Cortical Representation of Inward and Outward Radial Motion in Man

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We have used positron emission tomography to investigate the cortical areas of the normal human brain involved in processing inward (Expansion) and outward (Contraction) radial motion simulated with an optic flow stimulus. The optical flow display was made out of dots moving radially away from or toward the center of the display monitor. In the Control condition, the dots' motion was randomized in order to remove any sensation of radial motion. In the Expansion condition. several loci of activation were observed: visual areas V2-V3 and the superior parietal lobule (BA 7), predominantly in the right hemisphere. In the Contraction condition activation sites were found in the same visual areas (V2 and V3) in the right hemisphere but the increase in rCBF in these regions was much lower than in the Expansion condition. BA 7 was activated in both hemispheres. When the motion component of the stimulus was isolated by subtracting the static condition from the incoherent motion condition, we obtained activations of areas V2, V3, and MT (putative V5). These results indicate that the detection of radial motion derived from an optic flow stimulus is mediated by structures forming the dorsal part of the visual cortical system and confirm that area MT is not specifically involved in flow analysis. • 2001 Academic Press

Key Words: local dots; forward motion; backward motion; PET imaging; visual system; man; cortical areas; regional cerebral blood flow.

INTRODUCTION

The direction of locomotion could be determined from information defined by optical flow. Gibson (1950) proposed that the direction of self-motion can be directly perceived from the "focus of radial outflow" in the optical flow pattern. Numerous psychophysical experiments have indicated that the perception of heading depends on the perception of the global optical flow pattern across the visual field (Warren *et al.*, 1988, 1990, and for review Dyre and Andersen, 1997). Monkey studies have shown that extrastriate cortices are perfectly suited to analyze optic flow fields. Those motion cells have been described in the medial superior temporal area (MST) although it seems that neurons in the dorsal portion of this region (a cortical area adjacent to V5) are more selective for the complex components of the optic flow stimulus such as radial, circular, translational, and shear motion (Tanaka and Saito, 1989; Duffy and Wurtz, 1991a,b; Orban et al., 1992; Graziano et al., 1994; Duffy, 1998; Eifuku and Wurtz, 1998). Neurons in area MT, on the other hand, although they respond to motion and are highly sensitive to directionality, are not tuned to radial or circular motion (Mikami et al., 1986), indicating that the middle temporal area (MT) is not particularly involved in flow analysis. However, if disparity is added in the motion stimuli, neurons in area MT show an increased sensitivity (DeAngelis and Newsome, 1999). The disruption through electrical stimulation of clusters of disparity-selective neurons can bias the behavioral perceptual judgment of depth in monkeys, which adds to the importance of MT in analyzing motion in depth (De Angelis et al., 1998). In addition to area MST, the ventral intraparietal area (VIP) also receives projections from area MT (Ungerleider and Desimone, 1983; Maunsell and Van Essen, 1986). VIP neurons present response properties similar to area MST in that they have large receptive fields, are responsive to direction and speed of moving visual stimuli (Colby et al., 1993; Duhamel et al., 1991), and respond to optic flow. Interestingly enough, the vast majority of optic flow-responding cells in VIP prefer expanding stimuli to contracting ones, with a significantly stronger response for the former (see Bremer et al., 2000). Both VIP and MST project to area 7A, whose neurons are sensitive to optic flow stimuli with a strong preference for expanding stimuli (Read and Siegel, 1997; Siegel and Reid, 1997). It thus seems, from these monkey studies, that optic flow processing is achieved at higher stages along the dorsal pathway beyond area MT and involves areas MST, VIP, and 7A.

In humans, the results obtained from brain imaging studies are more controversial. Some have indicated that BA 17 and 18 (Rutschmann *et al.,* 2000), the dorsal cuneus (area V3), the lateroposterior precuneus (areas 19 and 7), and regions of the fusiform gyrus (but





not area V5 or MT) are especially responsive to an optical flow stimulus (de Jong *et al.*, 1994), whereas others have suggested that area V5 might also be involved in the analysis of this particular form of motion (Dupont *et al.*, 1997; Smith and Scott-Samuel, 1998). In addition, it appears that occipitotemporal regions (MT/MST) and occipitoparietal regions (V3a and area 7) are more sensitive to coherent motion (Cheng *et al.*, 1995). More recently, however, Morrone *et al.* (2000) reported the presence of two motion areas within the V5/MT complex, one coding translational motion, the other being responsible for processing radial and circular motion.

