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A binocular perimetry study of the causes and implications of sensory eye dominance

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ABSTRACT

Sensory eye dominance (SED) reflects an imbalance of interocular inhibition in the binocular network. Extending an earlier work (Ooi & He, 2001) that measured global SED within the central 6°, the current study measured SED locally at 17 locations within the central 8° of the binocular visual field. The eccentricities (radius) chosen for this, “binocular perimetry”, study were 0° (fovea), 2° and 4°. At each eccentricity, eight concentric locations (polar angle: 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°) were tested. The outcome, an SED map, sets up comparison between local SED and other visual functions [monocular contrast threshold, binocular disparity threshold, reaction time to detect depth, the dynamics of binocular rivalry and motor eye dominance]. Our analysis shows that an observer’s SED varies gradually across the binocular visual field both in its sign and magnitude. The strong eye channel revealed in the SED measurement does not always have a lower monocular contrast threshold, and does not need to be the motor dominant eye. There exists significant correlation between SED and binocular disparity threshold, and between SED and the response time to detect depth of a random-dot stereogram. A significant correlation is also found between SED and the eye that predominates when viewing an extended duration binocular rivalry stimulus. While it is difficult to attribute casual factors based on correlation analyses, these observations agree with the notion that an imbalance of interocular inhibition, which is largely revealed as SED, is a significant factor impeding binocular visual perception.

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1. Introduction

Binocular vision contributes to our abilities of figure-ground segmentation and fine depth discrimination. Retinal images of 3-D visual scenes from the two eyes usually have the same mean contrast energy over time. This suggests that the binocular visual system is built to treat the inputs from the two eyes equally in order to achieve a high proficiency. Indeed, for a standard observer, stimuli with equal contrast in each eye induce superior binocular perception than stimuli with unequal contrast levels (Halpern & Blake, 1988; Legge & Gu, 1989; Ooi & He, 1996; Schor & Heckman, 1989; Smallman & McKee, 1995; Wolfe, 1986; Xu, He, & Ooi, 2010, 2011a, 2011b).

The interocular integration and inhibitory mechanisms that are part of the binocular neural network support a variety of binocular visual functions including summation, fusion, stereopsis and suppression. Both mechanisms work together, with the interocular inhibitory mechanism suppressing dissimilar images from one or both eyes, to achieve a coherent 3-D representation of the visual

scene. Binocular visual processing is adversely affected in an observer whose eyes (monocular channels) are not equally strong, presumably, because the stronger eye has a larger weighted contribution to the binocular neural network. We have shown, for instance, that human observers with sensory eye dominance (SED) due to a significant degree of unbalanced interocular inhibition have reduced binocular depth perception (Xu, He, & Ooi, 2010, 2011a, 2011b). The magnitude of SED varies in the population along a continuum. At one end of the continuum, observers with minor SED have clinically normal stereoacuity, while at the other extreme observers with strong SED have little or no stereopsis. An extreme example of observers with strong SED is the clinical population with amblyopia. [The amblyopic eye also suffers from a host of visual deficits related to contour integration, spatial and temporal vision, as well as those related to higher level visual functions (e.g., Ciuffreda, Levi, & Selenow, 1991; Kiorpes & McKee, 1999; Kovacs, 2000; Levi, 2006).]

While SED is likely established during early visual development and persists through adulthood, there exists plasticity in the underlying neural circuitries (e.g., Harauzov et al., 2010; Hubel & Wiesel, 1970; Suzuki & Grabowecy, 2007). Using a psychophysical approach, we have found, for example, that training adult observers over a 10-day period using a novel push-pull perceptual

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learning protocol significantly reduced their SED. In addition, the observers' binocular depth perception improved after the training (Xu, He, & Ooi, 2010, 2011a, 2011b).

SED is often measured in the laboratory by presenting the observer with a binocular rivalry stimulus that triggers the interocular inhibitory network to cause suppression of one or the other dissimilar half-image (Leat & Woodhouse, 1984; Ooi & He, 2001; Xu, He, & Ooi, 2010; Yang, Blake, & McDonald, 2010). Fig. 1a and b illustrate an example of two pairs of dichoptic orthogonal gratings that measure SED at a peripheral retinal location (Xu, He, & Ooi, 2010). In the test, stimulus (a) is displayed for a brief interval and the observer reports the orientation of the perceived grating disk (while the other grating disk is suppressed). For the next test trial, and depending to the observer's report in the preceding trial, the contrast of the horizontal grating in the left eye (LE) is appropriately adjusted with an adaptive procedure (QUEST, Watson & Pelli, 1983) before stimulus (a) is again presented. This is done after each trial until the observer experiences an equal percentage of seeing the two gratings (point of equality). Since the contrast of the vertical grating in the right eye (RE) is kept at a constant level, the contrast of the horizontal grating obtained at the point of equality is referred to as the LE balance contrast. But as the LE balance contrast could also be caused by a difference in sensitivity to the grating orientation (e.g., better sensitivity to the vertical orientation), it is necessary to measure the RE balance contrast. This is obtained by switching the vertical and horizontal gratings between the two eyes as in stimulus (b), and adjusting the contrast of the horizontal grating now in the RE until the point of equality is obtained. The difference between the LE and RE balance contrast values defines the SED.

The method of measuring local SED described above was adapted from an earlier method employed in our laboratory to measure global SED (Ooi & He, 2001). In that earlier method, we

used a larger stimulus display that consisted of six pairs of dichoptic green and red gratings with orthogonal orientation and distributed around the fixation (~ 2.3 – 2.9° from the fovea). All six grating disks in each half-image had the same color and intensity level. To obtain an eye's balance contrast, say the RE's, we kept the intensity of the gratings in the LE half-image constant and tested the RE with six levels of grating intensity using the method of constant stimuli. Then the two half-images were switched between the eyes to obtain the LE balance contrast. It was found that among the observers tested, the strong (dominant) eye as determined by the global SED method is not always the same as the strong eye determined by the sighting method. The latter, sighting method, measures the perceived visual direction and is typically used to reveal motor eye dominance (MED). This finding indicates that the SED and MED are likely caused by two relatively independent processes. Furthermore, the strong eye in SED is not always more superior in detecting a monocular contrast grating, or in perceiving the brightness of a suprathreshold monocular grating. It is thus concluded that the global SED can be attributed to an interocular imbalance of the underlying inhibitory neural mechanism.

This paper extends the study of Ooi and He (2001) to investigate the mechanism of SED, using a technique we coin as "binocular perimetry". To do so, we measured SED locally at the fovea and 16 peripheral retinal locations along eight radial directions spanning the entire 360° visual field (Fig. 1c). Three other visual function tests were also conducted. These were tests of monocular contrast detection threshold, binocular depth (stereopsis) detection threshold and reaction time, and binocular rivalry tracking. Together, these measurements allow us to reveal the spatial characteristics of local SED and of the other three visual functions across the visual field. Moreover, we gain knowledge of the correlations between the local SED and these other visual functions. Such knowledge provides valuable insights into the interocular

