Rapid communication

Ocular dominance reverses as a function of horizontal gaze angle

Aarlenne Z. Khan, J. Douglas Crawford *

York Centre for Vision Research, CIHR Group for Action and Perception, and Departments of Psychology, Biology and Kinesiology & Health Science, York University, Toronto, Ont., Canada M3J 1P3

Abstract

Ocular dominance is the tendency to prefer visual input from one eye to the other [e.g. Porac, C. & Coren, S. (1976). The dominant eye. *Psychological Bulletin 83*(5), 880–897]. In standard sighting tests, most people consistently fall into either the left- or right eye-dominant category [Miles, W. R. (1930). Ocular dominance in human adults. *Journal of General Psychology 3*, 412–420]. Here we show this static concept to be flawed, being based on the limited results of sighting with gaze pointed straight ahead. In a reach–grasp task for targets within the binocular visual field, subjects switched between left and right eye dominance depending on horizontal gaze angle. On average, ocular dominance switched at gaze angles of only 15.5° off center. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Ocular dominance; Eye position; Eye–hand coordination; Sighting dominance

1. Introduction

Although two eyes with overlapping visual fields are required for stereo vision (Howard & Rogers, 1995), this arrangement complicates the selection of a unique egocentric reference point for vision and action (Flanders, Helms-Tillery, & Soechting, 1992; Milner & Goodale, 1995), particularly in visuomotor systems that show an oculocentric organization (Mushiake, Tanatsugu, & Tanji, 1997; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Batista, Buneo, Snyder, & Anderson, 1999; Vetter, Goodbody, & Wolpert, 1999). For example, many common sighting tasks — such as pointing a finger or aiming a gun — force subjects to align just one eye with the target and ignore visual input from the other eye. Despite methodological quibbles, the classic sighting literature agrees that most subjects show consistent ocular dominance in such tasks (Miles, 1930; Crider, 1944; Walls, 1951; Coren & Kaplan, 1973;

Porac & Coren, 1976; Osburn & Klingsporn, 1998), with 53–82% of the population preferring the right eye and 18–40% preferring the left eye (0–22% showing no preference) (Porac & Coren, 1976). However, all such results were obtained with the eyes pointed straight ahead.

For the most part, ocular dominance is considered to be static (Porac & Coren, 1976; Osburn & Klingsporn, 1998). However, this view has been questioned by recent studies, which suggest that ocular dominance varies with different depth planes as well as the position of objects relative to the two eyes in binocular vision (Erkelens & Van De Grind, 1994; Erkelens, Muijs, & van EE, 1996). Here, we provide data that further suggest that the static concept of ocular dominance needs to be replaced by a more dynamic model, one that depends on eye position as well.

We employed a reach–grasp task that combined the basic elements of eye–hand coordination in grasping (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Flanders et al., 1992; Milner & Goodale, 1995; Henriques et al., 1998; Vetter et al., 1999) with a classic method for evaluating ocular dominance in sighting (Fig. 1) (Crider, 1944). Within the bounds of this task,

---

* Corresponding author. Present address: Department of Psychology, York University, 4700 Keele Street, Toronto, Ont., Canada M3J 1P3. Tel.: +1-416-7362100, ext. 88621; fax: +1-416-7365814.

E-mail address: jdc@yorku.ca (J.D. Crawford).

we tested the effect of horizontal gaze angle, head orientation, handedness and the order of stimulus presentation on ocular dominance.

2. Methods

Ten subjects (aged 19–28) were tested in our basic task, with a subset of these proceeding to other experiments (see Section 3). Nine subjects were right-handed and one was left-handed. Normal optical prescriptions were worn. The following procedures were pre-approved by the York University Human Participants Review Sub-committee. Each subject sat with the head stabilized by a bite-bar, facing a semicircular array of target stimuli 53 cm from the center of the interocular line. Targets consisted of white disks, 3 cm in diameter, numbered one to 11, placed at eye level at 10° intervals horizontally from 50° left to 50° right. Five 4.7-cm metal rings were suspended over each target so that the disk was visible and centered in the rings.

In the basic paradigm (Fig. 1), a number randomly chosen from one to 11 was called out; the subject first fixated on the named target (A), then reached out to grasp the first ring (B) using their dominant hand. The subject was instructed to maintain fixation on the stimulus (as confirmed by scleral search coil signals in five subjects (Henriques et al., 1998)) and then bring the ring all the way back to their face in a smooth fluid motion, without allowing it to cross their line of sight (C,D). This implicitly forced them to choose the left (....) or right (----) gaze line, bringing the ring to only one or other eye — i.e. the one that is dominant (Crider, 1944).