In this experiment, using PET methodology, we examined the cortical areas involved in the processing of both inward (Contraction) and outward (Expansion) radial motion when normal subjects viewed optical flow stimuli. We show that both types of radial motion activate parts of the dorsal visual pathway (BA 18 and 19), including the posterior parietal cortex (BA 7), the activation being, however, much larger for the expanding stimuli. The lack of activation in area MT confirms that this region is not involved in the processing of optic flow but rather that this function in humans happens in higher parietal areas, predominantly in the right hemisphere.

MATERIALS AND METHODS

Subjects and Recordings

We studied 11 normal volunteers, 5 males and 6 females, whose ages ranged between 25 and 32 years; they were neurologically sound and their vision was excellent as tested by optometry examination. All subjects gave written informed consent and the PET protocol was approved by the Aarhus University Ethics Committee.

Experimental Paradigm

The experiment involved nine sequential measurements (three conditions repeated three times each) of rCBF during the presentation of different radial motion stimuli. The stimuli were produced by the software Pixx (v 1.65) and displayed on a Tektronix display monitor placed at 57 cm from the subjects' eyes. In a circular area of 30° in diameter, 64 black dots (diameter 6 min of arc) were continuously generated along 16 radial trajectories. The stimulus consisted of randomdot kinematograms with radial trajectories. Dot lifetime was two frames, after which a dot was randomly repositioned as signal or noise. One frame lasted 75 ms and the interframe interval was 15 ms. Dot speed increased with the square of the distance from the center of expansion (the inverse was true for the contraction condition). In other words, dot speed increased

by a factor of 4 as the distance doubled. Under the present conditions, the dots had a speed of 0.37, 1.46, 5.85, and 23.4° /s, at eccentricities of 2.5, 5, 10, and 20°, respectively. At the stimulus limit of 30°, the dot speed was 52.66° /s.

Three experimental conditions were used and were interleaved during scanning. In the first condition, all the dots moved at random along the radial trajectories leading to no motion-in-depth perception (baseline condition); in the second and third conditions, the dots moved toward (Expansion) and away from the subjects' eyes (Contraction), respectively, while the subject fixated on the center of the screen. For five subjects, an additional baseline condition consisting of static dots, which maintained the spatial structure of the optic flow stimulus, was tested to isolate the motion component. In this case, the number of conditions was 4 and each was repeated three times (for a total of 12 injections). This procedure, we believe, would increase the activation of the motion areas of the brain.

PET Data Acquisition and Image Analysis

An ECAT PET camera was used to detect changes in relative rCBF by recording the distribution of cerebral radioactivity caused by the freely diffusible, positron emitting, ¹⁵O-labeled tracer water (H₂¹⁵O) infused intravenously. Ten seconds prior to the injection, the visual stimulus was presented on the screen and the bolus (500 MBg or 13.5 mCi) was then injected at time 0 through an intravenous catheter. Data acquisition started at bolus arrival to the brain and continued for a period of 40 s. Images were reconstructed with a measured attenuation correction and filtered to 12 mm full-width at half-maximum isotropic with a Hanning filter of cut-off frequency 0.15 cycles/pixel. For anatomical localization PET images were coregistered to the subjects' MRI in Talairach coordinates (Talairach and Tournoux, 1988; Collins et al., 1994). After a voxel-byvoxel subtraction of the baseline conditions from the test conditions, a statistical parametric map of the rCBF change was created using a t statistic (Worsley et al., 1992). For t exceeding 3.6, the rCBF change was significant at P < 0.05 corrected for multiple comparisons.

