Relationship Between Ventral Stream for Object Vision and Dorsal Stream for Spatial Vision: An fMRI+ERP Study

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Abstract: Recent imaging studies indicated the existence of two visual pathways in humans: a ventral stream for object and form vision and a dorsal stream for spatial and motion vision. The present study was motivated by a stimulating question: Supposing shape and motion are processed separately in the two pathways, how do the respective cortical areas respond to the stimuli of “forms defined by motion”? fMRI and ERP recordings were combined in order to measure the spatiotemporal activation pattern in the two pathways responding to forms defined by motion, which were produced solely by coherent movement of random dots against a background of dynamic or static random dots. The fMRI data indicated that the stimuli of forms defined by motion indeed activated both dorsal MT/V5 and ventral GTi/GF. Furthermore, the RV curves resulting from fMRI-seeded dipole modeling indicated that each pair of dipoles located at MT/V5 or GTi/GF reached the same best-fit point; a single pair of free dipoles located near the fMRI foci of MT/V5 and GTi/GF could be identified at the corresponding best-fit point; and the source waveforms resulting from fixed dipole modeling also showed simultaneous activation of MT/V5 and GTi/GF dipoles in the time interval around the best-fit point. The present results, therefore, suggest that MT/V5 and GTi/GF appear to be activated in parallel and simultaneously responding to forms defined by motion. Such findings raise interesting issues about the hierarchical organization and the functional specialization in the two pathways. *Hum. Brain Mapping* 8:170–181, 1999. © 1999 Wiley-Liss, Inc.

Key words: visual cortex; forms defined by motion; functional MRI; event-related potential; dipole model; integration of fMRI and ERP; cognitive brain imaging

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INTRODUCTION

Visual processing of monkeys involves >30 cortical areas that occupy approximately one-half of the total cortex. These cortical areas appear to be organized mainly into two hierarchically arranged and functionally specialized processing pathways: a ventral stream for object vision and a dorsal stream for spatial vision [Ungerleider and Haxby, 1994; Van Essen and DeYoe,

1995]. The ventral stream is anatomically organized along the occipitotemporal cortical pathway and includes hierarchical areas V1, V2, V4, and further stations in inferior temporal areas. In contrast, the dorsal stream, the occipitoparietal pathway, includes areas V1, V2, V3, MT, and further stations in posterior parietal areas. The anatomically distinct pathways are also considered to be functionally specialized: the occipitotemporal pathway functions for perceiving visual features relevant to object identification, such as shape, whereas the occipitoparietal pathway functions for perceiving spatial aspects of stimuli, such as direction of motion and velocity. Recent brain imaging studies and neuropsychological studies suggested that human visual system, like that of monkeys, may be organized to include ventral and dorsal streams [reviewed in Tootell et al., 1996].

To address the question of what is the relationship between the two visual pathways, the present study was motivated by a stimulating question: Supposing shape and motion are processed separately in the two streams; how do the two pathways respond to “forms defined by motion”? As expressed by Van Essen and Deyoe [1995], “A simple dichotomy between temporal and parietal cortices leaves uncertain the assignment of intermediate visual tasks such as structure from motion.” Particularly, the stimuli of “forms defined by motion,” together with noninvasive brain imaging techniques, may serve as an effective probe to explore neural mechanism underlying the relationship between the two proposed streams. In the present study, fMRI (functional magnetic resonance imaging) and high-resolution (128-channel) ERPs (event-related potentials) were combined in order to measure the spatiotemporal activation pattern in the two pathways responding to forms defined by motion with millisecond temporal resolution and millimeter spatial resolution [Fox and Woldorff, 1994].

EXPERIMENT 1

Materials and methods

Seven male right-handed subjects were recruited from the University of Science & Technology of China. The subjects were between 22 and 33 years old and had normal or corrected vision. All subjects gave informed consent prior to undergoing these experiments.

Stimuli and tasks

As illustrated in Figure 1, there are four stimulus types: kinetic shape; dynamic random-dot field; static

Figure 1.

The main stimulus patterns used in Exp. 1 and Exp. 2.

random-dot field; and motion random-dot field. Kinetic shape was defined solely by a patch of contiguous random dots (subtended $5^\circ \times 5^\circ$) uniformly moving downward against a background of dynamic random dots at the velocity of $15^\circ/\text{sec}$, a clear indication that form perception can be derived from pure motion information [Zhang and Wu, 1990]. The presentation of one kinetic shape lasted for 150 msec, and the interval between successive shapes varied randomly between 525–675 msec during which only the background of dynamic random dots was presented. Kinetic shapes consisted of circles and squares, which comprised 95% and 5% of the whole stimuli, respectively.

