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Eye Dominance Predicts fMRI Signals in Human Retinotopic Cortex

Janine D. Mendola^{1,2,3} and Ian P. Conner²

¹ Department of Radiology and Center for Advanced Imaging, West Virginia University, Morgantown, West Virginia 26506-9236, USA

² Department of Neurobiology and Anatomy, West Virginia University, Morgantown, West Virginia 26506-9236, USA

³ Department of Ophthalmology, West Virginia University, Morgantown, West Virginia 26506-9236, USA

Abstract

There have been many attempts to define eye dominance in normal subjects, but limited consensus exists, and relevant physiological data is scarce. In this study, we consider two different behavioral methods for assignment of eye dominance, and how well they predict fMRI signals evoked by monocular stimulation. *Sighting eye dominance* was assessed with two standard tests, the Porta Test, and a 'hole in hand' variation of the Miles Test. *Acuity dominance* was tested with a standard eye chart and with a computerized test of grating acuity. We found limited agreement between the sighting and acuity methods for assigning dominance in our individual subjects. We then compared the fMRI response generated by dominant eye stimulation to that generated by non-dominant eye, according to both methods, in 7 normal subjects. The stimulus consisted of a high contrast hemifield stimulus alternating with no stimulus in a blocked paradigm. In separate scans, we used standard techniques to label the borders of visual areas V1, V2, V3, VP, V4, V3A, and MT. These regions of interest (ROIs) were used to analyze each visual area separately. We found that percent change in fMRI BOLD signal was stronger for the dominant eye as defined by the acuity method, and this effect was significant for areas located in the ventral occipital territory (V1v, V2v, VP, V4). In contrast, assigning dominance based on sighting produced no significant interocular BOLD differences. We conclude that interocular BOLD differences in normal subjects exist, and may be predicted by acuity measures.

Keywords

visual cortex; Portus; Miles; amblyopia; V1

The concept of eye dominance in normal subjects, i.e., a consistent preference or advantage for using one of the two eyes, is well known and has been discussed for decades [19,23,27]. Nevertheless, the functional significance of eye dominance remains elusive, and, if present, it

Corresponding Author: Janine Mendola, Ph.D, Associate Professor, Center for Advanced Imaging, HSC-S, Radiology, PO Box 9236, West Virginia University School of Med. Morgantown, WV 26506-9236, tel: (304)-293-0731, fax: (304)-293-7142, jmendola@hsc.wvu.edu, <http://www.hsc.wvu.edu/wvucn/people/Mendola/>.

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must differ from hemispheric laterality because the brain is not lateralized for the eyes, as it is for the limbs. Three definitions of eye dominance are generally recognized [41,6]. 1. The eye used for sighting objects. 2. The eye with better acuity or contrast sensitivity. 3. The eye that dominates during binocular rivalry. However, these three measures of eye dominance are generally not recognized to correlate with each other [6,19], and the correlation between eye dominance and handedness is weak [27,1].

Sighting eye dominance is popularly measured with the Portus Test, that determines which monocular view of a near target best matches the binocular view, or the Miles Test (hole-in-hand variant), that determines which monocular view of a distance target in an aperture matches the binocular view. These simple measures generally correlate, and test-retest reliability is high, but in recent years other complicating factors have been discovered. For example, sighting dominance can depend on the gaze angle, as well as the hand used for pointing in certain cases [15,3]. The lack of consensus has lead several authors to express a rather pessimistic view of the significance of eye dominance: "Other than being the 'preferred' eye in some viewing situations, the sighting dominant eye has no special role for visual or oculomotor processes for the normal population" [19].

In addition to the inconsistencies associated with sighting eye dominance, it has been unclear if this concept would have relevance to the processing of simple visual stimuli in retinotopic areas of visual cortex. One prior fMRI study by Rombouts et al., of 22 subjects found a slightly larger extent of activation in both occipital lobes when the sighting dominant eye was stimulated (with LED goggles) compared to the other eye [32]. Similar conclusions were reached by two VEP studies using monocular checkerboard stimuli [35,37]. However, none of these studies compared the different methods for assigning eye dominance.

In our own fMRI studies, we have measured brain activity during monocular stimulation in normal subjects, and have observed a difference between the amount of activity evoked by each eye. The question we address here is whether these differences can be explained by eye dominance. Moreover, we directly compared alternate methods for the assignment of eye dominance to determine which definition would better predict the BOLD signal evoked by simple hemifield stimuli.