RESULTS

Expansion

All subjects reported seeing the depth in the optical flow display. The group analysis for all 11 subjects revealed significant increases in rCBF in the posterior cortical visual areas (BA18 and BA19) and in the parietal cortex (BA 7). All these areas were more strongly active in the right hemisphere. The exact coordinates along with the *t* values and levels of statistical signif-

TABLE 1

BA		Talairach coordinates					
	Anatomical region	Side	X	У	Ζ	<i>t</i> value	P value
18	Middle occipital gyrus	Right	20	-98	12	5.8	0.0001
18	Middle occipital gyrus	Left	-30	-91	8	4.5	0.0001
19	Superior occipital gyrus	Right	36	-84	24	3.9	0.02
19	Middle occipital gyrus	Left	-28	-91	24	3.7	0.04
7	Superior parietal lobule	Right	23	-64	55	4.4	0.002
7	Superior parietal lobule	Left	-21	-71	51	3.5	0.04

Talairach Coordinates and t Values for Inward Radial Motion (Expansion)

icance are reported in Table 1 and the activated cortical areas obtained from a group analysis showing significant rCBF changes following full-field visual stimulation are illustrated in Fig. 1. The absence of activation of area MT (putative V5) could have been due to the subtraction paradigm used in the experiment, namely, Expansion minus Dynamic Baseline (incoherent motion). In this subtraction, the motion parameters included in both types of stimuli might have canceled out, thus eliminating the middle temporal activation. To test this possibility, we submitted 5 subjects to the same paradigm but with an extra condition in which the baseline stimulus (originally made out of incoherently moving dots) was static. When the Static condition was subtracted from the Dynamic Baseline condition, a strong activation of the middle temporal area emerged, in addition to areas V2 and V3 (Table 2). Activation of the parietal region (BA 7) was, however, lost.

Contraction

In this condition, the foci of activation were found in visual cortical regions similar to those activated by the contracting stimulus, namely, BA 18/19 (V2/V3) in the right hemisphere and BA 7 (precuneus), bilaterally. It is interesting to note that the levels of activation produced in this condition were much lower than those obtained in the contraction condition, thus confirming monkey electrophysiological experiments showing that single cells were more responsive to expanding that contracting stimuli (Bremer et al., 2000). The activation foci are illustrated in Fig. 2 and the results are summarized in Table 3. It is worth pointing out that the contraction foci were centered over the expansion foci in the occipital cortex, but that contraction and expansion foci were at different locations in parietal cortex.

DISCUSSION

Our results indicated that optic flow stimuli (whether contracting or expanding) activated visual and nonvisual cortical areas. The cortical areas showing significant elevation of rCBF included Brodmann's areas 18 and 19. predominantly in the right hemisphere, and BA 7 bilaterally. These results confirm the involvement of BA 18, 19, and 7 in the processing of optic flow stimuli. We did not find, however, selective activation of area MT (V5) with such stimuli, which is in agreement with what has been reported by de Jong et al. (1994) but at variance with others who showed activation of the MT-MST complex using optic flow stimuli (Zeki et al., 1991; Dupont et al., 1994; Smith and Scott-Samuel, 1998; Morrone et al., 2000). Although BA 17 was found to be related to the processing of optic flow, only the middle part of area 19 selectively responded to the direction components of the flow field (Rutschmann et al., 2000). Our results add to the consensus that BA 17 is not activated by optic flow stimuli. Moreover, in our study, BA 18, 19, and 7 were bilaterally activated with a predominance in the right hemisphere (Fig. 2). The predominantly active right hemisphere in the processing of optic flow stimuli has also been reported by de Jong et al. (1994) in normal human subjects and is supported by neuropsychological studies showing that patients with right hemispheric lesions (occipitoparietal) do not perceive simulated forward motion produced by a rotating cylinder display (Vaina, 1989).

The lack of activation of area MT (V5) following optic flow stimulation is not surprising in light of monkey single-unit and human brain imaging studies. Indeed, it has been shown that single cells in area MT respond to motion and are highly sensitive to directionality but are not tuned to all kinds of optic flow stimuli (e.g., radial, circular) (Mikami et al., 1986). In humans, results are more contradictory, some suggesting an involvement of area MT in the processing of optic flow (Dupont et al., 1997; Smith and Scott-Samuel, 1998; Morrone et al., 2000), others failing to show its selective activation (de Jong, 1994; Rutschmann et al., 2000). The contradiction seems to lie in the type of stimuli used in the experiments. For example, the field size of the visual stimulus seems to be an important parameter for activation since it has been shown that a small field size stimulus failed to activate area MT (Rustchmann et al., 2000), whereas a much larger field



FIG. 1. Activation sites for inward radial motion (Expansion). (A) 3-D reconstruction of the activation loci represented in the horizontal sections shown in (B). The levels of the sections on the dorsoventral (*z*) axis are indicated by the white lines. Note the stronger activation in the occipital and parietal areas of the right hemisphere.

size did (Cheng *et al.*, 1995). Numerous studies, however, using a wide variety of stimuli involving directionality, dot speed, dot coherence, etc., agree that the processing of various dot motion occurs in cortical areas beyond MT (Cornette *et al.*, 1998; Dupont *et al.*, 1997; Orban *et al.*, 1995). We show, moreover, and in agreement with others (McKeefry *et al.*, 1997), that area MT (V5) is more responsive to incoherent motion.