The dynamic random-dot field was constituted of a whole field of dynamic random dots that looked like the twinkling snow noise on TV; static random-dot field was a whole field of static random dots; and motion random-dot field was a whole field of random dots uniformly moving downward at a velocity of $40^\circ/\text{sec}$. All the mentioned stimuli were of equal luminance; the dots in the field (subtended $24^\circ \times 18^\circ$) were black or white with equal probability, and at the center of the random-dot field, a green cross was presented as the fixation. Three tasks were designed: (1) motion random-dot field vs. static random-dot field, (2) dy-

namic random-dot field vs. static random-dot field, and (3) kinetic shape vs. dynamic random-dot field.

Activation was expressed in percentage change relative to baseline.

MRI scanning

Subjects were scanned on a 1.5 T GE Signa scanner, using a homogeneous birdcage-type RF coil. They viewed the stimuli projected on a translucent screen through a mirror mounted on the head coil. Functional imaging used a single-shot, T2*-weighted EPI sequence [TR: 2000, TE: 40, FOV: 25–25, 7.5thk/0.5sp, 64–64] to acquire a set of 9 or 12 axial slices (from inferior to superior, AC-PC line is located at the 5th slice).

The fMRI scan were performed for four cycles of the four stimuli, in the order of ABCD for five subjects and in the order of DCBA for the other two, thus to obtain 48 (12×4) images for each stimulus in one slice and the first two of the 12 images of each scan were discarded to eliminate the effects of EPI onset. MR scan for each stimulus started after the stimulus had been presented for 20 sec for saturation of cerebral blood oxygenation. During each scan, the subjects were instructed to lie as still as possible and to concentrate on viewing the stimuli with fixation on the green cross. They were given at least 30 sec rest between two scans.

Analysis of fMRI data

The raw MR images were rearranged according to the three designed tasks and were analyzed by cross-correlating each pixel time course with a boxcar reference waveform by AFNI [Cox, 1996]. For a single subject, only pixels with a correlation coefficient larger than 0.42 ($P < 0.0001$) were taken as significant activation, which was overlaid on the T1-weighted image to anatomically illustrate activation sites. To assess the consistency of activation, individual data sets were transformed to Talairach coordinates [Talairach and Tournoux, 1988] through manually defined landmarks, followed by co-averaging across subjects to generate averaged correlation coefficient maps.

Movies were run of all raw images per slice, which furnished a dynamic view of head motion. When image head motion was greater than 1 pixel, or when it was not corrected by the reregistration algorithms (2D in-plane), the images were discarded. To measure the activation levels for each stimuli, time courses from the volume of interest were averaged in response to identical stimuli. For each task, levels of activation were calculated by subtracting the averaged baseline MR signal strength from the averaged activation.

ERP recording

The ERPs elicited by the identical stimuli of kinetic shapes were recorded in a separate session from the same seven subjects. Four blocks were run, each of which consisted of 100 trials of kinetic shapes. Subjects were instructed to discriminate kinetic circles and squares, which were presented on a PC monitor. On seeing a square (target), subjects were asked to press the key, and 128 channels of EEG (referenced to linked left and right ears) were continuously recorded by NeuroScan system (gain 15,000, bandpass 0.1–40Hz, sampling rate 250 Hz), including eight channels for recording the EOG. The horizontal EOG signals were recorded bipolarly with electrodes at the left and right outer canthi, and the vertical EOG signals were recorded bipolarly with electrodes below and above the two eyes. Trials contaminated by blinks and eye movements (exceeding 100 μ v) were automatically rejected during averaging, and only the standard stimuli were averaged. The positions of all the electrodes and of the three fiducial points (nasion and preauricular points) were measured by 3DSPACE ISOTRACKII digitizer.

