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Temporal characteristics of binocular rivalry: visual field asymmetries

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Abstract

Very little is known about the mechanisms that drive the alternation between the two views during binocular rivalry. A key property of the rivalry process is the rate at which the two views alternate. Understanding the factors that affect the rate of the alternation is critical to the final understanding of the underlying process. Using a circular and a radial grating as the rivalry stimuli, we observed a significantly faster binocular rivalry when stimuli were presented in the right visual field than that in the left visual field for the right-handed observers, and a reversed asymmetry for the left-handed observers. In both groups, rivalry was faster for stimuli presented in the lower visual field than that in the upper visual field. This pattern of results suggests that (1) rivalry is likely a locally driven process and (2) the visual brain in the left hemisphere may be the faster one of the two hemispheres in right-handed people.

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1. Introduction

When two different visual stimuli are presented dichoptically to the observer, often the perception is an alternation of the two eye's views. This binocular rivalry phenomenon has had a long history of study (Blake, 2001) and recently it has gained renewed attention (Blake & Logothetis, 2002), partly because it provides a clear dissociation between the stimulus and visual awareness. Although the stimulus information is constant, perception alternates between two states.

One of the fundamental problems in understanding the binocular rivalry process is to understand what drives the alternation between the two stimuli. A key aspect of the switching process is its rate, which is influenced by both the stimulus factors and observer factors. Stimulus factors, often referred to as "stimulus strength", have been shown to significantly affect the rivalry rate (Levelt, 1966). For example, increasing the contrast of both stimuli presented to the left and right eyes results in faster alternations (Alexander & Bricker, 1952; Whittle, 1965). Eccentricity of the stimulus from fovea can also affect the rivalry rate (Breese, 1909;

Fahle, 1987). On the observer side, there was an attempt to link the rate of binocular rivalry with intelligence (Crain, 1961), but the idea does not seem to hold (Hodges & Fox, 1965). More recently, Pettigrew and his colleagues showed that unilaterally stimulating one hemisphere by using caloric vestibular stimulation and transcranial magnetic stimulation could alter rivalry characteristics (Miller et al., 2000), and people with bipolar disorder perceived rivalry at significantly slower rates than normal controls (Pettigrew & Miller, 1998). Partly based on these results, they have proposed that rivalry is the result of left–right hemisphere competition, and, in their words, bipolar patients have a "sticker" switch. Although the idea that rivalry is due to competition between the two hemispheres and there is a "master switch" is controversial, there is no question that switch rate is an important property of the rivalry process.

In this paper we report a novel observation that competing stimuli presented to the right visual field generate faster binocular rivalry compared to the same stimuli presented to the left visual field at the same eccentricities for right-handed observers, and vice versa for left-handed observers. For both groups, the rivalry rate is faster for stimuli presented in the lower visual field than that in the upper visual field. Furthermore, this pattern of results cannot be explained by the possible difference in contrast sensitivity between these different

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visual fields. Our results suggest that the rate of binocular rivalry is determined in part by retinotopic specific mechanisms, and cast some doubts on models that leave the switching control to sites that are removed from the retinotopic specific processing.

2. Methods

2.1. Observers

Sixteen right-handed (including the two authors, 10 males and 6 females, ages between 20 and 38), and eight left-handed observers (4 males and 4 females, ages between 18 and 30) participated in this experiment. Observers' handedness was identified with the "Edinburgh Handedness Inventory" form. All observers had normal or corrected-to normal visual acuity. No formal stereo test was administered but all observers could see images in random dot stereograms. The experiments were performed under the approval of the University of Minnesota human subjects review committee. Except for the two authors, all participants received monetary compensation for their time.

2.2. Apparatus

Stimuli were generated with Vision Shell software (<http://www.mlink.net/~ml/>) running on a PowerPC Macintosh computer. A Sony 17seII monitor was used to present the stimuli. Through a mirror stereoscope, observers could see the image on the left half of the screen with their left eyes, and that on the right half with right eyes. At the same time, their head and eyes positions were fixed with the help of a chin-rest. Observers' responses were recorded with keyboard presses.

2.3. Stimuli

The stimuli were a red circular sine-wave grating and a green radial sine-wave grating; one was presented on the left part of the screen and the other on the right. This pair of stimuli was selected because it gave relatively

clean and crisp rivalry, with minimum mixture states. A fixation point was placed at the left, right, upper, or lower side of each grating, with a distance of 1.0° , 3.0° , or 5.0° between the centers of the grating and the fixation point. The diameters of the gratings were 1.5° , 2.0° , or 2.5° corresponding to the eccentricities used above. The red-circular grating had four cycles and the green-radial grating had eight cycles. Both gratings were set at full contrast, with the mean luminance at about 15 cd/m^2 . The stimuli were presented on a white background with the luminance set at about 30 cd/m^2 . A square frame surrounding each grating was used to help keeping two eyes' stimuli aligned (Fig. 1).