In the Contraction condition, we found that the same visual areas as in the Expansion condition were activated, namely, BA 18, 19, and 7. The rCBF elevation, in this condition, was, however, much lower that in the Expansion condition. This result is in agreement with electrophysiological studies that showed that single neurons in the parietal cortex (VIP), for example, prefer an expansion over a contraction stimulus. In fact, contraction stimuli result in a slight inhibition of the cells' activity (Bremer *et al.*, 2000).

Our results seem to support the suggestion that there might be two main sites of activation, both in the dorsal part of the visual stream, in response to an optical flow stimulus, namely, the superior parietal and occipitotemporal cortices (see Bremer *et al.*, 2000). When simple motion is viewed, area V1 is highly active

TABLE 2

BA			Tala	irach coordinates			
	Anatomical region	Side	X	у	Z	<i>t</i> value	P value
19	Cuneus	Right	24	-85	23	8.3	0.0001
37	Middle temporal gyrus	Right	46	-64	3	8	0.0001
37/19	Middle temporal gyrus	Left	-47	-75	2	7.1	0.0001
18	Lingual gyrus	Right	1	-87	-8	6.3	0.0001
18	Lingual gyrus	Left	-16	-83	-3	6	0.0001

Talairach Coordinates and P Values for Incoherent Motion

(Zeki *et al.*, 1991; Watson *et al.*, 1993). Complex motion information is funneled to areas V2 and V3 and then to higher order motion-processing areas such as MT. Neurons in this area are tuned for the direction and speed of a moving visual stimulus and cells with pre-

ferred directions are arranged in columns. Area MT, by its topographical organization and receptive properties of its neuronal population, is considered a relay station for visual motion processing. MT is connected to other structures along the dorsal pathway such as MST,

FIG. 2. Activation sites for outward radial motion (Contraction). (A) 3-D reconstruction of the activation loci represented in the horizontal sections shown in (B). The levels of the sections on the dorsoventral (*z*) axis are indicated by the white lines. Note the weak cortical activation compared to the Contraction condition.

TABLE 3

Talairach Coordinates and t Values for Outward Radial Motion (Contraction)

BA	Anatomical region		Та	lairach coordina			
		Side	X	У	Ζ	<i>t</i> value	P value
18	Cuneus	Right	20	-98	6	3.40	0.03
18	Cuneus	Left	-28	-95	4	2.90	0.10
7	Precuneus	Right	33	-50	55	3.30	0.06
7	Precuneus	Left	-18	-57	60	3.30	0.06
37	Fusiform gyrus	Right	24	-48	-15	2.90	0.10

whose neurons have different physiological properties, namely, a selective sensitivity to optic flow stimuli (expanding or contracting radial motion). MST is reciprocally connected to the VIP; neurons in VIP are particularly sensitive to expanding or contracting optic flow stimuli, with a majority of cells preferring expanding stimuli. These two areas are not the final stages in the motion-sensitive part of the dorsal stream of the monkey visual system, since both areas send projections to BA 7. Neurons in this area have been shown to be selective for radial optic flow patterns and they also prefer expanding to contracting coherent radiating patterns (see review by Bremer *et al.*, 2000).

It thus seems that the visual percept first processed in the occipital lobe is generated in the temporal lobe, whereas the parietal lobe is involved in visuomotor coordination (Goodale and Milner, 1992). The parietal lobe contains cells that are multimodal in nature since they respond to visual, tactile, and vestibular stimuli. This area of integration of various modalities is perfectly suited to the encoding of locomotion during heading since approaching objects in the environment have the potential to be touched. This confirms Gibson's original idea that direction of heading is specified by the global expansion of the moving stimuli and that the dorsal part of the cortical visual system is perfectly suited to handle this type of information.

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