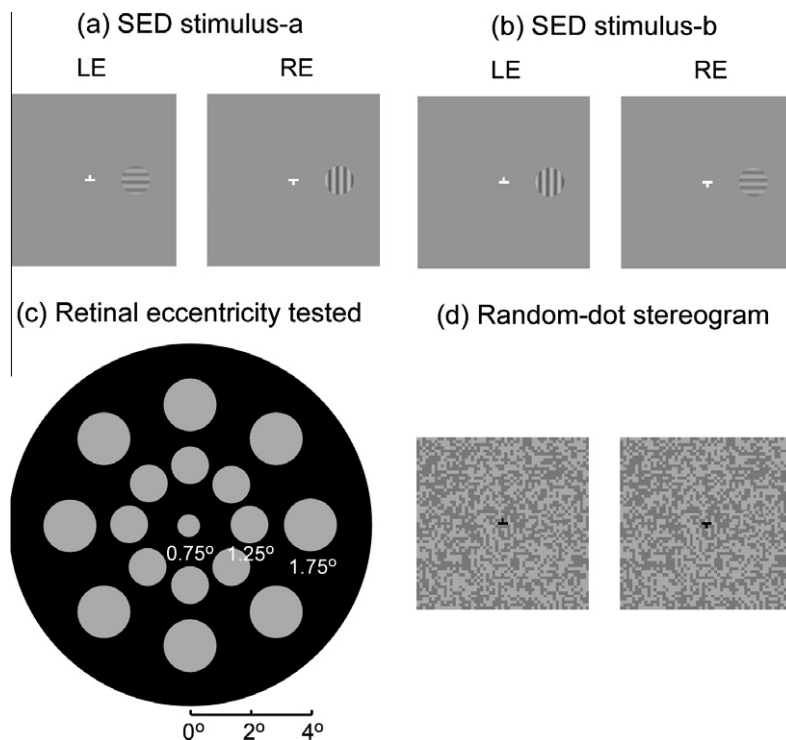


Fig. 1. (a and b) Sample stimulus used for measuring SED. (a) The LE balance contrast is obtained by varying the horizontal grating contrast while keeping the contrast of the vertical grating seen by the RE constant (SED stimulus-a). The LE balance contrast is reached when the two eyes obtain an equal percentage of perceiving the two gratings (point of equality). (b) The gratings are switched between the two eyes to obtain the RE balance contrast (SED stimulus-b). The difference between the LE and RE balance contrast values defines the SED. (c) Schematic of the binocular visual field indicating the 17 retinal locations tested with the stimulus sizes appropriately scaled to account for the cortical magnification factor. (d) The random-dot stereogram used to measure stereo threshold.

inhibitory mechanism underlying SED and binocular visual functions. For example, the measurement of local monocular contrast thresholds can provide clues as to whether the local SED could also be explained by an interocular difference before the convergence of monocular information. Lastly, we compared the observers' MED with foveal SED and found that both types of dominance may not necessarily reside in the same eye.

2. Materials and methods

2.1. Design

The stimuli were generated using either a Macintosh G4 or Mac-Pro computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), and presented on a 19-in. flat CRT monitor. The resolution of the monitor was set at 1280 × 1024 @ 100 Hz refresh rate for all experiments, except for the stereopsis experiment where the resolution was 2048 × 1536 @ 75 Hz. All observers (one author and eleven naïve observers with informed consent) had self-reported normal binocular vision. We measured each observer's performance in the following order: local SED, interocular difference in contrast threshold, stereo disparity threshold and stereo reaction time at 17 retinal locations (Fig. 1c). The 17 retinal locations were the fovea and eight concentric locations (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°), 2° and 4°, respectively, from the fovea. Additionally, we measured the observers' motor eye dominance (MED) and binocular rivalry performance with central viewing. For the binocular rivalry experiment, only ten out of the twelve observers were tested, as two observers were unavailable for the test.

2.2. Observers

All 12 adult observers (ages 21–29) had normal or corrected-to-normal visual acuity (at least 20/20), clinically acceptable fixation disparity (≤ 8.6 arc min) and stereopsis (≤ 40 arc sec). They also passed the Keystone vision-screening test. During the experiments they viewed the computer monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm.

2.3. Stimuli and procedure

2.3.1. Interocular imbalance test to measure SED

The stimulus comprised a pair of dichoptic vertical and horizontal sinusoidal grating disks (35 cd/m^2) on a gray background ($11^\circ \times 11^\circ$, 35 cd/m^2) (Fig. 1a). The contrast of the vertical grating was held constant (1.5 log unit) while the contrast of the horizontal grating was variable (0–1.99 log unit). For testing at the 2° or 4° eccentric retinal location, a trial began with central fixation on the nonius target ($0.45^\circ \times 0.45^\circ$, line width = 0.1° , 70 cd/m^2) and the presentation of the dichoptic orthogonal gratings (500 ms), followed by a 200 ms mask ($11^\circ \times 11^\circ$ checkerboard sinusoidal grating, 35 cd/m^2 , 1.5 log unit). It should be noted that the stimulus duration of 500 ms is sufficiently long to activate the underlying interocular inhibitory mechanism (Su, He, & Ooi, 2011a, 2011b; Wolfe, 1983). The testing at the foveal location was similar, except the nonius fixation was removed 200 ms before the presentation of the stimulus. The observer responded to his/her percept by key presses. If a mixture of vertical and horizontal orientation was seen, the observer would respond to the predominant orientation perceived. The horizontal grating contrast was adjusted after each trial with the QUEST procedure and ended after 50 trials (block). When the horizontal grating was presented to the LE (Fig. 1a) we refer to its contrast at equal predominance as the LE's balance contrast. To obtain the RE's balance contrast, the gratings were

switched between the eyes (Fig. 1b). The difference between the LE and RE balance contrast values is defined as the local SED for that tested retinal location. In all, the 17 retinal locations were tested with 34 stimulus combinations (17 locations × 2 eyes/orientation). The order of the retinal location tested was randomized and each location was tested twice.

Because the SED was measured at different retinal eccentricities (0°, 2° and 4°), we applied the cortical magnification factor to the stimulus parameters used for testing. We fixed the grating disk stimuli for the foveal location at 5 cpd and 0.75° (disk diameter). For the eccentric stimulation, the stimuli's spatial frequency and disk diameter were proportionally scaled using the cortical magnification factor given by the formula: target frequency (cpd) = foveal frequency/[1 + eccentricity (°)/3]; target size (°) = foveal size × [1 + eccentricity (°)/3] (Rovamo & Virsu, 1979). Accordingly, [3 cpd, 1.25°] was used for the grating at 2° eccentricity, and [2.14 cpd, 1.75°] was used for the grating at 4° eccentricity. The spatial frequency used for the checkerboard mask was consistent with that of the grating disk.

2.3.2. Monocular contrast detection threshold

The tested eye viewed a monocular sinusoidal grating (35 cd/m^2 , 500 ms) that was oriented either horizontal or vertical. The fellow eye viewed a homogeneous field. The contrast sensitivity test was conducted using a 2AFC method in combination with the QUEST procedure. The 2AFC stimulus presentation sequence was: fixation, interval-1 (500 ms), blank (400 ms), interval-2 (500 ms), blank (400 ms) and mask ($11^\circ \times 11^\circ$ checkerboard sinusoidal grating, 35 cd/m^2 , 1.5 log unit contrast, 200 ms). The monocular grating was presented at one interval while the other interval had a blank field. For testing at the fovea, the nonius fixation was removed 200 ms before the presentation of the stimulus. The observer responded by key press whether he/she saw the grating in interval-1 or -2, and an audio feedback was given. The grating contrast was adjusted after each trial (by QUEST) to obtain the contrast threshold.

The monocular contrast threshold was measured at the same 17 retinal locations used to measure SED. The cortical magnification factor was appropriately accounted for by scaling the grating spatial frequency and disk diameter at each retinal eccentricity (fovea: 5 cpd, 0.75°; 2°: 3 cpd, 1.25°; 4°: 2.14 cpd, 1.75°). A total of 68 stimulus combinations (17 locations × 2 eyes × 2 orientations) were tested in a randomized order. Each stimulus combination was repeated over two blocks of trials (50 trials/block).

