, flip angle = 90° , matrix = 64×64 , FoV = 192 mm, thickness = 4 mm, slice gap = 0 mm, 30 slices), showing BOLD contrasts. A custom-made bite bar was used to minimize head motion.

Visual Area Specification fMRI Experiment

Procedure

The task procedure was the same as that in the selective attention fMRI experiment, except for the stimulus. Under the color condition, 50% of the dots changed their color to the target 1 with the stimulus onset but remained stationary. Under the motion condition, 50% of the dots started moving in the target direction with the stimulus onset but their color remained white.

There were 128 scans performed in 1 session (TR = 3 s). Data from the first 4 and last 4 scans were not included in analysis, and the remaining 120 scans were alternately divided into 6 task blocks and 6 fixation blocks. Each block contained 10 scans. Three of the 6 task blocks were for the color condition; the other 3 blocks were for the motion condition.

fMRI Acquisition

Acquisition was performed as it was in the selective attention fMRI experiment.

Analysis

fMRI Analysis

The images were preprocessed and analyzed using an SPM 99 (<http://www.fil.ion.ucl.ac.uk/spm/spm99.html>). After correcting the slice timing, the images were realigned to the first image as a reference, spatially normalized to the Montreal Neurological Institute (MNI) space and spatially smoothed with a Gaussian kernel (9 mm, full-width at half-maximum). The block design analysis was conducted using boxcar regressors, convolved with a hemodynamic response function as the reference waveform for both color and motion conditions.

Cortical Current Estimation

A polygon model of the cortical surface was constructed based on individual MRI image slices for each subject using Brain Voyager software (Brain Innovation, Maastricht, Netherlands). The total number of vertex points for each subject was $26,783 \pm 585$ (mean \pm standard error [SE]). The task-related cortical regions were determined by logical OR operation between the results of the color and motion conditions in the selective attention fMRI experiment. Within these regions, a single-current dipole was assumed perpendicular to the cortical surface at each vertex point. Here, the total number of dipoles for each subject was 3871 ± 291 (mean \pm SE). The lead field matrix was calculated using a sphere model. Cortical currents were estimated with the recorded MEG data under 2 conditions using the hierarchical Bayesian method (Sato et al. 2004). Because the forward model was identical between color and motion conditions, the difference of the estimated currents between the 2 conditions reflects the difference of the MEG data between the 2 conditions.

Using the hierarchical Bayesian estimation, a linear spatial filter to estimate the cortical current for each dipole was calculated using the MEG data (see Supplementary Methods for more details). We assumed that the pattern of cortical activity changed during the cue period (from the cue onset to the stimulus onset: 1000 ms) and the stimulus period (from the stimulus onset to the stimulus offset: 500 ms). To prevent these states being mixed, we divided the time of 1 trial (from 250 ms before cue onset to 500 ms after stimulus onset: 1750 ms) into 34 time windows (100 ms in length: 50-ms overlap); the linear spatial filter was calculated separately for each time window. The cortical current was then estimated with the MEG data using an estimated linear spatial filter at each time window. In the overlap period, the cortical currents were averaged between 2 time windows.

Estimated Current Normalization

A cortical current estimation with the MEG data is necessarily inexact due to several factors, including noise in the measured data. Therefore, it is essential to quantitatively evaluate the uncertainties and potential errors of the estimated current by normalization (Dale et al. 2000). Thus, we normalized the current by dividing the estimated currents by the posterior variance of the cortical current at each dipole (Friston et al. 2002). We then conducted a statistical comparison of the normalized estimated currents between the 2 conditions.

Results

Behavioral Results

We compared the subjects' task performance in the selective attention MEG experiment between 2 conditions. When the ISI was 1000 ms, reaction time (color condition, 757 ± 55 ms [mean \pm SE]; motion condition, 833 ± 111 ms; Wilcoxon signed rank test, $P = 0.29$) and accuracy (color condition, $96 \pm 2\%$ [mean \pm SE]; motion condition, $93 \pm 2\%$; Wilcoxon signed rank test, $P = 0.16$) were not significantly different between 2 conditions. Similarly, when the ISI was 500 ms, reaction time (color condition, 783 ± 37 ms; motion condition, 834 ± 97 ms; Wilcoxon signed rank test, $P = 0.56$) and accuracy (color condition, $95 \pm 3\%$; motion condition, $93 \pm 4\%$; Wilcoxon signed rank test, $P = 0.38$) were not significantly different between 2 conditions. These results suggest that the task difficulty was similar in both conditions, and subjects kept their attention on the assigned feature in both ISI trials.

Task-Related Areas Defined by fMRI

Figure 2A and B show the results of the selective attention fMRI experiment for the color condition (Fig. 2A) and the motion condition (Fig. 2B) for subject YS. Under both conditions, significantly activated areas were found in the bilateral dorsolateral prefrontal cortex (DLPFC; left and right), bilateral precentral gyrus (prCG; left and right), supplementary motor area (SMA), anterior part of the bilateral intraparietal sulcus (aIPS; left and right), posterior part of the bilateral intraparietal sulcus (pIPS; left and right), and occipital cortex. All subjects showed similar activity patterns as shown in Figure 2A and B. These areas were used as a spatial constraint for the cortical current estimation. Nine significant areas within the extravisual cortex were used to specify the regions of interest (ROIs) for frontal and parietal areas.

Figure 2C shows the results of the visual area specification fMRI experiment for subject YS. The responses to the color stimulus were seen in the bilateral fusiform gyrus (Fig. 2C, left), and the responses to the motion stimulus were seen in the bilateral MT gyrus (Fig. 2C, right). All subjects showed similar activity patterns as shown in Figure 2C. These areas were used to specify the ROIs for color- and motion-sensitive visual areas.