2.4. Experimental conditions

All observers completed four experimental sessions. Each session contained four experimental conditions corresponding to the four visual field positions of the stimuli (left, right, upper, lower visual field). In two sessions the red-circular grating was presented to the left eye, green-radial grating to the right eye, and vice versa for the other two sessions. Each session contained four 2-min trials, one trial for one experimental condition. Overall, there are 8 min of rivalry tracking data for each visual field location from each observer.

2.5. Procedure

Each observer was first positioned on the chin-rest and the mirrors of the stereoscope were adjusted so that the fixation points and the frames presented to the two eyes were precisely fused, and the two gratings were perfectly aligned. After taking two practical trials, the observer ran four sessions of test trials. They were instructed to maintain fixation at the fixation point throughout the trials. Each test trial lasted for 2 min, during which the observer saw and tracked the alternations of the two gratings. Key presses on a standard keyboard were made when the observers perceived the switches from one grating to the other. They pressed the space key with the left hand for the perceptual onset of one grating and the "0" key on the numerical keyboard for the perceptual onset of the other grating.

3. Results and discussion

Since the current study focused on the rate of rivalry, optimal stimuli for generating clean and crisp alternations were used. The dependent measure is rivalry rate (or mean dominance time) and the independent variable is the position of the stimuli presented in the different parts of the visual field. In particular, the key comparisons are between symmetrical positions (left vs. right,

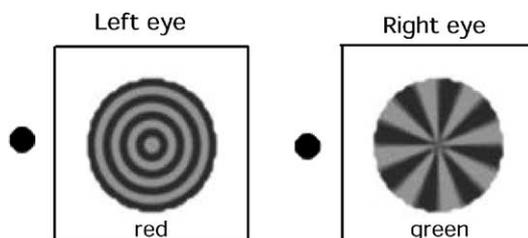


Fig. 1. Sample stimuli for generating binocular rivalry. Shown here is an example of stimuli presented to the right visual field. Observers were asked to fixate on the black dot while tracking the rivalry alternations between the red-circular pattern and the green-radial pattern.

upper vs. lower) across the visual field. Below we report the key findings.

3.1. Handedness and visual field dependence

One characteristic feature of binocular rivalry is that observer’s dominance time follows a gamma distribution, which is true in our results. Fig. 2 shows the typical frequency distributions, based on the data from a right-handed observer. The four curves represent the frequency distributions of the dominance time for the stimuli presented in the left, right, upper, and lower visual fields. Although all the distributions follow gamma functions, the difference among them is quite apparent. For the right-handed observer, stimuli presented in the right and lower visual field generated higher peaks in the relatively shorter duration range compared to the stimuli presented in the left and upper visual field, respectively (Fig. 2). Given that there were minimum mixture phases with the rivalry stimuli used, shorter dominance duration means faster rivalry switch. Thus, the data in Fig. 2 mean that, on average, this right-handed observer had a faster switch rate for the lower visual field stimuli than the upper visual field stimuli, and a faster switch rate in the right visual field than that in the left visual field.

Fig. 3 summarizes visual field asymmetry for all observers. X-axis represents the ratio of switch rate for the right visual field to that for the left (right/left), and the Y-axis represents the ratio of the switch rate for the lower visual field to that for the upper (lower/upper). Each observer contributed one data point to this plot. If there is no significant difference between the switch rates in different visual fields, then the ratios will be centered around 1 on both axes. Points above the dashed horizontal line represent the observers who had a faster switch rate in the lower visual field than that in the upper visual field (14 out of 16 in the right-handed observers, 6 out of 8 in the left-handed observers). Points to the right of the dashed vertical line represent the

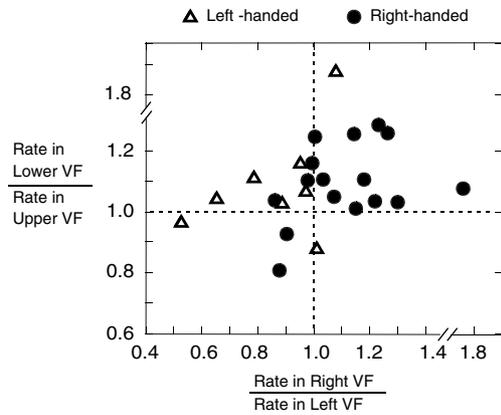


Fig. 3. Ratios of the switch rate in the lower visual field (VF) over that in the upper VF and the right over left VF. If the ratio is larger than 1 (indicated by the dashed lines), then the switch rate in the lower or right VF is higher than that in the upper or left VF. Most of the right-handed observers (11 of 16) had higher rate in the right VF; on the contrary, most of the left-handed observers (6 of 8) had higher rate in the left VF. Most of the right- and left-handed observers (20 of 24) had higher rate in the lower VF.

