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Spatio-temporal Analysis of Feature-Based Attention

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The cortical mechanisms of feature-selective attention to color and motion cues were studied in humans using combined electrophysiological, magnetoencephalographic, and hemodynamic (functional magnetic resonance imaging) measures of brain activity. Subjects viewed a display of random dots that periodically either changed color or moved coherently. When attention was directed to the color change it elicited enhanced neural activity in visual area V4v, previously shown to be specialized for processing color information. In contrast, when dot movement was attended it produced enhanced activity in the motion-specialized area human MT. Parallel recordings of event-related electrophysiological and magnetoencephalographic responses indicated that the attention-related facilitation of neural activity in these specialized cortical areas occurred rapidly, beginning as early as 90–120 ms after stimulus onset. We conclude that selection of an entire feature dimension (motion or color) boosts neural activity in its specialized cortical module much more rapidly than does selection of one feature value from another (e.g., one color from another), as reported in previous electrophysiological studies. By combining methods with high spatial and temporal resolution it is possible to analyze the precise time course of feature-selective processing in specialized cortical areas.

Keywords: attention, color, ERP, feature-based attention, fMRI, MEG, motion

Introduction

Visual stimuli can be readily selected from the environment and attended on the basis of their simple features such as color, brightness, size, or shape (Wolfe 2003). Neuroimaging experiments over the past 15 years have provided many insights into the neural systems that mediate feature-selective attention. In pioneering studies using positron emission tomography, Corbetta et al. (1990, 1991) found that attending to a specific feature (color, shape, or motion) of a multifeature array boosted the neural activity in the cortical region that was specialized to process that feature. This enhancement of feature-specific processing was proposed to be orchestrated by an attentional control network that included posterior parietal and frontal cortical areas. Subsequent neuroimaging studies have confirmed the general principle that paying attention to a particular feature is associated with increased neural activity in its specialized cortical module, which in the case of color has been localized to the inferior occipital area V4/V8 (Martin et al. 1995; Clark et al. 1997; Chawla et al. 1999) and in the case of motion to area V5/hMT (Beauchamp et al. 1997; O'Craven et al. 1997; Chawla et al. 1999; Saenz et al. 2002).

Although neuroimaging studies have given a detailed picture of the anatomical regions participating in feature-selective attention, these techniques do not reveal the precise time course of the selective stimulus processing. Such timing information has come from studies using event-related brain potentials (ERPs) and magnetoencephalography (MEG), beginning with the groundbreaking studies of Harter and Aine (1984). Their general finding was that stimuli possessing an attended-feature value elicited an enhanced negative ERP component termed the "selection negativity" (SN), which has a latency of onset in the range of 140- to 200-ms poststimulus. Harter and Aine proposed that the SN reflects enhanced processing in a feature-specific "channel" resulting from the allocation of attention, which accords well with the neuroimaging data of Corbetta et al. (1990, 1991). Modulations of the SN and associated components have been observed during selective attention to a variety of features including color, motion, shape, spatial frequency, and orientation (Harter and Aine 1984; Kenemans et al. 1993; Anllo-Vento and Hillyard 1996; Anllo-Vento et al. 1998, 2004; Smid et al. 1999; Torriente et al. 1999; Kenemans et al. 2000; Ruijter et al. 2000; Martinez, Di Russo, et al. 2001; Martinez, DiRusso, et al. 2001; Baas et al. 2002; Beer and Roder 2004, 2005).

There have been several attempts to localize the anatomical generators of the SN and associated components by dipole modeling techniques. For feature selections based on color (Anllo-Vento et al. 1998) and spatial frequency (Martinez, DiRusso, et al. 2001; Baas et al. 2002), the dipolar sources of the SN were estimated to lie in ventral occipital cortex, in the same general region as the color-selective area V4/V8 identified with functional magnetic resonance imaging (fMRI) (McKeefry and Zeki 1997; Hadjikhani et al. 1998). The accuracy of such unconstrained dipole models is open to question, however, due to the uncertainties inherent in the inverse problem of source localization. The anatomical sources of ERP components or their magnetic counterparts (event-related fields or ERFs) may be localized with greater validity by combining dipole source analysis with convergent evidence from hemodynamic measures of cortical activity in the same task situation (Heinze et al. 1994; Martinez et al. 1999; Mangun et al. 2001; Noesselt et al. 2002; Schoenfeld et al. 2002; Di Russo et al. 2003, 2005; Schoenfeld, Tempelmann, et al. 2003; Vanni et al. 2004; Rodriguez-Fornells et al. 2005). To our knowledge, such a convergent analysis has not been reported for the neural activity associated with selective attention to nonspatial stimulus features.

The present study combined ERP and ERF recordings with fMRI in order to investigate both the time course and cortical substrates of feature-selective attention to color and to motion. Although previous studies have employed one or another of these methods, it is important that electromagnetic and hemodynamic methods can be combined in the same task

situation to obtain spatially and temporally sensitive measures of feature-selective processing. The present design was aimed to maximize selective processing of either the color or motion feature of a random dot display by presenting separate blocks of attend-color and attend-motion trials. This type of design, in which attention is directed to a feature dimension rather than to a particular feature value within a dimension, is typical of hemodynamic studies of feature-selective attention (Corbetta et al. 1991; Clark et al. 1997; Chawla et al. 1999) but to our knowledge has not been employed in ERP/MEG studies.

Methods

Subjects

Eighteen healthy subjects (8 males, ages 19–35 years) with normal or corrected-to-normal vision participated as paid volunteers in the ERP/ERF experiment. Six of these subjects (4 males) also participated in the fMRI experiment. All gave informed consent, and the study was approved by the local ethics committee.

Stimuli

In the ERP/ERF experiment moving dot stimuli were presented on a projection screen situated at 120 cm in front of the subject. The stimuli were presented against a dark background (0.22 cd/m^2) within a squared aperture (4° × 4°) that was centered on the vertical meridian with its lower edge situated 3° above a central fixation cross. One hundred stationary white dots (200 cd/m^2) were continuously present in this aperture during the intertrial intervals. On each trial on a random basis the dots either moved coherently to the right (movement trials) or changed color from gray to isoluminant red or orange (color trials) for 300 ms (see Fig. 1). On movement trials the velocity of the dot movement could either be slow (standards: 6° s-1, on 70% of the trials) or fast (targets: 8° s-1, on 30% of the trials). On color change trials the dots could change either to isoluminant red (standards: on 70% of the trials) or to orange (targets: on 30% of the trials). Red/orange/white isoluminance was established through heterochromatic flicker photometry. The intertrial interval randomly varied between 620 and 800 ms.