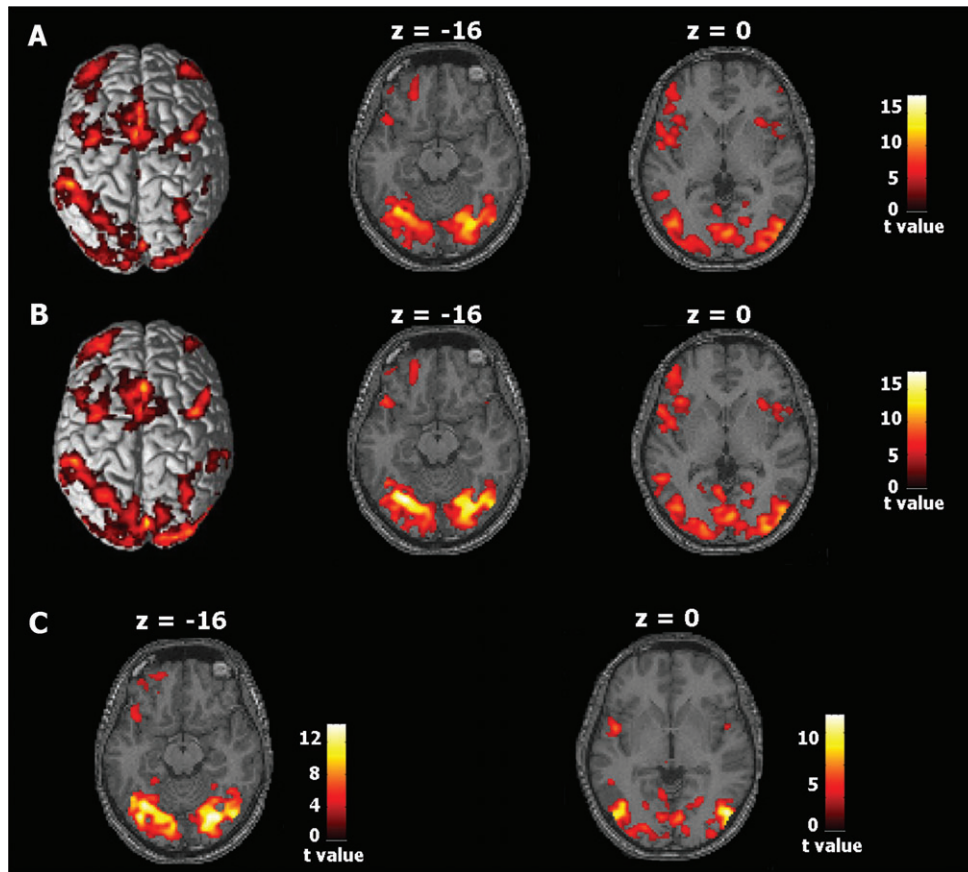


Figure 2. Activated brain areas in the fMRI experiments for subject YS. (A) Results of the selective attention fMRI experiment in the color condition ($P < 0.001$, uncorrected; extent threshold of 30 voxels). (B) Results from the selective attention fMRI experiment in the motion condition ($P < 0.001$, uncorrected; extent threshold of 30 voxels). (C) Bilateral responses to the color stimulus (left) and motion stimulus (right) in the visual area specification experiment ($P < 0.001$, uncorrected; extent threshold of 30 voxels).

MEG Channel-Level Analysis

Global Field Magnetic Power

Figure 3 shows the recorded MEG data for subjects YS and MS plotted as global magnetic field power (GFP) over time. GFP was calculated as:

$$GFP(t) = \sqrt{\frac{1}{N} \sum_{i=1}^N (S_i(t))^2},$$

where $S_i(t)$ is the trial average of the observed magnetic signal in channel i at time t , and N is the number of channels. For each subject, GFPs for both color and motion conditions remained virtually superimposed throughout the entire time period, and peaks of GFP to the stimulus ranged from 150 to 200 ms after the stimulus onset (gray area in Fig. 3), in agreement with the results of previous MEG studies using a color or motion stimulus (Toyama et al. 1999; Kuriki et al. 2000, 2005).

Channel-Level Analysis

We compared the MEG signal amplitudes between 2 conditions for all channel. To separately examine the effects of feature attention before and after the stimulus onset, we calculated the mean signal amplitudes for each period and condition and compared them between 2 conditions. In each period, several channels showed significant differences between 2 conditions within each subject (t -test, $P < 0.05$). For the cue period (from

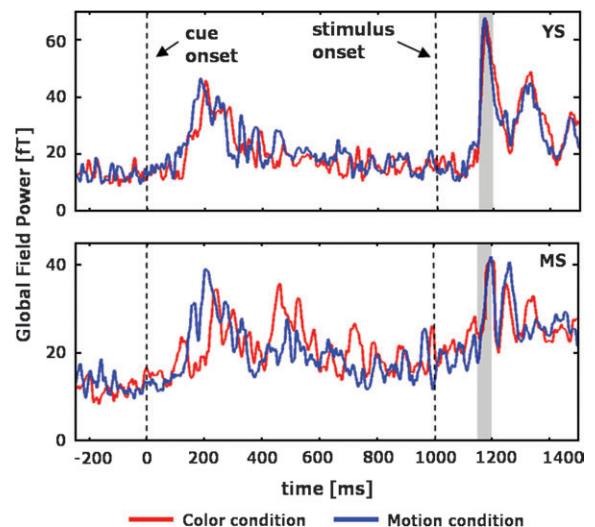


Figure 3. GFP plotted as a function of time for subject YS and MS. The onset times of the visual cue (0 ms) and stimulus (1000 ms) are demarcated by vertical dotted lines. GFP is shown for attention to color (red line) and attention to motion (blue line). The gray shading shows the period of time used for the specification of ROIs.

the cue onset to the stimulus onset), there were 26 ± 9 significant channels (mean \pm SE), and for the stimulus period (from the stimulus onset to the stimulus offset), there were

16 ± 4 significant channels (mean \pm SE) for each subject. However, between subjects, we did not find any common tendency in the number of the channels that showed significant differences or in the spatial configuration of the channels showing significant difference.