Specifically, we studied 7 adults aged 21 to 30 years (3 male, 4 female) with normal or corrected to normal visual acuity, each passing a clinical eye exam. Informed consent was obtained from all subjects in a project approved by the WVU Institutional Review Board for the Protection of Human Subjects (protocol #14788), in accordance with the Declaration of Helsinki. The subjects' handedness was assessed with the Edinburgh Survey [24]. Each of these subjects had previously participated in an experiment to define the boundaries of multiple retinotopic visual areas using standard phase-encoded methods [34] that have been previously described by us in detail [5]. We defined regions of interest (ROI) corresponding to retinotopic areas V1, V2, (ventral and dorsal branches) V3, VP, V3A and V4v. The eccentricity range of these ROIs was approximately 1–15°. In addition, the motion sensitive area MT was also delineated using a separate scan of low contrast moving versus stationary circular square-wave gratings [39]. Specifically, Freesurfer software was used to draw the ROIs for each hemisphere on flattened patches of occipital cortex (<http://www.nmr.mgh.harvard.edu/freesurfer>). However, all ROIs exist in native (folded) coordinates when measurements are made. The necessary surface reconstructions of each subject's cerebral cortex were generated from high resolution anatomical images obtained in a separate experiment, using previously validated techniques [10,5]. ROIs are applied to the native images by reversing this cortical surface transformation, in combination with manual registration of the functional images to the high resolution anatomical images.

For each subject, we determined the dominant eye according to the sighting criteria as well as according to the visual acuity criteria. *Sighting eye dominance* was determined with the Portus and Miles Test [30,8,14] (Table 1). For the Portus test the dominant eye was the eye whose monocular view of a near vertical target (finger or pencil) best matched the binocular view. For the Miles test the dominant eye was the eye whose monocular view of a distant target (the corner of a room where walls meet ceiling) seen through an aperture (created by subject's hands) best matched the binocular view. We encountered no subject with conflicting results from the Portus and Miles tests.

Acuity dominance was determined based on visual acuity measured with the Snellen eye chart (Lombart Instruments, Norfolk VA, USA) as well as by a test of grating acuity, if Snellen was the same in each eye. The average of Snellen and grating acuity was always better in the eye assigned to be dominant. For grating acuity, stimuli were generated using the Psychophysics Toolbox [2,26] and MATLAB 5 for Macintosh OS 9 and a calibrated high resolution CRT monitor (Hitachi Super Scan 812) at 5.9 meters. For each trial, the subject viewed two temporally sequenced screens identified by audible tone, containing either a vertical sinusoidal grating (80% physical contrast, subtending 8 degrees of visual angle) or an isoluminant gray screen. Grating contrast was ramped-on over 200 msec, plateaued for 500 msec, and then ramped-off over 200 msec. The subject identified the grating epoch using a two-alternative forced choice paradigm (2-AFC). Spatial frequency was varied by a staircase procedure that increased spatial frequency following two correct responses and decreased spatial frequency after one incorrect response (2-up, 1-down), terminating after seven reversals. The acuity threshold was taken as the geometric mean of the last four reversals. The results of behavioral testing are shown in Table 1. Notably, in our sample, there was little correspondence between sighting and acuity dominance assignment, consistent with previous results [28,31,25; but see 7]. Specifically, 4 out of 7 subjects showed opposite sighting versus acuity dominance assignments.

To further pursue this discrepancy we compared these behavioral results with the results of monocular fMRI. Subjects were scanned in a General Electric 3 Tesla MR scanner using a visual surface coil (Nova Medical, Inc., Wilmington, MA), as has been previously described [5]. We acquired 20 interleaved oblique 4 mm fMRI slices with 1.72×1.72 mm in-plane resolution, oriented perpendicular to the calcarine sulcus, beginning at the occipital pole. We used a spiral gradient echo sequence (TE = 40 ms, Flip Angle = 65 deg, TR = 2000 ms, 128 time points) [12].

The experiment used a blocked design, showing 16 s periods of a high-contrast, radially moving wedge in the left or right visual hemifield, alternating with a fixation-only condition (total 256 sec). The wedge spanned either 100 degrees or 160 degrees, and spared the central 0.5 degrees of visual space, where the fixation target was presented (Figure 1A). These stimuli were designed to avoid the cortical representation of the vertical meridian, similar to those used in an earlier study of the ipsilateral visual field representation in subjects with normal vision [40]. In this study, we report data from the hemisphere contralateral to the stimulated field in order to focus on direct, retinogeniculate input to visual cortex.

