

Form-From-Motion: MEG Evidence for Time Course and Processing Sequence

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Abstract

■ The neural mechanisms and role of attention in the processing of visual form defined by luminance or motion cues were studied using magnetoencephalography. Subjects viewed bilateral stimuli composed of moving random dots and were instructed to covertly attend to either left or right hemifield stimuli in order to detect designated target stimuli that required a response. To generate form-from-motion (FFMo) stimuli, a subset of the dots could begin to move coherently to create the appearance of a simple form (e.g., square). In other blocks, to generate form-from-luminance (FFLu) stimuli that served as a control, a gray stimulus was presented superimposed on the randomly moving dots. Neuromagnetic responses were observed to both the FFLu and FFMo stimuli and localized to multiple visual cortical stages of analysis. Early activity in low-level visual cortical areas

(striate/early extrastriate) did not differ for FFLu versus FFMo stimuli, nor as a function of spatial attention. Longer latency responses elicited by the FFLu stimuli were localized to the ventral-lateral occipital cortex (LO) and the inferior temporal cortex (IT). The FFMo stimuli also generated activity in the LO and IT, but only after first eliciting activity in the lateral occipital cortical region corresponding to MT/V5, resulting in a 50–60 msec delay in activity. All of these late responses (MT/V5, LO, and IT) were significantly modulated by spatial attention, being greatly attenuated for ignored FFLu and FFMo stimuli. These findings argue that processing of form in IT that is defined by motion requires a serial processing of information, first in the motion analysis pathway from V1 to MT/V5 and thereafter via the form analysis stream in the ventral visual pathway to IT. ■

INTRODUCTION

Studies in macaque monkeys have suggested that the extrastriate cortex is divided in two major processing systems (Van Essen & DeYoe, 1995; Desimone & Ungerleider, 1989; Maunsell & Newsome, 1987; Moran & Desimone, 1985; Ungerleider & Mishkin, 1982). One pathway is directed ventrally into the temporal lobe and supports the analysis of nonspatial stimulus features and object analysis. A parallel pathway is directed dorsally into the parietal lobe and supports spatial perception and visuomotor performance. A third pathway may also exist that is directed into the posterior temporal region to analyze visual motion or for the integration of spatial and object vision (Baizer, Ungerleider, & Desimone, 1991; Boussaoud, Ungerleider, & Desimone, 1990). Various functional neuroimaging studies (Malach et al., 1995; Tootell, Reppas, Dale, et al., 1995; Watson et al., 1993; Corbetta, Miezin, Shulman, & Petersen, 1991; Haxby et al., 1991; Zeki et al., 1991) have presented evidence for the existence of similar systems in humans.

In everyday vision complex objects have to be perceived and identified while they are moving, and motion helps to bind the features of objects in complex scenes. This raises the question of how these systems integrate information (e.g., Merigan & Maunsell, 1993). Although there is some evidence of interstream communication on the basis of anatomical studies and single-cell recordings (reviewed in Felleman & Van Essen, 1991), there is relatively less knowledge about their functional role in interstream integration.

Several studies have investigated the neural substrates of motion and object processing in humans. Some have provided evidence that V5 (referred to here as MT/V5), the human homologue of monkey MT, is part of a system for motion processing (Dupont et al., 1997; Barton et al., 1996; Tootell, Reppas, Kwong, et al., 1995; Watson et al., 1993; Zeki et al., 1991). Other studies have shown the inferior temporal cortex (IT) to be part of the system for form processing (Kanwisher, Woods, Iacoboni, & Mazziotta, 1997; Malach et al., 1995; Haxby et al., 1993; Kohler, Kapur, Moscovitch, Winocur, & Houle, 1993; Schacter et al., 1993; Sergent, 1982). One study (Dupont et al., 1997) found a specific area, KO, near MT/V5 that is involved in the processing of kinetic boundaries, while two other studies (Grill-Spector,

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Kushnir, Edelman, Itzchak, & Malach, 1998; Malach et al., 1995) identified an area on the lateral aspect of the occipital lobe (LO) that is specific for luminance and motion-defined object silhouettes.

Although brain areas involved in the processing of shape and those involved in the processing of motion have been identified, there is little knowledge about the timing of the activations of these areas, especially under conditions where these areas might be expected to have to interact to accomplish object identification. There are several possibilities for the processing sequence of form-from-motion (FFMo) information in the visual cortex (e.g., Britten, Newsome, & Saunders, 1992). A first simple possibility, but one which is most likely incorrect, would be serial processing of motion and luminance information involving only the ventral stream through V1, V2, V3, V4 towards IT. It is, of course, well known that IT plays an important role in shape perception (e.g., Britten et al., 1992) and to be active when a shape has to be perceived (Sary, Vogels, & Orban, 1993). But, in addition, it has been demonstrated that V2 neurons (e.g., Burkhalter & Van Essen, 1986; Orban, Kennedy, & Bullier, 1986; Zeki, 1978; Baizer, Robinson, & Dow, 1977) as well as V3 neurons (Felleman & Van Essen, 1987; Zeki, 1978) and V4 neurons (Albright & Desimone, 1987; Zeki, 1978) are also sensitive to motion. Thus, motion might be integrated with luminance cues within the ventral visual processing stream to extract form information. However, Britten et al. (1992) demonstrated by lesioning MT, a dorsal stream area, that this region is necessary for the perception of FFMo, a finding that indicates that processing of FFMo cannot rely only on ventral stream processing.

A second possibility for human FFMo processing that would still involve a serial processing account would entail the initial analysis of visual motion inputs in the dorsal stream via V1 towards MT/V5 extracting motion information, which would then be directed into the ventral visual stream towards IT for form analysis and object identification. Such an interstream connection between monkey MT and V4 has been described by Maunsell and Van Essen (1983) and Ungerleider and Desimone (1986).

A third possibility would be an initial parallel processing out of V1 to MT/V5 (dorsal stream) and from V1 towards IT (ventral stream), converging later on a higher-order region where the information from both streams is integrated. A candidate for this region would be the anterior portion of the superior temporal sulcus (Baizer et al., 1991; Boussaoud et al., 1990). Yet another possibility was proposed by Shipp and Zeki (1989). Stimulus-induced activity would flow from V1 to MT/V5, where movement would be analyzed and then, via reafferent projections, would reenter the ventral stream through V1 for further processing in order to complete object analysis.

In humans, fMRI and PET provide excellent localization of activity supporting visual processing, but do not reveal the temporal sequence of activities that underlie complex neural processing such as the extraction of FFMo cues. For such a purpose, a method is needed that offers higher temporal resolution of the activations of the areas involved. Magnetoencephalography (MEG) permits one to track the processing sequence of FFMo and form-from-luminance (FFLu) in order to investigate serial versus parallel processing models of visual object recognition. In humans, one would expect that shape information would be processed in the IT (Kanwisher et al., 1997; Tanaka, 1996; Sary et al., 1993) mainly in the right hemisphere (Farah, 1990), while motion would be processed in dorsal stream areas (Dupont et al., 1997; Barton et al., 1996; Tootell, Reppas, Kwong, et al., 1995; Watson et al., 1993; Zeki et al., 1991). However, when form must be extracted from only motion cues, then interactions between the two streams should be observed, and the time course of these processes can be tracked using MEG. MEG also provides significant information about the localization of neural activity, and thus, is uniquely suited for studying the time course and localization of brain processes.

In the present study, subjects were presented with two squares formed by randomly moving dots located to the left and to the right of a central fixation cross. In these squares, two shapes (square or rectangle) were defined either by dots moving in a coherent manner (FFMo task) or by luminance differences (FFLu) (see also Figure 6 and Methods section). Subjects were instructed to maintain fixation, and to covertly attend to one lateral field location in order to discriminate the shapes at the attended location only. They were required to press a button to the designated target shape (e.g., square or rectangle).

