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The functional basis of ocular dominance: functional MRI (fMRI) findings

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Abstract

Changes in cortical metabolism and cerebral perfusion may be recorded non-invasively with functional magnetic resonance imaging (fMRI). In pilot experiments, using fMRI with photic stimulation, we found differences between activated areas when the left or the right eye was stimulated separately. In this study we investigated whether this could be explained by ocular dominance. We studied 26 healthy volunteers (mean age 23.3 ± 3.5 years). Ocular dominance was determined by means of the near-far alignment test. fMRI-measurements consisted of a double-slice gradient echo sequence. Slices were acquired placed parallel on either side of the calcarine fissure. Visual stimulation was done with goggles with two LED matrices (red light, 8 Hz); each in front of one eye. In each subject, the left and right eye were stimulated separately and together, in a randomly alternating order. Twenty-two subjects showed activation, of whom eight subjects had a dominant left eye and 14 a dominant right eye. In general the size of the activated area was bigger upon stimulation of the dominant eye. The difference with the area upon stimulation of the non-dominant eye was statistically significant in the right eye dominant group. These results indicate that the dominant eye actually activates a larger area of the primary visual cortex than the non-dominant eye. This provides for the first time a functional basis for the concept of ocular dominance.

Keywords: Functional magnetic resonance imaging; Ocular dominance; Blood oxygenation

Changes in cortical metabolism and cerebral perfusion may be recorded non-invasively with functional magnetic resonance imaging (fMRI). The possibilities of the blood oxygenation level dependent (BOLD) fMRI technique were first investigated by Ogawa et al. [10,11]. The technique makes use of the fact that de-oxyhemoglobin acts as an intravascular paramagnetic contrast agent [18]. Using fMRI successful early attempts have been made to visualize the activated human visual cortex upon photic stimulation [2,3,7,8,12]. In most fMRI studies of the visual system both eyes were stimulated, with the exception of the study by Hedera et al. [6] in which monocular and biocular photic flash stimulation was administered to albinos and controls. No studies have been reported in which activation patterns upon monocular stimulation are compared.

Since there is a semi-decussation of the optic fibers at the optic chiasm (except in albinos), stimulation of either eye reaches both cerebral hemispheres. However, in several pilot experiments, we observed that the bilateral activated area in the visual cortex differed when the left or the right eye was stimulated [16]. In this study we investigated whether this could be explained by ocular dominance, a concept first described by Porta in 1593 [14], in which the input of one eye is favored over the other.

Twenty-six healthy volunteers (14 male, 12 female, mean age 23.3 ± 3.5 years, range 19–32 years) without ocular refraction anomalies, history of vision loss or color blindness underwent a complete visual stimulation study.

Ocular dominance was determined by means of the near-far alignment test first described by Porta [14]. In this test the subject is asked to hold a pencil in one hand directly in front of himself. Then, the subject is asked to align the tip with a point on a distant wall with both eyes

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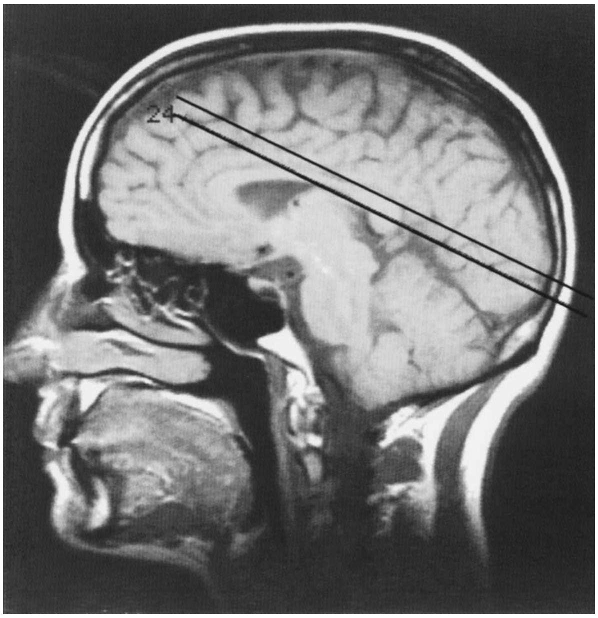

Fig. 1. Illustration of the placement of the two slices of the fMRI measurement, on either side of the calcarine sulcus.

open. The subject is then asked to alternatively close one eye. Only when the dominant eye is open and the other eye closed, the tip of the pencil will remain in good alignment with the point on the wall. This test is repeated with the pencil in the other hand. When in doubt, a variant of Miles test [9] was administered, in which the subject is asked to focus on a point on a distant wall through a hole formed by the opposed thumb and index finger of one hand. Then the hand is moved towards the face while focusing on the same point, until one of the eyes is reached, which indicates the dominant eye.

