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Brain activation during dichoptic presentation of optic flow stimuli

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Abstract The processing of optic flow fields in motion-sensitive areas in human visual cortex was studied with BOLD (blood oxygen level dependent) contrast in functional magnetic resonance imaging (fMRI). Subjects binocularly viewed optic flow fields in plane (monoptic) or in stereo depth (dichoptic) with various degrees of disparity and increasing radial speed. By varying the directional properties of the stimuli (expansion, spiral motion, random), we explored whether the BOLD effect reflected neuronal responses to these different forms of optic flow. The results suggest that BOLD contrast as assessed by fMRI methods reflects the neural processing of optic flow information in motion-sensitive cortical areas. Furthermore, small but replicable disparity-selective responses were found in parts of Brodmann's area 19.

Key words Functional magnetic resonance imaging · Optic flow · Visual cortex · Disparity · Stereo vision

Introduction

The analysis of visual motion processing is mostly confined to the dorsal visual pathway (V2, V3, MT, and MST or V5/V5a, respectively; see Van Essen et al. 1981; Albright 1984; Albright et al. 1984; Zeki 1978). Motion information is further relayed to cortical regions in the parietal cortex as part of an analysis of spatial relation-

ships between objects in the environment and the viewer (Andersen 1995, 1997; Colby 1998).

Neurons in the middle superior temporal area (MST) in macaque monkey appear to participate in the analysis of optic flow stimuli. These neurons have large receptive fields (typically $>20^\circ$) that extend to the ipsilateral hemifield (Raiguel et al. 1997; Duffy and Wurtz 1991). Furthermore, differentiated responses of MST neurons to complex motion gradients presented in optic flow fields have been reported (Saito et al. 1986). Neurons in MST(d) but not MT seem to contribute to flow analysis (Duffy 2000; Lagae et al. 1994; Duffy and Wurtz 1991; Lappe et al. 1996). Beyond occipital regions neurons in the parietal cortex show selective responses to optic flow stimuli (Siegel and Read 1997).

Relevant studies on the processing of optic flow stimuli with positron emission tomography (PET) employing coherently and incoherently moving random dots have been performed by Zeki et al. (1991), Dupont et al. (1994), and De Jong et al. (1994). These authors reported activation in the human V5/V5a complex (MT/MST) in the border region between areas 19 and 37, in the inferior cuneus in area 18 (V3), in the insular cortex, and in the lateral extent of the posterior precuneus in occipitoparietal cortex (areas 19/7). Cheng et al. (1995) measured responses in subjects who monocularly viewed an 80 deg (virtual) field while luminous dots moved coherently in one of eight directions. The control conditions consisted either of incoherent motion sequences or mere fixation. The results indicate that some of the occipitotemporal (V5/V5a, BA 19/37) and occipitoparietal (V3A, BA 7) visual areas exhibit a more pronounced response during coherent motion perception.

Recent investigations show that neurons in area MT are also sensitive to the disparity contained in motion stimuli (DeAngelis and Newsome 1999). Electrical stimulation of MT neurons, found to be sensitive to binocular disparity, affects the depth judgements of monkeys performing visual motion discrimination tasks. Binocular disparity could potentially provide an important cue in resolving depth information inherent in dichoptically presented motion sequences. There is evidence (Bradley and Andersen 1998) that neurons in area MT analyse

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binocular disparity and this information can be used to define motion planes of different depth.

Studies using functional magnetic resonance imaging (fMRI) identified areas V5/V5a and V3a to be selectively sensitive to expanding stimuli, the human homologue of V3a being more sensitive to motion-defined borders than V5/V5a (Tootell et al. 1995; Reppas et al. 1997).

In the present study, we recorded the BOLD responses to optic flow using dynamic, random-dot kinematograms comparing two types of flow field stimuli with a random walk type stimulus. Optic flow fields were presented either binocularly in plane (both eyes viewing identical stimuli, i.e. monoptic presentation) or with stereo depth (two eyes viewing disparate images, i.e. dichoptic presentation), using speed gradients combined with different amounts of disparity.