In the FFMo task, it is only possible to extract the shape information by processing motion information first, because the shape is defined "only" by the motion (luminance cues were eliminated by careful stimulus design). If MEG activity to FFMo stimuli in ventral stream regions that analyze stimulus form is preceded by activity in dorsal stream areas and is delayed relative to processing of luminance-defined forms, then this will provide evidence for serial processing in which information is first processed in dorsal stream areas and fed into ventral stream structures for object analyses. If, however, dorsal and ventral areas show simultaneous activity, or activities with considerable temporal overlap, and the time course of processing in ventral stream areas (e.g., IT) is not different from those defined by luminance, then this would support the idea that the processing of FFMo occurs in parallel in dorsal and ventral streams, feeding forward to a higher-order region for integration. In contrast, in the FFLu task, no motion processing is needed to get the shape information

because perception can proceed based on luminance differences. Hence, the MEG activity that is time locked to the onset of the luminance information should be confined to ventral stream regions and not be observed in MT/V5.

This study also investigates a second important issue concerning the role of attention in motion and object perception. Previous studies have demonstrated that attention influences the processing of motion in the dorsal stream (Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998; O’Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Anllo-Vento & Hillyard, 1993; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991). For example, Corbetta, Miezin, Dobmeyer, et al. (1991) found that selective attention to stimulus features, such as form or motion, modulated the activity in the brain areas, which are believed to process the attended stimulus feature.

These studies investigated attention to specific stimulus features. At present, however, it remains unclear what role spatial attention might play in the integration of ventral and dorsal stream processing. A fundamental goal of attention research is to discover which levels of information processing can be influenced by top-down attentional processes. Spatial attention is thought to modulate processing of information at early stages through filtering mechanisms (Broadbent, 1970; Treisman, 1969). In addition, it has been proposed that an important role for focal attention is to provide the “glue” for integrating the various features of an object. (e.g., Treisman & Gelade 1980). Following this line of thinking, one possible role for spatial attention might be the integration of dorsal and ventral stream activity in object perception. Hence, another goal of the present study was to ask what the role of spatial attention might be when objects required integration of information regarding motion and form. To address this question in the present study, the processing sequences elicited by FFMo and FFLu stimuli are investigated in attended and unattended conditions. Competing views of attention have argued that the unit of attentional selection in object and motion processing is not spatial, but rather is based on the feature or form attended (O’Craven, Downing, & Kanwisher, 1999), but these studies did not manipulate spatial attention, and thus, could not address its role in the processing of

motion, form, or FFMo stimuli. The present study specifically manipulates spatial attention toward and away from the stimuli streams.

RESULTS

Behavioral Results

A repeated-measures ANOVA with the factor of Attention (left vs. right) and Condition (FFMo vs. FFLu) was performed for the reaction times in Table 1. There was no significant main effect for Attention [$F(1,7) = 1.076, p = .334$], but a significant main effect of Condition [$F(1,7) = 54.532, p < .0001$]. There was also a significant interaction between Attention and Condition [$F(1,7) = 10.03, p < .001$]. ANOVAs for specific contrasts showed this to be the result of differences in RT as a function of the task condition (FFLu vs. FFMo) for attend-left versus attend-right conditions. Specifically, the reaction times were delayed for the FFMo versus the FFLu condition for both the attend-left condition [$F(1,7) = 10.4, p < .01$] and the attend-right condition [$F(1,7) = 9.39, p < .01$], but the delay was larger for the attend-left condition (FFMo – FFLu delays were 92.3 and 67.2 msec for the attend-left and attend-right conditions, respectively). There were no significant differences for attend-left versus attend-right conditions for either the FFLu [$F(1,7) = 0.92, p > .05$] or the FFMo [$F(1,7) = 0.95, p > .05$] conditions. No significant differences were found for the rates of false alarms or misses.

MEG and Timing Analyses

Overview

To assess the time course of differences between FFLu and FFMo processing, as well as the effects of spatial attention, analyses were directed at activity over relevant scalp regions and at various latencies in order to investigate both early sensory input processing and high-order perceptual analyses related to motion and form processing. We will first present analyses aimed at determining whether input processing (as indexed by short latency responses over striate and early extrastriate cortex) was different in either latency or amplitude as a function of stimulus type (FFLu vs. FFMo) or spatial attention. Then we will describe detailed analyses of the occipito-temporal responses at longer latencies that reflect processing of motion and form.

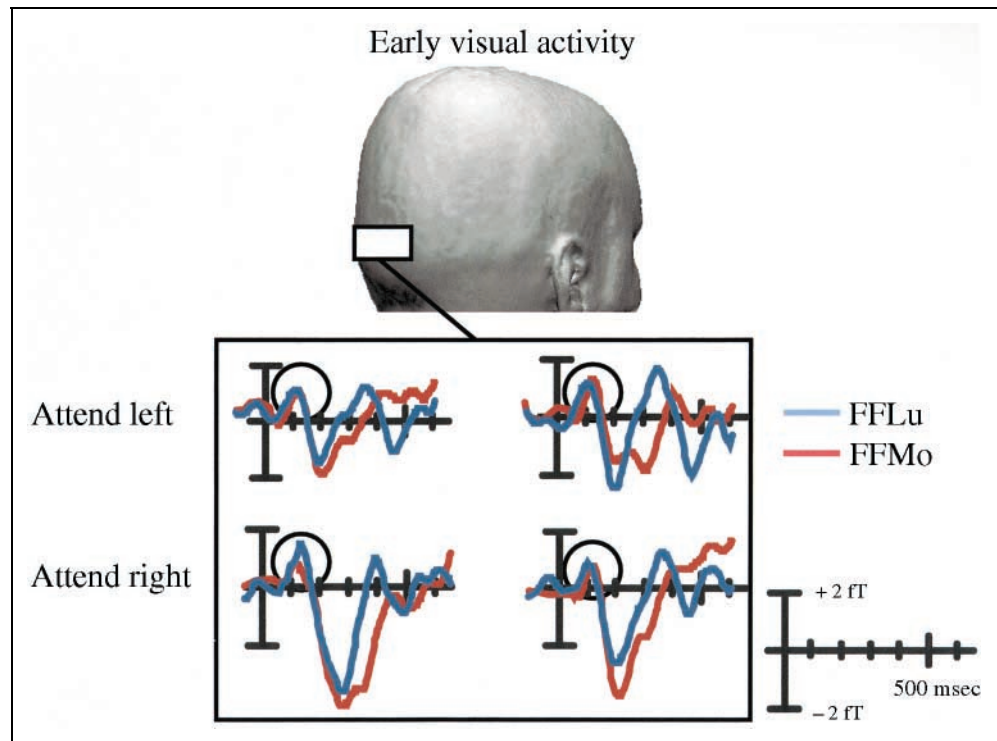
Short Latency Occipital Responses

Over occipital sensors, both FFLu and FFMo elicited responses. Between 50 and 150 msec latency, these responses were highly similar in latency and amplitude regardless of stimulus type or attention. Figure 1 shows the attended waveforms for FFLu and FFMo. The

Table 1. Behavioral Data

Condition	RT (msec)	Hits (%)	Misses (%)	FA (%)
FFMoL	822.68	84.5	11.5	4
FFMoR	792.16	82.5	12.5	5
FFLuL	730.41	87.0	10	3
FFLuR	724.97	85.5	11.5	3

Figure 1. MEG waveforms from sensors located over the striate cortex (indicated by box over representative head viewed from right rear). Shown are the responses to the attended FFLu and FFMo stimuli over left (left column) and right (right column) occipital sensors. The responses are shown for both the attend-left (top row) and attend-right (bottom row) conditions. The tick marks are placed every 50 msec on the scale with stimulus onset at the upright amplitude scale bar. The responses from early visual areas are circled. No significant differences were obtained in latency or amplitude of these early responses as a function of stimulus type or attention (see text).



latency of the responses (collapsed across attention conditions) at 25% of its peak amplitude was 108 msec for FFLu and 113 msec for FFMo (the latency at a percentage of peak amplitude provides a measure that is less sensitive to noise in the waveforms, although it is neither the onset nor the peak of the response; these responses peaked between 120 and 125 msec). The latencies of these short latency occipital responses were not statistically different for FFLu versus FFMo stimuli [$F(1,7) = 0.35, p > .50$]. Neither were the latencies of these responses significantly affected by spatial attention [$F(1,7) = 0.34, p > .50$]. The amplitudes of the occipital responses at their peaks (collapsed across attention conditions) were 0.5 fT for FFLu and 0.4 fT for FFMo, and were “not” significantly different [$F(1,7) = 0.78, p > .30$]. These peak amplitudes also did not differ significantly as a function of attention [$F(1,7) = 3.09, p > .08$]. No interactions of stimulus type (FFLu vs. FFMo) with attention were observed for the latency measure [$F(1,7) = .26, p > .60$] or peak amplitude [$F(1,7) = .88, p > .30$]. Thus, at the level of input processing in striate/early extrastriate cortex, there were no significant differences in the processing of the FFLu versus FFMo stimuli.