The studies were done on a 1.5 T Siemens SP63 (Siemens, Erlangen, Germany) using a standard cp head coil. Subjects were positioned in the magnet using the standard equipment and immobilized with foam cushions. In all three directions subjects were checked for positioning with a localizer scan at the beginning of each study. Next, sagittal images were acquired to detect the calcarine fissure and first order shimming was performed manually. The fMRI-measurements consisted of a double-slice flow-compensated (read direction and through-plane) fast low angle shot sequence [5] (TR, 91 ms; FA, 15° in order to reduce inflow-effects [4]; TE, 60 ms; slice thickness, 5 mm; FOV, 250 mm; matrix, 128^2 interpolated for display purposes to 256^2; interslice gap, 1 mm; acquisition time, 14 s). Two slices were acquired placed parallel on either side of the calcarine fissure (Fig. 1). In each measurement, 25 images of both slices were acquired in an alternating manner: five during rest, five during visual stimulation, and so on. All subjects underwent this visual paradigm three consecutive times: left and right eye were stimulated separately and together, in a randomly alternating order. They were wearing modified goggles (Grass Instruments, Quincy, MA, USA) with two 5 × 6 LED matrices, each in front of one eye. It was made sure that the goggles fitted all subjects well and subjects were instructed to lie completely still during the study and to keep their eyes open. During the rest periods, subjects were lying in the dark, since the goggles were turned off and no light from outside could reach the eyes. During the stimulation periods, the goggles were turned on and the visual field of either eye individually or both eyes simultaneously was illuminated with a flashing red light (8 Hz). In an earlier study, this procedure showed to have a low intra-subject variation for stimulation of both eyes [15]. At the end of each study, anatomical images were acquired at the same location as the fMRI images.

During postprocessing, images were corrected for possible small translational movement artifacts with a simplified version of the algorithm described by Woods et al. [19], correcting for in-plane translations. Activation was detected with the correlation method [1]. A box car function with the same on-off period as the stimulus was used as a reference. No delay was used since acquisition time

Table 1

Ratios l/b and r/b and mean signal increases of the activated areas upon monocular stimulation

Subject number	1/b	r/b	% Signal change left eye	% Signal change right eye
Right eye dominant group				
1	0.62	0.76	5.60	7.30
2	0.28	0.49	6.30	8.20
3	0.22	0.64	5.10	5.20
4	0.35	0.75	8.00	6.50
5	0.65	0.55	5.50	5.90
6	0.55	0.67	6.10	6.90
7	0.72	0.61	6.60	7.60
8	0.88	0.18	6.30	3.80
9	0.02	0.44	5.00	5.30
10	0.00	0.94	0.00	12.30
11	1.70	1.77	4.00	5.00
12	0.76	0.87	6.30	6.50
13	0.66	0.82	5.80	5.50
14	0.41	0.50	5.00	5.40
Means ± SD	0.56 ± 0.43	0.71 ± 0.39*	5.40 + 1.82	6.53 ± 2.03
Left eye dominant group				
1	0.85	0.46	5.30	4.40
2	0.67	0.13	5.30	4.10
3	1.09	0.67	7.10	5.00
4	0.55	0.48	4.60	4.40
5	0.17	0.34	5.60	7.10
6	0.22	0.30	4.90	4.00
7	0.88	0.69	5.00	5.10
8	1.26	0.90	5.40	5.00
Means ± SD	0.71 ± 0.36	0.50 ± 0.25	5.40 ± 0.76	4.89 ± 0.99

Most subjects show the smallest area of activation and lowest signal increase with stimulation of the non-dominant eye and the largest area and highest signal increase when the dominant eye is stimulated. Note that in most subjects the largest area is activated upon biocular stimulation; $^*P = 0.04$ for the difference with stimulation of the left eye (two-sided Wilcoxon signed rank test).