Time Series of the Spatial Map of the Estimated Currents

Cortical currents in task-related areas defined by fMRI were estimated with MEG signals using the hierarchical Bayesian method (Sato et al. 2004). Figure 4 shows the spatial map of the estimated current amplitude for subject YS (see Supplementary Movie for the detailed time series). In the cue period (from the cue onset to the stimulus onset), activity was observed in the parietal and frontal cortex as well as in the visual cortex (Fig. 4, left). In the stimulus period (from the stimulus onset to the stimulus offset), strong responses to color and motion stimuli were observed in the visual cortex (Fig. 4, right). Spatiotemporal patterns of the brain activity were generally similar in the color and motion conditions, and this tendency was observed in all subjects.

ROI Specification

Parietal and Frontal Areas

In the selective attention fMRI experiment, we found 9 significant areas in the parietal and frontal cortex (Fig. 2A,B). The estimated currents involved with the task were located in these areas, but they were predominantly focalized within the area. Thus, for further analysis, we determined the ROIs in

frontal and parietal areas for each subject as follows: 1) specify 9 areas based on the results of the selective attention fMRI experiment, 2) find the dipole with the largest intensity in the spatial pattern of the estimated current amplitude temporally averaged from the cue onset to the stimulus offset within each area, and 3) specify a circular region with a 6-mm radius centered at the dipole found in step 2 and set it as an ROI. Nine ROIs (left DLPFC, right DLPFC, left prCG, right prCG, SMA, left aIPS, right aIPS, left pIPS, right pIPS) were determined for each subject. Each ROI contained 19 ± 2 dipoles (mean \pm SE). These areas are known to belong to the front-parieto attention network (Corbetta and Shulman 2002; Shulman et al. 2002; Giesbrecht et al. 2003; Liu et al. 2003; Serences et al. 2005). As the time courses of the estimated currents were very similar among the dipoles within each ROI (correlation coefficient averaged more than 0.8), we averaged the estimated currents of dipoles in each trial and regarded this as the estimated current for the ROI.

Lower Visual Areas

To examine the effect of feature attention within the lower visual areas, Brodmann areas (BAs) 17 and 18, 4 ROIs (left BA17, right BA17, left BA18, right BA18) were determined for each subject. We used the results of selective attention fMRI experiment and the probabilistic cytoarchitectonic map in the SPM Anatomy toolbox (Eickhoff et al. 2005) to specify lower visual areas. For each subject, we determined the ROIs within lower visual areas as follows: 1) specify BA17 and BA18 in the left and right hemispheres by taking the common area between the results of the selective attention fMRI experiment

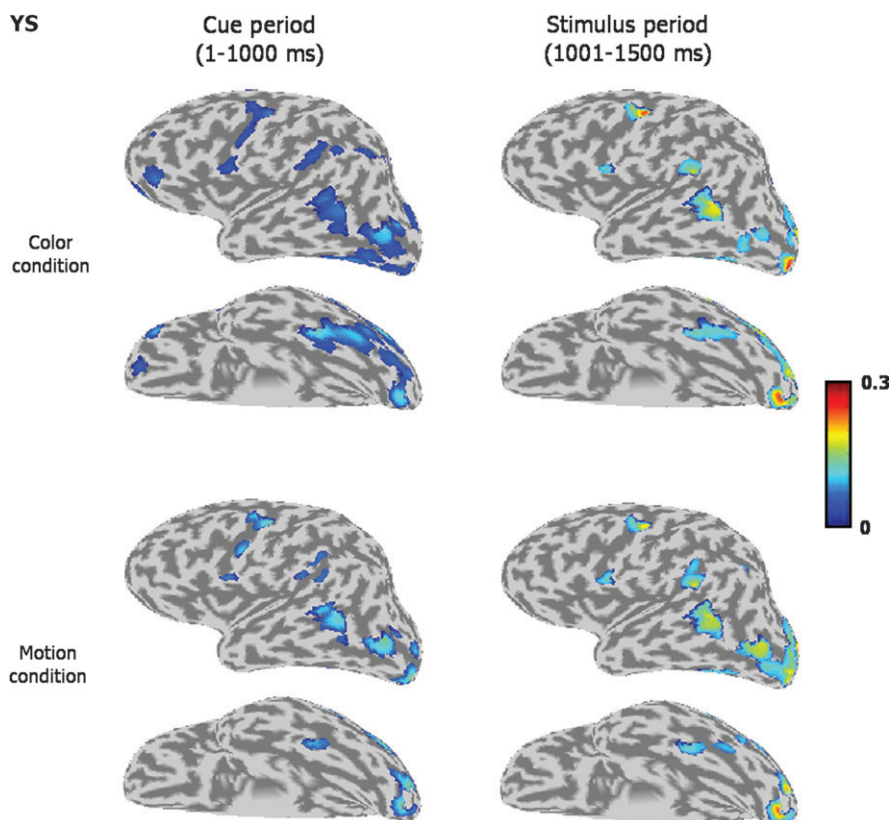


Figure 4. The spatial map of the mean current amplitude in the left inflated brain of subject YS during the cue period (left) and the stimulus period (right) in the color condition (top) and the motion condition (bottom).

and Brodmann areas 17 and 18 specified by the probabilistic cytoarchitectonic map, 2) find the dipole with the largest intensity in the spatial pattern of the estimated current amplitude temporally averaged from 150 to 200 ms after the stimulus onset within each area, and 3) specify a circular region with a 6-mm radius centered at the dipole found in step 2 and set it as an ROI.

Color- and Motion-Sensitive Areas

To examine the effect of feature attention within feature-sensitive areas, 4 ROIs (left and right color-sensitive area and left and right motion-sensitive area) were determined for each subject. In step 1, we used the results of the visual area specification fMRI experiment (Fig. 2C) to specify color- and motion-sensitive areas. The subsequent procedure (steps 2 and 3) was the same as that used in ROI specification for lower visual areas. Figure 5 shows the location of each ROI for subjects YS and MS. These locations were roughly consistent with the locations of color-sensitive areas (V4 complex) and motion-sensitive areas (MT+) as reported in previous fMRI studies (Zeki et al. 1991; Tootell et al. 1995; Chawla, Ress and Friston 1999; Bartels and Zeki 2000; Schoenfeld et al. 2003; Grill-Spector and Malach 2004).