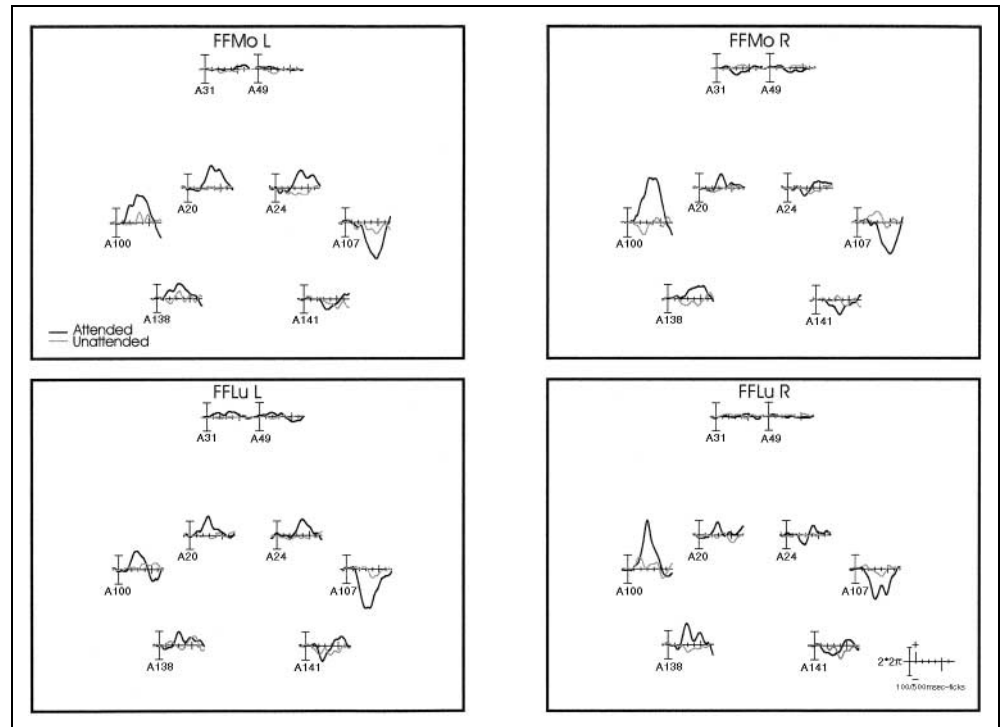
Long Latency Responses at the Lateral Occipital and Temporal Sites

At longer latencies over the lateral occipital and posterior temporal scalp areas, both stimulus types (FFLu and FFMo) evoked a slow wave with an onset between 100 and 200 msec and highest amplitudes

over the occipital and posterior temporal sensor positions when the location of the evoking stimuli was attended but were greatly attenuated when the stimuli were presented to the ignored location (Figure 2). Separate repeated-measures ANOVAs with the factor of attention (attended vs. unattended) were performed for FFLu and FFMo conditions for left and right targets. These analyses were restricted to occipital and temporal sensors (spatial averages) where the responses were maximal. The analyses revealed highly significant attention-related differences between the responses for all comparisons (i.e., left and right hemi-field FFMo and FFLu stimuli) (Table 2). Because the unattended waveforms of the long latency responses were so greatly attenuated, it was not possible to quantify their latencies in individual subjects, and hence, the analyses of the time course and topography of these for FFLu versus FFMo were performed only for the attended stimulus waveforms.

A delay in the late wave was revealed when event-related fields for FFLu stimuli were compared with FFMo stimuli in attended conditions. This wave had a later onset in the FFMo conditions compared with the FFLu conditions. The delays were calculated and are shown in Figure 3 along with the corresponding mean reaction time delays, and the grand average associated waveforms. The greatest delays in these long latency MEG responses were found over the right temporal (TR) sensors for both attend-left and attend-right conditions. One-way ANOVA across subjects, with sensor location as a factor, revealed highly significant differences between the delays for the temporal right (TR) sensors versus the

Figure 2. MEG waveforms elicited by FFMo and FFLu stimuli in attended and unattended conditions. FFMoL = form-from-motion left visual field, FFMoR = form-from-motion right visual field, FFLuL = form-from-luminance left visual field, FFLuR = form-from-luminance right visual field. Black traces depict activity of stimuli in attended conditions, while gray traces depict activity elicited by the same stimuli when they were unattended. The analysis period is from 100 msec before to 700 msec after stimulus onset. Significant activity was only elicited by attended stimuli, indicating a strong suppression for the unattended ones.



occipital right (OR) sensors for both the attend-left [$F(1,7) = 38.1, p < .001$] and attend-right [$F(1,7) = 45.2, p < .001$] conditions, with the activity over right temporal sensors having around a 50–60 msec greater delay compared with right occipital sensors in the FFMo compared with FFLu responses. There was a trend for a similar delay between the occipital left (OL) and temporal left (TL) sensors, but this did not reach significance for either attend-left [$F(1,7) = 5.3, p > .055$] or attend-right condition [$F(1,7) = 3.4, p > .1$].

Source Analyses

In order to relate MEG activity obtained in the FFLu and FFMo conditions to underlying cortical anatomy, and hence to the extant literature on the localization of motion and form processing areas, source modeling was employed. Two different approaches using realistic head models derived from MRI were used for this purpose, and these were: (i) a cortical-surface con-

strained current–source distribution analysis, and (ii) an equivalent current dipole method.

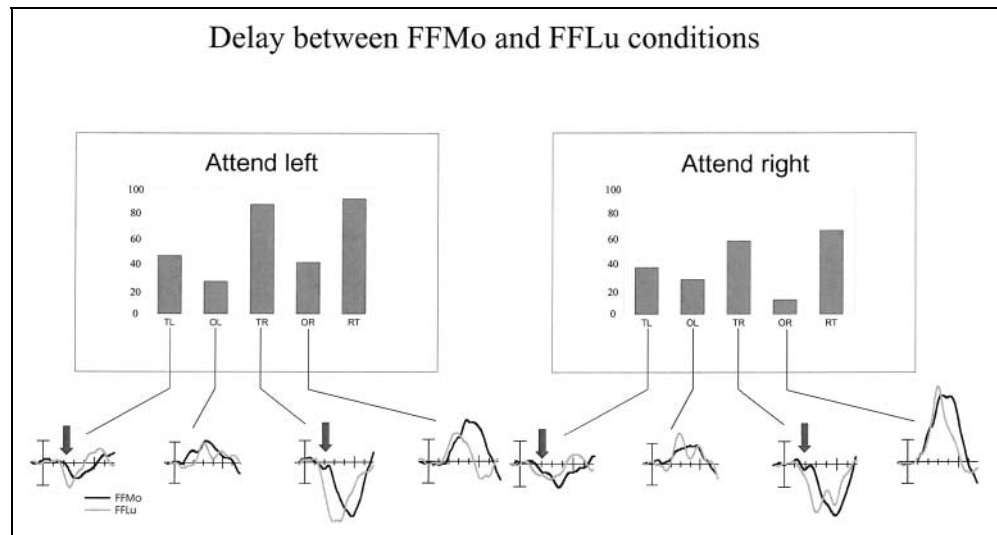
Cortical Surface Current Density

Data from single subjects were analyzed using current–source distribution maps for the whole brain. In these analyses, the individual brain and head were modeled using MRI data, and the extracranial magnetic fields were used to estimate the electrical activity at the cortical surface of the brain. The same analyses were also performed using the grand average fields (i.e., average across subjects), primarily for illustrative purposes. In addition, the modeling focused on the extrastriate activity for two reasons. First, the main focus was on the processing sequence in extrastriate regions, and second, the activity in the primary visual cortex was small and did not reach a signal-to-noise ratio of at least 4:1, which we established as necessary to allow reliable source analysis (see Fuchs, Wagner, Kohler, & Wischmann, 1999).