We achieved monocular stimulation with the Avotec SilentVision dichoptic projector (Stuart, FL, USA). The stimuli were generated using the Psychophysics Toolbox and MATLAB 5 for Macintosh OS 9 on a PowerMac G4 computer with dual SVGA display drivers (output resolution = 832×624 pixels, 30 deg horizontal $\times$ 23 deg vertical). Subjects used the eyepieces' built-in optical correction to achieve image focus. Therefore, all testing was done with subject's best corrected acuity. For each functional scan, one eyepiece displayed the stimulus and fixation target while the other displayed an isoluminant gray screen. The fixation target was a small arrowhead (0.5 deg) pointing in one of four directions, randomly changing direction

approximately every 4 s. Subjects reported the orientation of the fixation point with a 4-button fiber-optic pad. In addition, fixation stability was measured during the scans and no interocular differences in accuracy were observed. Left and right eye stimulation was alternated during each experiment. Eight total runs were collected.

The statistical analysis was completed using the FS-FAST software tools freely available at <ftp://ftp.nmr.mgh.harvard.edu/pub/flat/fmri-analysis>. For each subject, MR images were first motion-corrected and then intensity-normalized using the average in-brain voxel intensity. Then, for each eye, the epochs corresponding to the high-contrast wedge, and those corresponding to the fixation point alone were selectively averaged. To visualize results on the cortical surface, a voxel-wise *F*-test was performed to compute the significance of the difference between the fMRI signal for the wedge stimulus and the control (Figure 1B). The statistical maps were viewed as *p* values on a logarithmic pseudocolor scale ($0.0003 < p < 0.01$, uncorrected). For display purposes, the low end of the scale was set at the minimum typically used, but all of the regions that we emphasize in the results include regions with considerably higher thresholds. For quantitative analysis, the previously defined ROIs were applied to the data, and the time course of the fMRI signal was averaged for all voxels within. Then the average magnitude for the stimulus and control epochs were calculated separately, and the percent signal change computed, factoring in a 4-second hemodynamic delay. The process was performed separately for stimulation of each subject's left and right eye.

We then compared the percentage increase in fMRI BOLD signal generated by dominant eye to that generated by non-dominant eye stimulation, using either the *sighting* or the *acuity* method of dominance assignment. These signal changes were averaged across subjects for each visual area separately, and analyzed statistically. The results are shown in Figures 2 and 3. When the acuity method was used, significant interocular differences in evoked fMRI signal were seen in V1v and V2v, favoring the dominant eye with a two-tailed paired *t*-test (Figure 2A). All seven subjects showed greater activation for the dominant eye based on acuity in V1v and V2v (Table 1). When all ROIs were averaged, 6 out of 7 subjects showed greater activation for the acuity dominant eye. These data were further analyzed by computing an eye dominance index, defined as the interocular difference in percent signal divided by the sum of each eye's percent signal. This index was significantly greater than zero for V1v, V2v, VP, and V4v (Figure 2B). Although this index was calculated from fMRI signal magnitude, it also strongly correlated across all subjects with an analogously calculated index of number of significant vertices, in all ROIs ($R^2 = 0.62$, $p < 0.0002$), supporting the known relationship between signal magnitude and extent of activation. In contrast to these results, when eye dominance was assigned based on sighting, there was no clear relationship between BOLD signal and dominance (Figure 3).

Our finding that fMRI signals are better predicted by visual acuity than by sighting dominance does not necessary conflict with Rombouts et al. [32]. Those authors found that sighting dominance did predict their fMRI, but they did not use acuity dominance as a comparison. Moreover, in studies with a small number of subjects, like ours, there could be differences in the correlation between acuity and sighting dominance due to random sampling bias. We consider our results to be provocative, but requiring replication with a larger number of subjects. It is also possible that brain regions not assessed in our study might show a better correlation with sighting than acuity dominance. For example, evidence linking sighting eye dominance and motor control suggests that areas of parietal cortex might show such a correlation during appropriate tasks [27,29,33]. These ideas could be addressed in future fMRI studies.

Our current results indicated a correlation between visual acuity and the ventrally located visual areas. Previous studies have in fact highlighted the anatomically interconnected ventral stream

as a critical neural substrate of high acuity pattern perception. In particular, the correlation between V1 and hyperacuity has been firmly established [9]. V2 and V4 are also strongly implicated in pattern and shape perception [e.g., 11,21,8]. Finally, it may be relevant that many subtle aspects of form perception are known to develop relatively late in humans and not mature until adolescence [16,36]. Perhaps a slight advantage in the effective connectivity of one eye over the other can develop over the course of experience.