During the fMRI experiment, the stimuli were presented via a projector/mirror system. The stimulus parameters were identical to those of the ERP/ERF sessions, except that the intertrial intervals were varied between 1.0 and 7.0 s following a gamma function in order to allow trial separation in an event-related analysis (Worsley et al. 1992; Hinrichs et al. 2000).

Procedure

Prior to each block of 10–12 trials, a symbolic cue (the letter "B" from the German word "Bewegung" for movement or "F" from the German word "Farbe" for color change) replaced the fixation cross for 400 ms indicating the feature to be attended on that block. During each block a target stimulus (either fast movement or color change to orange) could occur 2–3 times at random. Subjects were instructed to press a button as quickly as possible upon detecting an attended-feature target. After 10–12 trials a new cue appeared, which was followed by the next block of trials. In the ERP/ERF experiment, each experimental run consisted of 50 blocks and had a duration of 9–10 min, and the experiment was carried out in 4 runs. Prior to the experimental sessions, subjects were trained to maintain fixation on the central cross. Eye movements were continuously monitored by recording the electrooculogram.

For the fMRI experiment each experimental run consisted of 18 blocks, and a total of 6 runs were carried out.

ERP/ERF Recordings

Data Acquisition

ERPs and ERFs were recorded simultaneously using a BTI Magnes 2500 WH (Biomagnetic Technologies, Inc.) whole-head system with 148 magnetometer channels and 32 electroencephalography (EEG) channels (NeuroScan, Inc.). The recording bandpass was DC-50 Hz with a sampling rate of 254 Hz for both. Artifact rejection was performed offline by removing epochs with peak-to-peak amplitudes exceeding a threshold of 3.0 × 10^{-12} T, as well as epochs before, during, and after button presses. Following artifact rejection, data were filtered with a bandpass of 0.1–20 Hz. Individual head shapes were coregistered with the sensor coordinate system by digitizing (Polhemus 3Space Fastrak) skull landmarks (nasion, left, and right preauricular points) and determining their locations relative to sensor and electrode positions using signals from 5 coils that were located at 5 different positions on the head. These landmarks enabled the coregistration of ERP/ERF activity with individual anatomical MR scans.

Data Analysis

Separate ERP and ERF averaged waveforms time-locked to motion or color change onsets were computed for each of the 8 trial types (4 stimulus conditions × 2 attention conditions). Only responses to the

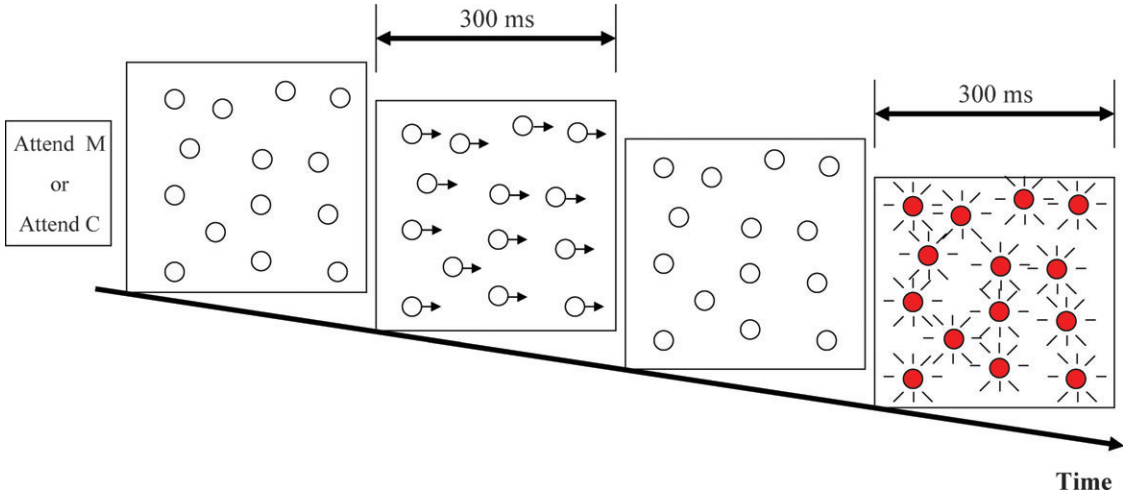

Figure 1. Schematic diagram of the experimental design. Each block of trials started with a symbolic cue indicating the stimulus feature to be attended (motion or color). The dots were stationary in the interstimulus interval and then either moved rightwards or changed color for 300 ms. Motion and color stimuli were presented equiprobably, in random order. For each feature there were 2 alternative stimuli (fast vs. slow movement and red vs. orange color change). Subjects were instructed to press a button as quickly as possible upon detecting fast motion when motion was the attended feature or the orange color change when color was the attended feature.

more frequent nontarget stimuli (slow movements and color changes to red) were analyzed in the present study. To determine the effect of attention on motion processing, difference waves were formed by subtracting the ERP/ERF waveforms elicited on trials in which the dots moved but color was the attended feature (unattended movement) from those elicited on trials where the dots moved and the attended feature was motion (attended movement). The effect of attention on color processing was similarly determined by subtracting the ERP/ERF waveforms elicited on color change trials when motion was the attended feature (unattended color change) from those elicited by the same stimuli but when color was the attended feature (attended color change). Attention effects were quantified in these difference waves as mean amplitude measures over specified latency intervals (with respect to a 200 ms prestimulus baseline) at the sensor/electrode sites showing the largest amplitudes. Statistical tests were performed using repeated-measures analysis of variance (RANOVA). To determine the time of onset of the sensory and attention effects, amplitude measures were taken over successive 10-ms intervals and tested for deviation from baseline with a criterion of $P < 0.05$ (Guthrie and Buchwald 1991). The earliest significant interval followed by 5 (or more) successive significant intervals was taken as the onset latency (Molholm et al. 2002; Schoenfeld, Tempelmann, et al. 2003; Schoenfeld, Woldorff, et al. 2003).