2.3.3. Stereo threshold and reaction time

An $11^\circ \times 11^\circ$ random-dot stereogram (dot size = 0.0132° , 35 cd/m^2 , 1.5 log unit contrast) with a variable crossed-disparity disk target was used (disk diameters: 0.75° at fovea; 1.25° at eccentricity 2°; 1.75° at eccentricity 4°) (Fig. 1d). The standard 2AFC method in combination with the staircase procedure was employed to measure the stereo disparity threshold. The temporal sequence of the stimulus presentation was fixation, interval-1 (200 ms), blank (400 ms), interval-2 (200 ms), blank (400 ms), and random-dot mask (200 ms, $11^\circ \times 11^\circ$, 35 cd/m^2). For testing at the fovea, the nonius fixation was removed 200 ms before the presentation of the stimulus. The observer indicated whether the crossed-disparity disk (front depth) was perceived in interval-1 or -2, and an audio feedback was given. Each block comprised 10 reversals (step size = 0.8 arc min, total ~ 50–60 trials), and the average of the last eight reversals were taken as the stereo threshold. Stereo threshold was measured at each of the same 17 retinal locations in a randomized testing order. Each block was repeated twice.

The binocular disparity of the dichoptic disk target used to measure stereo reaction time (RT) was either ± 6 arc min. The disk diameter was appropriately adjusted for cortical magnification as

in the above. The observer began a trial by aligning his/her eyes on the nonius fixation. The target was then presented at one of the seventeen retinal locations (the nonius fixation would be removed 200 ms before the stimulus presentation if the fovea was tested). The observer's task was to press one of two keys immediately upon detecting the stereo disk to indicate whether it was in front or back. Upon his/her response, the stimulus was removed

and a blank screen (400 ms) was presented. This was followed by a mask (200 ms) that ended the trial, after which an audio feedback was given. If depth (target) was not detected, the stimulus timed-out after 2500 ms. Each test block consisted of 60 trials, with 30 front-trials and 30 back-trials that were randomly interleaved. Three blocks were tested at each of the 17 retinal locations.

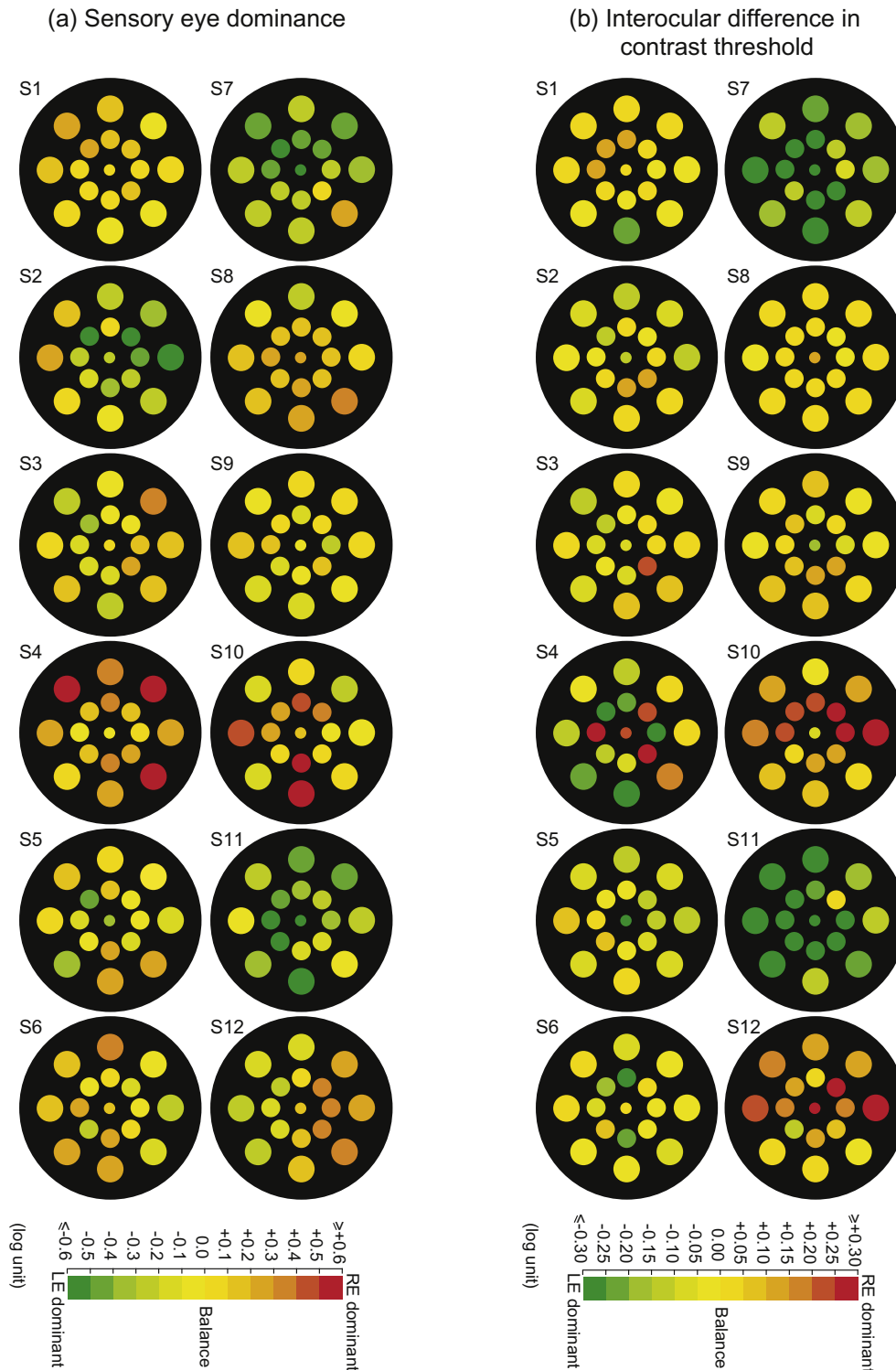


Fig. 2. Binocular visual fields of individual observers showing the distributions of their (a) sensory eye dominance (SED) and (b) interocular difference in contrast threshold, at the 17 tested locations. The data are represented with a green–yellow–red color spectrum that corresponds to the extent and sign of SED or interocular difference in contrast threshold. Red and green, respectively, indicate RE and LE being stronger, while yellow indicates no interocular difference (i.e., balanced). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

To control for the accuracy of response in the RT task, each observer was given several practice blocks until he/she achieved an accuracy of 70% or higher (accuracy is defined as the ratio of correct trials to the total number of trials). Moreover, only correct trials whose response times were longer than 100 ms were used in the final data analysis. Fewer than 0.05% correct trials had an RT of <100 ms. We also found that our observers' average accuracy was quite high (90%) during the test sessions.

2.3.4. Binocular rivalry tracking

The stimulus comprised a pair of dichoptic vertical and horizontal grating disks (1° , 5 cpd, 35 cd/m^2 , 1.99 log unit contrast) surrounded by a $7.5^\circ \times 7.5^\circ$ gray square (35 cd/m^2). The observer aligned his/her eyes on the nonius fixation ($0.45^\circ \times 0.45^\circ$, line width = 0.1° , 70 cd/m^2) to prepare for a trial. He/she then pressed the spacebar to remove the nonius fixation. This was followed 200 ms later, by the presentation of the binocular rivalry stimulus