Table 2. ANOVA Results for the Factor Attended versus Unattended

Location	FFLuL	FFLuR	FFMoL	FFMoR
Left occipital	$F = 17.79; p = 0.001$	$F = 16.33; p = 0.001$	$F = 13.02; p = 0.003$	$F = 15.28; p = 0.002$
Left temporal	$F = 12.16; p = 0.004$	$F = 11.04; p = 0.005$	$F = 16.44; p = 0.001$	$F = 11.99; p = 0.004$
Right occipital	$F = 12.91; p = 0.003$	$F = 9.45; p = 0.008$	$F = 9.40; p = 0.008$	$F = 18.08; p = 0.001$
Right temporal	$F = 16.54; p = 0.001$	$F = 14.17; p = 0.002$	$F = 13.77; p = 0.002$	$F = 16.92; p = 0.001$

Figure 3. The calculated late component delays between FFMo and FFLu are presented for TL, TR, OL, and OR sensors for the attend-left and attend-right conditions along with the reaction times (RT) (right side of each panel). MEG waveforms elicited by FFLu (gray traces) and FFMo (black traces) in attended conditions are presented on the bottom. The delay for the late wave onset between the waveforms elicited by the two stimulus types was maximal over TR sensors for attend-left and attend-right conditions. Note that the difference in delay between waveforms elicited by FFLu and FFMo stimuli was less pronounced over OL, OR, and TL sensors compared with TR sensors.



In single subjects, FFMo stimuli appeared to elicit activity in three distinct regions of the brain (Figure 4, left). The first region inferred to be active was located around the occipito-temporal junction of the hemisphere contralateral to the attended side, a region that seems likely to correspond to area MT/V5. The next region that appeared to be activated was located more inferior in the lateral occipital cortex and may correspond to the so-called LO region. At longer latency, estimates of activity were localized to the inferior parts of the temporal lobe, presumably corresponding to IT. In contrast, the estimates of activity elicited by the FFLu stimuli were first observed in the LO region followed by activity in IT regions of the hemisphere contralateral to the attended side. With the exception of the activity in MT/V5 being elicited only for FFMo stimuli, both stimulus types had highly similar estimated sources (i.e., in LO and IT) for the long latency response, but with different timing (LO being activated at shorter latencies for the FFLu than for the FFMo stimuli).

A similar analysis was also performed on the grand average MEG data (Figure 4, right). In this analysis, the head of one subject was used as the estimated volume conductor, and this brain was used to provide an approximate cortical surface to which to attribute source activity estimates (see Methods for a description of how this “canonical brain” was selected). Due to these approximations, this analysis was performed primarily for illustrative purposes. Nonetheless, as can be seen in Figure 4 (right), this analysis yielded highly similar estimated sources as were derived in single subjects, with the exception that only the “left” MT/V5 region was estimated to be active in the FFMo conditions regardless of the attended side. This latter pattern may have resulted from the use of grand average data in a single subject’s realistic head model,

but parallel analysis (below) using equivalent current dipole modeling revealed a similar pattern. In any case, here in the grand average model, the regions which were estimated to be active after MT/V5 are LO and IT, contralateral to the attended side, just as in the single subject data.

Equivalent Current Dipole Modeling

A second approach was also employed in order to validate the localization of the observed cortical sources in single subjects and to gain more precise information about the relative timing of activity in different brain regions. The grand average magnetic fields were modeled with equivalent current dipoles, again using a realistic head model. This model was computed using the MRI scan of one subject as described earlier (see also Methods). In this approach, using a dipole model for intracranial activity, no cortical surface constraints are needed because the head model is only used as a volume conductor. Although using the head of one subject as the volume conductor model for the grand average data across the group involves approximations, it is substantially more accurate than using a multi-shell sphere as the model head volume conductor (Fuchs et al., 1999; Waberski et al., 1998).

Because the cortical surface information is not used for the modeling here (despite the rendition in Figure 5), modeling of grand average dipoles in the realistic head is less problematic than for the cortical surface current density case presented in Figure 4 (right side). This is because if the actual active cortical surface sources within subjects would result in similar single equivalent current dipoles across subjects (with respect to localization and orientation), which is likely for some cortical regions, the grand average equivalent current dipoles

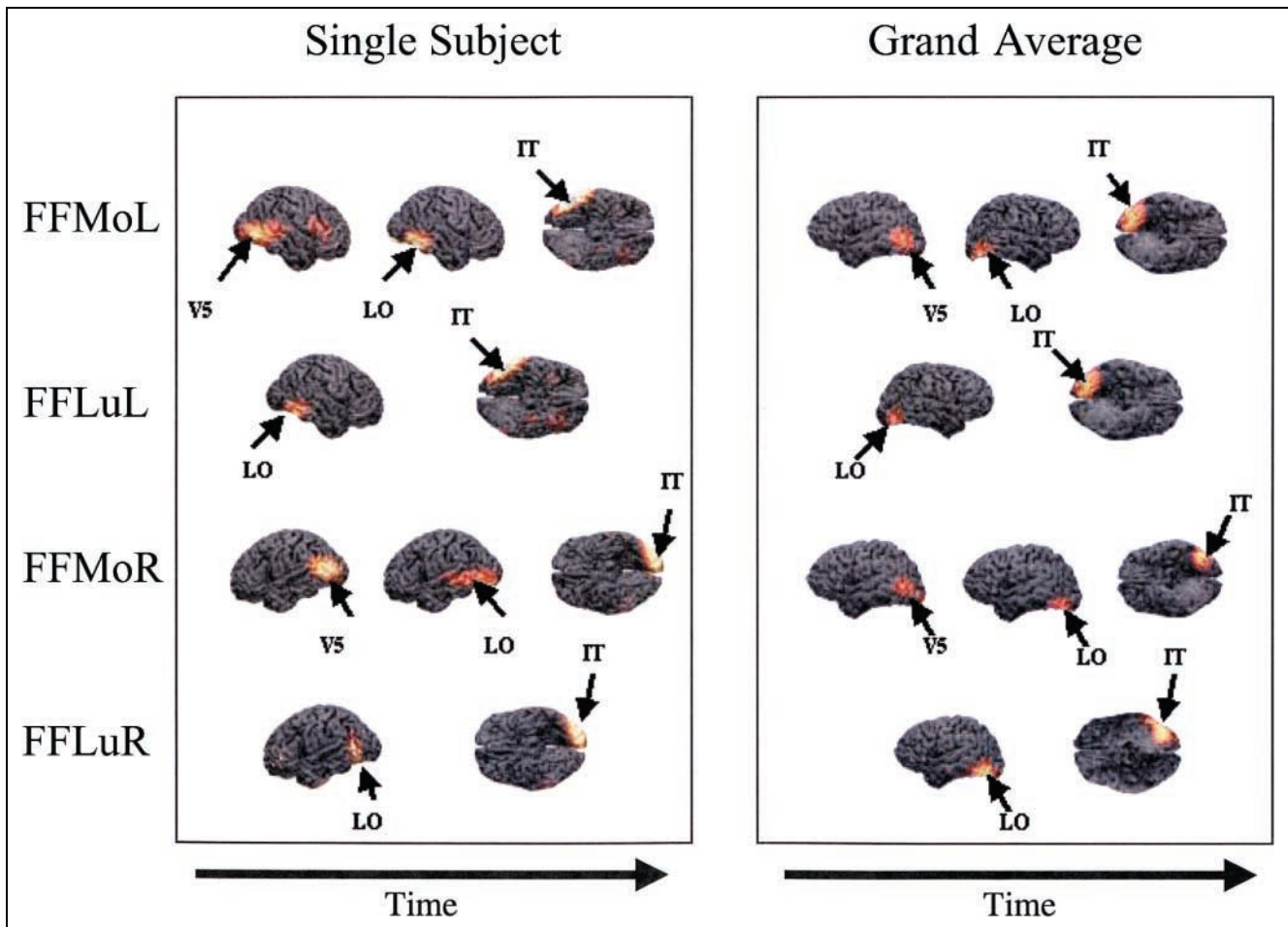


Figure 4. Current source density (CSD) using minimum-norm sources are presented for each of the four attended conditions in a representative single subject (left box) as well as for the grand average (right box). FFMoL = form-from-motion attend-left, FFMoR = form-from-motion attend-right, FFLuL = form-from-luminance attend-left, FFLuR = form-from-luminance attend-right. The time flow direction is from the left to the right (arrow in the bottom). FFMo stimuli related activity was first observed in the MT/V5 region, followed by activity in the bilateral LO region, and IT regions. FFLu stimuli related activity was first observed in the bilateral LO region and later in the IT regions.

will yield meaningful models (e.g., auditory cortex in the supratemporal plane—see Woldorff, Hillyard, Gallen, Hampson, & Bloom, 1998). However, the foregoing caveats should be kept in mind in interpreting the findings. The results are presented in Figure 5 and described in the following.