Source analysis was carried out using multimodal neuroimaging software (Curry 4.0, Neuroscan, Inc.). Source modeling was performed using regional equivalent current dipoles (ECDs) in a realistic boundary element model (BEM) of the head derived from a structural MR scan. The magnetic field distribution as measured by the MEG is oriented perpendicularly with respect to the voltage field distribution measured by the EEG. Consequently, the electric (ERP) and magnetic fields (ERF) produced by a given dipolar source will have different (nearly orthogonal) surface topographies. The ERP and ERF surface topographies were fit concurrently to obtain maximal localization power (Fuchs et al. 1998; Schoenfeld, Tempelmann, et al. 2003). This fitting procedure requires that the conductivities of the volume conductor model are matched for the EEG and MEG recordings. A conductivity factor was therefore determined to scale the EEG data with respect to the MEG data on the basis of a tangential dipole evoked by tactile stimulation of the index finger by an air puff at 30–40 ms latency (Fuchs et al. 1998). Reliably across these subjects, the conductivity factor could be approximated to 0.8 and this value was used for all subjects. Dipoles were modeled to fit to the grand average ERP/ERF difference fields (attended minus unattended) using the BEM from the subject whose brain dimensions were closest to the mean of all subjects (Schoenfeld, Woldorff, et al. 2003). The following procedure was used for source modeling. First, the difference fields were modeled using a single, unconstrained, ECD. Because these single-dipole models explained less than 90% of the field variance, a second additional dipole was introduced into the model. During the iterative best-fitting estimation calculations, the dipoles were allowed to move within the volume conductor without any constraints. For both the color and movement difference fields this best-fitting procedure resulted in 2 dipoles settling into nearly symmetrical locations in the occipital cortex of both hemispheres.

MR Imaging

Subjects were scanned with a neuro-optimized GE Signa LX 1.5-T system (General Electric, Milwaukee, WI). In a structural session whole-head T_1-weighted images (spatial resolution 1 mm × 1 mm × 1.5 mm, in-plane resolution: 256 × 256, 124 slices, no gap) were acquired with a circular polarized head coil using a 3D spoiled gradient echo sequence (time repetition/time echo [TR/TE]/flip angle = 24 ms/8 ms/24°).

For the functional session a 5-inch surface coil was centered beneath the subjects' occipital pole. During task performance functional data from 20 slices (matrix 64 × 64, field of view 18 cm, slice thickness 3 mm, no gap, oriented perpendicular to the calcarine fissure) covering the occipital cortex were collected using an echo planar imaging (EPI) gradient echo sequence (TR/TE/flip angle = 2000 ms/40 ms/80°, ramp sampling on). The order of slice acquisition was first impair followed by the pair slices (1, 3, . . ., 19, 2, 4, . . ., 20). The experiment consisted of 6 runs, each lasting 8 min and 40 s (260 volumes).

fMRI—Eye Movement Control

During functional runs the movements of the left eye of the subject were recorded by a custom system using an infrared light transmission device with fiber optic cable. The resolution of this system for the detection of eye movements was better than 0.5°. Performance was monitored online, and all subjects were able to maintain fixation with less than 1° deviation.

fMRI Analysis

Data from each subject were at first analyzed individually (Statistical Parametric Mapping 99 [SPM], Wellcome Department of Cognitive Neurology, London, UK). The first 4 images of each run were removed to exclude saturation effects. The remaining images were time-sliced, realigned to the fifth scan of the first run, normalized on the Montreal Neurological Institute (MNI)-template, resliced to 2 × 2 × 2 mm^3 cubic voxels and spatially smoothed (Gaussian kernel of 6 mm). Individual anatomical scans were coregistered with the functional images and normalized to 2 × 2 × 2 mm^3 to serve as an overlay for the activated areas.

Functional data were temporally high- and low-pass filtered. Statistical analysis of the data was performed using the standard hemodynamic-response function (SPM) in an event-related design for each subject (SPM99). As in the ERP/ERF experiment, trials were grouped according to the 2 stimulus conditions (movement or color) and the 2 attention conditions (attend-movement or attend color). Group analyses were performed using the fixed effects model approach. The effects were thresholded at $P = 0.01$ corrected for multiple comparisons (family-wise error) and for cluster size (Poline et al. 1997) with a cluster size threshold of 15 voxels. For coregistration fMRI and ERP/MEF data were brought into the MNI space frame. The coordinates of the electromagnetic sources and fMRI activations were then transformed into Talairach space coordinates using the mni2tal-transform (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html).

Retinotopic Mapping

Mapping of the borders between the retinotopic visual areas was carried out using the Freesurfer program package (http://surfer.nmr.mgh.harvard.edu). The overlay of the functional SPM-results upon the occipital cortical surface was accomplished by manual alignment of the inversion recovery prepared EPI and T_1-weighted high resolution data, including rotation, translation, and linear scaling.

Results

Behavioral Results

Subjects were faster and more accurate at detecting targets during the color task. The mean reaction time (RT) was 429 ms, and the hit rate was 91.7%. False alarms were rare (0.2%). In the motion task the mean RT was 622 ms, whereas the hit rate was 73.8%. The false alarm rate was slightly higher (2%). These differences were substantiated in an RANOVA with the factor task (motion vs. color discrimination). A significant main effect was found for the RTs ($F_{1,17} = 141.49$; $P < 0.0001$) as well as for the hit rate ($F_{1,17} = 54.18$; $P < 0.0001$) and for the false alarms ($F_{1,17} = 38.81$; $P < 0.0001$).