ERP source analysis

Source analysis was constrained by seeding with fMRI activation foci, using the CURRY (Philip Co.) and EMSE [Greenblatt, 1993] programs. This method places a proposed set of voltage dipoles in a three-shell spherical head model and adjusts the positions and orientations of the dipoles iteratively to obtain the best possible fit between the observed and computed voltage distributions [Scherg and Berg, 1991]. For each subject, coregistration of the ERP electrode reference frame with the MRI reference frame was accomplished by transformation matrices derived from common fiducial points in the two reference frames. The fMRI activation foci defined as the averaged center of the activation in the corresponding cortical area were used to seed [Heinze et al., 1994; Woldorff et al., 1997] the dipole modeling for every sample slice of the ERPs (every 4 msec) to obtain the time courses of residual variance (RV) between the observed and computed voltage distributions by CURRY. Besides, moving dipole modeling without position constraint was also applied to evaluate the adequacy of fMRI-seeded modeling. Fixed dipole modeling was used as an additional means to obtain the source waveforms. As

Figure 2.

Averaged correlation coefficient maps (for the 7 subjects) in Exp. 1. Functional maps are shown superimposed upon transverse sections of an individual MR-image that had been Talairach normalized; shows the axial slices at $z=0$ and $z=-10$. Intensity of activation is normalized between the minimum and maximum of activation.

well as being applied to the individual ERPs, fixed dipole modeling was also applied to the grand-average ERPs waveforms using grand-average electrode locations and fMRI activation foci by EMSE.

RESULTS

fMRI Task 1. Motion random-dot field vs. static random-dot field

Areas involved in coherent motion perception were explored by searching for preferential cortical activation in response to motion random-dot field, compared

with static random-dot field. Figure 2 of the averaged correlation coefficient maps shows motion random-dot field primarily produced activation in posterior lateral occipitotemporal areas; the averaged Talairach coordinates of these areas ($x=47$ $y=-65$ $z=0$) were in good agreement with those of motion-specific area MT/V5 described in previous studies [Eden et al., 1996, $x=44$, $y=-66$, $z=4$; Tootell et al., 1995, $x=45$, $y=-76$, $z=3$; Watson et al., 1993, $x=42$, $y=-69$, $z=0$]. This pattern of activation was evident in six of the seven subjects. Motion random-dot field also produced activation in posterior occipital areas, including the lingual gyrus (GL) and cuneus (Cu), corresponding to BA 17/18.

Figure 3.

Averaged relative signal changes elicited by the three designed tasks of Exp. 1, derived from three visual areas (GL/Cu, MT/V5, and GTi/GF).

This pattern of activation was evident in all seven subjects.

Figure 3 of the averaged relative signal changes shows motion random-dot field produced 1.3% signal enhancement in MT/V5, and 2.2% signal enhancement in GL/Cu, compared with static random-dot field.

Task 2. Dynamic random-dot field vs. static random-dot field

This task was designed to explore cortical areas involved in kinetic motion perception. As shown in Figure 2, dynamic random-dot field mainly produced activation in posterior occipital areas, including the lingual gyrus and cuneus, whereas in MT/V5, there was little activation. This pattern of activation was evident in six of the seven subjects. Figure 3 shows dynamic random-dot field produced 1.4% signal enhancement in GL/Cu compared with static random-dot field, whereas in MT/V5 the signal change was only 0.35%.

Task 3. Kinetic shape vs. dynamic random-dot field

Areas involved in kinetic shape perception were explored by searching for preferential cortical activation in response to kinetic shape, compared with dynamic random-dot field, since it contains many visual features common to kinetic shape, except for significant shape perception. As shown in Figure 2, kinetic shape produced activation in posterior lateral

Figure 4.

The display of the two pairs of dipoles and the voltage distribution maps on the 3D MRI views of a single subject. The above pair represents MT/V5 and the underlying pair represents GTi/GF. Note this subject shows stronger activation in the right cortex.

occipitotemporal areas with averaged Talairach coordinates of ($x=45$ $y=-53$ $z=1$). These areas were close to and overlapping the motion-specific area MT/V5 found in the first task. This pattern of activation was evident in six of the seven subjects. Kinetic shape also produced activation in inferior ventral areas, primarily including the fusiform gyrus (GF) and inferior temporal gyrus (GTi) corresponding to BA 37/19; weaker activation was found in the lingual gyrus as well. The averaged Talairach coordinates of these areas were ($x=41$ $y=-58$ $z=-10$). To all the subjects, this pattern of activation was evident.

As shown in Figure 3, kinetic shape produced 0.85% signal enhancement in MT/V5 and 1.05% signal enhancement in GTi/GF, compared with dynamic random-dot field. Whereas in GTi/GF, dynamic random-dot field produced only 0.1% signal enhancement, motion random-dot field even produced negative signal change of -0.15% compared with static random-dot field. In GL/Cu, kinetic shape produced only 0.3% signal enhancement compared with dynamic random-dot field. These data indicated that the stimuli of kinetic shapes indeed activated both MT/V5 in the dorsal stream and GTi/GF in the ventral stream, but produced only mild activation in GL/Cu.