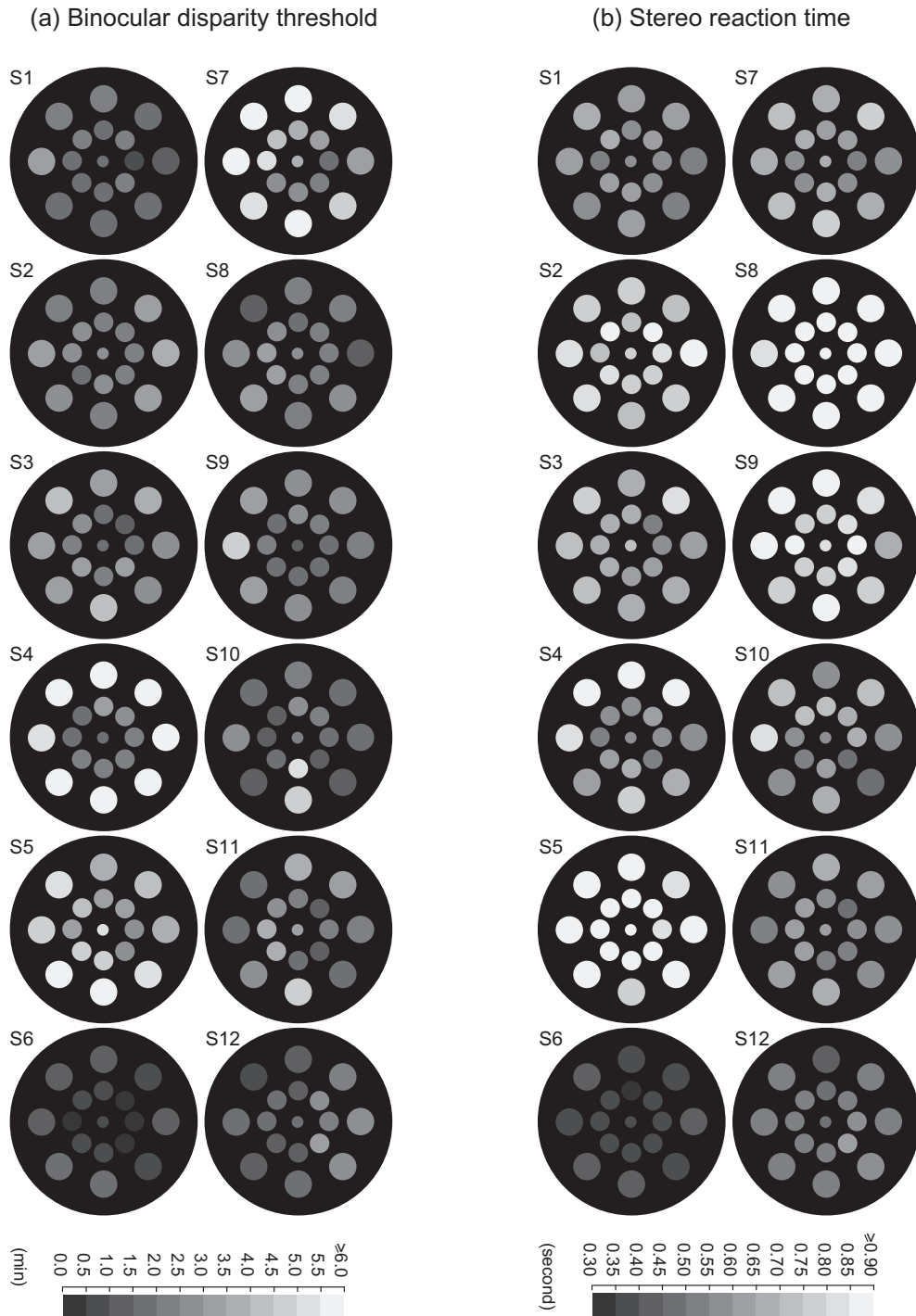


Fig. 3. Binocular visual fields of individual observers showing the distributions of their (a) binocular disparity threshold and (b) reaction time to detect binocular depth. These data are plotted with a dark-light gray shade that represents the different gradients of the data. A smaller measured value is represented with a darker gray shade that is closer to the black background.

(30 s). A 1-s mask ($7.5^\circ \times 7.5^\circ$ checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2 , 1.99 log unit contrast) terminated the trial. The observer's task was to report (track) his/her instantaneous percept of the binocular rivalry stimulus over the 30 s stimulus viewing duration. Depending on the percept, vertical, horizontal, or a mixture of both, he/she would depress the appropriate key until the next percept took over. A total of eight trials were performed (two orientation/eyes \times four repeats).

2.3.5. Motor eye dominance

A variation of the Ring sighting test was used (Borish, 1970; Ooi & He, 2001). To perform the test, the observer brought both hands simultaneously to the front of his/her face at arms length, and formed a ring (2–3 in. in diameter) by bringing together the index finger and thumb from each hand. He/she then sighted a target with both eyes opened through this "ring", while carefully placing the sighted target in the center of the ring. After this, he/she closed each eye alternately to determine whether the right or left eye saw the target as more centered in the ring. The eye that saw the target as more centered is defined as the motor-dominant eye.

3. Results

3.1. Perimetry results of individual observers ($n = 12$)

Fig. 2a and b, respectively, plot each observer's sensory eye dominance (SED) and interocular difference in contrast threshold at the 17 tested locations. The data are represented with a green–yellow–red color spectrum that corresponds to the extent and sign of SED or interocular difference in contrast threshold (red indicates RE being stronger while green indicates LE being stronger). Clearly, most plots have a varying color spectrum rather than a single color. This indicates that SED and the interocular difference in contrast threshold vary across the visual field both in extent and sign. Furthermore, a careful comparison between the SED and interocular difference in contrast threshold measurements at the same test location reveals that they do not always indicate the same eye to be superior. Consider, for example, the results of observer 12 (S12) at the leftmost test location. S12's SED measurement indicates left eye superiority (green) whereas the interocular difference in contrast threshold measurement reveals right eye superiority (red). This finding supports those of our earlier study (Ooi & He, 2001) that a difference in monocular contrast detection between the two eyes is not always correlated with SED. Our SED data are also comparable to those of Leat and Woodhouse (1984) who measured SED along the horizontal meridian at the fovea, 1° , 2° and 4° on the left and right visual field. They found that the sign of SED is not uniform across the retinal locations and there exists individual differences.

Fig. 3a and b, respectively, plot each observer's binocular disparity threshold and reaction time to detect binocular depth. These data are plotted with a dark-light gray shade that represents the different gradients of the data (a smaller measured value has a darker gray shade). As in the SED and interocular difference in contrast threshold data in Fig. 2, the general trend of the depth perception data exhibits an inhomogeneity across the visual field. To further understand the implications of these results and their relationships, we next performed a series of further data analyses. These are presented below.

3.2. Analysis of visual field eccentricity and symmetry

We first averaged the data from the same retinal eccentricity for each of the measured function (SED, interocular difference in

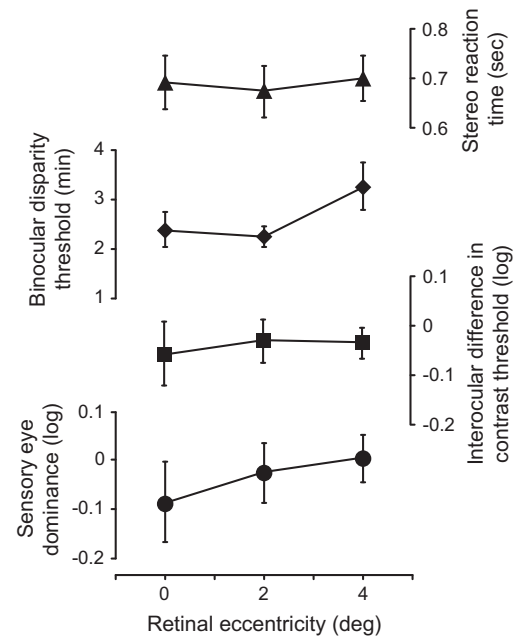


Fig. 4. Assessing the effect of eccentricity. Data from the same retinal eccentricity for each of the measured function (SED, interocular difference in contrast threshold, binocular disparity threshold, and stereo reaction time) were averaged and plotted as a function of the tested retinal eccentricity (fovea: 0° ; parafovea: 2° , 4°). Only binocular disparity threshold increases significantly with retinal eccentricity. Please note that for convention, we use a negative value (of SED or interocular difference in contrast threshold) to indicate LE superiority and a positive value to indicate RE superiority.

contrast threshold, disparity threshold, and stereo reaction time). These are plotted in Fig. 4 as a function of the tested retinal eccentricity (fovea: 0° ; parafovea: 2° , 4°). We then applied one-way ANOVA with repeated measures to each set of test results. We found that binocular disparity threshold (diamonds) significantly increases with retinal eccentricity [$F(2,22) = 4.187$, $p = 0.029$]. On the other hand, the remaining three measurements do not reliably change with eccentricity ($p > 0.15$) (SED: circles; interocular difference in contrast threshold: squares; reaction time to detect depth: triangles).