Attention Effect for Motion

ERP and ERF Measures

The ERPs and ERFs elicited by the standard (slow) motion stimulus were compared while subjects were engaged in the attend-motion versus attend-color task. The comparison between the ERP waveforms (spatial average over posterior occipital scalp sites) revealed a significant difference over the time range 100–350 ms, in that the ERP to the motion stimulus was significantly more negative when attended compared with when it was unattended ($F_{1,17} = 16.46$; $P < 0.005$) (Figs. 2*A*, 3*A*

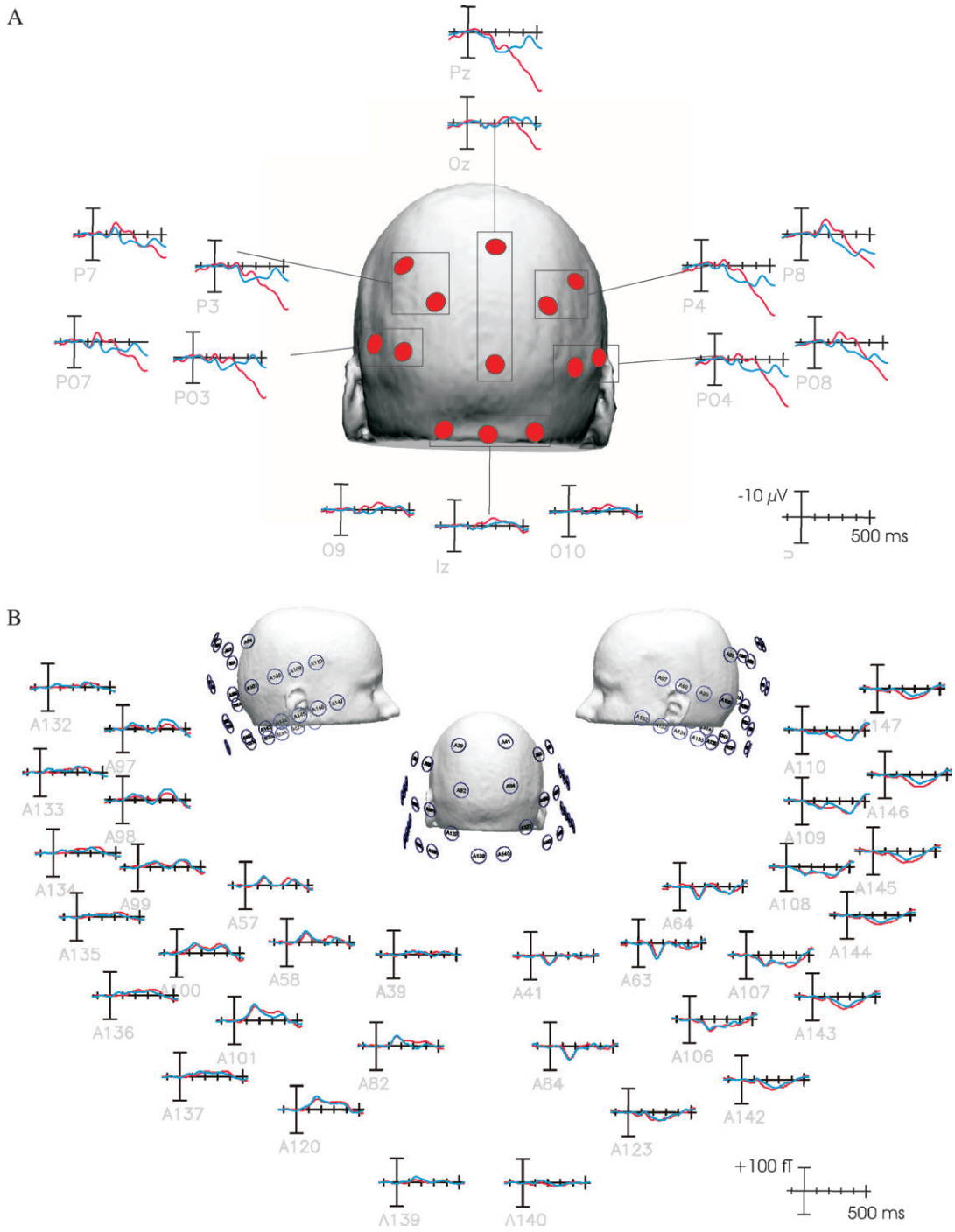

Figure 2. (*A*) ERP waveforms elicited by the motion stimulus under attended (red tracings) and unattended (blue tracings) conditions, averaged over all subjects. (*B*) ERF waveforms elicited by the motion stimulus under attended and unattended conditions, averaged over all subjects.

and *B*). This negativity was maximal bilaterally over lateral occipital–parietal electrode sites giving rise to 2 foci in the ERP topography (Fig. 3*C*, left topography map). Statistical comparisons of the amplitude in successive 10-ms epochs after stimulus onset with respect to the prestimulus baseline indicated that the difference between the waveforms started to become significant at 110 ms.

The ERF waveforms exhibited a similar difference for the same comparison in the time range 100–350 ms ($F_{1,17} = 9.58$; $P < 0.014$, spatial average over right maximum) (Figs. 2*B*, 3*A* and *B*). Successive testing of 10-ms epochs after stimulus onset versus the baseline showed that the difference started to become significant at 120 ms. The topographical distribution of this difference field consisted of symmetrically located pairs of maxima and minima over left and right occipital–temporal sensors (Fig. 3*C*, right topography map). The right maximum/minimum pair was more prominent than the left pair.

In the time range 120–280 ms the distributions of the ERP and ERF difference waveforms were modeled with 2 dipolar sources located in the left and right lateral occipital cortex posterior to