Comparison of Estimated Current Amplitudes within the ROI

Previous studies have reported that covert spatial attention continually modulates the neural activity within specific cortical areas before a stimulus onset (Luck et al. 1997; Worden et al. 2000; Yamagishi et al. 2005; Thut et al. 2006). For this reason, for the cue period, we calculated the time-averaged amplitude of the estimated current for each trial and for both conditions and then compared it between the 2 conditions. On the other hand, previous EEG studies (Hillyard and Anllo-Vento

1998; Luck et al. 2000) have reported that the attentional effects on the sensory stimulus were observed at peaks of stimulus-evoked potentials. Thus, for the stimulus period, we calculated and compared the peak amplitudes and latencies of the estimated current between conditions.

Parietal and Frontal Areas

We examined the effect of feature attention on 9 ROIs within frontal and parietal areas: left DLPFC, right DLPFC, left prCG, right prCG, SMA, left aIPS, right aIPS, left pIPS, and right pIPS. For the cue period, there was no significant difference between the 2 conditions in current amplitude for each ROI (Wilcoxon signed rank test, $P > 0.094$). For the stimulus period, no significant difference in current amplitudes was observed ($P > 0.156$). Similarly, latencies were not significantly different between conditions for each ROI ($P > 0.156$).

Lower Visual Areas

Regarding the frontal and parietal areas, we compared the time-averaged amplitudes of the estimated current between conditions for the cue period, whereas we compared the peak amplitudes and latencies of the estimated current between the 2 conditions for the stimulus period within 4 lower visual areas: left BA17, right BA17, left BA18, and right BA18. We found no significant difference between conditions for both the cue and stimulus periods in each ROI (Wilcoxon signed rank test, $P > 0.156$). There was also no significant difference between conditions in the latency in each ROI during the stimulus period ($P > 0.219$).

Color- and Motion-Sensitive Areas

We conducted the same comparisons within each feature-sensitive area. During the cue period, within the left color-sensitive area, the estimated current amplitude was significantly greater in the color condition than in the motion condition

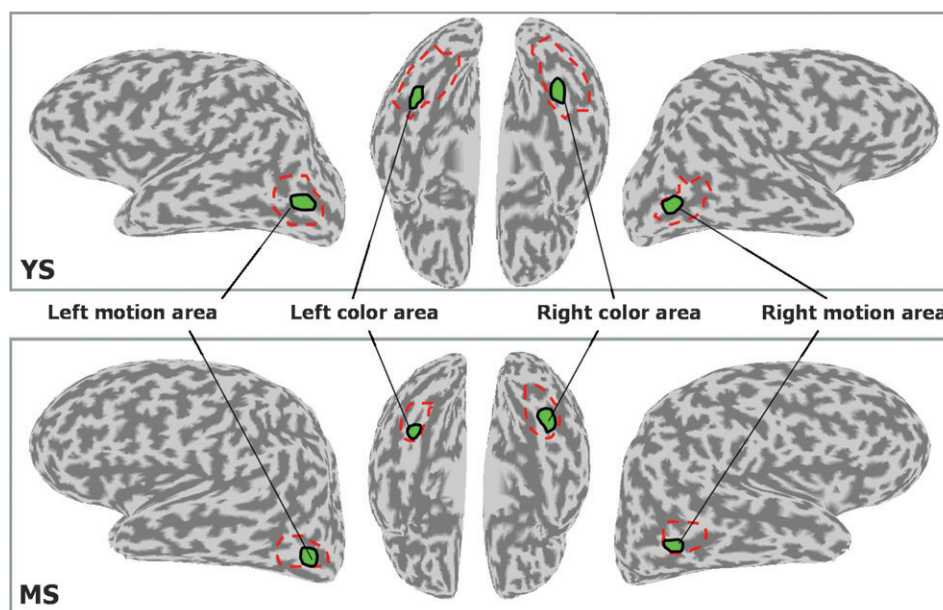


Figure 5. Four ROIs within feature-sensitive areas for subject YS and MS. Each ROI (indicated by green enclosure) was placed within the region determined by the visual area specification fMRI experiment (indicated by red broken lines). The Talairach coordinates of the ROI center for subject YS are (−34, −64, −16) for the left color-sensitive area; (45, −62, −14) for the right color-sensitive area; (−44, −67, 0) for the left motion-sensitive area; and (46, −66, 2) for the right motion-sensitive area. The Talairach coordinates of the ROI center for subject MS are (−32, −50, −20) for the left color-sensitive area; (36, −54, −18) for the right color-sensitive area; (−49, −61, −2) for the left motion-sensitive area; and (58, −60, −1) for the right motion-sensitive area.

(Wilcoxon signed rank test, $P = 0.031$). Within the right color-sensitive area, although not statistically significant ($P = 0.312$), a similar tendency was observed in 5 out of 6 subjects. Within the right motion-sensitive area, the estimated current amplitude was significantly greater in the motion condition than in the color condition ($P = 0.031$). Within the left motion-sensitive area, although not statistically significant ($P = 0.062$), a similar tendency was observed in 5 out of 6 subjects. During the stimulus period, within both the left and right color-sensitive areas, the peak of the estimated current amplitude was significantly greater in the color condition than in the motion condition ($P = 0.031$), whereas within both the left and right motion-sensitive areas, the peak of the estimated current amplitude was significantly greater in the motion condition than in the color condition ($P = 0.031$). Figure 6 summarizes the amplitude (i.e., root-mean-square) comparison between the color condition (red bar) and the motion condition (blue bar) within each feature-sensitive area (see Supplementary Fig. 1 for the individual subject statistics). The average latencies of the peak amplitude from the stimulus onset were 234 ± 24 ms (mean \pm SE, left color-sensitive area), 253 ± 29 ms (right color-sensitive area), 202 ± 33 ms (left motion-sensitive area), and 183 ± 28 ms (right motion-sensitive area). We did not find any significant differences in peak latency ($P > 0.312$).