We also examined whether there is a performance asymmetry between the upper and lower visual field, or left and right visual field. Paired t -test analysis reveals that the reaction time to detect binocular depth in the right visual field is 23 ms faster than in the left visual field. However, this difference is not significant after applying the pairwise t -test with the Bonferroni correction [$t(11) = 2.435$, $p = 0.033$, which is larger than acceptable $p = 0.05/2 = 0.025$]. Other measurements also do not show any significant asymmetric effect ($p > 0.105$).

3.3. Gradual spatial variation of SED and interocular difference in contrast threshold

As mentioned earlier and plotted in Fig. 2, individual measures of SED and interocular difference in contrast threshold vary across the visual field (inhomogeneity). Yet, an inspection of the plots shows that the variations between adjacent locations are more gradual than abrupt. To quantify this impression of a gradual change, we first examined the correlation between adjacent SEDs on the same side of the retina along the same radial direction. This is done by correlating adjacent SEDs at the 2° and 4° eccentricity, as shown in Fig. 5a. Since there are eight pairs of data points for each observer, and we tested 12 observers, Fig. 5a has a total of

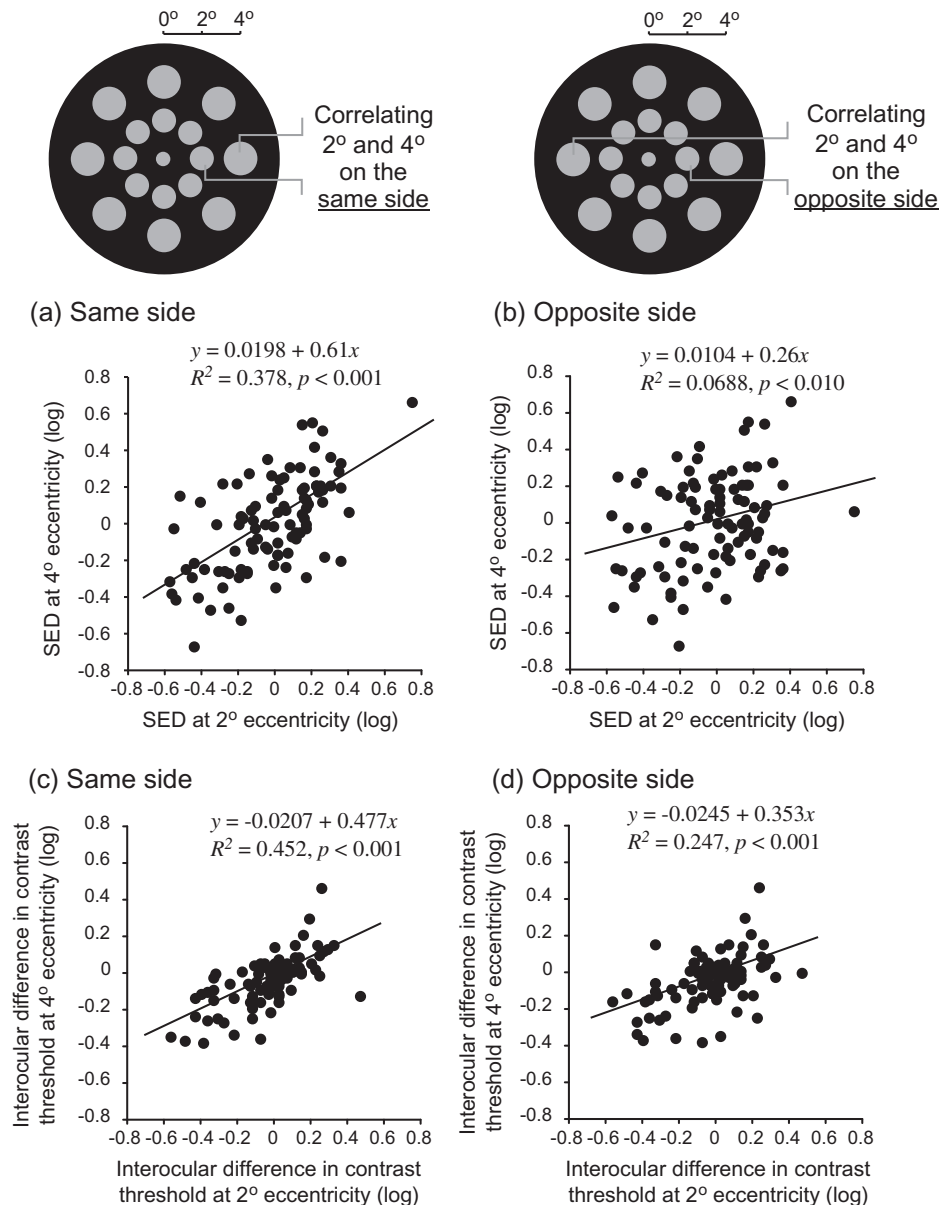


Fig. 5. We correlated the measured attributes at the 2° and 4° retinal eccentricities from either the same side of the retina, or across the fovea on the opposite side. A more gradual change (larger R^2 value) in SED and interocular difference in contrast threshold is found when the correlation is done on the same side of the retina (a and c), than when it is done on the opposite side (b and d).

96 data points. Secondly, we correlated the SED at 2° with the SED at 4° across the fovea (i.e., along the opposite radial direction) and plotted them in Fig. 5b. Consistent with the notion of a gradual change, we found a larger correlation in Fig. 5a (adjacent location) ($R^2 = 0.378$, $p < 0.001$) than in Fig. 5b (across fovea) ($R^2 = 0.0688$, $p = 0.010$).

We applied a similar analysis to the interocular difference in contrast threshold data and also found a stronger correlation between the 2° and 4° data points when they are adjacent on the same side of the retina (Fig. 5c, $R^2 = 0.452$, $p < 0.001$) than when they are across the fovea (Fig. 5d, $R^2 = 0.247$, $p < 0.001$).

In addition, we examined the correlation between the fovea and the parafoveal regions (average of all 2° and 4° data). Each data point in Fig. 6a represents the results of one observer, where the x -value is foveal SED and y -value is the mean of 16 SEDs from the 2° and 4° test locations. We found a reliable correlation between the foveal and parafoveal SED ($R^2 = 0.670$, $p = 0.001$). We

also plotted the data of the interocular difference in contrast threshold in a similar manner (Fig. 6b) and found a similar trend ($R^2 = 0.412$, $p = 0.024$). Altogether, the data in Fig. 6 suggest that for both the SED and interocular difference in contrast threshold, a sample measurement at the fovea can provide a reasonably good prediction of the global trend in the parafoveal region.

Finally, we examined the visual field variation of stereopsis using similar analyses. For both binocular disparity detection threshold and reaction time, there are significant correlations between the fovea and parafoveal performance (binocular disparity: $R^2 = 0.384$, $p = 0.031$; reaction time: $R^2 = 0.908$, $p < 0.001$). In the parafoveal region, there is a stronger correlation between the 2° and 4° disparity threshold data when they are adjacent on the same side of the retina ($R^2 = 0.255$, $p < 0.001$), than when they are across the fovea ($R^2 = 0.102$, $p < 0.001$). However, this trend is not found for the stereo reaction time data (adjacent: $R^2 = 0.646$, $p < 0.001$; across: $R^2 = 0.642$, $p < 0.001$).