In the form-from-motion attend-right condition (FFMoR), brain activity was best modeled by four dipoles located in the left MT/V5, left and right LO, and left IT. The left (contralateral) MT/V5 source explained activity in the time range 200–240 msec and was followed by two (bilateral) LO sources at 230–310 msec, which were then followed from 330 to 460 msec by a right IT source. Neural activity in the FFMo attend-left condition (FFMoL) was again best modeled by four different sources with only a little temporal overlap. At 180–220 msec, a source in the “left” MT/V5 region best explained the measured magnetic field. The second source located more inferior in the region of the left LO explained activity from 230 to 360 msec. From 330 to 370 msec, activity was well accounted for by a third source

located in the right LO region and joined by a fourth source explaining activity from 350 to 480 msec located in the right IT.

Activity in the form-from-luminance attend-right condition (FFLuR) was well modeled by two sources. At 240–310 msec, a source located in the left LO region was found, followed by a source located in the left IT region in the time range 280–380 msec. In the form-from-luminance attend-left condition (FFLuL), the activity was modeled by three sources—bilateral LO sources and a right IT source. These sources were the same as found in the FFMoL condition but did not include the left MT/V5 source. However, the timing was different. The activity was explained by two sources located in the bilateral LO region in the time range 250–320 msec followed by a third source in the right IT region from 280 to 340 msec.

The dipole solutions all explained at least 90% of the variance of the magnetic field distributions, and the dipoles were highly stable with regard to their localization in their relevant time ranges. The Talairach

coordinates of the inferior temporal dipole solutions described in the foregoing are provided in Table 3.

Summary of Modeling

Both cortical surface density and equivalent current dipole modeling approaches identified similar sources for each condition (i.e., FFMo or FFLu). In the attend-left and attend-right FFMo conditions, a sequence of

(left) MT/V5, bilateral LO, and contralateral IT (contralateral to the attended side) was found to underlie the processing of these stimuli that required extraction of FFMo. In contrast, FFLu conditions activated a sequence of LO and IT, primarily contralateral to the attended side. Importantly, there was a difference in the timing of activities in LO and IT, in that the activity evoked by FFMo, especially in the IT region, was delayed in time compared with activity evoked by FFLu.

Figure 5. Results from the source analyses on the late wave component of the grand average using equivalent current dipoles, as well as the time courses of the activity explained by each dipole, are depicted for each attended condition. The dipole located in the left MT/V5 region and its time course are presented in red, the dipoles in bilateral LO and their time courses are presented in orange, and the contralateral inferior temporal dipoles (IT) and time courses are presented in yellow. The analysis period was from 150 to 500 msec after stimulus onset. There was little temporal overlap between the different sources. Differences were apparent between the peaks of the late wave in the FFLu and FFMo conditions, when the same location was attended. Similar delays were observed for the onset of the late wave (Figure 3) and for the activations of IT areas between FFLu and FFMo conditions.

FFMoL = form-from-motion attend-left, FFMoR = form-from-motion attend-right, FFLuL = form-from-luminance attend-left, FFLuR = form-from-luminance attend-right.

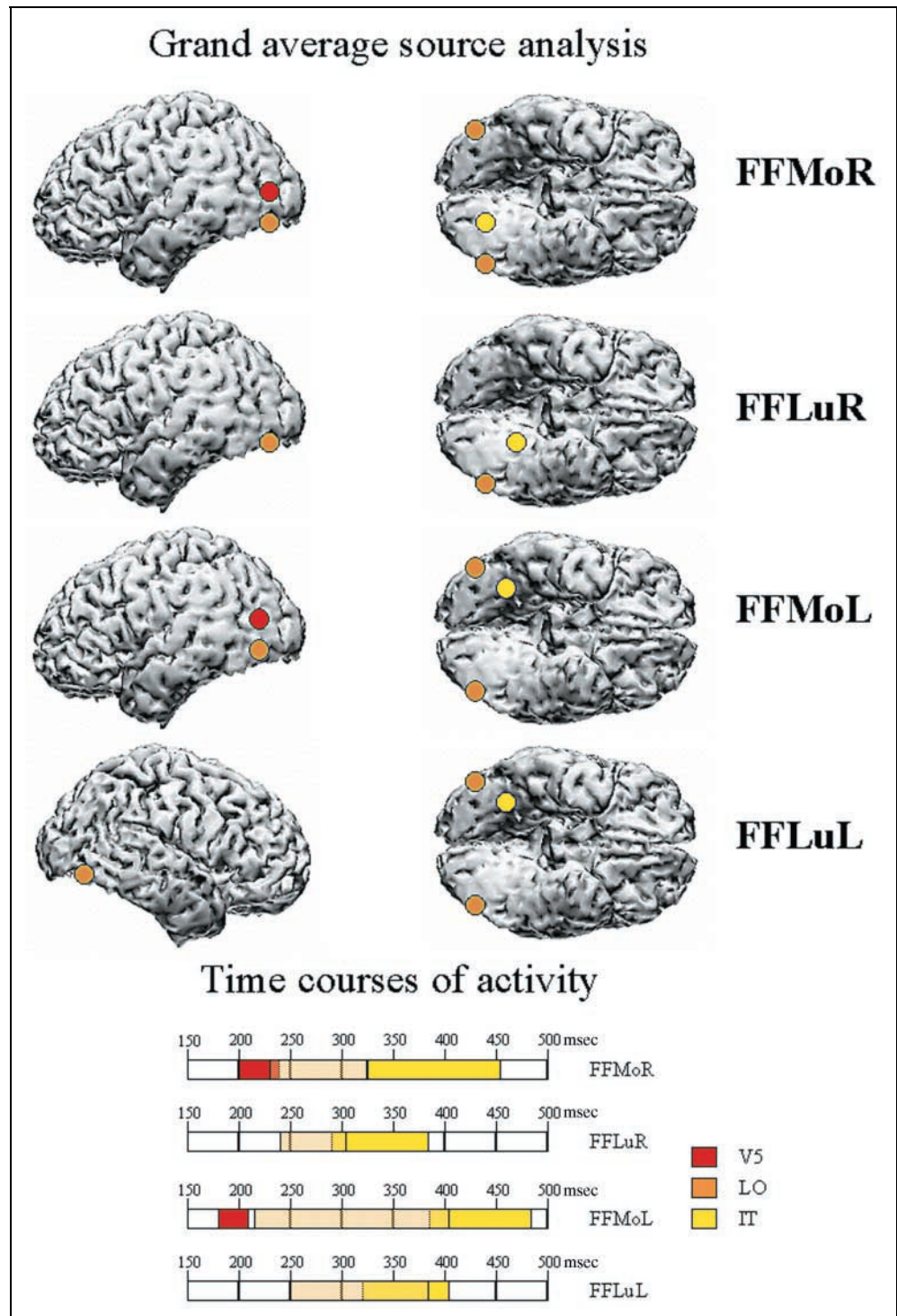


Table 3. Talairach Coordinates

<i>Condition</i>	<i>x</i>	<i>y</i>	<i>z</i>
FFMoL	37R	-63	-14
FFMoR	25L	-64	-9
FFLuL	43R	-62	-14
FFLuR	29L	-64	-9

DISCUSSION

The present study investigated the neural mechanisms of FFMo processing, as well as the influence of spatial attention on visual analysis. Four different models for the analysis and extraction of FFMo were tested. The results support a serial model in which information from FFMo stimuli is first analyzed in the dorsal stream (area MT/V5) prior to integration with ventral stream areas that extract stimulus form. The timing of the MEG, as well as the behavioral data, provides evidence that FFMo processing took longer than FFLu processing. In the MEG, this was observed as a significant delay in the responses generated in LO and IT areas when form was defined by motion as compared to luminance. We interpret this delay as the added cost of first having to process motion information prior to the engagement of form analysis. Our results show that these effects were not the result of differences in early visual cortical processing for FFMo versus FFLu stimuli (e.g., striate/early extrastriate processing). In addition, spatial attention was found to significantly influence stimulus processing. Activity in both dorsal and ventral stream areas was robust for stimuli at attended locations, but greatly attenuated for stimuli at unattended locations. This pattern supports early selection theories of attention that posit that top-down attentional influences can modulate perception processes prior to complete feature analysis.