Figure 5.

A. Curves of averaged residual variance (RV). Fitting was done every 4 msec for each subject; then the mean RV was calculated. **B.** Topographic maps (nose down) of the observed and forward calculated voltage distributions at the best-fit point (252 msec) using two pairs of dipoles. **C.** The source waveforms of the two pairs of fixed dipoles resulting from source analysis of the grand-average ERPs./LEG

Dynamic analysis with fMRI + ERP

In order to determine the time dependence of neural activation in MT/V5 and GTi/GF in response to kinetic shape, inverse source analysis constrained by fMRI results was performed on the ERPs elicited by the stimuli of kinetic shapes. For each participant, the fMRI foci of MT/V5 and GTi/GF observed in the third fMRI task were set as the positions of two pairs of dipoles with the orientations being allowed to vary. Figure 4 shows the display of two pairs of dipoles and the voltage distribution map on the 3D MRI views of a single subject. Three kinds of fMRI-seeded dipole modeling were applied to the ERPs for every sample time slice, namely, one pair of dipoles located at MT/V5 or GTi/GF and the combination of them. As plotted in Figure 5A of the averaged RV curves, each pair of dipoles located at MT/V5 or GTi/GF reached the same best-fit points at 252ms (MT/V5: RV=9.47%; GTi/GF: RV=10.29%). A combination of MT/V5 and GTi/GF dipoles yielded good fit (averaged RV= 7.47%) for the observed ERPs in the 200–260 msec time interval, with the best-fit point at 248 msec (RV=5.3%). Figure 5B compared the forward calculated voltage distribution with the observed data. Ideally, if two cortical areas A and B are activated consecutively, each dipole located at A or B would reach the best-fit point consecutively. So the present results suggested that MT/V5 and GTi/GF appear to be the major contributing sources of the ERPs in the 200–260 msec time interval, and they are activated simultaneously. However, such orientation-only modeling has certain deficits, for instance, gradual changes of dipole locations might be muffled by gradual changes of dipole orientations. In order to evaluate this possibility and obtain the source waveforms, fixed dipole modeling was applied to the ERPs in the 200–260 msec time interval. Source analysis of the grand-average ERPs indicated two pairs of dipoles with fixed positions and orientations located at MT/V5 and GTi/GF were able to account for 98.3% of the variance in the 200–260 msec time interval. Figure 5C of the source waveforms shows MT/V5 and GTi/GF dipoles appear to be synchronously and simultaneously activated in the 200–260 msec time interval (although the peak latencies of the source waveforms were not exactly at the same time, this discrepancy was not significant according to the individual data), and this modeling behavior was evident in six of the seven subjects. These data provided additional evidence for the coincidence of the excitement of MT/V5 and GTi/GF in response to the stimuli of kinetic shapes.

In order further to evaluate the adequacy of such fMRI-based dipole modeling, moving dipole modeling without position constraint was used. The results turned out that one single pair of moving dipoles could be defined within the 200–260 msec time interval with the best-fit point at 252 msec (RV=6.67%), and the positions of the moving dipoles were near the fMRI foci of MT/V5 and GTi/GF. These data indicated the adequacy to use fMRI-based dipoles located at MT/V5 and GTi/GF. However, probably due to the limitation of the dipole modeling, in the dipole procedure to use more than one pair of free dipoles was unable to reach a proper solution. This result indicated that inverse dipole modeling alone without constraints derived from fMRI localization may not be sufficient to discern the two cortical areas.

DISCUSSION

So far, we have explored the cortical areas involved in the perception of kinetic shape, coherent and kinetic motion in the fMRI experiment. The preliminary results indicated the stimuli of kinetic shapes activated both dorsal MT/V5 and ventral GTi/GF, whereas motion perception mainly produced activation in MT/V5. Furthermore, fMRI-based ERP source analysis suggested that these two areas appear to be activated in parallel and simultaneously.

