Stereoscopic processing in the human brain as a function of binocular luminance rivalry

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Received 31 January 2003; accepted 26 February 2003

DOI: 10.1097/01.wnr.0000075419.59944.ad

We investigated the neural substrates of a recent model of human stereodepth perception by obtaining measurements of regional cerebral blood flow (rCBF) using PET. Subjects experienced the perceptual properties of stereopsis by viewing rival-luminance stereograms displaying an identical random-dot pattern in their central portion while the backgrounds exhibited correspondent dots contrasting in black/white luminance. The stereoscopic vision induced by retinal luminance rivalry coincided with a significant elevation of rCBF in the dorsal visual pathway. Area V5 (MT) was activated bilaterally by the experimental condition while the remaining active loci were restricted to the right hemisphere. The neural sites that responded to this novel stereoscopic stimulus are similar to those activated by traditional stereograms containing horizontal disparities. *NeuroReport* 14:1163–1166 © 2003 Lippincott Williams & Wilkins.

Key words: Area MT; Binocular luminance rivalry; Brain imaging; Human; Stereopsis; Visual areas

INTRODUCTION

Stereovision is dependent upon the brain's ability to process binocular disparity, representing the difference between corresponding points in interocular retinal images [1]. The Julesz random-dot stereograms rely on a slight horizontal displacement of dots (positional disparity) within a specific region in order to generate depth perception [2]. A near or far depth effect can also result from viewing a pair of rival-depth stereograms containing a region of binocularly uncorrelated points directly adjacent to an area displaying perfectly correlated dots [3]. The corresponding elements contained in a set of such stereograms are randomly disparate in several ways (i.e. vertical, oblique or horizontal alignment and luminance level). Any of these variables may be responsible for the depth perceived in this visual stimulus.

A luminance-based stereogram was developed by Howard [4] within the last decade. It contains binocularly correspondent discs showing opposite black/white luminance. Pairs of these stereograms exhibit no positional disparity; the correlated discs comprised therein fall precisely on the same region in both retinae. In order to produce a strong illusion of depth, the white discs must nevertheless be smaller in size than their black counterpart. This indicates that the depth cue inherent to the stimulus is not solely related to the interocular retinal rivalry produced by the opposing disc luminance.

Faubert [5] recently designed a pure luminance-based pair of stereograms with central portions displaying a similar random-dot pattern while the surrounding regions of dots contrast in terms of black/white luminance. The retinal cells that are activated by the binocularly contrasting points send rival inputs to the brain regarding the luminance of a given point in the physical world. These rival-luminance stereograms produce a strong depth effect in that the central region of the stimulus appears to float above the surround. This illusion of depth cannot be attributed to the density, spatial location or size of the constituent dots. The stereoscopic stimulus designed by Faubert [5] only shows disparity in terms of luminance, which clearly makes the latter its only depth cue.

To our knowledge, no previous experiments have been conducted to evaluate how the neural processing of luminance disparity signals ultimately leads to a cognitive representation of a 3D image. We exposed subjects to Faubert rival-luminance stereograms while measuring regional cerebral blood flow (rCBF) with PET, allowing us to determine how the brain processes binocular luminance rivalry in order to generate the perceptual experience of stereopsis.

MATERIALS AND METHODS

Ten volunteers (age 21–31 years) participated in the study. All had normal stereopsis, as determined psychophysically while the subject was lying in the PET scanner prior to the actual recording. All participants gave written informed

consent in accordance with the guidelines approved by Aarhus University and the Montreal Neurological Institute Ethics committees.

Stimuli: The subjects were presented two stimulus conditions: Faubert rival-luminance stereograms and a form (control) stimulus. The pair of rival-luminance stereograms contained a central square region showing an identical pattern of random-dots, whereas the surround was comprised of corresponding points displaying opposite black/white luminance (Fig. 1a). The background dots were designed to send rival and non-alternating inputs to the retina, where the binocular coordinates contrasted in terms of luminance. No shape or depth was apparent by looking at the stereograms independently. However, a fusion of the two with the use of red–green glasses produced an illusion of depth in that a square appeared closer to the observer than the surrounding area. The form stimulus consisted of the same stimulus but free of luminance disparities leading to the perception of a monocularly visible square in its center. It hence displayed a different level of luminance relative to the background, but it did not produce the sensation of a 3D surface. Six sets of PET scans (PC-2048B tomograph) were obtained for each participant under both stimulus conditions. To ensure that the rCBF values recorded during the Faubert stereogram presentations reflected only the neural processing of depth information and not the visual inputs related to the form of the stimulus, the responses elicited by the form (baseline) stereograms were subtracted from the metabolic activity derived from retinal luminance rivalry.