Time Course and Functional Anatomy

Following initial analysis of stimulus inputs in early visual cortical areas at short latencies, FFMo stimuli elicited robust activity (in response to attended stimuli) starting at a latency of 180–200 msec in the region of the middle temporal and middle occipital gyri. This location corresponds well to area MT/V5 that has been described in other studies in humans, and which have provided strong evidence for the specialization of this region in motion processing (Dupont et al., 1997; Barton et al., 1996; Tootell, Reppas, Kwong, et al., 1995; Watson et al., 1993; Zeki et al., 1991). In the present study, activity in this region was primarily contralateral to the attended hemifield, but was also bilateral in some subjects. However, in the grand average data (collapsed over all the participants), only activity in the left hemisphere was reliable. A key

finding is that the FFLu stimuli did not appear to produce any activity in this region, as determined by source analysis (see Figures 4 and 5), thereby reinforcing the interpretation that this activity is generated by motion-specific neuronal processing in human MT/V5.

In addition to the MT/V5 activity, the FFMo stimuli also elicited longer latency activity (220–240 msec latency) that was generated more anterior and inferior to MT/V5, near the junction of the temporal and occipital lobes. This area likely corresponds to the region LO, described in prior hemodynamic imaging studies and that has been proposed to have a role in object analysis, being specialized for the processing of object silhouettes derived from luminance cues, as well as from motion cues (e.g., Grill-Spector et al., 1998; Malach et al., 1995). Importantly, in contrast to the pattern in MT/V5, activity in LO was also elicited by the FFLu stimuli, but at shorter latencies (see Figure 5). Together, the findings in the literature regarding LO and the present data suggest that this area may be involved in the extraction of the shape information both from luminance *and* from motion cues. Our findings provide key information about the timing of these processes, showing that the LO region is activated at a later point in time for FFMo than for FFLu stimuli, suggesting that for FFMo stimuli motion information must first be analyzed in MT/V5 prior to being available to LO and structures downstream in the IT (described next).

As with activity in region LO, responses were elicited by *both* FFMo and FFLu stimuli in the IT of the hemisphere contralateral to the attended side. The IT activity occurred later than the MT/V5 or LO responses, and importantly, was also delayed for the FFMo stimuli relative to the FFLu stimuli.

The localizations of the effects in MT/V5, LO, and IT were based on both cortical surface density estimates and single dipole analyses of the late response in the MEG, which allowed a more precise localization of the active regions. The anatomical localization of MT/V5, LO, and IT observed here (see Figures 4 and 5 and Table 3) are highly similar to those reported in other studies which used hemodynamic methods (Grill-Spector et al., 1998; Kanwisher et al., 1997; Malach et al., 1995; Tootell, Reppas, Kwong, et al., 1995; Zeki et al., 1991). These results are also consistent with data from single-cell recordings in monkeys suggesting that IT neurons are specialized in visual shape analysis (Tanaka, 1996).

To summarize these effects, the source analyses revealed a sequence of activity in MT/V5, LO, and IT for FFMo stimuli, but the FFLu stimuli activated only LO and IT. The localization of the best-fit dipoles for LO and IT activity was the same for FFLu and FFMo stimuli, but these areas were delayed in the time course of their activity for the FFMo stimuli. As noted, only the FFMo stimuli elicited activity in MT/V5, and this preceded the activity in LO and IT.

Importantly, none of the latency differences reported here for activity in MT/V5, LO, and IT regions of the cortex for FFLu versus FFMo stimuli resulted from differences in early visual cortical processing for these two types stimuli. This was demonstrated by quantifying the amplitude and latency of short-latency occipital responses that were consistent with processing in striate and/or early extrastriate visual areas and showing that these responses did not differ for FFLu and FFMo stimuli (see Figure 1).

Implications for Models of FFMo Processing

Many possibilities have been proposed for the processing sequence for FFMo stimuli. Britten et al. (1992) showed that monkey MT is necessary for FFMo. In the present study, MT/V5 activity was elicited exclusively by FFMo stimuli, strongly supporting the involvement of a dorsal stream area in the processing of FFMo stimuli in humans, and arguing against the idea that FFMo is processed in the ventral stream only. Another model proposes parallel processing in the ventral and dorsal stream, with a later activation of a region in the superior temporal sulcus to integrate the outputs of the two streams. In this case, more overlap in the time course of activity in MT/V5 versus LO and IT might be expected. In the present study, FFMo stimuli elicited activity in MT/V5, LO, and IT with relatively little temporal overlap (Figure 5). In addition, no activity was observed in the anterior part of the superior temporal sulcus or in the parietal cortex. Therefore, we find little support for the idea that parallel streams converge on higher-order areas for FFMo analysis.

Shipp and Zeki (1989) proposed another model in which FFMo would be processed in the dorsal stream, such that motion information was extracted in MT/V5 and then directed via V1 to the ventral stream for shape analysis. This model would require activity in the striate cortex following the MT/V5 activity and prior to the activation of IT. The present MEG data do not support this model because no V1 activity was observed between the activation of MT/V5 and the activation of LO or IT, although such activity might have been difficult to discern. This pattern fits well with the observation that lesions in the human homologue of ventral V4 (V4v) does not impair motion perception (Gallant, Shoup, & Mazer, 2000).

The model that is most consistent with the present data is one in which the processing of FFMo stimuli involves both visual streams but in a hierarchical and serial manner. Work in animals has led to the suggestion that the interstream connection is from MT/V5 to V4 (Ungerleider & Desimone, 1986; Maunsell & Van Essen, 1983). In the present study, the FFMo stimuli elicited activity first in MT/V5 then in LO, a ventral stream region very close to V4, and finally, in IT with little overlap in time. FFLu stimuli elicited activity in LO followed by

activity in IT, without involving MT/V5, fitting the pattern of serial processing entirely in the ventral stream when motion cues were not required for form analysis.

Convergence versus Segregation of Visual Cues

What other evidence supports the hierarchical and serial model for FFMo processing we argue for here? There are conflicting findings in the literature concerning convergence versus segregation of visual cues in the visual system. One study (Gulyas, Heywood, Popplewell, Roland, & Cowey, 1993) found segregation, concluding that the discrimination of visual form can be produced by different cortical networks depending on the underlying visual submodalities. However, most studies have found some convergence of visual cues, especially for the regions found to be active in this study. MT/V5 has been shown to be activated by motion (Ffytche, Skidmore, & Zeki, 1995), LO by luminance or by motion-defined object silhouettes (Grill-Spector et al., 1998), and IT when shape analysis is required (Kanwisher et al., 1997; Sary et al., 1993). The present study found that activity in LO and IT was present for both FFMo and FFLu stimuli, in line with the idea that there is a convergence of visual cues in the human visual system, and here we support the view that this convergence results from interstream communication.