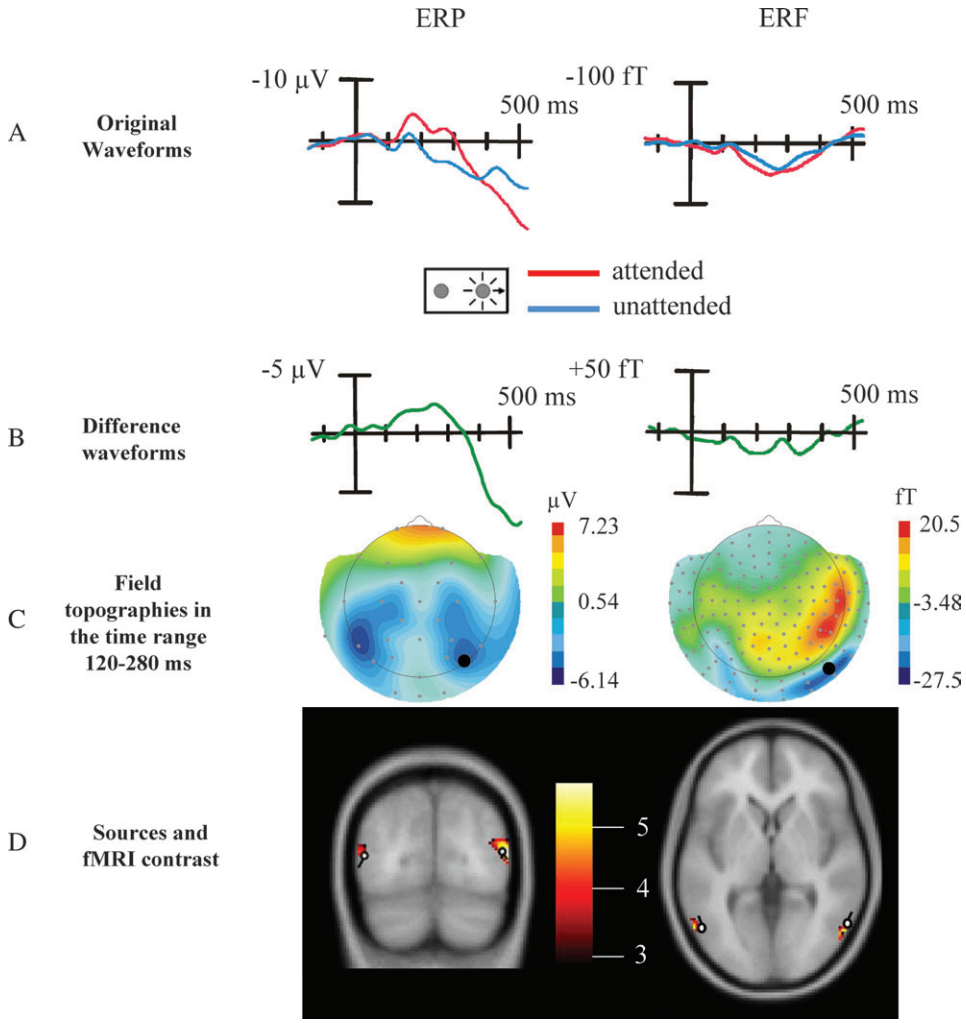

Figure 3. The effect of attention on the processing of motion. (*A*) Concurrently recorded ERP and ERF waveforms elicited by the slow motion stimulus (standards) when motion was attended (red tracings) and unattended (blue tracings), averaged over all subjects. Time zero of recording epoch is when the dot array begins to move. Recording sites are indicated with dots on part *C*. (*B*) Difference waveforms formed by subtracting the unattended from the attended waveforms shown in part *A*. (*C*) Topographical field distributions of the ERP and ERF difference waveforms shown in part *B* averaged over the time range 110–280 ms. (*D*) Locations of estimated source dipoles accounting for the surface topography of the difference waveforms shown in part *C* coregistered with fMRI activations in the corresponding contrast (attended vs. unattended motion trials).

the occipito-temporal junction (Talairach coordinates of the dipoles: –48/–67/4 and 57/–63/5) (Fig. 3*D*). This model explained 92% of the field variance. It should be emphasized that although these 2 dipoles turned out to be almost bilaterally symmetrical, no symmetry constraint was imposed in the fitting of either the motion or color difference waves.

Hemodynamic Measures

The contrast for the hemodynamic response to the motion stimulus comparing the attended versus unattended conditions revealed 2 nearly symmetrical foci of event-related activity, which were located bilaterally in lateral occipital cortex in the vicinity of the occipito-temporal junction (Talairach coordinates: –49/–67/5 and 56/–64/5) (Fig. 3*D*). No other activations were observed at the level of $P = 0.01$ corrected for multiple comparisons.

To compare the localizations of activity based on the ERP/ERF and the hemodynamic measures the results from the dipole source analysis were brought into MNI space and coregistered with the hemodynamic activations. This revealed a close spatial coincidence of the hemodynamic activations with the 2 modeled sources (Fig. 3*D*).

Additional analyses were performed in the single subjects in which the hemodynamic activations were overlaid on individual retinotopical maps. In all subjects, the activations were found to be located within the V5/human-MT+ (hMT) regions of both hemispheres (Fig. 6).

Attention Effect for Color

ERP and ERF Measures

The ERP/ERF waveforms elicited by the standard (red) color stimulus were compared while subjects were engaged in the color versus the speed discrimination task. The comparison between the ERPs (spatial average over parieto-occipital channels) revealed a significant difference over the time range 100–190 ms, in that the amplitude of the ERP was more positive when the color change stimulus was attended compared with when it was unattended ($F_{1,17} = 6.86$; $P < 0.032$) (Figs. 4*A*, 5*A* and *B*). This positivity was maximal over centro-parietal