Eye movements: The subjects' oculomotor behavior during stimulus presentations was recorded using an infrared video camera (ISCAN, Cambridge, MA) that tracks the center of the pupil and the corneal reflection. Horizontal and vertical movements of the left eye were analyzed dedicated scripts written in Matlab, which allowed us to identify and remove blink artifacts, and subsequently detect and measure the amplitude of saccadic eye movements. Data showed that the number of saccades $> 0.5^\circ$ and the mean amplitude varied across subjects but did not differ across conditions (Friedman ANOVA, $p > 0.5$), thus ruling out the contribution of eye movements to the observed brain activations.

Subject preparation and procedure: Prior to brain imaging, a fine needle-catheter was inserted into the brachial vein for the administration of a radioactive substance with a short half-life (10 mCi $H_2{}^{15}O$). Three scans were taken during each of the two experimental conditions, yielding a total of 60 CBF volumes. All scans (50s duration) were carried out 10 s after the subject began to observe the stimulus on the display monitor (Tektronik), placed at a viewing distance of 57 cm (1 cm = 1°). The two stimuli showed equal visibility (50% light and 50% dark dots) and displayed the same average luminance on the screen. The stimuli were 27.16 cm in size (280 pixels on the screen), with a central square of 19.4 cm (200 pixels). The size of each pixel was 0.097 cm.

Images of each participant's brain were collected with high-resolution MRI technology (Philips Gyroscan ACS, 1.5 T). The individual MRI scans were co-registered with PET images and spatially normalized according to standard stereotaxic space [6]. The PET images were reconstructed as 128×128 matrices of $2 \times 2 \times 2$ mm pixels using an 18 mm Hanning filter. The purpose of the filter was to limit the residual anatomic variability that may persist following stereotaxic standardization. Individual MRI images were subjected to the same averaging procedure as the PET scans. MRI and PET images were superimposed to allow the direct localization of *t*-statistic peaks. Using the DOT program, the data were analyzed for the following voxel by voxel subtraction pairs: rival-luminance minus form (activity elicited by luminance rivalry and form−form = pure depth processing). The presence of a significant focal change was tested with a method based on 3D Gaussian random-field theory [7]. An exploratory search strategy was used. Specifically, the only peaks considered statistically significant were those with $t \geq 3.5$; $p < 0.0004$, 2-tailed, uncorrected), given a brain (gray matter) volume estimate of 200 resels.

RESULTS

The brain areas that were activated by the experimental luminance-based stimulus are depicted in Table 1. The cerebral activity due to the form of the stimulus has been subtracted from the reported values. Rival-luminance stereogram presentations significantly increased rCBF in areas BA 18 and 19 of the right occipital lobe. Two peaks of activation were also apparent in the superior (BA 7) and inferior (BA 40) parietal lobules of the right hemisphere. An elevation in blood flow was further noted in the frontal lobe (area BA 9) and it was specific to the right side of the brain. Activations were also detected in the middle temporal visual area (MT), but these were bilateral. These results are illustrated in Fig. 1.

DISCUSSION

We used a pure form of luminance-based stereogram in combination with neuroimaging techniques to examine how the human brain processes rival inputs originating from the retina in order to generate a 3D percept. Our data show that the occipital, parietal and temporal cortices are all implicated in depth information processing. The results further indicate that although MT was bilaterally activated by retinal luminance rivalry, the other cortical regions all demonstrated a right hemispheric dominance, in agreement

Table I. Brain areas showing a significant activation during the experimental condition.

Brain area	H	X	Y	Z	*t*
BA 18	R	34	−68	21	4.5
BA 19	R	25	−80	35	3.6
MT	R	44	−72	8	4.2
	L	−30	−77	−3	3.8
BA 7 (SPL)	R	29	−64	60	4.5
BA 40 (IPL)	R	34	−49	51	5.2
BA 9 (GFM)	R	44	13	42	4.2

MT, middle temporal area; SPL, superior parietal lobule; IPL, inferior parietal lobule; GFM, medial frontal gyrus.