Effects of Spatial Attention

Another goal of the present study was to investigate the influence of spatial attention on the processing of FFLu and FFMo stimuli. A long-standing view in attention research is that attention can modulate processing of stimulus information at early stages (Broadbent, 1970; Treisman, 1969). Under this view, spatial attention is thought to act at early stages of visual analysis as a gain control mechanism, relatively enhancing the processing of stimuli coming from attended locations compared with unattended ones (for a review, see Mangun, Hillyard, & Luck, 1993). Neurophysiologically, it has been shown using ERPs in humans and single-unit studies in monkeys that effects of spatial attention begin as early as 70–100 msec after the onset of task-relevant stimuli in early extrastriate regions (e.g., Mangun, Hansen, & Hillyard, 1987; Woldorff et al., 1997; Heinze et al., 1994; Moran & Desimone, 1985; Van Voorhis & Hillyard, 1977). The short latency of such effects strongly argues that voluntary spatial attention involves preset or tonic changes in cortical excitability that result in changes in processing gain for incoming sensory activity (e.g., Hillyard & Mangun, 1987). Such effects may be manifest as early as the primary visual cortex (area V1) (e.g., Kastner & Ungerleider, 2000; Gandhi, Heeger, Boynton, 1999; Ito & Gilbert, 1999; Somers, Dale, Seiffert, & Tootell, 1999; Motter, 1993; Oakley & Eason, 1990), although not all studies have found effects of spatial attention this

early (e.g., Martinez et al., 1999; Gratton, 1997; Luck, Chelazzi, Hillyard, & Desimone, 1997; Clark & Hillyard, 1996; Moran & Desimone, 1985). Thus, when all the evidence is taken into consideration, one can conclude that if voluntary spatial attention influences input processing in V1, such effects are relatively small, and may occur only under a limited set of stimulus and task circumstances (e.g., McAdams & Maunsell, 1999).

Using other paradigms, it has also been shown that attention to motion modulates processing in motion-related areas of the brain (Valdes-Sosa et al., 1998; O'Craven et al., 1997; Anllo-Vento & Hillyard, 1993; Corbetta, Miezin, Dobmeyer, et al., 1991). Furthermore, attention to other stimulus features may also modulate processing of irrelevant motion stimuli (e.g., Rees, Frith, & Lavie, 1997, 2001).

In the present experiment, spatial attention did not significantly modulate the earliest processing, particularly medial occipital activity before 100 msec, activity which would be consistent with input analysis in the striate cortex (see Figure 1). These findings are consistent with a significant body of literature (reviewed above) finding no effect of attention on the first volley of activity through V1, but rather beginning with early processing in the extrastriate cortex. In the present experiment, it is also important to note that not only did spatial attention not affect this earliest processing, but this early activity did not differ as a function of the FFMo versus FFLu conditions, providing evidence that this earliest input analysis was the same in all conditions. After 100 msec, however, the effects of attention were striking. More specifically, significant longer latency activity in MT/V5, LO, and IT was elicited only when the stimulus location was attended. Notably, however, this was true for both the FFMo and FFLu conditions.

Other studies have provided support for the idea that the processing of features of unattended visual stimuli are relatively suppressed. For example, ERP studies (e.g., Anllo-Vento & Hillyard, 1993) have demonstrated suppression of processing of moving stimuli at unattended locations. A similar mechanism has also been found in an object-based attention study showing a strong suppression of the feature processing of unattended objects (Valdes-Sosa et al., 1998).

In the present study, the observed attention effects in the later time range were due to the strong relative attenuation of the spatially unattended stimuli. In the absence of a neutral (sensory) condition, it is not possible to know whether these effects specifically reflect facilitation of processing at the attended location or suppression of processing in the unattended location. However, regardless, in the present study employing highly focussed spatial attention, significant activity in these higher-level motion and form analysis areas only occurred for stimuli in the attended location. Moreover, because this strong modulation of the longer latency feature processing occurred for both the

FFMo and FFLu conditions, this suggests that attention gated the input at a level prior to these analysis stages.

Conclusions

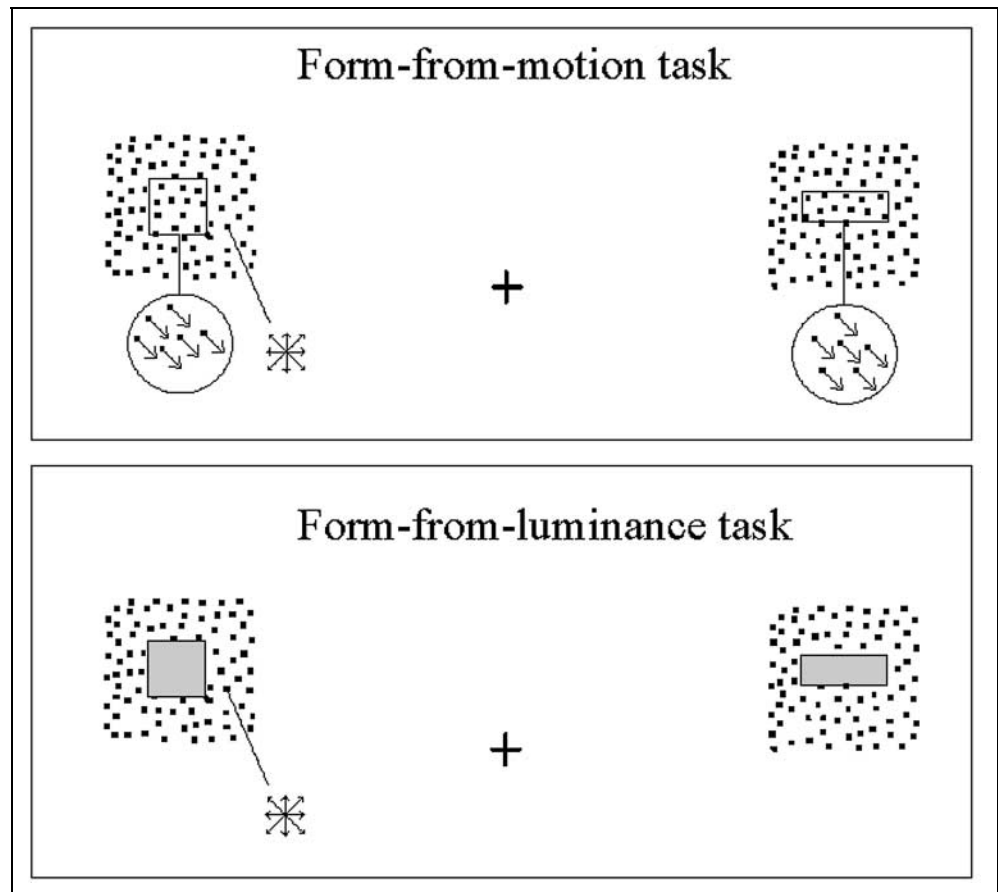
The present study investigated the timing and sequence of activation of cortical areas involved in FFLu and FFMo processing, as well as the influence of spatial attention. The goal was to understand how the visual cortex extracts and analyzes form when defined only by motion cues. The present findings support a model whereby initial processing of motion cues occurs in dorsal stream areas, but the output of these analyses is fed into ventral stream areas for form identification. This pattern can be described as a hierarchical and serial model, where motion information extracted in areas such as MT/V5 is then combined with processing in the ventral stream at an intermediate point in the ventral stream hierarchy. The present data do not support models in which FFMo is processed entirely in the ventral stream (or dorsal stream), nor is it consistent with reentrant activation of V1 from the dorsal motion system to derive FFMo cues, or with models that propose a complete parallel set of analyses in the dorsal and ventral stream prior to convergence on higher-order areas for integration of motion and luminance information. Spatial attention produced significant modulations of the processing in the extrastriate cortex, with stimuli at unattended regions of space eliciting greatly attenuated responses. This relative attenuation was observed for activity in both the dorsal and ventral visual processing streams, thereby arguing for an early effect of spatial attention on sensory processing, at a stage prior to the extraction of simple stimulus features such as motion or form information.