Materials and methods

Stimuli

Stimuli were created using a VSG graphics board (Cambridge Research Systems) in a standard PC and projected with an LCD Projector (Panasonic) onto a screen covering the rear of the scanner, each pixel measuring $0.033\text{--}0.033\text{ deg}^2$. Subjects viewed the projection by means of a mirror (monoptic) or a mirror prism device in combination with polarizing filters (dichoptic condition). There was negligible crosstalk between the eyes using this device.

In a square area of $16.5 \times 16.5\text{ deg}^2$ ($12.5 \times 12.5\text{ deg}^2$ during dichoptic stimulation) 80 gray dots (dot size $0.1 \times 0.1\text{ deg}^2$) were animated on a dark background in one of three fashions (expansion, random walk, spiral motion) while subjects had to fixate a central white spot of $0.26 \times 0.26\text{ deg}^2$. The appearance of new dots was controlled to maintain constant dot density.

Expansion

All dots were simultaneously moving outward and, as soon as a dot disappeared in the periphery, one appeared near the centre of the screen. To simulate optic flow fields, dots had to have increasing speed from the centre to the periphery (as indicated by the length of the arrows in Fig. 1a). Dots accelerated in six steps from 4.75 deg/s to 13.06 deg/s (average speed 8.91 deg/s).

Spiral motion

The dots were moved as in the expanding flow field condition with an added rotational component of 108 deg of rotational angle per second (18 rpm), resulting in a spiral motion. The rotational component was either clock- or counterclockwise.

Random walk

As the dots moved they changed their direction and speed randomly. Time between direction and speed changes was also varied randomly with an average of 250 ms. Average speed was as in the expanding flow field condition (see Fig. 1b).

Stereo depth

During monoptic stimulation (same stimulus in both eyes) the dots had zero disparity, whereas during dichoptic stimulation the disparity varied with horizontal eccentricity ranging from 0 to

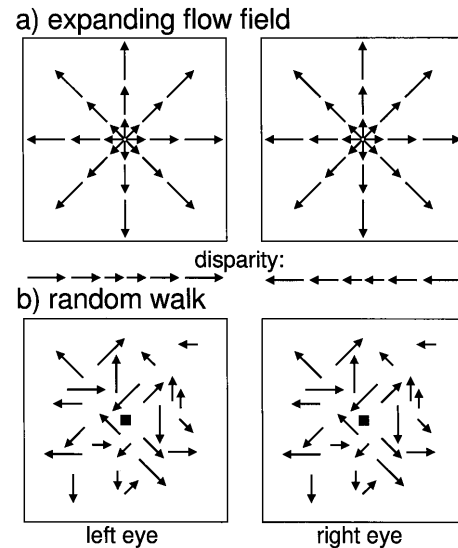


Fig. 1a, b Scheme of the flow field and random walk stimulus for dichoptic stimulation with disparity. *Arrow sizes* approximately represent dot speeds or disparity angle during dichoptic stimulation

1.2 deg in steps of 0.24 deg (indicated by the length of the arrows in the middle of Fig. 1).

MRI data acquisition

Imaging was performed using a 1.5-T Siemens Magnetom (Vision) scanner, which has 25-mT/m gradients with a 0.3-ms rise time. The subject was positioned in the RF receive-transmit full head coil, and the head was stabilized with a vacuum cap and forehead rests.

Twelve to 16 contiguous T2*-weighted EPI slices ($TE=66\text{ ms}$, $TR=3\text{ s}$, flip angle $=90^\circ$, 128×128 matrix, voxel size $=2 \times 2 \times 4\text{ mm}$), positioned approximately parallel to the calcarine sulcus, and encompassing occipital and posterior parietal lobes were taken as functional images. To map functional slices into Talairach space (Talairach and Tournoux 1988), whole-head anatomical data were acquired using sagittal T1-weighted 3D MP-RAGE images (magnetization-prepared rapid-acquisition gradient echo; Siemens AG, Erlangen, Germany) with 1-mm^3 voxels.