During preliminary tests, subjects reported occurrences of double vision while bringing the rings toward their eyes. This caused some confusion, i.e. some subjects paused and/or switched hand trajectories midway. However, we found that this mainly occurred when the ring was brought toward the eyes slowly. We, therefore, instructed the subjects to bring the ring toward them as quickly and smoothly as possible without crossing their line of sight to the target. This diminished the perception of double vision and eliminated 'trajectory switching'.

For five subjects, the eye to which the subject brought the ring was quantified by recording the 3-D trajectory of the subjects' arm (Henriques et al., 1998). However, in most cases we used a simpler method that proved to be equally accurate, wherein the experimenter viewed the ocular dominance selection process via a mirror and coded the choice manually onto a computer. After the eye selection was recorded, the subject dropped the ring and a new target number was called out. In every case, a total of ten repetitions per stimulus were used, with a brief rest period midway in the
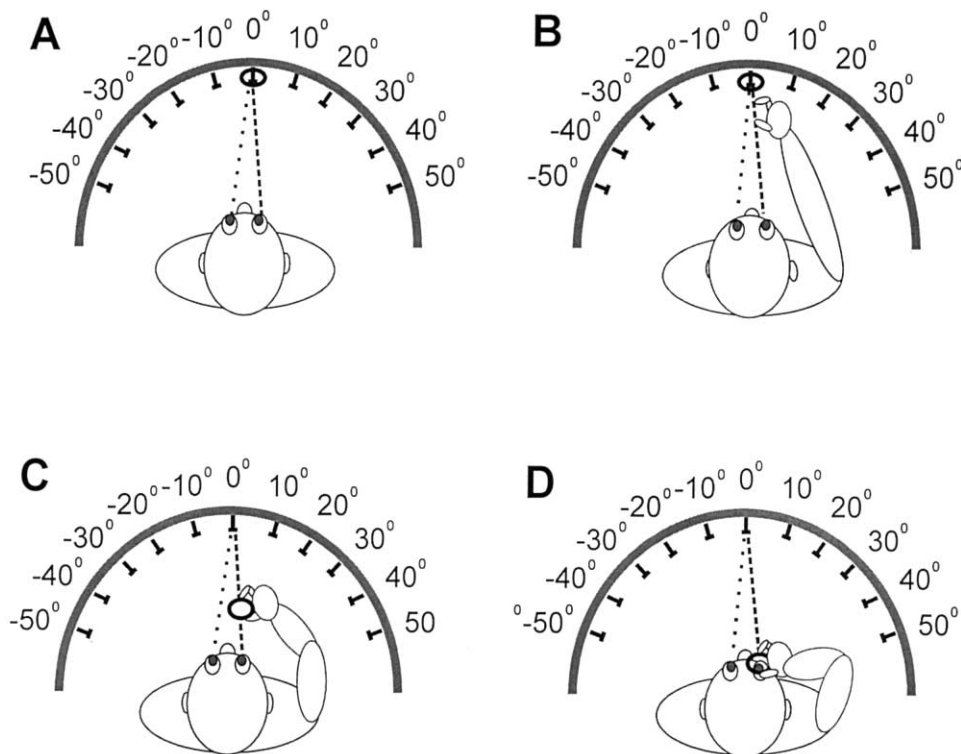

Fig. 1. Method: a number from one to 11 was called out; the subject fixated that particular target (A), then reached out to grasp the first ring (B). The subject was instructed to bring the ring all the way back to their face in a smooth fluid motion, without allowing it to cross either line of gaze (C,D).