METHODS

Stimuli

Stimuli consisted of two squares containing 100 white randomly moving dots each, forming a 1° by 1° square of visual angle at 5° eccentricity to the left and to the right of a fixation cross. These were presented on the horizontal meridian on a black background, using a back projection (microcomputer-controlled video projector) at a distance of 120 cm (Figure 6). The fixation cross and the two squares of randomly moving dots were present continuously on the screen during every run. Target and nontarget (standard) shapes were presented asynchronously on the left and right background squares of randomly moving dots with interstimulus intervals (ISI) varying randomly between 480 and 960 msec. The duration of the stimuli was 500 msec. In the FFMo conditions, these shapes consisted of 25 of the 100 dots moving in the same direction coherently (from upper left to bottom right) and thereby forming the shape. The luminance and contrast were controlled in that the

Figure 6. Both tasks are shown. Two squares of 100 randomly moving dots were forming the background of the stimuli and were present continuously during the task. In the FFMo conditions, a subset of 25 out of the 100 dots, in either the left or the right box, started to move coherently, defining either a square or a rectangle. In the FFLu conditions, the same shapes were defined by gray figures presented on the moving dots background. The subjects were instructed to maintain fixation on the fixation cross and to attend to either one or to the other side during each trial (e.g., appeared in the left or right locations in a random trial sequence within each block). However, the background dots were present bilaterally on each trial.



shapes were only defined by their correlated motion, whereas the background motion was random. Two possible shapes (a square and a rectangle) having the same area and number of dots had to be discriminated. For one half of the subjects, the square served as a target, while for the other half, the rectangle did. The ratio of targets to nontargets was 20:80. In the FFLu condition, the same two shapes were defined by luminance rather than by moving dots. Gray figures were presented on top of the random-dot background with the same ISI and the same target/nontarget probability as in the FFMo conditions. All dot movements had a frequency of 60 Hz in order to avoid any interactions with the refresh cycle (60 Hz) of the presentation system.

Task

Subjects were instructed to carefully maintain fixation and to minimize blinking during the experiment. Fixation was monitored by an infrared video zoom lens system. The experiment was run in one session with short breaks between the runs and consisted of four types of blocked conditions: FFMoL, FFMoR, FFLuL, FFLuR. In each condition, 10 runs of 100 shape stimuli were presented, with the presentation of the FFMo and FFLu stimuli also being blocked (e.g., only FFMo stimuli

were presented in the FFMo conditions). The subjects were instructed to maintain fixation, attend either to the left or right side, and to press a button upon detecting the occurrence of a target shape that was designated to them prior to the run. Eight subjects (five females and three males) participated as paid volunteers in the experiment. They were all right-handed and had normal or corrected-to-normal visual acuity.

Data Acquisition

MEG was recorded on a BTI Magnes 2500 WH (Biometric Technologies, San Diego, USA) whole-head system with 148 magnetometers using a DC to 50 Hz bandpass. An on-line noise reduction system was used, which removes a weighted sum of environmentally induced magnetic noise (first-order spatial gradients of the field) recorded by eight remote reference sensors (three magnetometers and five gradiometers). Data from one magnetometer sensor were discarded because of hardware-related artifacts. Artifact rejection was performed off-line by removing epochs with peak-to-peak amplitudes exceeding a threshold of $3.0E^{-12}$ T. Individual head shapes and the sensor-frame coordinate system were coregistered by digitizing (Polhemus 3Space Fastrak) individual landmarks (nasion, left and right preauricular points) whose locations in relation to sensor

positions were derived based on precise localization signals provided by five head coils with a fixed spatial relation to the landmarks. These landmarks, in turn, served to enable coregistration to individual anatomical MR scans that were recorded to constrain realistic source modeling. To adjust for sensor location variability across subjects for computing the grand average responses, the sensor-frame coordinate system of each subject was readjusted to the sensor-frame coordinate system of one subject whose anatomical MR scan was used for displaying the source analysis results. The readjustment was done by computing a hypothetical current distribution from the original data on a spherical shell using the least squares algorithm using a commercial software package (ASA, Enschede, The Netherlands). In a second step, the magnetic fields are recomputed as a forward solution from this current distribution for the sensor positions of the sensor-frame coordinate system of one subject. These fields are then used to compute the grand average. After source analysis, the MR scan was fitted into the reference frame of the three-dimensional proportional system of the co-planar stereotactic atlas of the human brain (Talairach & Tournoux, 1988).

Data Analysis

Separate averages to the standards were computed for every condition. In this way, eight different standard-shape event-related field (referred to as MEG throughout for simplicity) averages were obtained (attended FFMo left, attended FFMo right, nonattended FFMo left, nonattended FFMo right, attended FFLu left, attended FFLu right, nonattended FFLu left, nonattended FFLu right) that are free from activity associated with the button presses to the targets.

MEG source analysis was performed using the multimodal neuroimaging software Curry 3.0 (Neuroscan Inc., El Paso, TX). Single-subject data were analyzed using distributed source models. These models were computed based on the minimum L2-norm method constrained on the surface using individual realistic head models (boundary element method, BEM). A BEM was computed for every subject using the individual MRI scan. In order to find a realistic model to be used for the source analysis of the grand average, the dimensions of each individual brain in all three axes were compared with the mean dimensions. The brain of one subject that was closest to the mean in the three dimensions was considered to be the most canonical and was used for the purposes described below.

The BEM of this brain was used as the volume conductor for further analysis. Dipole fits were computed using moving dipoles employing the realistic head model of the canonical brain without any cortical surface constraints. The dipoles were allowed to move within the volume conductor without any restrictions. The analysis

started with a single dipole and additional dipoles were introduced into the model until it explained over 90% of the variance of the magnetic field. A further requirement was that the dipoles had to remain stable over the fitted time period.

Statistics and Timing Analyses

Statistics and timing analyses were performed using MATLAB V5.2 (Mathworks, Natick, MA). Behavioral measures were submitted to repeated-measures ANOVA with the factors: Condition (FFMoL, FFMoR, FFLuL, FFLuR) and Subjects ($N = 8$). Statistical analyses on MEG data were performed on temporal left (TL), occipital left (OL), temporal right (TR), and occipital right (OR) sensors, using repeated-measures ANOVA with the factors: Attention (attended, unattended), Condition (FFMoL, FFMoR, FFLuL, FFLuR), and Subjects ($N = 8$) in the time range of the main effect (250–400 msec).

Timing analyses were performed to substantiate the delay between the onsets of the MEG waves of the FFLu versus FFMo conditions. The MEG waveforms to the FFLu and FFMo stimuli in the same attended visual field location were compared with one another in the following manner. First, a direct measure of the onset latency of the late wave for the FFMo condition was determined for each subject. To accomplish this, the prestimulus baseline was divided into 10 epochs of 8-msec duration each, and the mean amplitude of each of these 8-msec epochs was measured (with reference to the mean amplitude of the entire prestimulus period) yielding 10 values that served as a “baseline reference set” (BaselineRS). Deviations in the response from this BaselineRS were determined in the poststimulus period by determining a consecutive series of “data reference sets” (DataRS), and comparing each of these sets of values with the BaselineRS of values using t tests. This was done as follows. In the poststimulus period, beginning at time zero (stimulus onset), 10 consecutive epochs of 8-msec duration each were defined, and the mean amplitude in each 8-msec epoch was measured (again, with reference to the mean amplitude value of the entire prestimulus period) to yield one poststimulus DataRS of 10 values. The first DataRS was compared to the BaselineRS using a t test, and was considered significant if $p < .05$. Then, this time window was “slid” to the right by 8 msec, creating the next DataRS (consisting of 10 values, consisting of the last seven from the prior DataRS, and one new value). This new DataRS was also compared to the BaselineRS using a t test. This procedure was continued until a series of seven consecutive DataRS were significantly different from the prestimulus BaselineRS. The first time point of the first epoch of these seven DataRS that were significantly different from the DataRS was considered the onset latency of the response in the FFMo condition. Indeed, this rather conservative measure coincided

well with the visually observed deviations of the waveforms from baseline.

The second step was to determine the “difference” in onset latency between the FFMo and FFLu responses for each subject. To do this, the rising phase of the response for the FFMo condition (consisting of 80 msec of the waveform following the onset latency of the wave as determined above) was “shifted backward in time,” time point by time point, and correlated against the corresponding time points for the FFLu condition until the best correlation was found. This was sensible because the waveshapes of the FFMo and FFLu responses looked very similar but appeared to differ in onset latency. The amount of shift that gave the highest correlation between these waveform segments from the two conditions was interpreted as being the best estimate of the delay between the late waves of the two conditions. Again, the difference value obtained using this method was highly consistent with the observed latency onset difference in the waveforms when inspected visually. This analysis was performed separately for the waveforms of the FFLuR versus FFMoR conditions, and those for the FFLuL versus FFMoL conditions, for each of the selected MEG sensors. Four groups of sensors were formed: OL, OR, TL, TR. The late-wave onset delays from these sensor groups were submitted to repeated-measures ANOVA with the factor location (OL vs. OR, TL vs. TR, OL vs. TL, OR vs. TR) to investigate whether the onset delays were different for different brain regions.

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