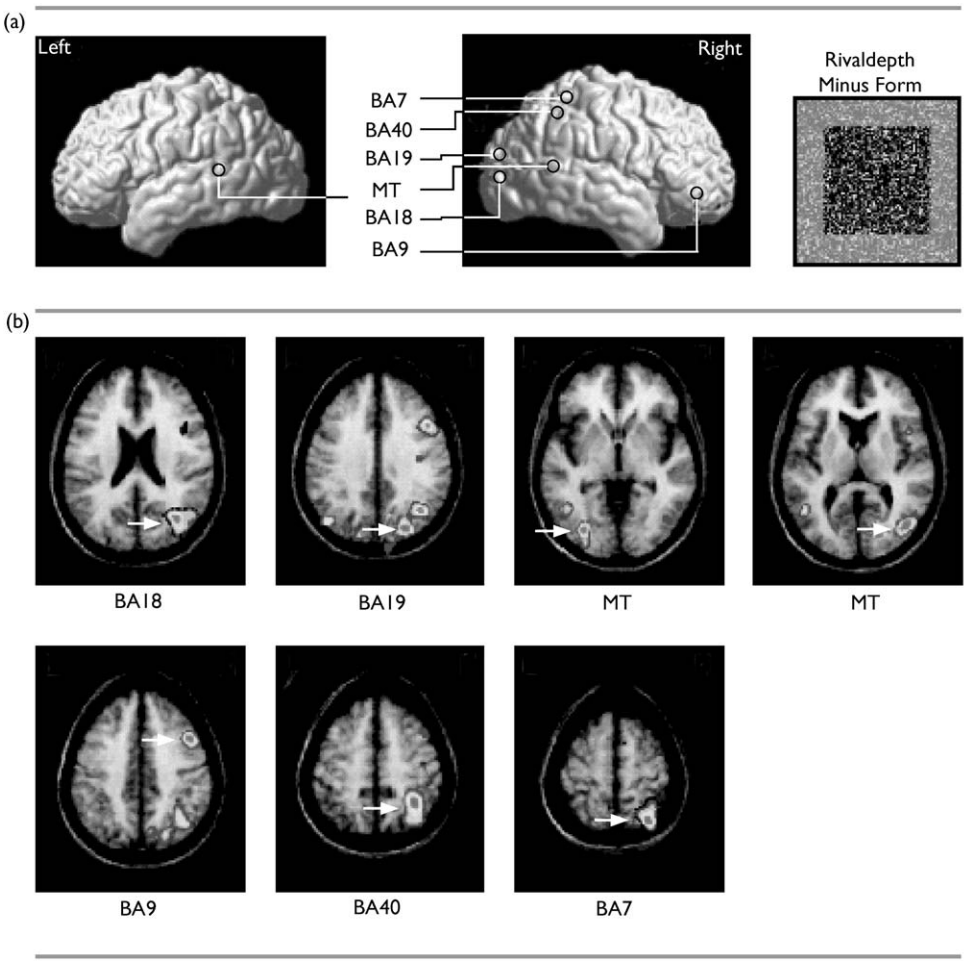

Fig. 1. Active brain sites after the form of the stimulus has been accounted for. (**a**) Coordinates (derived from the sections in b) of activated cortical regions are placed on 3D cerebral hemispheres. The luminance-based stereogram is on the right. (**b**) Sections showing the activation sites (arrows).

with earlier reports showing the lateralization of stereoscopic processing in the human brain [8–12].

Our results revealed that the frontal cortex, predominantly in the right hemisphere, is metabolically activated by rival-luminance stereograms. Frontal lobe activity during exposure to stimuli that produce a sensation of depth has also been noted by others investigators [8–11,13]. However, patients who have been subjected to a right frontal lobectomy do not have difficulty extracting depth information from positional disparity-based stereograms [14], suggesting that the frontal cortex is not directly involved in the processing of stereoscopic information. It is interesting to note that sustained attention is associated with increased neural activity in the prefrontal region of the right hemisphere [15,16]. It can therefore be argued that frontal lobe activation during stereoscopic stimulation is simply an indicator of the attentional requirements of the visual task as opposed to a true representation of stereodepth information processing.

We show for the first time that the depth information derived from retinal luminance rivalry is treated in the same regions of the human brain as that generated by random-dot stereograms containing horizontal disparities [8–13,17,18]. The neuronal components of the occipital, parietal and temporal lobes that are activated by luminance and positional disparity-based stimuli constitute the occipito-parietal pathway or dorsal stream, which is known to play a crucial role in spatial perception [19]. The brain regions comprising this dorsal pathway appear to be hierarchically organized (in monkeys, [20] and in humans [8,21–24]) in that the visual inputs originating from V1 are sequentially processed in V2, V3, MT, the medial superior temporal area and finally the parietal cortex.

In conclusion, we show that the anatomical structures of the human brain that mediate stereoscopic vision form a neural pathway comprising areas in the occipital, parietal and temporal cortices. Our data provide strong evidence to show that stereodepth analysis are primarily carried out in the right cerebral hemisphere. The findings further demonstrate that the cortical neurons implicated in depth perception can be activated by visual inputs that are disparate in terms of luminance or their spatial location on the retina. It would now be interesting to demonstrate with single-cell recordings that the neural elements selectively activated by binocular horizontal disparity also respond to retinal luminance rivalry.

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Acknowledgements: This work was supported by grants from le Ministère de l'Education du Québec (Fonds FCAR) and the Danish medical research council. The authors wish to thank Dr M.-H. Grosbras for her help in recording ocular movements and analyzing the data.