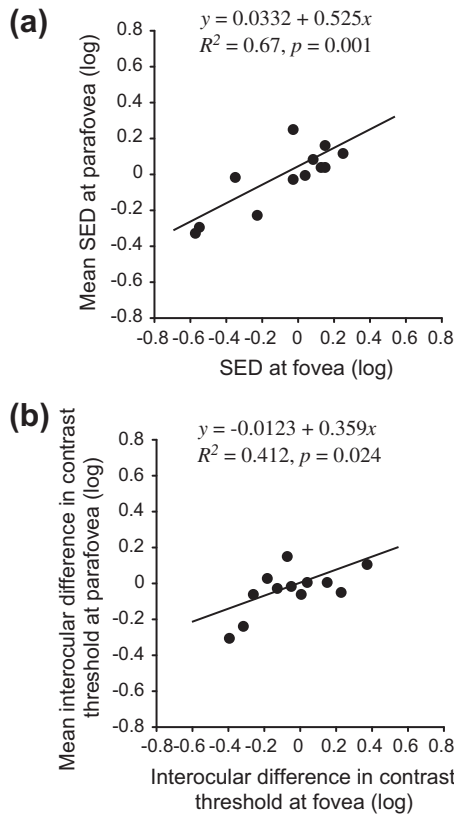


Fig. 6. Correlations between the foveal and parafoveal measurements of (a) SED and (b) interocular difference in contrast threshold. The parafoveal data were derived from averaging all the 2° and 4° results (16 positions).

3.4. SED cannot be fully accounted for by a difference in interocular contrast threshold

Fig. 7a plots all 12 observers' paired data points between the SED and interocular difference in contrast threshold obtained from the parafoveal region (2°: small black circles; 4°: large gray circles). There are 96 data points (12 observers × 8 locations) for each retinal eccentricity. Although there exists a reliable correlation (2°: $R^2 = 0.241, p < 0.001$; 4°: $R^2 = 0.1, p = 0.002$; both 2° and 4°: $R^2 = 0.169, p < 0.001$), it needs to be emphasized that while the majority of the data points fall in the first and third quadrants (where the two measurements consistently reveal the same eye as superior), there is a noticeable number of data points that fall in the second and fourth quadrants (inconsistent quadrants). These latter data points that fall in the inconsistent quadrants indicate that SED cannot be attributed to a difference in interocular contrast threshold. We also correlated the 12 observers' foveal SED and interocular difference in contrast threshold data. As shown in Fig. 7b, several data points also fall in the second and fourth quadrants. In fact, about 40% of the variability in foveal SED is not accounted for by variations in the difference in interocular contrast threshold ($R^2 = 0.612, p < 0.003$).

To further emphasize the lack of strong correlation, we obtained from among the 204 locations tested (12 observers × 17 locations), 110 locations (54%) where the difference in interocular contrast threshold is smaller than 0.1 log unit. We found that 72 of the 110 locations (67%) have SED larger than 0.1 log unit. Taken together, these data provide further support for our earlier finding (Ooi & He, 2001) that SED cannot be fully accounted for by the monocular contrast sensitivity explanation. However, it is important to note that such a conclusion does not exclude the

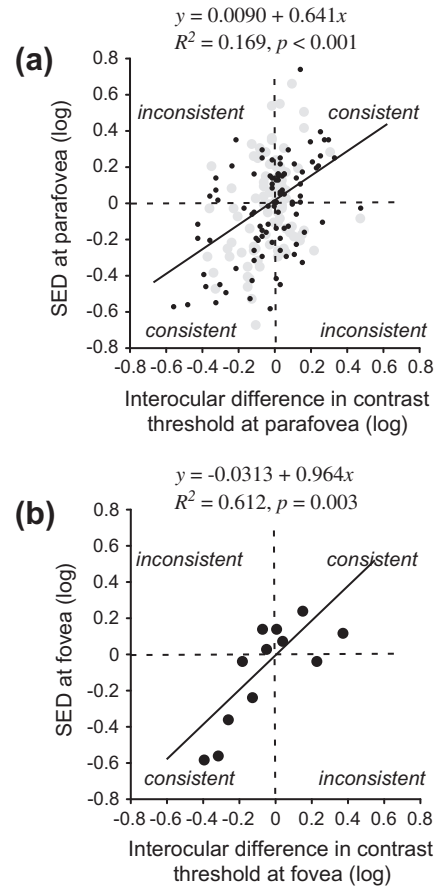


Fig. 7. Correlating SED and interocular difference in contrast threshold in the (a) parafovea (small and large dots for 2° and 4°, respectively) and (b) fovea. Data points falling in the first and third quadrants (consistent) indicate superiority in the same eye for both measures, whereas data falling in the second and fourth quadrants (inconsistent) indicate opposite eye superiority.

contribution of the interocular difference in contrast threshold to SED. In fact, our findings indicate a partial contribution. Thus, the measured SED may not be entirely caused by an asymmetric gain of mutual inhibition in the interocular inhibitory cortical network.

3.5. Stereopsis is affected more by SED than by a difference in interocular contrast threshold

Fig. 8a and b correlate binocular disparity threshold with the absolute value of the SED, respectively, at the parafoveal and foveal locations. Both at the foveal and parafoveal regions, binocular disparity threshold increases with the absolute SED (foveal: $R^2 = 0.537, p = 0.007$; 2°: $R^2 = 0.3, p < 0.001$; 4°: $R^2 = 0.222, p < 0.001$; both 2° and 4°: $R^2 = 0.204, p < 0.001$), suggesting that an imbalance in the interocular inhibitory network can degrade the binocular depth process. We then correlated binocular disparity threshold with the absolute value of the interocular difference in contrast threshold (Fig. 8c and d). In comparison to SED, there is only a weaker tendency for the binocular disparity threshold to increase with the absolute interocular difference in contrast threshold (foveal: $R^2 = 0.254, p = 0.096$; 2°: $R^2 = 0.0203, p = 0.166$; 4°: $R^2 = 0.0337, p = 0.073$; both 2° and 4°: $R^2 = 0.00719, p = 0.242$). This difference further underscores the important role of the interocular inhibitory mechanism in processing binocular depth information.

Similar results are found in correlation analyses of the relative reaction time to detect a target in depth (average of crossed and uncrossed disparity trials) with the absolute SED (Fig. 9a and b),