a Raw Data from All Subjects
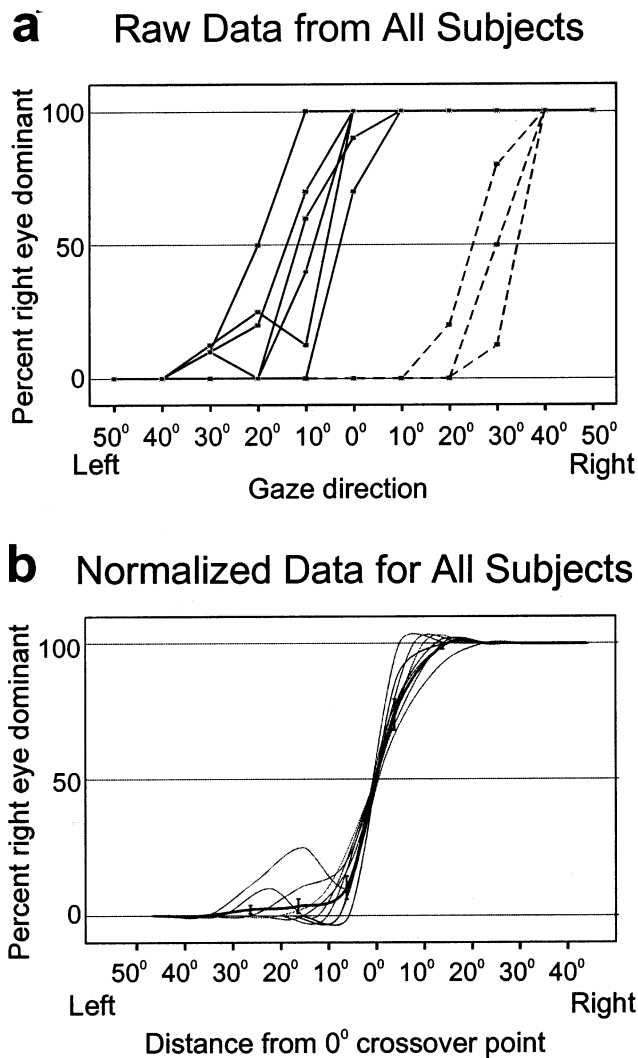

b Normalized Data for All Subjects

Fig. 2. Gaze position-dependence of ocular dominance in Experiment 1. (a) Raw data collected from ten subjects. The abscissa shows the angle of gaze direction, the ordinate shows the percent of trials where the right eye was dominant (where 0% indicates that the left eye was always dominant). —: Right eye dominant at center. ----: Left eye dominant at center. Two of the right-eye dominant subjects' data overlapped exactly with one other. (b) Same data normalized (shifted so that the 50% crossover point aligns with zero on the abscissa) and smoothed. The thick line shows the average across all subjects ± S.D. Two subjects could not see target 11 (50° right) with their left eye, but this proved to be well in the periphery of their 50% crossover point.

experiment while the experimenter replaced the hoops. Variations on this basic paradigm are described in Section 3.

3. Results

3.1. Experiment 1: gaze angle dependence

As required by the task, subjects only brought the ring to one or other eye for a given trial. However,

across trials, all ten of our subjects aligned the ring with both eyes — the left eye on some trials and right eye on other trials. This always occurred in a highly stereotypical fashion, showing a switch of ocular dominance as a function of eye position (Fig. 2a). Subjects showed a rather abrupt transition from left to right eye dominance; seven to the left (—; i.e. right eye dominant at center) and three to the right (----; i.e. left eye dominant at center). Since only one of the latter left-eye dominant subjects was left-handed and all the other subjects were right-handed, these results were only loosely related to hand preference.

Before each experiment, it was verified that the subject could see most or all of the targets with both eyes. All targets up to 40° eccentricities left and right were visible to both eyes for all subjects, but three subjects were unable to see one or both targets located 50° from center with both eyes. Data from these subjects were included in the graphs for completeness but made no difference to the overall curve since their reversal points (shift from left to right eye dominance) occurred several target steps before 50°. In fact, the average gaze angle, where subjects were equally likely to bring the ring to the left or right eye, was shifted by only 15.5° ± 11.3° (± S.D.) in the direction of the non-dominant eye, i.e. well within the binocular visual field.

To average the data, the individual subject's crossover functions were horizontally aligned at 0°. The data were then smoothed to remove any angularities without affecting the data. As illustrated in Fig. 2(b), this process revealed a consistent, quasi-sigmoidal ocular dominance function. The thick line shows average performance (± S.E.). This convention is used henceforth to illustrate the data from three further control experiments, which study other relevant aspects of ocular dominance.