Experimental design

Subjects were shown the stimuli blockwise, separately for each stimulus type. Each block consisted of 30 s of fixation with dark background (fix), 30 s of an animated stimulus series (anim) – either expansion, spiral motion, or random walk – and 30 s of static dots (stat), where the dots shown in the last position of the animated phase were presented as stationary. This was repeated 4 times, one stimulus block thus lasting 360 s. Functional images were acquired every 3 s. During dichoptic stimulation two of the four phases were presented with and two without disparity. This allowed for the comparison of dichoptic and monoptic presented optic flow stimuli and thus the influence of stereoscopic depth on processing of optic flow.

Data analysis

Functional images were corrected for head movements and smoothed with a gaussian ($FWHM=4\text{ mm}$) using Robert Cox' AFNI package (Cox 1996). Further analysis was done using Krish Singh's BrainTools (<http://www.pc.rhbc.ac.uk/vision/BrainTools.html>; see

also Smith et al. 1998). Functional images were correlated pixelwise with a smoothed stimulus time course to allow comparison between animated phases and static or fixation phases. Animated phases of dichoptic and monoptic stimuli were compared with each other and separately to fixation phases.

Clusters of areas activated during animation as compared to fixation ($r > 0.5$) were then defined in each subject as region of interests (ROIs). These ROIs were compared across all subjects. The z -transformed correlation coefficients multiplied with the variance of the signal defined the level of activation (Bandettini et al. 1993). Talairach coordinates were averaged over subjects for each ROI.

The ANOVA for repeated measurements was calculated in each ROI and for each contrast (animation vs static, animation vs fixation, static vs fixation) with stimuli (expansion, spiral, random) as a factor. Activation during dichoptic presentation with disparity was compared to periods with monoptic stimuli (no disparity) separately for each ROI and stimulus type.

Subjects

Fourteen (seven female) subjects participated in the experiment. Five (two female) of those were also tested with the dichoptic stimulus. All subjects were neurologically healthy and had normal or corrected-to-normal (contact lenses) vision. Informed consent was obtained in all cases.

Results

The time course clearly indicated a larger response during the animated phases compared to stationary dots (e.g. Fig. 2d). A typical activation in two prominent ROIs in one subject is shown in Fig. 2a–c.

A total of six ROIs with high activation during the animated stimulation phases could be identified in all subjects. These ROIs were found in Brodmann's areas 17, 18, 37, and dorsal, middle, and ventral locations within BA 19, subsequently called 19d, 19m, and 19v (Table 1). Some subjects showed activation in extrastriate dorsal areas BA 39 and 7. These ROIs were not further investigated since they could not be found in all subjects.

An ROI analysis was performed on the data of all 14 subjects. The results are presented in Fig. 3. The mean activation, as defined in "Materials and methods", is shown for each stimulus condition (see insert) and for each ROI. As can be seen in Fig. 3, there is significant activation in all areas investigated and all these areas respond to the three types of motion.

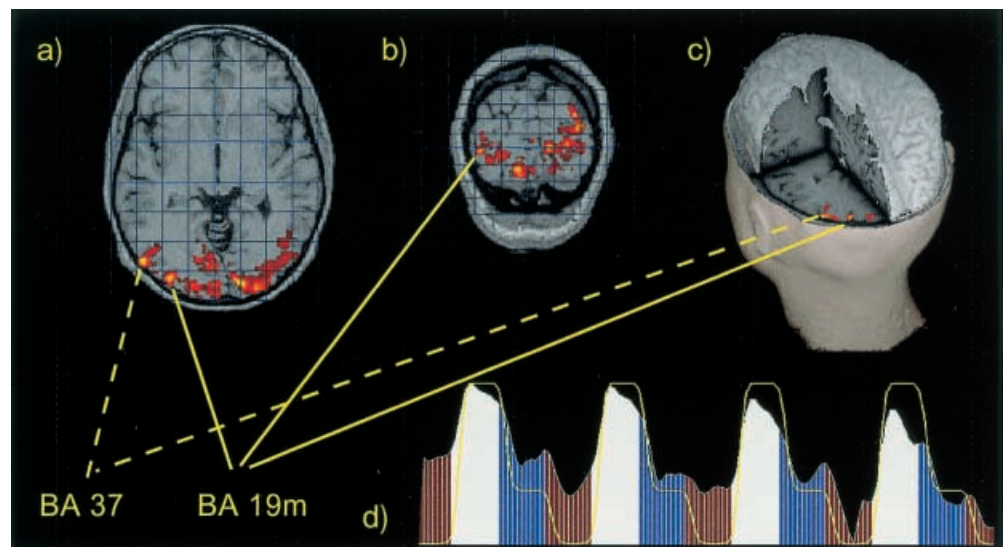
Area 19m is the only area that shows a significant difference in activation for the expanding flow field vs the random walk stimuli ($P \leq 0.009$, Scheffé). The difference between the spiral motion and the random walk stimuli did not reach significance level ($P \leq 0.077$, Scheffé).