Figure 7 shows the trial averages of the estimated current time courses for the color (red line) and motion (blue line) within each feature-sensitive area for subjects YS and MS (note that it is not root-mean-square). In each area, after the stimulus onset, the estimated currents peaked at approximately 200 ms, and the peak amplitudes differed between experimental conditions as shown in Figure 6. All subjects showed the same pattern of results. In contrast, during the stimulus period, we did not find any consistent peaks across subjects during the cue period. In addition, the pattern of experimental differences shown in Figure 6 was not always observed around the prominent peak but was observed around smaller peaks for

some cases. For example, in the left color-sensitive area of subject YS, the peak amplitude around 200 ms after the stimulus onset was greater in the color condition than in the motion condition as shown Figure 6. In contrast, in the right motion-sensitive area of subject MS, the peak amplitude around 300 ms after the cue onset was rather smaller in the motion condition than in the color condition. Nevertheless, time-averaged amplitude was significantly greater in the motion condition (see the individual statistics of subject MS in Supplementary Fig. 1). In the next section, Temporal Characteristics of the Effect of Feature Attention within Color- and Motion-Sensitive Areas during the Cue Period, we will focus on temporal characteristics of the amplitude differences between conditions during the cue period.

Temporal Characteristics of the Effect of Feature Attention within Color- and Motion-Sensitive Areas during the Cue Period

Figure 8 shows the difference of current amplitudes calculated by subtraction of the amplitude in the motion condition from that in the color condition for each ROI and averaged across subjects. Consistent with our previous statistics, the differences tended to be positive for color-sensitive areas and negative for motion-sensitive areas. We divided the estimated current amplitudes during the cue period into bins of 500 ms and compared time-averaged amplitudes between conditions in each bin. No significant difference was observed in each bin or each ROI between subjects (Wilcoxon signed rank test, $P > 0.062$). Similarly, when the length of the time bin was 250 ms, no significant difference was observed ($P > 0.094$).

Figure 9A shows the amplitude difference between 2 conditions for each ROI and each subject. Each colored broken line corresponds to 1 subject, and each square marker corresponds to the amplitude difference averaged over 100 ms, calculated by subtraction of the amplitude in the motion condition from that in the color condition. Because magnitude of the difference varied across subjects, for the purpose of data

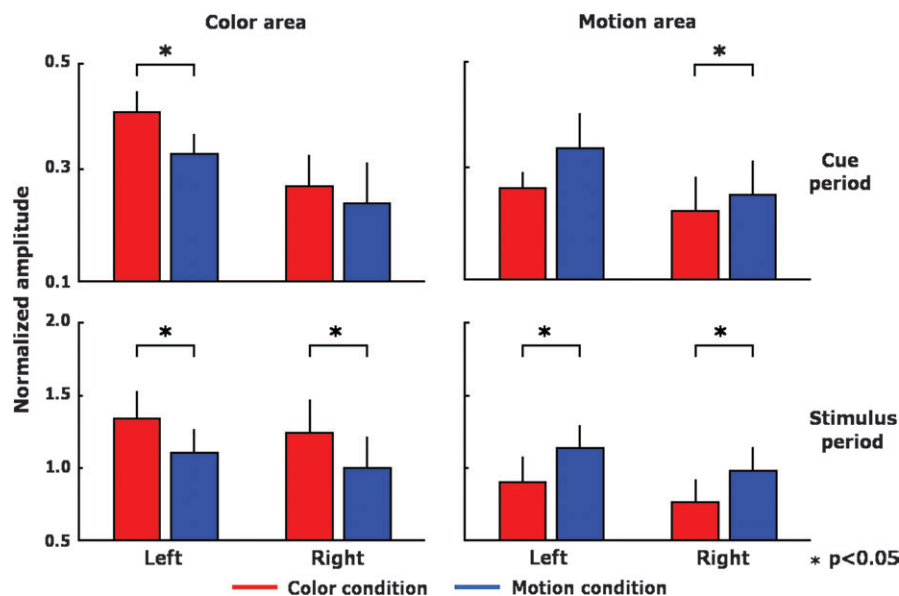


Figure 6. Comparison of the mean current amplitudes within each feature-sensitive area and each period (6 subjects). Each bar (\pm SE) shows the mean current amplitudes for color (red bars) and the motion (blue bars) conditions.