The focus of this study was to compare left versus right eye stimulation in the same cortical hemisphere. A few other studies have also made this comparison, but in a different context. One study by Liu et al. assessed the fMRI asymmetry between left versus right eye stimulation using the voxel-wise *t*-statistic [18]. However, they did not relate that data to behavioral eye dominance. Other studies have attempted to resolve separate ocular dominance regions with high spatial resolution [e.g., 20,13,4]. However, these studies have not generally reported on fMRI asymmetry between the two eyes or behavioral eye dominance in normal subjects [but see 20]. Like Liu et al. [18], our methods pooled signals across multiple ocular dominance columns to compute mean eye dominance in larger cortical regions, in order to assess global differences in evoked signal between eyes. Therefore, this type of ‘eye dominance’ measure is more global than specific anatomical or electrophysiological measures from single neurons. We fully expect that our fMRI signal comes from both binocular and monocular neurons.

We also point out that two previous fMRI studies using monocular full-field stimuli have focused on differences between signal evoked from the hemisphere contra- versus ipsilateral to the tested eye [22,38]. In general, a small advantage was found for the contralateral hemisphere, and this was thought to be due to the purely monocular crescent of the peripheral nasal retina or a more generalized increase in the connectivity and sensitivity of the nasal retina (although attention factors are also possible [33]). Our study was designed differently, to make intra-hemisphere comparisons, so we cannot perform the same comparison between hemispheres. Moreover, with our stimuli, we found no difference between the strength of evoked fMRI signal in our ROIs between nasal and temporal retina, so those conditions were combined.

This study is the first to compare two different definitions of eye dominance with the fMRI signals evoked from monocular visual stimulation. We conclude that interocular differences in evoked fMRI BOLD signals are found in normal subjects. Measures based on BOLD magnitude were similar to those based on activation extent. For this dataset, acuity-based dominance predicted interocular BOLD differences in ventral occipital-temporal areas. This topic of normal eye dominance is readily amenable to future studies with fMRI using a variety of stimuli, and such physiological measures are needed to fully understand the functional significance. In addition, understanding the extent of eye dominance in normal subjects is important for the study and interpretation of monocular clinical eye diseases like amblyopia.

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Figure 1.

A. Depiction of stimuli. B. The fMRI signal evoked from dominant eye of one subject (DW) shown on flattened representation of left occipital pole ($0.01 > p > 0.0003$). Light and dark grays indicate the unfolded gyri and sulci, respectively. ROIs are shown overlaid, clockwise from upper left, V3A, V3, V2d, V1d, V1v, V2v, VP, V4v, and MT.

Figure 2.

A. Magnitude of fMRI signals produced by monocular stimulation of each eye for each visual area, when eye dominance is defined based on visual acuity. Solid bars = dominant eye; open bars = non-dominant eye. Asterisk indicate significant difference between monocular conditions ($p < 0.05$). Ventrally located areas are placed on the left side of the figure while dorsal areas are placed on the right. B. Dominance index for each visual area. Asterisk indicate significant difference from zero ($p < 0.05$).

Figure 3.

A. Magnitude of fMRI signals produced by monocular stimulation for each visual area, when eye dominance is defined based on sighting tests. Solid bars = dominant eye; open bars = non-dominant eye. No differences are significant. B. Dominance index for each visual area; none are significantly different from zero.

Table 1

Handedness, Eye Dominance Assignments, Acuity and fMRI Measures

Subject	Hand	Acuity Dom.	Sighting Dom.	DE Snellen (MAR)	NDE Snellen (MAR)	DE Grating (MAR)	NDE Grating (MAR)	DE Avg. (MAR)	NDE Avg. (MAR)	DE - NDE (MAR)	DE - NDE (BOLD)
AZ	R	R	R	1.00	1.00	0.62	0.70	0.81	0.85	0.04	0.13
AW	R	R	L	1.00	1.00	0.83	1.00	0.92	1.00	0.08	0.11
NC	R	R	L	1.25	1.25	0.69	0.83	0.97	1.04	0.07	0.05
DW	R	L	L	0.80	1.00	0.77	0.77	0.79	0.88	0.09	0.04
LW	R	L	R	1.25	1.60	1.03	0.77	1.14	1.19	0.05	0.29
IC	R	L	R	0.80	1.00	0.75	0.77	0.78	0.88	0.10	0.09
CA	L	L	L	1.00	1.25	0.74	1.04	0.87	1.15	0.28	0.29

DE = Dominant Eye; NDE = Non-dominant eye

MAR = minimum angle of resolution in arc min

Avg = Average of Snellen and Grating acuity

Note: for each subject the eye with best acuity for each test is shown in bold text

DE-NDE = difference between eyes

BOLD = fMRI percent signal change in V1v and V2v