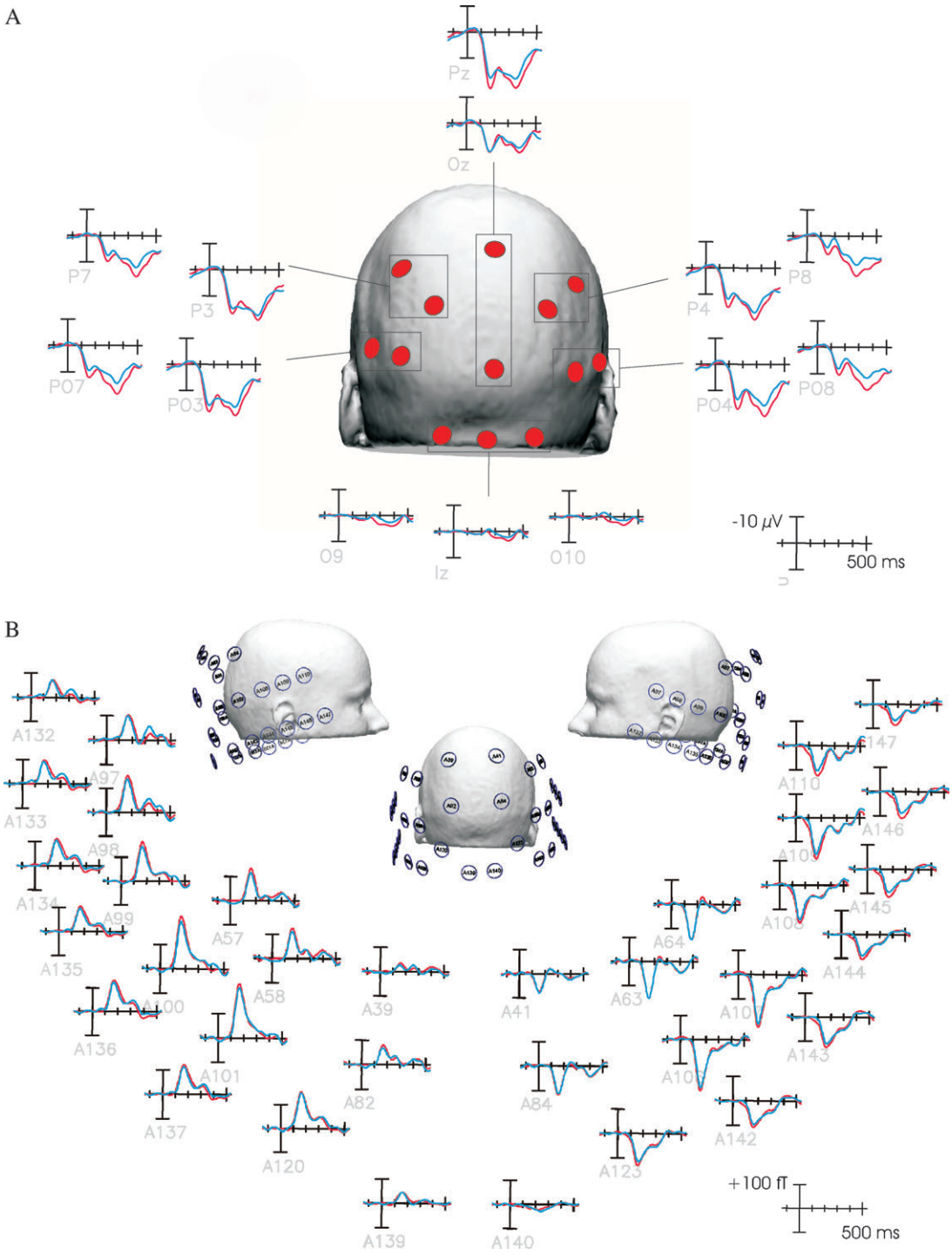

Figure 4. (*A*) ERP waveforms elicited by the standard color change stimulus under attended (red tracings) and unattended (blue tracings) conditions averaged over all subjects. (*B*) ERF waveforms elicited by the color change stimulus in attended and unattended conditions averaged over all subjects.

electrode sites giving rise to a focal maximum in the ERP topography (Fig. 5*C*, left topography map). Statistical comparisons of the amplitudes in successive 10-ms epochs after stimulus onset with respect to the prestimulus baseline indicated that the difference between the attended and unattended waveforms started to become significant at 110 ms.

The ERF waveforms exhibited a similar difference for the same comparison in the time range 90–220 ms ($F_{1,17} = 6.64$; $P < 0.03$, spatial average over right maximum) (Figs. 4*B*, 5*A* and *B*). Successive testing of 10-ms epochs after stimulus onset versus the baseline showed that the difference started to become significant at 90 ms. This difference had a complex field topography due to cancellation effects, with one maximum located over left occipital–temporal sensors and a minimum located slightly more anterior over right occipital–temporal sensors (see Fig. 5*C*, right topography map). The distributions of the ERP and ERF difference waveforms in the time range 90–220 ms were modeled with 2 dipolar sources located bilaterally in