3.2. Experiment 2: cognitive set

We wondered if these functions were "hard-wired" into the eye–hand coordination program or whether they were affected by some sort of top-down decision processes, i.e. a cognitive set. If cognitive set was a factor, then one would expect that performance in the previous trial would affect the dominance state in the next trial, if the next trial were predictable. To test for this, we presented targets sequentially in left-to-right (—) versus right-to-left (----) order (Fig. 3a) for six subjects. These two conditions produced a small relative shift (3.8° ± 3.2°) in the ocular transition curve, but this was not statistically significant for any target. Thus, cognitive set did not appear to be an important factor in determining the ocular dominance function in this task.

a Sequential Stimulus Order

b Left/Right Hand Performance

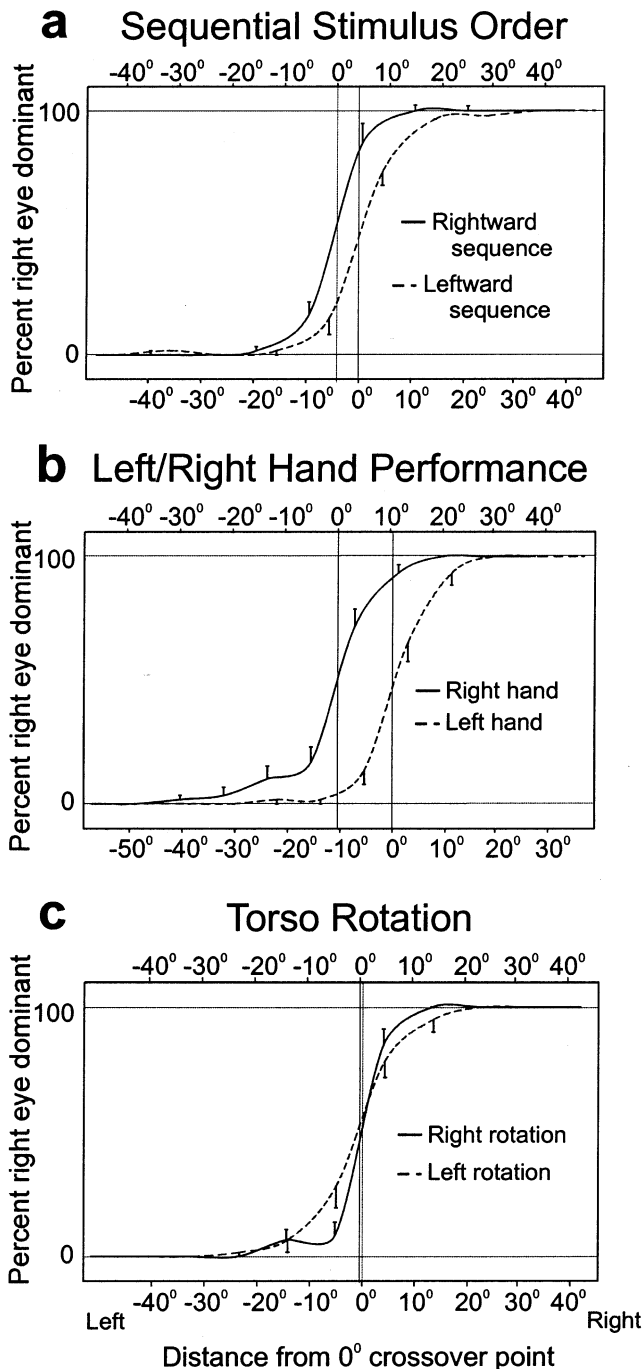## c Torso Rotation

Distance from 0° crossover point

Fig. 3. Effect of stimulus order, handedness, and arm/body position. (a) In this experiment, the targets were presented in sequence going from left-to-right and back again. Data are plotted using conventions used in Fig. 2(b), except that the average crossover curves for the leftward sequence of targets (bottom scale; ---) are shifted from the rightward sequence curves (top scale; —) by the average actual shift between these data at the 50% crossover point. (b) Similar plot for Experiment 3, where the random presentation was made using both the left and right hand. In this case, the average crossover curves for the left hand (bottom scale; ----) and right hand (top scale; —) are shifted with respect to each other by the average actual shift between these data at the 50% crossover point. (c) Similar plot contrasting the average curve for a random, dominant hand task with the head still fixed in its original position but the body rotated 20° to the left (bottom scale; -----) or right (top scale; —).

3.3. Experiment 3: hand effect

In our third experiment, we tested the effect of hand used, repeating the original random target presentation for both hands (Fig. 3b) for six subjects yielding two transition curves. They completed a set of ten trials in which they alternated using their left or right hand (five trials each). When using the left hand, subjects exhibited a curve (----) was shifted by $12.2° \pm 12.4°$ to the right relative of the right-handed curve (—) (this means that subjects tended to choose the left eye more with the left hand and vice-versa, as one might expect). Using a t-test, we found the curves to be significantly different from one another ($P \leq 0.002$). Thus, within a given individual, the choice of hand had a moderate but consistent effect on the dominance transition curve, i.e. the hand used changed the point at which the reversal of dominance occurred, however the shape of the curve itself remained unchanged.