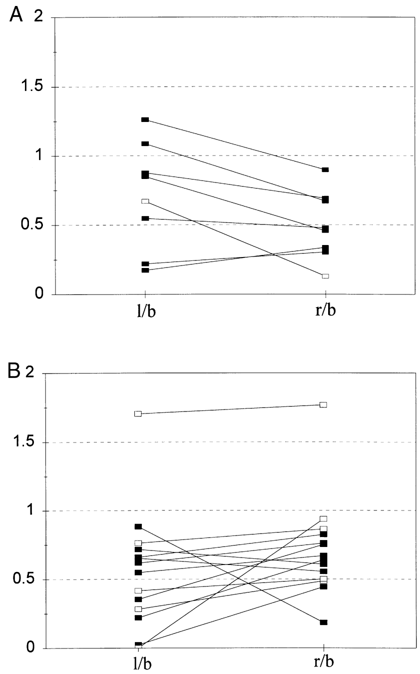

Fig. 2. (a) Ratios l/b and r/b for the group with a dominant left eye (n = 8). Six subjects show a larger area activated when the dominant eye is stimulated (l/b>r/b) compared to the other eye. (b) Ratios l/b and r/b for the group with a dominant right eye (n = 14). Eleven subjects show a larger area activated when the dominant eye is stimulated (r/b>l/b) compared to the other eye.

was longer than the expected hemodynamic response time. Areas were considered as being activated when the correlation value was 0.5 or higher ($P < 0.01$ per pixel) and when the area consisted of at least four connected pixels showing activation. Next, the size of the total activated area in the occipital region was measured for each paradigm.

To take into account the large intersubject variability of visual activated areas [15], ratios of the size of the activated areas during stimulation of the right and left eye separately divided by the size of the activated area upon biocular stimulation, respectively given as r/b and l/b, were calculated, when comparing monocular stimulation results.

Three subjects did not show activation upon both monocular stimulation paradigms. Two of them also showed no activation upon biocular stimulation. Twenty-three subjects showed activation in the biocular and at least one monocular paradigm. Of these, eight subjects had a dominant left eye, 14 a dominant right eye and one subject had no eye dominance. The 22 subjects with a dominant eye that showed activation were used for further analysis.

In Table 1 the ratios l/b and r/b and mean signal increases of activated areas are given for the two groups of subjects. In Fig. 2a,b, the l/b- and r/b-ratios are plotted for the groups with a dominant left and a dominant right eye, respectively. Only in the dominant right eye group the