It might be argued, however, that since the stimulus of kinetic shape, which was defined by coherent movement of random dots, also moved as a whole itself, such kinetic shape might induce multiple interactions between the two pathways. Thus the apparent simultaneous activation in MT/V5 and GTi/GF may be caused not by forms defined by motion per se, but by the iterated perception of motion and shape (i.e., motion→shape→motion). One more possible argument might be that unidirectional movement of the random-dot field would induce nystagmus [Tootell et al., 1995], which might confound the present result. Considering such arguments, in the following experiment, motion-defined shape defined by only two successive cinematogram frames was used as the stimulus to eliminate the effect of the motion of the stimulus itself, and the random dots were changing moving directions to avoid nystagmus.

EXPERIMENT 2

Materials and methods

Five male right-handed subjects were recruited from the university. The subjects were between 19 and 25

years old and had normal or corrected vision. All subjects gave informed consent prior to undergoing these experiments.

Stimuli and tasks

As illustrated in Figure 1, there were three stimulus types: motion-defined shape; static random-dot field; and motion random-dot field. Motion-defined shape was made visible by displacing the random dots within the figure region (subtended $4^\circ \times 4^\circ$) in one of four motion directions against the background of stationary random dots; note that the figure itself was stationary. The dots in the figure region were shifted for a displacement of 0.15° that lasted for 150 msec until the dots were shifted back. The interval between successive motion defined shapes varied randomly between 600–750 msec during which only the background of stationary random dots was presented. Motion-defined shapes consisted of three shapes: circle, square, and triangle, which comprised of 1/3 of the whole stimuli, respectively. Static random-dot field was a whole field of static random dots and motion random-dot field was a whole field of random dots uniformly moving at the velocity of $5^\circ/\text{sec}$ in one of the eight directions, randomly changing direction every 375 msec. Other features of the stimuli were identical to those in Experiment 1. Two additional tasks were designed: motion random-dot field vs. static random-dot field, and motion-defined shape vs. static random-dot field.

MRI scanning and analysis of fMRI data

The fMRI scan were performed for four cycles of the three stimuli, in the order of ABC for three subjects and in the order of CBA for the other two. MRI scanning and analysis of the fMRI data were identical to those in Experiment 1.

ERP recording and source analysis

The ERPs elicited by the identical stimuli of motion-defined shapes were recorded in a separate session from the same five subjects. In order to avoid the possible incompatible task demands in the fMRI and ERP experiments, the subjects were instructed to concentrate on viewing the stimuli of motion defined shapes without making any response. The methods for ERP recording and dynamic analysis were identical to those in Experiment 1.

RESULTS

fMRI

Task 4. Motion random-dot field vs. static random-dot field

This task design aimed at exploring cortical areas involved in coherent motion perception. Figure 6 of the averaged correlation coefficient maps shows motion random-dot field primarily produced activation in posterior lateral occipitotemporal areas; the averaged Talairach coordinates of these areas ($x=45$ $y=-64$ $z=6$) were in good agreement with those of a motion-specific area MT/V5 described in the mentioned previous studies. This pattern of activation was evident in four of the five subjects. Motion random-dot field also produced activation in posterior occipital areas, including the lingual gyrus and cuneus. This pattern of activation was evident in all five subjects.

Figure 7 of the averaged relative signal changes shows motion random-dot field produced 1.35% signal enhancement in MT/V5 and 1.4% signal enhancement in GL/Cu, compared with static random-dot field.

Task 5. Motion-defined shape vs. static random-dot field

This task design aimed at exploring cortical areas involved in motion-defined shape perception. As shown in Figure 6, motion-defined shape produced activation in posterior lateral occipitotemporal areas; the averaged Talairach coordinates of these areas ($x=46$ $y=-62$ $z=7$) were quite consistent with MT/V5 found in the fourth task. Motion-defined shape also produced activation in posterior occipital areas, including the lingual gyrus and cuneus. This pattern of activation was evident in all five subjects. In addition, there was also activation in the areas inferior to MT/V5, including the fusiform gyrus and inferior temporal gyrus, and weaker activation in the medial occipital gyrus (GOm). The averaged Talairach coordinates of these areas were ($x=45$ $y=-62$ $z=-8$). To all the subjects, this pattern of activation was evident.

As shown in Figure 7, motion-defined shape produced 1.43% signal enhancement in MT/V5 and 1.45% signal enhancement in GTi/GF, compared with static random-dot field, whereas motion random-dot field only produced 0.2% signal enhancement in GTi/GF. In GL/Cu, motion-defined shape produced 1.1% signal enhancement compared with static random-dot field. Hence, although the motion stimuli activated only

Figure 6.