3.4. Experiment 4: coordinates

The latter experiment raised the possibility that our effect was not due to eye position at all, but rather arm position. To control for this, seven subjects repeated the random target task with the head in the same fixed central position; once with the body rotated 20° left and once with the body 20° right. If the 'ocular dominance' curve was actually determined by arm position (or otherwise fixed in body coordinates), this should produce a 40° shift between these two curves. However, no such shift was observed (Fig. 3c). The two resulting curves were shifted apart by only $0.8° \pm 1.4°$, with no statistically significant effect at any point. Thus, arm position did not play a role in this task; rather ocular dominance was a function of eye position in head coordinates.

4. Discussion

Our main finding is that ocular dominance reverses as a function of ocular dominance, with some modulation determined by the hand used. The functional significance of these results seems to be straightforward. Although the binocular field of view is $\approx 100°$ when looking straight ahead, as the eyes rotate peripherally, the monocular field of the inward turning eye is increasingly occluded (largely by the nose) by up to 50%. Therefore, it makes sense for the eye–hand coordination system to choose the eye with best overall field of view. At the same time, in most subjects this gating function is shifted slightly to the left or right (Fig. 2a), most likely to avoid dominance 'flickering' at the commonplace central range (i.e. the range tested in previous studies). This strategy allows for preferential gating of

visual input from the eye with the best field of view, while avoiding ambiguity at the most common central gaze position.

From the current data, several questions arise that can only be answered through further experimentation, but invite some discussion here. First, is this gaze-dependent phenomenon specific to the current task, common to everyday sighting tasks, or common to all binocular behaviors, including perceptual phenomenon like binocular rivalry? Second, given the nature of our task, is its underlying mechanism visual or motor?

We regard it most fruitful to consider these questions in terms of the overall visuomotor transformation for the task. For example, if this phenomenon is a strategy particular to certain sighting tasks, then one might look for its underlying mechanism within particular sub-modules of the 'dorsal stream' posterior parietal complex (Milner & Goodale, 1995). Moreover, the finding that the hand used (right versus left) had a slight modulation in our task could suggest visuomotor mechanisms as far downstream as frontal cortex. (Although one cannot, on the basis of our results, rule out the possibility that the hand effect was due to vision of the hand.) Another possibility is that the hand may have occluded vision to the eye contralateral to the target at more extreme angles (from center front) while bringing the ring towards the eyes. This may also have caused the shift in the reversal curves between the left and right hand.

In light of the potential general utility of optimizing the eye with the best vantage point, it seems reasonable to hypothesize that the dynamic gating of ocular dominance could be a general effect and this process could be initiated as early as layer IV of primary visual cortex, where neural signals from the two eyes first combine (Hubel, 1979). In support of this, Trotter and Celebrini (1999) found that gaze direction modulates the response gain of neurons in V1. Moreover, Rombouts, Barkhof, Sprenger, Valk, and Scheltens (1996) found that the dominant eye activated a greater proportion of the primary visual cortex than the non-dominant eye, as measured by fMRI. Similarly, Menon, Ogawa, Strupp, and Ugurbil (1997) found the human equivalent to primate ocular dominance columns, which also showed a prevalence of right eye dominant pixels in the ocular dominance columns of right eye dominant subjects.

Of course, none of these speculations informs us about the basic mechanism for the gating of ocular dominance. One possibility is that the gating that we observed in this study was related to the greater size of the retinal image on the closer eye. At our average 15.5° crossover point, the difference in the visual angle was 0.03° or $\approx 3\%$. Ogle (1938) showed that differences of $< 2\%$ in the visual angle of the two eyes affected the perceived slant of targets. These differences of image size may be a potential mechanism causing these shifts in ocular dominance, however this cannot be determined without further experimentation.

In our view, a more robust source of gating information would be direct internal estimates of eye position. Such information, in the form of eye position 'gain fields', has been observed in such diverse cortical areas as V1 (Trotter & Celebrini, 1999), parietal cortex (Snyder, Grieve, Brotchie, & Anderson, 1998; Batista et al., 1999) and frontal cortex (Mushiake et al., 1997; Tehovnik, 1995). Previous studies have emphasized the possible role of these signals in the maintenance of the spatial constancy of visual stimuli (Nakamura, Chung, Graziano, & Gross, 1999; Battaglia-Mayer, Ferraina, Mitsuda, Marconi, Genovesio, Onorati, Lacquaniti, & Caminiti, 2000).