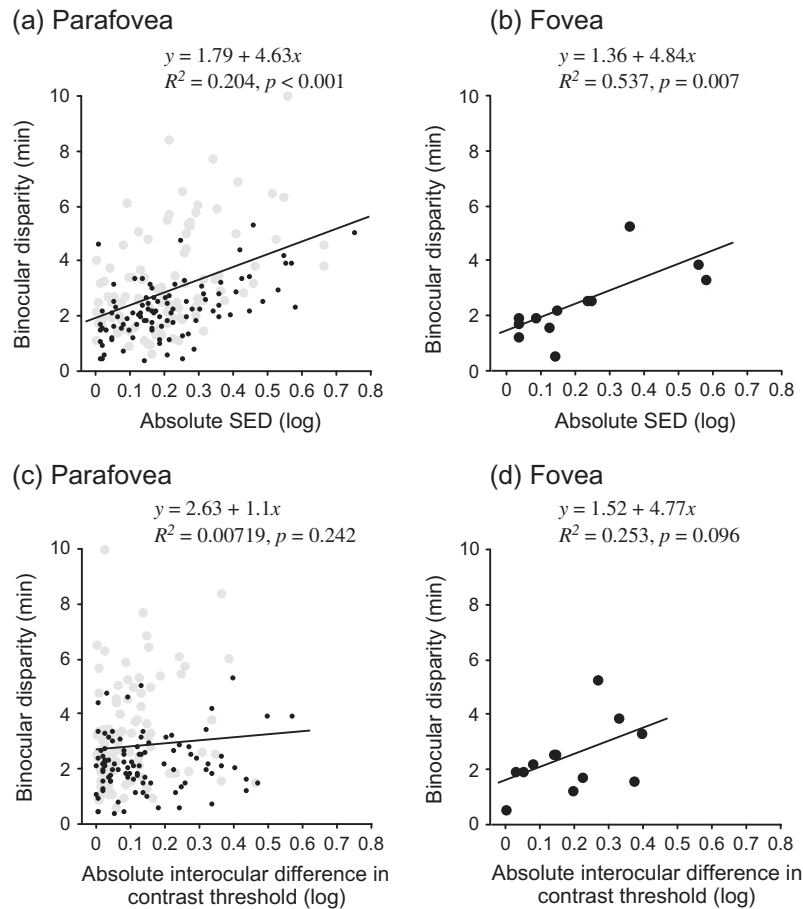


Fig. 8. (a and b) Correlate binocular disparity threshold and absolute SED, respectively, in the parafovea and fovea. (c and d) Correlate binocular disparity threshold and absolute interocular difference in contrast threshold, respectively, in the parafovea and fovea. Generally, the correlation between binocular disparity threshold and absolute SED is higher than between binocular disparity threshold and absolute interocular difference in contrast threshold. Note that in (a and c), the small and large dots depict the 2° and 4° data, respectively.

and with the absolute interocular difference in contrast threshold (Fig. 9c and d). Relative reaction time to detect a target in depth increases with the absolute SED (foveal: $R^2 = 0.247$, $p = 0.100$; 2°: $R^2 = 0.161$, $p < 0.001$; 4°: $R^2 = 0.252$, $p < 0.001$; both 2° and 4°: $R^2 = 0.197$, $p < 0.001$), but barely increases with the absolute interocular difference in contrast threshold (foveal: $R^2 = 0.000157$, $p = 0.969$; 2°: $R^2 = 0.011$, $p = 0.310$; 4°: $R^2 = 0.0153$, $p = 0.230$; both 2° and 4°: $R^2 = 0.00105$, $p = 0.656$).

We also examined the tested locations in the parafoveal area where the difference in interocular contrast threshold is smaller than 0.1 log unit. We found that the correlation coefficient between binocular disparity threshold and SED ($R^2 = 0.178$, $p < 0.001$), and between relative reaction time and SED ($R^2 = 0.209$, $p < 0.001$), are significant. This further implicates the contribution of the interocular inhibitory mechanism to binocular depth perception.

3.6. Correlation between SED and predominance in binocular rivalry with extended viewing duration

We measured the observers' percepts while tracking a 30 s binocular rivalry stimulus with foveal vision to reveal the dynamics of binocular rivalry (dominance shifts) (Blake, 1989; Fox, 1991; Kovacs, Papathomas, Yang, & Fehér, 1996; Levelt, 1965; Suzuki & Graboweky, 2002, 2007). We then correlated the data with the foveal SED. For each observer, we calculated his/her interocular difference in predominance measured in proportion, which is defined as:

$$\begin{aligned} & [\text{Predominance}(\text{RE}, \text{H}) - \text{Predominance}(\text{LE}, \text{H})] \\ & + [\text{Predominance}(\text{RE}, \text{V}) - \text{Predominance}(\text{LE}, \text{V})] \end{aligned}$$

In the above, H and V denote the perceived horizontal and vertical image, respectively. We then paired each observer's interocular difference in predominance with his/her foveal SED and plotted these in Fig. 10a. The graph reveals a strong correlation ($R^2 = 0.795$, $p = 0.001$). Data falling in the first and third quadrants indicate the superior eye in SED also enjoys a higher predominance when tracking binocular rivalry. Nevertheless, one of the ten observers tested had her data point falling in the second quadrant; however, it is likely that this data point is affected by the fluctuation of the visual system's intrinsic noise level since both measurements are rather small in magnitudes. We also examined whether the foveal SED has a similar relationship with the dominance duration and dominance frequency in the binocular rivalry tracking task. We found a reliable correlation between SED and dominance duration ($R^2 = 0.6403$, $p = 0.005$), but not between SED and alternation frequency ($R^2 = 0.0023$, $p = 0.894$). Overall, we conclude that there is a general agreement between eye dominance based on the SED task and that based on the binocular rivalry tracking task.

3.7. A non-significant correlation between sensory and motor eye dominance

The previous study by Ooi and He (2001) examined the relationship between global SED and motor eye dominance, and found

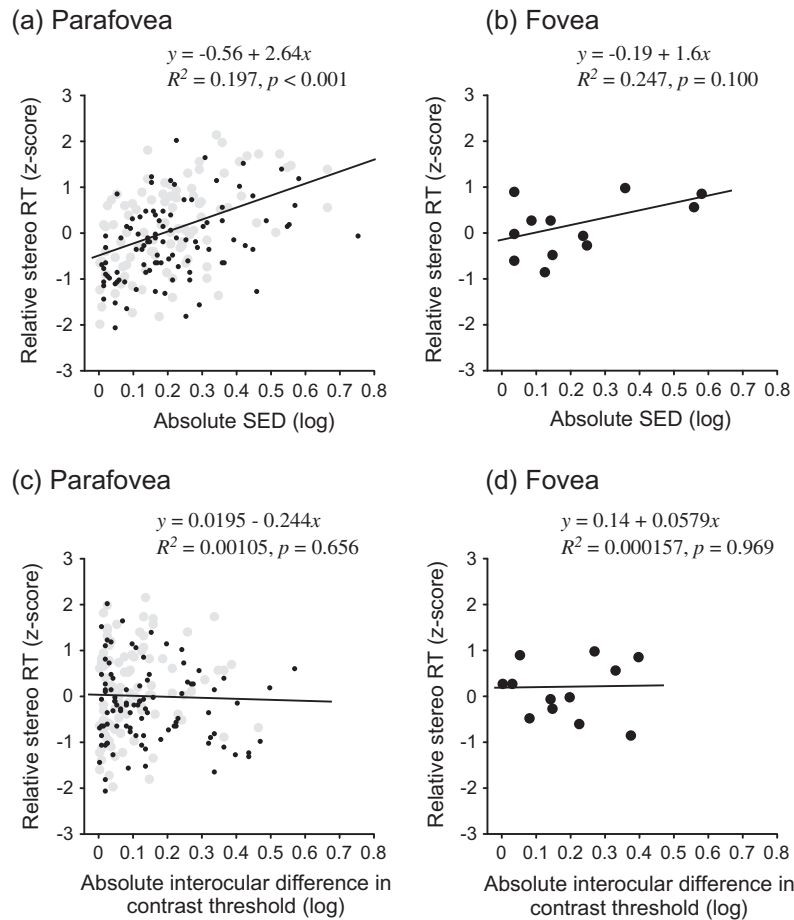


Fig. 9. (a and b) Correlate relative RT (z-score) for seeing depth and absolute SED, respectively, in the parafovea and fovea. (c and d) Correlate relative RT (z-score) for seeing depth and absolute interocular difference in contrast threshold, respectively, in the parafovea and fovea. Generally, the correlation between relative RT (z-score) for seeing depth and absolute SED is higher than between relative RT (z-score) for seeing depth and absolute interocular difference in contrast threshold. Note that in (a and c), the small and large dots depict the 2° and 4° data, respectively.

that a substantial number of observers exhibited an opposite dominance in the sensory and motor domain. This suggests that the underlying mechanisms of SED and motor eye dominance (MED) are different. Our present study provides further support for this conclusion. We compared the observers' foveal and parafoveal SED with MED. The parafoveal SED result for each observer was obtained by averaging his/her SED data from the 2° and 4° eccentricities. Fig. 10b depicts the 12 observers' SED and MED data. Clearly, there are at least four observers whose data (both foveal and parafoveal) fall in the inconsistent regions. This indicates that eye dominance is independent for the motor and sensory modalities.