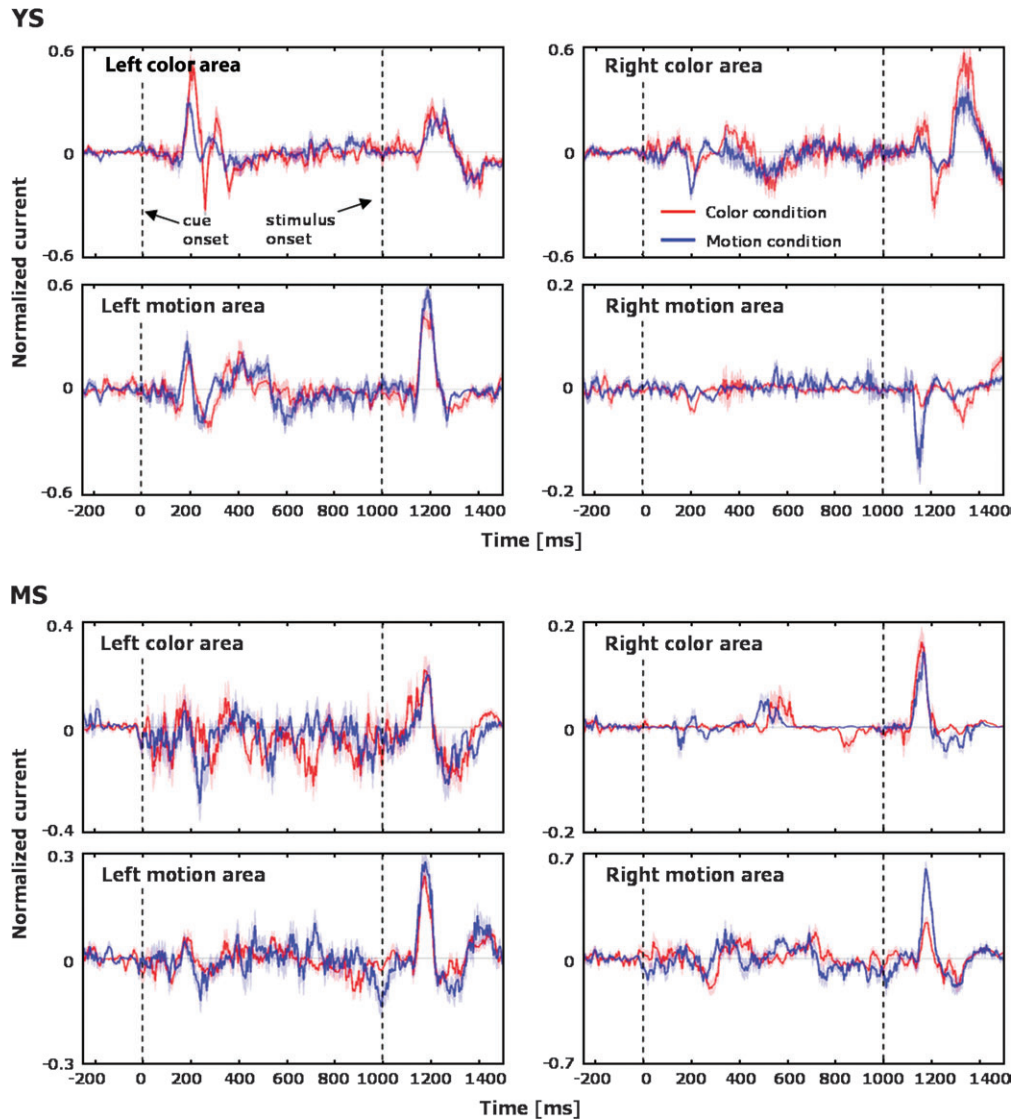


Figure 7. Trial average of the estimated current time courses within each feature-sensitive area for subject YS and MS. The onset times of the cue (0 ms) and the stimulus (1000 ms) are demarcated by vertical broken lines. Current is shown for attention to color (red line) and attention to motion (blue line). Red and blue shadings indicate the SE for the color and motion conditions, respectively.

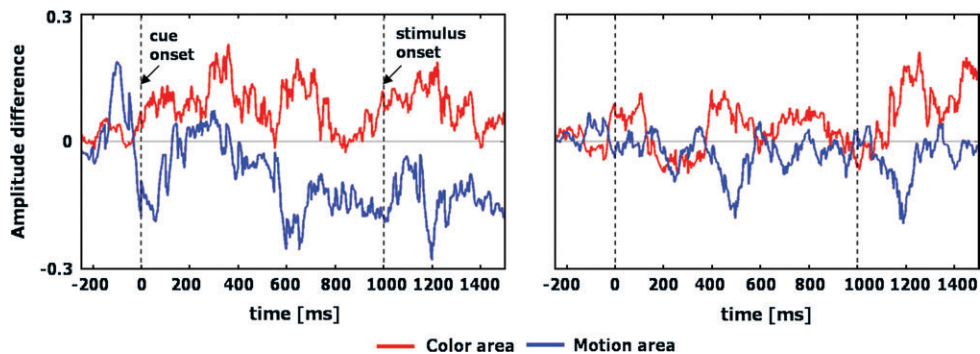


Figure 8. Mean differences of current amplitudes in the left hemisphere (left) and right hemisphere (right) across subjects, as calculated by subtraction of the amplitude of the motion condition from that in the color condition. Red and blue lines show the time course for color- and motion-sensitive areas, respectively.

visualization, we normalized them by dividing the amplitude difference by the absolute value of the maximum difference for each subject. As shown in Figure 9A, the time-points when

differences were observed during the cue period varied among subjects. In addition, the amplitude difference was rather transient, not sustained, during the cue period in each subject.

To show this characteristic quantitatively, we examined individual subject data and quantified how long the conditional difference lasted during the cue period. Figure 9B shows a histogram representing the continuity index for all feature-sensitive areas and all subjects. The continuity index was calculated for each feature-sensitive area and for each subject as follows: 1) calculate significance levels of the amplitude difference between the 2 conditions in each 100-ms bin, 2) count how many bins successively showed significant differences (t -test, $P < 0.05$, corrected for multiple comparisons with 10 of 100-ms bins) between conditions (note that only positive differences were accounted for color-sensitive areas and only negative differences were accounted for motion-sensitive areas), and 3) the maximum number of such successive bins was regarded as a continuity index for the area and for a subject. As shown in Figure 9B, the distribution of the continuity index is skewed, and the index less than 3 contains 75% of the total cases, indicating that significant amplitude differences typically lasted 100–300 ms during the cue period.

Discussion

In the present study, we investigated the effects of feature attention on neural activity before stimulus onset, using MEG in combination with fMRI. First, we compared the signal amplitudes of the recorded MEG data between the 2 conditions at the channel level. We found that, in several channels, the signal amplitudes were significantly different between the 2 conditions. However, we did not find a common tendency in most subjects. Next, cortical currents were estimated in the order of millimeters and milliseconds in each cortical area using the hierarchical Bayesian method. We found that spatiotemporal patterns were generally similar between the 2 conditions (Fig. 4). Then, we examined the effects of feature attention for each ROI and found that no significant difference between conditions was observed in frontal, parietal, and lower visual areas. By contrast, the current amplitude within the color-sensitive area was larger when subjects directed their attention to color than when they directed their attention to motion. On the other hand, the current amplitude within the motion-sensitive area was greater when subjects directed their