On average most areas showed somewhat higher activation during dichoptic than during monoptic stimuli (Fig. 4). This effect might reflect the neural processing associated with stereo depth. The combination of expansion or spiral motion and disparity led to a relatively larger response in BA 19m and BA 19d than when random walk was combined with disparity. The mean increment in response in those areas is clearly above zero for the flow conditions (exp, spi in Fig. 4) unlike in the random walk condition. However, only for the flow-field condition in BA 19m is this trend significant (sign-test, $P < 0.02$).

Table 1 Average Talairach coordinates for the six investigated ROIs ($n=14$ subjects)

BA	Left hemisphere			Right hemisphere		
	TC x	TC y	TC z	TC x	TC y	TC z
17	-5.57	-87.78	-11.95	9.61	-86.92	-10.84
18	-14.71	-95.20	-6.51	14.29	-94.74	-4.80
19d	-19.93	-86.91	21.49	20.49	-87.57	22.87
19m	-31.26	-86.86	-3.76	31.63	-85.23	-0.91
19v	-18.40	-80.40	-18.64	16.66	-80.48	-18.84
37	-47.61	-69.05	-0.10	44.54	-67.42	-0.75

Fig. 2 Localization of BA 37 and 19m in one subject: **a** Axial slice 1 mm ventral to AC; **b** coronal slice 90 mm posterior to AC; **c** 3D visualization; **d** a typical detrended time course of the BOLD signal in movement-sensitive areas. White regions indicate animated stimulation phases, blue regions stationary dots, and red regions fixation phases. The yellow line represents the shifted and smoothed stimulus time course. One segment represents one scan every 3 s



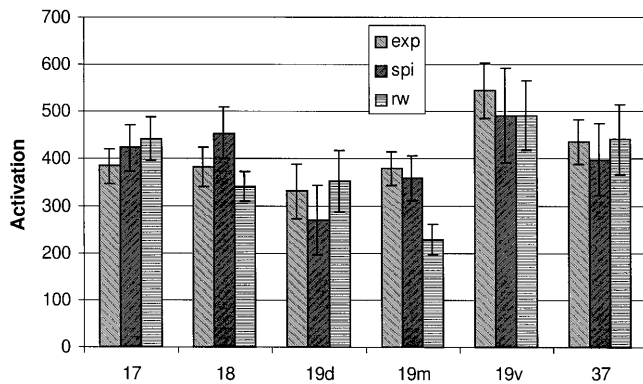


Fig. 3 Activation during animated phases compared to fixation in all regions of interest signified by the Brodmann's area numbers. Error bars indicate 1 standard error ($n=14$ subjects)

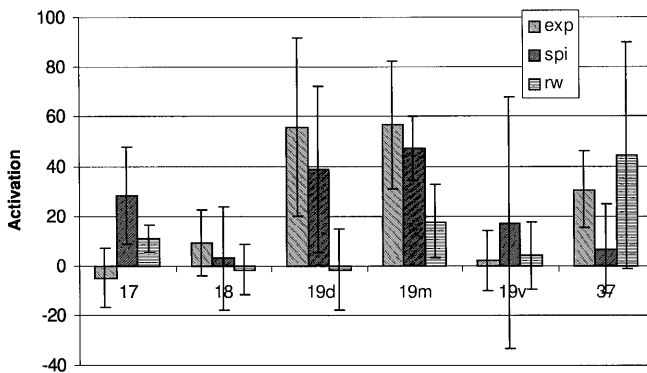


Fig. 4 Comparison of activation during dichoptic and monoptic stimuli. Positive values denote stronger activation during dichoptic stimulation. Error bars indicate 1 standard error ($n=5$ subjects)