4. Discussion

Our study extends the previous one by Ooi and He (2001) on global SED by measuring SED locally at seventeen different retinal locations (SED perimetry). We also measured monocular contrast detection threshold, binocular depth detection threshold and reaction time, and binocular rivalry tracking percept at the tested retinal locations. Supporting Ooi and He (2001)'s study, we first found that the strong eye in SED does not always have higher monocular contrast sensitivity. Secondly, the foveal SED and MED do not always reside in the same eye. Thirdly, we are able to reveal from the perimetry test data that all measured performance vary gradually across the retina. There is no significant upper/lower or left/right field asymmetry for the local SED and monocular contrast

detection threshold data. Fourthly, in agreement with the notion that the interocular inhibitory mechanism contributes to stereo processing, we found a significant correlation between local SED and binocular depth perception. There also exists a significant correlation between local SED and the dynamics of binocular rivalry, indicating the common role of the interocular inhibitory mechanism in both tasks. While the goal of the current study is to reveal the causes and implications of SED across the binocular visual field through a battery of psychophysical tests, our findings also demonstrate the potential uses of the binocular perimetry test in a clinical setting. Specifically, binocular perimetry testing can be used to address the various visual functions associated with binocular vision.

It should be emphasized that to measure local SED, we employed a pair of orthogonal gratings to stimulate the interocular inhibitory network (Blake, 1989; Fox, 1991; Wolfe, 1986). Thus, the measured SED reflects the output of the interocular inhibitory network. However, it is reasonable and also important to ask whether the measured SED is attributable to an interocular difference between the two monocular channels that provide their inputs to the interocular inhibitory network, or the difference between the monocular channels at the site of the mutual interocular inhibition, or a combination of both. While our psychophysical method cannot directly gauge the monocular inputs before their convergence at the site of interocular inhibition, we could estimate the monocular inputs by measuring the monocular contrast detection threshold. By doing so, we found that our observers' interocular difference in monocular contrast detection thresholds is not

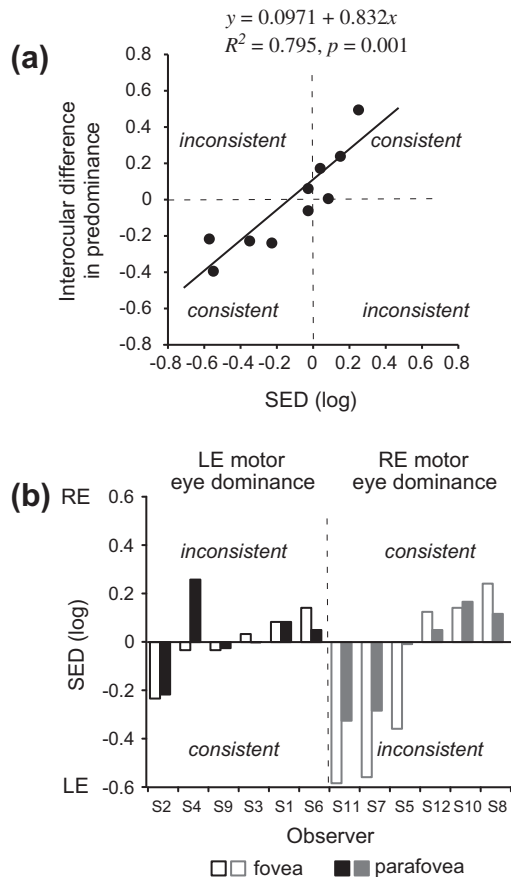


Fig. 10. (a) Correlating interocular difference in predominance (from tracking binocular rivalry percepts) and SED. Data falling in the first and third quadrants indicate the superior eye in SED also enjoys a higher predominance when tracking binocular rivalry. (b) Comparing each observer's motor eye dominance with his/her foveal SED and mean parafoveal SED. Data falling in the inconsistent quadrants indicate the sensory and motor dominant eye is opposite.

always consistent with the sign of their local SED. This suggests that, at least for our observers with clinically normal binocular vision, the local SED cannot be fully accounted for by an imbalance in the monocular inputs to the interocular inhibitory network. Related to this assertion, we found in a separate study that the change in monocular contrast threshold cannot account for the reduction in SED that occurs after our observers underwent a push–pull perceptual learning paradigm to reduce SED (Xu, He, & Ooi, 2010, 2011a).

We also found a significant correlation between SED and binocular depth detection threshold. This finding supports the view that binocular depth perception depends on the interaction between the interocular integration and interocular inhibitory mechanisms. Specifically, the interocular inhibitory network has been assumed to play a critical role in eliminating false matches during the process of forming a single 3-D object representation.

Finally, we found a strong correlation between local SED and the favored eye when viewing a binocular rivalry stimulus with an extended duration. This implies that the interocular inhibitory network responds not only to briefly presented binocular rivalry stimuli, such as the stimulus used for measuring SED, but also mediate the dynamics of binocular rivalry when the viewing duration is long (Su, He, & Ooi, 2009, 2010, 2011a; Wolfe, 1983). Furthermore, we observed in Xu, He, and Ooi (2011b) that when SED is decreased after the push–pull training, the trained (weak) eye improves in its ability to maintain image dominance when

tracking the binocular rivalry stimulus. Taken together, these findings indicate that measuring SED with briefly presented stimuli is sufficient (and efficient) for revealing the imbalance nature of the interocular inhibitory network.

The measurement of eye dominance has a long history that dates back to the sixteenth century (e.g., Crider, 1935; Li et al., 2010; Ooi & He, 2001; Pascal, 1926; Porac & Coren, 1976; Sheard, 1923; Xu, He, & Ooi, 2010; Xu et al., 2011a,b; Walls, 1951; Yang et al., 2010). Besides being a scientific curiosity, eye dominance is also a condition that the layperson is quite familiar with. This is because, particularly for MED, the preference to use one eye when viewing through a monocular contraction (e.g., telescope, camera, etc.) naturally reveals to oneself the dominant eye. It is harder to discover one's own SED since it requires a specialized setup that stimulates binocular rivalry at corresponding retinal points. This paper has focused primarily on SED to investigate its correlation with various visual functions. While it is difficult to attribute causal factors from correlation analyses, our data lead us to favor the notion that a large SED, which reflects an imbalance of interocular inhibition, is a significant factor impeding binocular visual perception. In fact, as we have suggested, excessively large SED could be akin to the clinical condition of amblyopia. We have also shown elsewhere that SED could be reduced through the process of perceptual learning. Thus, given the significant interactions among the cortical networks responsible for various visual functions, it is foreseeable that the amblyopic patient could be simultaneously trained on various visual functions, including spatial localization, contrast detection, orientation discrimination, SED, etc. (Huang, Tao, Zhou, & Lu, 2007; Levi & Li, 2009; Sasaki, Nanez, & Watanabe, 2010; Schor, 1991; Su et al., 2009; Wolfe, 1986; Xu, He, & Ooi, 2010).

5. Conclusions

Using a new binocular perimetry test to locally measure SED at 17 discrete retinal locations, we found that not all retinal locations have the same SED. SED between adjacent locations tend to be more similar than those between locations further apart. Nevertheless, despite the inhomogeneity, a correlation exists between the average parafoveal SED and the foveal SED. SED is not completely predictable from the measurements of MED or monocular contrast sensitivity. However, SED is significantly correlated with binocular depth perception. Locations with larger SED tend to have degraded stereo performance. The sensory dominant fovea, as identified by the short duration imbalance (SED) test, very often predominates when viewing a long duration binocular rivalry stimulus.

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