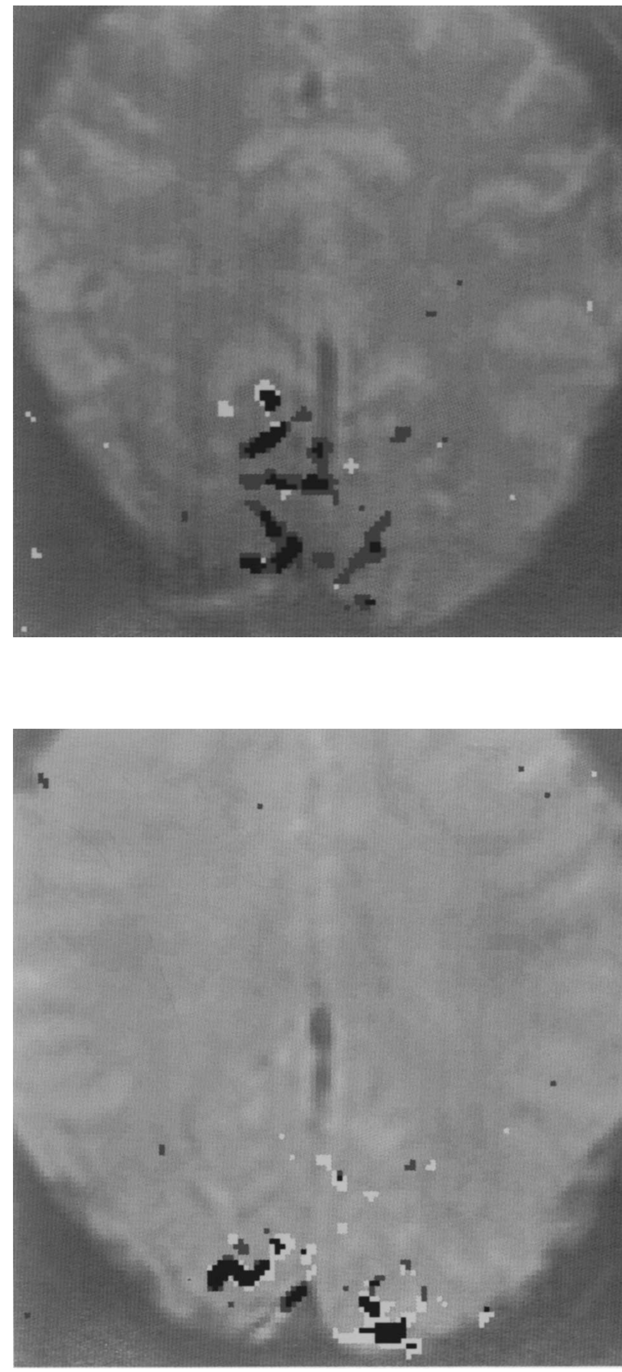

Fig. 3. Upper part, activated areas in the visual cortex of a subject with a dominant right eye, projected on an anatomical image. In yellow is the area that is activated both during stimulation of the right and the left eye. The area in red is activated upon stimulation of the left eye and the area in blue is activated when the right eye (the dominant eye) was stimulated. Note that nearly the complete area that is activated when the left eye is stimulated, is also activated with stimulation of the right (dominant) eye and that the activation pattern upon stimulation of the dominant eye is more extensive. Lower part, as in upper part for a subject with a dominant left eye. Again, the activated area of the dominant eye contains the area of the other eye, but is greater in size. Note that the pattern of activation is inverted compared to the subject with the dominant right eye.

difference in size between the activated areas upon left and right eye stimulation reaches statistical significance, with higher values upon right eye stimulation.

In Fig. 3 two examples are shown of activated areas upon stimulation of the left and the right eye. The upper half of the figure shows the activated areas in the occipital region of one slice of a subject with a dominant right eye. In the lower half, activated areas are seen of a subject with a dominant left eye. The subjects in the figure clearly showed more activation when the dominant eye was stimulated.

We found that subjects showed more activation in both primary visual cortices when the predetermined dominant eye was stimulated, although the difference only reached statistical significance in the right eye dominant group.

Our findings cannot be explained by incorrect positioning since all three paradigms were done during one scanning session without repositioning between paradigms. The high variability of the primary visual cortex in humans [17] can explain differences between the sizes of activated areas upon binocular stimulation on fMRI between subjects, as we showed earlier [15], but not the differences found in activation of both visual cortices upon stimulation of each eye separately. The fact that we did not find a significant difference in the left eye dominant group is probably due to the small sample size.

In previous fMRI studies that used photic stimulation thus far usually both eyes were stimulated. In the study of Hedera [6] the six controls showed symmetric patterns of activation during monocular stimulation, but no attention was given to whether the size of the activated area differed between left and right eye stimulation.

The concept of ocular dominance was already formulated in 1593 by Porta [14], and is of important, but mostly unconscious, practical use to everyone, but received little research attention thus far. There exist several forms of ocular dominance, but sighting dominance is the most commonly measured and most reliably obtained form [13]. In an extensive overview of the pertinent literature, Porac and Coren found that 65% of the subjects studied showed right eye dominance, 32% left eye dominance and 3% no consistent dominance, which is in accordance with the findings in our small sample [13]. It is independent of age, race, cultural differences, and handedness or footedness. To our knowledge, no pathophysiological correlate for this concept has ever been found. Our fMRI results indicate that the dominant eye actually activates a larger area of the primary visual cortex than the non-dominant eye. This may prove fMRI to be a useful tool in studying the functional basis of ocular dominance. Moreover, our results point to the fact that in fMRI studies using photic stimulation of the visual cortices ocular dominance should be taken into account, especially when studies are designed to discover differences between the left and right visual pathways, i.e. in studies of optic neuritis in multiple sclerosis patients.

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