Averaged correlation coefficient maps (for the 5 subjects) seen in Exp. 2. Functional maps are shown superimposed upon transverse sections of an individual MR-image that had been Talairach normalized; the figure shows the axial slices at $z=5$ and $z=-8$. Intensity of activation is normalized between the minimum and maximum of activation.

MT/V5, the stimuli of motion defined shapes indeed activated both MT/V5 and GTi/GF. In addition, the primary visual areas were also activated by motion-defined shape, compared with static random-dot field.

Dynamic analysis with fMRI + ERP

As plotted in Figure 8A of the averaged RV curves resulting from dipole modeling seeded by fMRI foci in the fifth fMRI task, each pair of dipoles located at MT/V5 or GTi/GF reached the same best-fit points at 336 msec (MT/V5: $RV=6.81\%$; GTi/GF: $RV=6.92\%$). As Figure 8B shows, the combination of MT/V5 and GTi/GF dipoles yielded good fit (averaged $RV=7.01\%$) for the observed ERPs in the 312–352 msec time interval, with the same best-fit point at 336 msec ($RV=5.38\%$).

Source analysis of the grand-average ERPs indicated fMRI-based fixed dipole modeling was able to account

Figure 7.

Averaged relative signal changes elicited by the two designed tasks in Exp. 2, derived from three visual areas (GL/Cu, MT/V5, and GTi/GF).

for 97.7% of the variance in the 312–352 msec time interval. Figure 8C of the source waveforms shows MT/V5 and GTi/GF dipoles appear to be synchronously and simultaneously activated in the 312–352 msec time interval, and this modeling behavior was evident in all five subjects. When the dipole positions were set free, one single pair of moving dipoles could be defined within the 312–352 msec time interval with the best-fit point at 336 msec (RV=5.02%). The positions of the moving dipoles were close to the fMRI foci of MT/V5 and GTi/GF.

DISCUSSION

In summary, controlling for the possible confound of the iterated perception of motion and form, Experiment 2 duplicated the main results of Experiment 1. The stimuli of motion defined shapes elicited by only two frames of random dot display—the continuously presented stationary random dots background and otherwise the same display except for the random dots within the figure region shifted for a displacement, indeed activated both dorsal MT/V5 and ventral GTi/GF and the dynamic analysis with integration of fMRI and ERP indicated they appeared to be simultaneously activated.

Although the gap of about 100 msec between the best-fit points of the stimuli of motion-defined shapes and kinetic shapes suggested the time courses of neural activation in MT/V5 and GTi/GF may strongly depend on the pattern of the stimuli, the similarity between the two voltage distribution maps (Figs. 5b,8b) at the respective best-fit time points suggested that the two kinds of forms defined by motion may be processed by the same underlying neural mechanism but excited at different latencies.

GENERAL DISCUSSION

Using two kinds of forms defined by motion, we found consistent activation both in the dorsal MT/V5 and ventral GTi/GF areas. This finding indicates that the perception of forms defined by motion involves both the ventral and dorsal pathways. As indicated by earlier physiological studies in nonhuman primates [reviewed by Barton et al., 1996], lesions of the MT or MST [Marcar and Cowey, 1992], or inferotemporal cortex [Britten et al., 1992] impair perception of motion-defined form in monkeys. Schiller [1993] found combined lesions of both the MT and V4 cause moderate defects for the perception of motion-defined forms. Based on these observations, some authors proposed decisions regarding form-from-motion are based on

information in the ventral pathway involving IT cortex and the dorsal motion areas such as MT and MST [Britten et al., 1992; Regan et al., 1992]. Recent PET study on human cortex [Gulyas et al., 1994] showed perception of motion-defined forms mainly involved the inferior and lateral occipital gyri, the lingual, the left fusiform, and right inferior temporal gyri. The present results are consistent with these previous findings and suggest that “motion” and “form” sub-systems cooperate to carry out the perception of forms defined by motion. However, probably limited to the technologies and methods available now, so far not very much research literature has discussed the relationship between the two visual pathways, and particularly little literature dealt with the causal relationship and time dependence of the activation of the areas in the two pathways. The present study, applying the technology of integrating fMRI and ERP, measured the spatiotemporal activation pattern in the two pathways with both high spatial and temporal resolution. The results turn out that MT/V5 and GTi/GF appear to be activated in parallel and simultaneously in response to forms defined by motion. These data seem to be in contradiction with the commonly accepted hierarchical model of anatomic and functional organization of brain cortex and raise interesting issues about the relations between and the functional specialization in the two visual pathways.

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