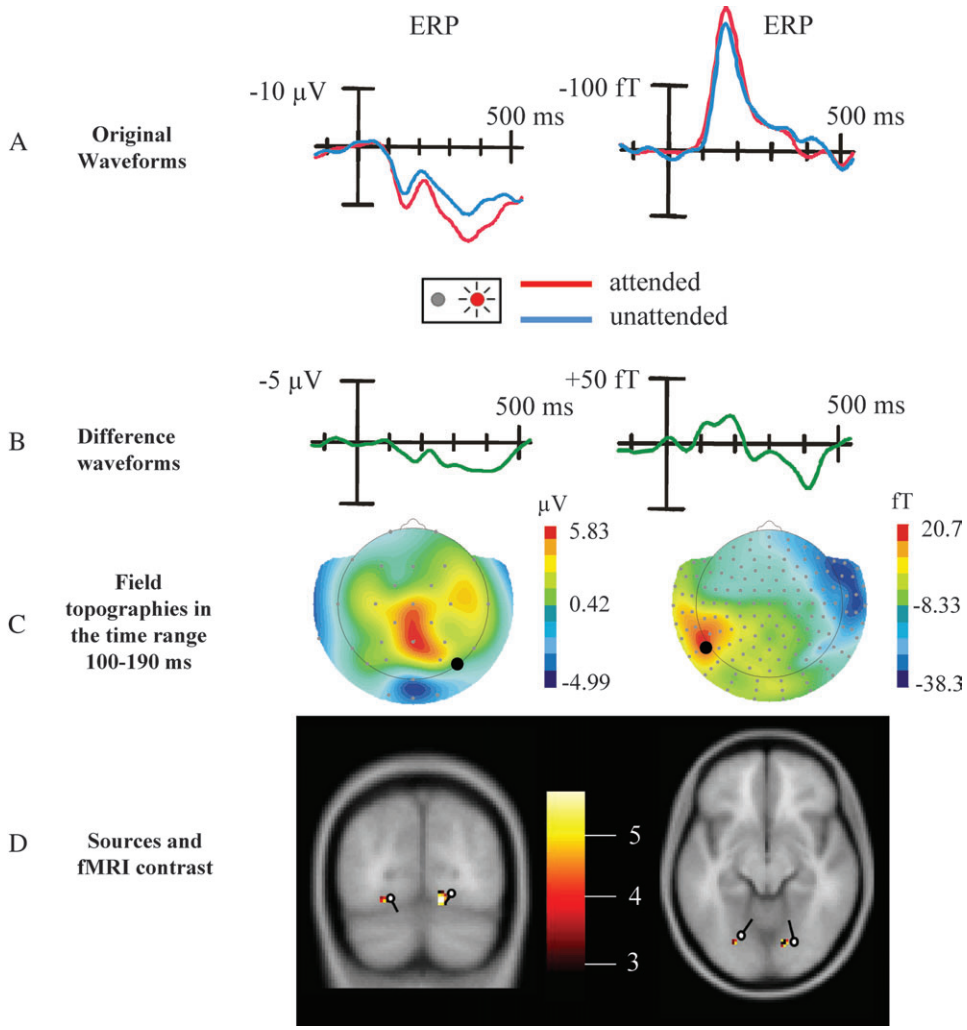

Figure 5. The effect of attention on the processing of color. (*A*) Concurrently recorded ERP and ERF waveforms elicited by the standard color change (to red) stimulus averaged over all subjects on trials when color was attended (red tracings) and unattended (blue tracings). (*B*) Difference waveforms formed by subtracting the unattended from the attended waveforms shown in part *A*. (*C*) Topographical field distributions of difference ERP and ERF waveforms shown in part *B* averaged over the time range 105–210 ms. (*D*) Locations of estimated source dipoles accounting for the surface topography of the difference ERP and ERF waveforms shown in part *C* coregistered with fMRI activations in the corresponding contrast (attended vs. unattended color trials). Note that given the orientation of the dipolar sources, the magnetic field configurations elicited by each source are very similar (left positivity–right negativity shown in part *C*) but are spatially shifted corresponding to the distance between the source locations. This results in an overlap of a negative (from the source located in the left fusiform gyrus) and a positive magnetic field (from the source located in the right fusiform gyrus) in the central part of the topographical distribution canceling each other out. Consequently, a nearly isoelectric field distribution can be observed centrally.

the posterior fusiform/lingual gyrus (Talairach coordinates of the dipoles: −21/−72/−5 and 17/−73/−3) (see Fig. 3*D*). This model explained 91% of the variance of the field.

Hemodynamic Measures

The attended versus unattended contrast for the color change stimulus revealed nearly symmetrical activations in the right and left hemispheres (Fig. 5*D*). In the left hemisphere the activation was located in the fusiform gyrus (Talairach: −22/−73/−5). In the right hemisphere the activation was located more medially, along the collateral sulcus between the fusiform and lingual gyrus (Talairach: 16/−73/−4). The coregistration with the modeled dipolar sources revealed a close spatial coincidence (Fig. 5*D*). The overlay of the hemodynamic activations on the retinotopic maps indicated that these activations were located in the region V4v of both hemispheres (see Fig. 6 for a representative subject).

Discussion

The present study investigated the neural mechanisms underlying attentional selection for motion and color features in humans. By combining ERPs and ERFs with fMRI it was possible to delineate both the cortical substrates and the temporal dynamics of feature-based selection. When attention was directed to a specific feature (motion or color), an enhancement of the event-related blood oxygen level–dependent (BOLD) response in the corresponding feature-specific cortical module was observed. The neural sources of attention-related ERP/ERF modulations were localized using dipole modeling to these same feature-specific cortical areas. This spatial correspondence between the independently determined BOLD activations and dipole locations provides strong evidence that the hemodynamic and ERP/ERF measures arose from a common neural source. The ERP/ERF waveforms indicated that this attention-related enhancement of neural activity occurred

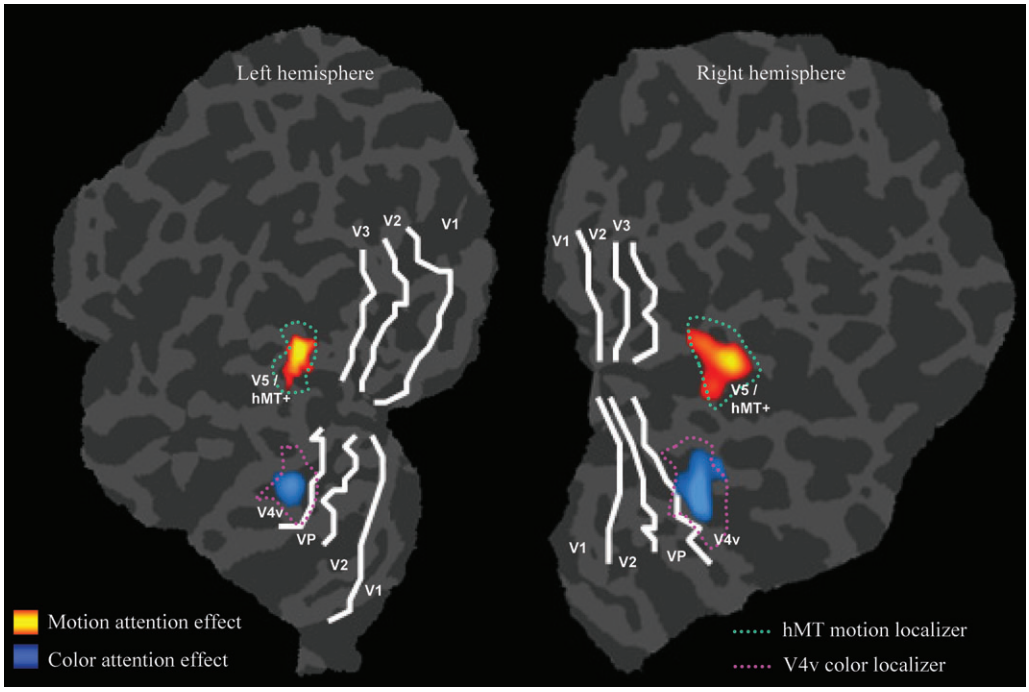

Figure 6. Hemodynamic attention effects of a representative subject projected on flattened cortical surfaces of the 2 hemispheres. The event-related hemodynamic activation for the contrast attended versus unattended motion is shown in red. The corresponding activation for the contrast attended versus unattended color is shown in blue. The borders between the visual areas were defined by retinotopic mapping. Motion (green dotted line) and color (pink dotted line) localizers were obtained by contrasting all moving and all color change stimuli, respectively, versus the stationary isoluminant gray stimuli in the baseline. Note that the localizers also elicited activity to a smaller extent in earlier visual areas (V1, V2, V3, V3a) not shown in the figure.

very rapidly, beginning as early as 90–120 ms after stimulus onset. These findings confirm the original hypothesis of Corbetta et al. (1991) regarding the modular organization of feature-selective attention and provide a time frame in which the attention-related enhancement of neural activity occurs.