Our study suggests that these signals may also perform another important role — in the selective gating of monocular information and the selection of the egocentric visual reference point. Thus, these dynamic gating mechanisms would be an important yet uninvestigated aspect of visual-motor neuroscience.

Acknowledgements

References

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centred coordinates. *Science*, *285*, 257–260.

Battaglia-Mayer, A., Ferraina, S., Mitsuda, T., Marconi, B., Genovesio, A., Onorati, P., Lacquaniti, F., & Caminiti, R. (2000). Early coding of reaching in parietooccipital cortex. *Journal of Neurophysiology*, *83*, 2374–2391.

Coren, S., & Kaplan, C. P. (1973). Patterns of ocular dominance. *American Journal of Optometry and Archives of American Academy of Optometry*, *50*, 283–292.

Crider, B. A. (1944). A battery of tests for the dominant eye. *Journal of General Psychology*, *31*, 179–190.

Erkelens, C. J., & Van De Grind, W. A. (1994). Binocular visual direction. *Vision Research*, *34*(22), 2963–2969.

Erkelens, C. J., Muijs, A. J. M., & Van Ee, R. (1996). Binocular alignment in different depth planes. *Vision Research*, *36*(14), 2141–2147.

Flanders, M., Helms-Tillery, S. I., & Soechting, J. F. (1992). Early stages in a sensorimotor transformation. *Behavioural Brain Science*, *15*, 309–362.

Henriques, D. Y. P., Klier, E. M., Smith, M. A., Lowy, D., & Crawford, J. D. (1998). Gaze-centered remapping of remembered visual space in an open-loop pointing task. *Journal of Neuroscience*, *18*, 1583–1594.

Howard, I. P., & Rogers, B. J. (1995). *Binocular vision and stereopsis*. New York: Oxford Press.

Hubel, D. H. (1979). The visual cortex of normal and deprived monkeys. *American Scientist*, *67*, 532–542.

Menon, R. S., Ogawa, S., Strupp, J. P., & Ugurbil, K. (1997). Ocular dominance in human V1 demonstrated by functional magnetic resonance imaging. *Journal of Neurophysiology*, *77*(5), 2780–2787.

Miles, W. R. (1930). Ocular dominance in human adults. *Journal of General Psychology*, *3*, 412–420.

Milner, A. D., & Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford: Oxford University Press.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size and orientation of objects for grasping in neurons in monkey parietal area AIP. *Journal of Neurophysiology*, *83*, 2580–2601.

Mushiake, H., Tanatsugu, Y., & Tanji, J. (1997). Neuronal activity in the ventral part of premotor cortex during target-reach movement is modulated by direction of gaze. *Journal of Neurophysiology*, *78*, 567–571.

Nakamura, K., Chung, H. H., Graziano, M. S. A., & Gross, C. G. (1999). Dynamic representation of eye position in the parieto-occipital sulcus. *Journal of Neurophysiology*, *81*, 2374–2385.

Ogle, K. N. (1938). Induced size effect. I. A new phenomenon in binocular space-perception associated with the relative sizes of the images of the two eyes. *Archives of Ophthalmology*, *20*, 604–623.

Osburn, D. M., & Klingsporn, M. J. (1998). Consistency of performance on eyedness tasks. *British Journal of Psychology*, *89*, 27–37.

Porac, C., & Coren, S. (1976). The dominant eye. *Psychological Bulletin*, *83*(5), 880–897.

Rombouts, S. A., Barkhof, F., Sprenger, M., Valk, J., & Scheltens, P. (1996). The functional basis of ocular dominance: Functional MRI (fMRI) findings. *Neuroscience Letters*, *221*, 1–4.

Snyder, L. H., Grieve, K. L., Brotchie, P., & Andersen, R. A. (1998). Separate body- and world-referenced representation of visual space in parietal cortex. *Nature*, *394*, 887–891.

Tehovnik, E. J. (1995). The dorsomedial frontal cortex: eye and forelimb fields. *Behavioural Brain Research*, *67*, 147–163.

Trotter, Y., & Celebrini, S. (1999). Gaze direction controls response gain in primary visual-cortex neurons. *Nature*, *398*, 239–242.

Vetter, P., Goodbody, S. J., & Wolpert, D. M. (1999). Evidence for an eye-centered spherical representation of the visuomotor map. *Journal of Neurophysiology*, *81*, 935–939.

Walls, G. L. (1951). A theory of ocular dominance. *American Medical Association and Archives of Ophthalmology*, *45*, 387–412.