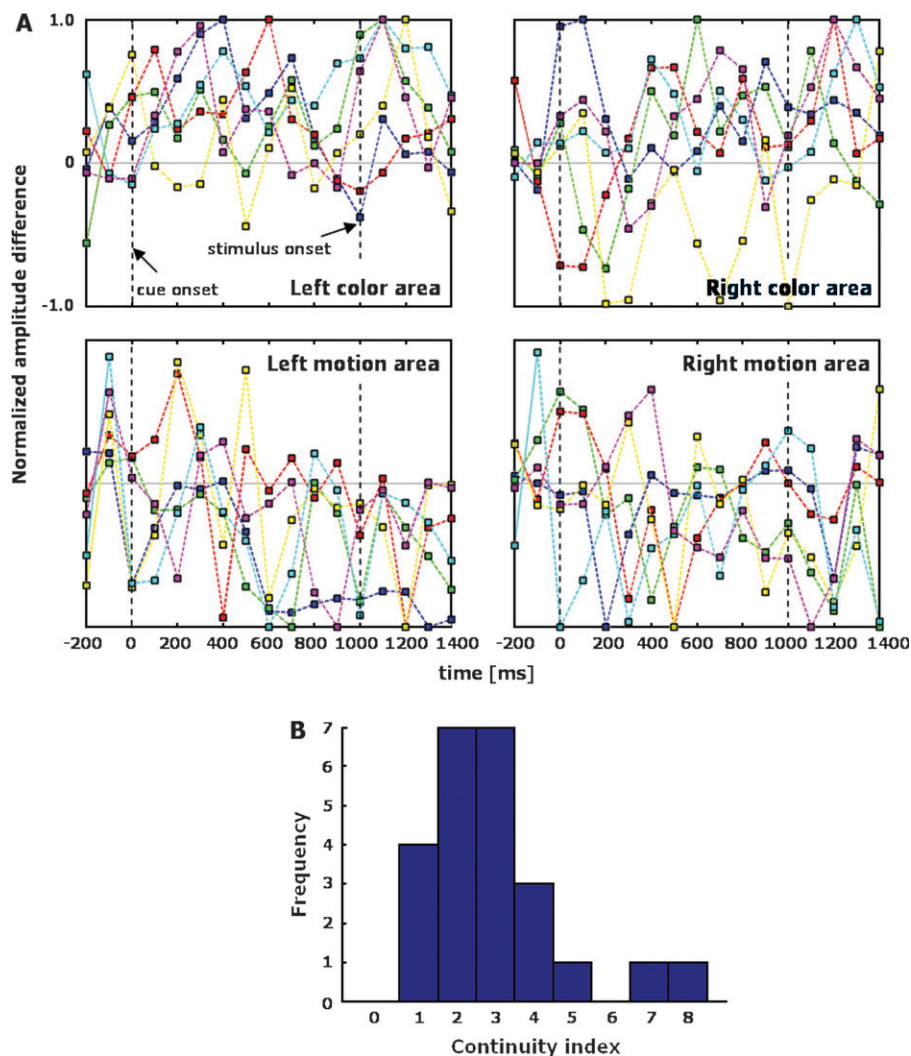


Figure 9. (A) Normalized difference of the estimated current amplitudes plotted for each subject within each feature-sensitive area. Each colored broken line corresponds to 1 subject, and each square marker corresponds to the amplitude difference between 2 conditions averaged over 100 ms. (B) Histogram of a continuity index for all feature-sensitive areas and all subjects. See text for a definition of the continuity index.

attention to motion than when they directed their attention to color. Furthermore, within each feature-sensitive area, and for the averaged data across subjects, we did not find any significant differences between the 2 conditions when we divided current amplitudes during the cue period into several time bins (500 or 250 ms) and compared them in each bin. This, at first, seems puzzling and in contrast with the significant differences (Fig. 6) obtained from the averaged data across subjects during the cue period. Plots of the differences between the 2 conditions for each subject (Fig. 9A) explain the seemingly contradictory statistical results for time-averaged data (significant) versus short time bin analyses (nonsignificant). That is, for each individual, the feature-sensitive area activity was generally greater when a subject attended to that feature, but the time for the difference differed from subject to subject. In addition, the difference between the 2 conditions was transient, not sustained, during the cue period (Fig. 9B). Thus, when the average is taken for both time and subjects, we obtained significant results, but the difference within each time bin did not reach significance because of individual fluctuations in the difference time.

The effect prior to the stimulus onset was observed while white stationary dots were presented at the center of a display without any changes in the visual presentation. Therefore, this effect may reflect top-down attention control processes to sensory processing areas. Regarding research on nonhuman primates, no study has measured single-unit activity from different feature-sensitive areas simultaneously and examined the effects of feature attention within each area. To date, only 1 study has reported activity changes in the visual cortex induced by motion attention without a stimulus in the context of working memory (Ferrera et al. 1994). Recently, some fMRI studies (Chawla, Ress and Friston 1999; Wylie et al. 2006) have reported that attention to a specific feature selectively modulates the activity in the corresponding feature-sensitive areas, even before stimulus onset. However, the BOLD signal does not have sufficient resolution to investigate the temporal nature of the attentional effect that may change in the order of a few hundred milliseconds (Muller et al. 1998; van Velzen and Eimer 2003; Slagter et al. 2005; Yamagishi et al. 2005). Although EEG and MEG have high temporal resolution, it has been difficult to examine the effect of feature attention within particular cortical areas by using these techniques because of the ill-posed inverse problem. In this study, we overcame these difficulties using the MEG source estimation in combination with the fMRI data (Sato et al. 2004). However, there might be some worries about how much fMRI predefined area information affects current estimation results, even though it is soft constrained. To answer this question, we conducted the current estimation without the fMRI data and compared the results with and without fMRI data (see Supplementary Results for details). The current estimation results without fMRI data showed very similar pattern of activities to the results with fMRI data. The resultant spatial patterns of activities were similar (compare Supplementary Fig. 2A,B), and the amplitude comparisons showed the same pattern of results with and without fMRI data (compare Supplementary Fig. 3A,B). This supports the reliability of the hierarchical Bayesian method that we used in this study.