When attention was directed to motion, the moving stimulus elicited an enhanced hemodynamic response in bilateral occipital regions posterior to the occipital–temporal junction. This region corresponds to the hMT, which is considered to be the homologue of the well-known MT region in the monkey that is highly specialized for the perception of motion (Zeki et al. 1991). Neurophysiological studies in monkeys have shown that attending to a moving stimulus results in enhanced neural firing in this cortical region (Treue and Maunsell JHR 1996; Treue and Martinez Trujillo 1999; Treue and Maunsell JH 1999). Converging evidence has come from studies in humans in which hemodynamic activity in hMT was shown to be enhanced when motion was attended (Corbetta et al. 1990, 1991; O'Craven et al. 1997; Buchel et al. 1998; Chawla et al. 1999; Saenz et al. 2002). The Talairach coordinates of the attention-related modulations in area hMT reported in these previous studies correspond closely with those observed here.

ERP studies have shown that attending to the direction of a moving stimulus leads an enlarged negativity over the posterior scalp starting at around 150–160 ms (Anllo-Vento et al. 1998). This negative component has been termed SN and is elicited during attention to a variety of feature dimensions (Harter and Aine 1984; Kenemans et al. 1993; Anllo-Vento and Hillyard 1996; Anllo-Vento et al. 1998; Smid et al. 1999; Torriente et al. 1999; Kenemans et al. 2000; Ruijter et al. 2000; Martinez, DiRusso, et al. 2001; Baas et al. 2002; Beer and Roder 2005). In the present study, the attended moving stimuli also elicited an enlarged posterior negativity in the ERP, which was accompanied by a corresponding modulation of the ERF. The source analysis of this attention effect revealed 2 bilateral sources that were spatially coincident with the region that exhibited hemodynamic activity and was identified as area hMT. The onset latency of this negativity was earlier (110–120 ms) than in previous studies of attention to motion, however, most likely because the present experimental design involved a between-feature selection (motion vs. color) rather than a within-feature selection (e.g., right vs. left motion) as in the studies cited above. These data suggest that an entire feature dimension can be selected more rapidly than a particular value within a feature dimension.

When color was the attended-feature dimension the colored stimulus elicited enhanced hemodynamic activity in the fusiform/lingual gyrus. Retinotopic mapping indicated that the activated region corresponds to visual area V4v. Although there is some controversy about how this region should be named (McKeefry and Zeki 1997; Hadjikhani et al. 1998), there is general agreement about its location and color sensitivity. The present findings are in agreement with previous hemodynamic studies showing that neural activity is enhanced in this V4v region when attention is directed to the color feature of a stimulus (Corbetta et al. 1991; Clark et al. 1997; Chawla et al. 1999). The Talairach coordinates of the attention-related activations in area V4v reported in these previous studies correspond closely with those observed in the present study.

In the ERP/ERF recordings, the attended colored stimuli elicited a more positive ERP waveform in the time range 110–200 ms over the parietal scalp than did the same stimuli when unattended. A corresponding ERF modulation was seen over 90–220 ms. This attention-related ERP/ERF modulation was

localized to neural generators that coincided spatially with the hemodynamic activations in area V4v. Previous ERP studies also reported an enhanced posterior positivity during color selection (Anllo-Vento et al. 1998; Lange et al. 1998) but the onset latencies were generally longer than those observed here, ranging from 130 to 180 ms. As with the motion attention effect, these latency differences among the various studies most likely result from differences in experimental design. Whereas the present study required selection between the color and motion feature dimensions, the previous studies required selection of a particular color within the color dimension. Another important difference between the present ERP waveforms associated with color selection and those reported previously is the complete absence of a SN component. This surprising absence of the most ubiquitous ERP sign of color selection might also be a consequence of the present experimental design (i.e., selection between feature dimensions rather than within a dimension) but other factors such as our use of isoluminant stimuli might also have played a role.

Although the ERP/ERF modulations associated with selection of the nonspatial features of motion and color began quite early under the present conditions (90–110 ms), the modulations associated with spatial attention typically begin even earlier. In particular, stimuli at an attended location elicit a characteristic sequence of enhanced ERP components over the posterior scalp including P1 (onset at 70–80 ms) and N1 (onset at 120–150 ms) deflections (Heinze et al. 1994; Anllo-Vento 1995; Martinez et al. 1999; Martinez, DiRusso et al. 2001; Di Russo et al. 2003). This ERP signature of spatial attention is quite different from the ERP configurations associated with selection of nonspatial features, which supports the proposal that spatial attention has a distinctive underlying mechanism. Studies that have combined spatial and feature-selective attention (Hillyard and Munte 1984; Anllo-Vento and Hillyard 1996; Karayanidis and Michie 1996; Lange et al. 1998) found that the ERP indices of feature selection are suppressed for stimuli at an unattended location. This suggests that one of the functions of spatial attention is to control access of feature information to the specific processing modules in a hierarchical manner.

In a previous study (Schoenfeld, Tempelmann, et al. 2003) we found that paying attention to a moving dot array produced an enhanced positive ERP deflection (and corresponding ERF modulation) beginning at 230–240 ms when the attended array included a task-irrelevant color feature. This ERP/ERF modulation had topographical properties (and source localization) very similar to those of the color selection effect observed in the present study. A parallel fMRI experiment showed an enhanced hemodynamic response in area V4v that corresponded precisely to the source of the ERP/ERF modulation (Anllo-Vento et al. 2004). This enhanced processing of the irrelevant color feature belonging to an attended "object" (moving dot surface) was interpreted as providing a neural basis for the feature binding process that underlies the perceptual unity of attended objects.

In sum, the present findings and those of previous studies show that color processing in area V4v is strongly modulated by selective attention, and the latency of this modulation depends on the type of selective process that is engaged. When a color feature is to be selected from another feature such as motion, the enhanced processing in area V4v begins very early (90–110 ms), whereas if one color is to be selected from another color the enhancement begins somewhat later (130–180 ms). And if the color feature is irrelevant and is selected only by virtue of belonging to an object that is being attended, the activation of the color-specific module takes still longer to begin, in the neighborhood of 230–240 ms. A similar finding was obtained for selection of motion information in area hMT. When the motion dimension itself is being attended, the selection begins quite early (110–120 ms), whereas selection of one direction of motion from another does not occur until 150–160 ms. To our knowledge, the present study is the first to demonstrate that selection between feature dimensions can occur as rapidly as 90–110 ms. These ERP/ERF data thus add essential information about the time course of feature-selective processing in specialized cortical areas that is unavailable from hemodynamic studies alone.

Notes

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