Discussion

We have demonstrated BOLD responses in posterior cortex that are related to the processing of optic flow stimuli. Significant responses were found in BA 17, 18, 19 and 37. However, only the middle part of area 19 selectively responded to the direction components of the flow field ($\text{exp} > \text{spi} > \text{rw}$) and these differences are significant (see Table 2, Fig. 3). We interpret this finding as evidence for a selective role of V3b (also called area KO by van Oostende et al. 1997) in the processing of optic flow.

Contrary to our original expectation, we did not find a stimulus-selective response in the MT/MST region in BA 37. This lack of selectivity to optic flow might be related to the smaller field size of our stimulus: normal viewing 16.5 deg, dichoptic viewing 12.5 deg compared to 80 deg in the study by Cheng et al. (1995). A more recent PET study by McKeefry et al. (1997) found V5 to be more responsive to incoherent than to coherent motion.

In a series of studies, Cornette et al. (1998), Dupont et al. (1994), van Oostende et al. (1997), Dupont et al. (1997), and Orban et al. (1998) assessed brain activation using either PET and fMRI in subjects who performed

Table 2 Differences in BA 19m between the three stimulus types as calculated by ANOVA (Scheffé) (*exp* expansion, *spi* spiral motion, *rw* random walk)

	Mean difference	Critical difference	P-value
exp, spi	22.123	140.363	0.9253
exp, rw	151.661	119.702	0.0092
spi, rw	129.539	140.363	0.0767

psychophysical tasks of direction and speed discrimination. Several visual areas responded to various forms of dot motion, suggesting that areas beyond V5/V5a, including areas in the lingual gyrus and cuneus, show selective responses to the direction and speed of visual motion. Orban and colleagues identified an area in the ventral portion of extrastriate cortex, which they refer to as the kinetic occipital (KO) cortex (Orban et al. 1995; van Oostende et al. 1997; Dupont et al. 1997). KO responds well to motion-defined borders within complex motion displays. Smith et al. (1998) compared BOLD responses to first- (luminance-derived) and second-order (contrast-derived) motion stimuli. The results suggest that several areas respond to both types of motion. Area KO/V3b appears to respond preferentially to certain types of second-order motion.

A subset of our subjects also viewed the motion stimuli under dichoptic viewing conditions. By introducing binocular disparity into these images, we could assess the effect of stereoscopic vision on the responses of optic flow. As can be seen in Fig. 4, the introduction of disparity usually led to an increase, albeit small, in the BOLD response in BA 19 and 37 (V5). In BA 19m (putative V3b) and BA 19d (putative V3a) we further found an increase in the response that was coupled to the directional components in the flow field. In BA 19m the disparity-selective component of the response was pronounced for the conditions with expanding and spiral optic flow fields with little effect in the random walk condition. BA 37 did not show this selectivity (Fig. 4). This small response to disparity in flow fields would represent a correlate of the additional processing associated with the neural analysis of 3D optic flow. Orban et al. (1999) have recently reported that areas V5/V5+ respond to simulated 3D motions in 2D stimuli. The activation differences between stimuli with and without disparity were generally low, which could mean that the BOLD level generated by the moving stimuli was already at saturation level, masking any small effects related to disparity.

In summary, our results support a role of motion-sensitive areas in the encoding of 3D optic flow stimuli. A subarea within BA 19, which could correspond to V3b or KO, appears to be differentially activated by the directional coherency of the motion vectors in the flow fields. This same area has the largest differential response to disparity. These differences could not be found in the putative area MT/MST in BA 37. Our results suggest that areas apart from MT/MST play an important role in the processing of complex 3D motion signals.

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