Figure 6 shows that attention to color and motion selectively enhanced the current amplitude within color- and motion-sensitive visual areas within a 1-s prestimulus period. Previous

neuroimaging studies of spatial attention have suggested that the effect of spatial attention starts several hundred milliseconds after subjects attended to 1 visual field within the corresponding visual areas (Muller et al. 1998; Worden et al. 2000; Slagter et al. 2005; Yamagishi et al. 2005; Thut et al. 2006). Our results suggest that, like spatial attention, the effect of feature attention starts within several hundred milliseconds after subjects direct their attention to a particular feature within the corresponding feature-sensitive visual areas.

However, the temporal nature of the effect of feature attention might be different from that of spatial attention. When we compared current amplitudes throughout the cue period, time-averaged amplitudes were significantly different between conditions. By contrast, there was no significant difference when we divided the estimated current amplitudes into shorter time bins and compared them. Moreover, the time-points in which conditional differences were observed during the cue period varied between subjects (Fig. 9A). The amplitude differences between conditions lasted mostly for a short period time (100–300 ms, Fig. 9B). To clarify that this result was not led by a particular estimation window size, we calculated the continuity index of the estimated current for 3 different time windows: time window 1 (200 ms in length, 100-ms overlap), time window 2 (100 ms in length, 50-ms overlap), and time window 3 (50 ms in length, 25-ms overlap) (see Supplementary Results for details). Resultant histograms of the continuity index show similar pattern of continuities and peaked at 2 (corresponding to 200 ms) for all time windows (A, B, and C in Supplementary Fig. 4). This suggests that, therefore, temporal characteristics of the estimated current we obtained were not particularly led by the time window we used.

It is unclear why an observed amplitude modification occurred at a different time for each subject even though we asked subjects to maintain their attention to color or motion during the entire cue period, with randomly interleaved catch trials (an ISI was 500 ms). Our results suggest that the effect of feature attention before the stimulus onset is transient rather than sustained, at least, for the frequency components that are higher than 1 Hz because of a 1- to 100-Hz band-pass filter we used. By contrast, previous EEG and MEG studies have suggested that the effect of spatial attention starts from several hundred milliseconds after subjects attend to 1 visual field and persists until the stimulus onset (Worden et al. 2000; Yamagishi et al. 2005; Thut et al. 2006). Previous psychophysical (Kanai et al. 2006) and physiological (McAdams and Maunsell 2000; Hayden and Gallant 2005) studies indicated that spatial and feature attentions are based on distinct neural substrates. Taken together, although both spatial and feature attention modulate neural activity within specific visual areas before the stimulus onset, mechanisms underlying these attentional effects may differ.

There was no significant amplitude difference between the conditions within the lower visual areas as well as the parietal and frontal areas. Does this mean that the difference of the effect of feature attention is represented within the corresponding feature-sensitive areas only? According to previous studies, this is not necessarily the correct view. Watanabe et al. (1998) reported that the effect of attention to motion within V1 is task dependent. They found that attention to expanding motion enhanced the activity in MT/MST, whereas attention to translating motion enhanced the activity not only in MT/MST

but also in V1. We used expanding or contracting motion in our study. Additionally, the effect of attention can be represented by a spatial pattern of cortical activity. Kamitani and Tong (2006) showed that the pattern of activity in lower visual areas can predict whether subjects attend to clockwise or counter-clockwise motion. Although we cannot conclude that the difference in feature attention is represented only at the corresponding feature-sensitive visual areas, at least, we can assert that feature-sensitive visual areas are central to the effect of feature attention.

One might argue that the difference of current amplitudes between the conditions during the cue period is not derived from a difference in top-down processes, but from the differences in bottom-up visual information, as the visual cue preceding the stimulus presentation was different in each condition (color condition: C and motion condition: M). However, the difference in cue shapes is not sufficient to explain the differences in current amplitude for the cue period as it does not seem plausible that color-sensitive areas and motion-sensitive areas selectively respond to C and M, respectively. Rather, top-down processes, which shift subjects' attention to a particular feature, are important factors that help to explain the differences between the conditions during the cue period.

Consistent with previous fMRI (Chawla et al. 1999) and EEG/MEG (Schoenfeld et al. 2007) studies, the amplitude of the stimulus-evoked response within each ROI was significantly different between the 2 conditions. Because the visual stimulus was identical under both conditions, this difference should also reflect the effects of feature attention. As there was no significant difference in peak latency within feature-sensitive visual areas, the effects of feature attention to a sensory input may be represented by an increase or a decrease in the neural firing rate or the degree of synchronization between neurons, rather than the latency of neural firing or neural synchronization. These effects of feature attention may help to facilitate our visual processing by improving information transmission to subsequent processing in the visual cortex (Fries et al. 2001; Salinas and Sejnowski 2001) or decoding accuracy of the stimulus in higher cognitive brain functions (Nakahara and Amari 2002).

How do attentional effects before and after the stimulus onset relate to each other? One hypothesis is that the effect of feature attention before the stimulus onset acts as a preparatory activity to enhance the stimulus-evoked signal within feature-sensitive areas (Driver and Frith 2000). Some computational (Chawla, Lumer and Friston 1999, 2000; Borgers et al. 2005) and physiological studies (Cossart et al. 2003; McCormick et al. 2003; Shu et al. 2003) have proposed that background activity before sensory inputs contribute to the modulation of stimulus-locked transients. Previous fMRI studies of both spatial and feature attention have reported changes in the BOLD signal within each feature-sensitive or retinotopic area without a visual stimulus (Chawla et al. 1999; Kastner et al. 1999; Hopfinger et al. 2000; Wylie et al. 2006). These effects may reflect a change in background neural activity. However, the difference between spatial and feature attention has remained largely unclear as the BOLD signal reflects time-integrated neural activity within the local neural population. According to our data, it is possible that feature and spatial attention before the stimulus onset contribute to the modulation of the stimulus-evoked signal via different neural mechanisms.

Supplementary Material

Supplementary Figs 1–4, Methods, Results, and Movie can be found at: <http://www.cercor.oxfordjournals.org/>.

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Notes

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