observers who had a faster switch rate in the right visual field than that in the left visual field (11 Out of 16 in the right-handed observers, 2 out of 8 in the left-handed observers). Clearly, the data plotted in Fig. 3 show that most right- and left-handed observers had a faster switch rate for binocular rivalry in the lower visual field. The mean ratio for both the left- and right-handed groups is 1.11 ± 0.20 (mean \pm SD), significantly greater than 1 (*t*-test, $t = 2.645$, $p = 0.014$). Another salient feature of Fig. 3 is the separation along the horizontal axis between the right- and left-handed groups. The mean R/L ratio in the right-handed observers is 1.12 ± 0.22 , significantly greater than 1 (*t*-test, $t = 2.237$, $p = 0.041$); and in the left-handed group it is 0.86 ± 0.19 , not significantly less than 1 (*t*-test, $t = -2.113$, $p = 0.072$). But, the difference between these two handedness groups reached statistical significance (*t*-test, $t = 2.903$, $p = 0.008$).

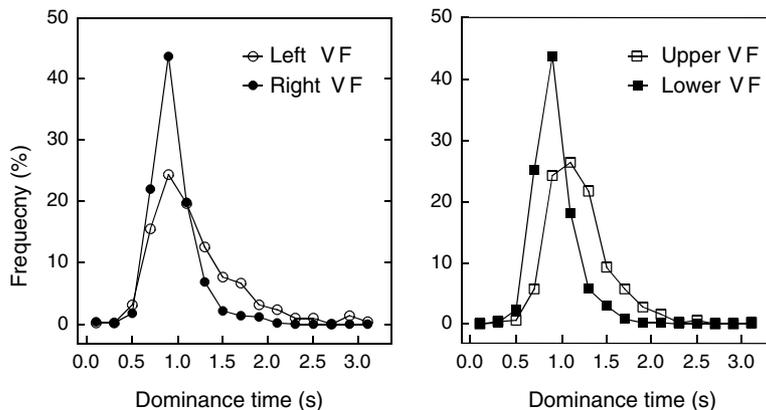


Fig. 2. Distribution of the dominance times for different visual fields (VFs) of one right-handed observer. Time bin width is 0.2 s.

Very limited data related to the binocular rivalry in different parts of the visual field exist in the literature. For example, Breese (1909) reported his own observation on the rivalry in the right/left/upper/lower visual fields at two eccentricities from the fixation point. Although there was no mention of the visual field asymmetries, the data of his own observation seemed to suggest that it was true in him that rivalry in the lower visual field was faster than that in the upper visual field. The asymmetry between the right and left visual field was less clear in his data (Breese, 1909). Kaushall (1975) studied the eye, pathway, and hemisphere asymmetries of rivalry in the right- and left-handed subjects. His data showed that the uncrossed visual pathways (stimuli received by the temporal part of the retina) were dominant over the crossed pathways (stimuli received by the nasal part of the retina) in a binocular rivalry task (Kaushall, 1975). More recently, O'Shea and Corballis (2001) reported a very interesting observation of visual field asymmetry of rivalry rates in two split-brain observers. The two split-brain observers showed faster rivalry when the stimuli were presented to the left visual field compared to those to the right visual field, which is in the opposite direction to our finding. However, the four normal observers in their study had either no asymmetry or faster rivalry in the right visual field (O'Shea & Corballis, 2001).

3.2. Contrast and eccentricity dependence

As noted earlier, some stimulus factors can affect the switch rate in binocular rivalry. One of them is stimulus contrast: faster switch rate with increasing contrast of both rival targets (Alexander & Bricker, 1952; Whittle, 1965). Is it possible that the visual field asymmetry we observed was due to differential contrast sensitivities in the different visual fields? Existing measurements of contrast sensitivity have not revealed significant differences in different visual fields (Rovamo & Virsu, 1979). Our own observation (adjustment method, data not shown) also confirmed that neither in contrast sensitivity, nor in contrast matching performance, any systematic difference between different visual fields appeared when eccentricities are equated. However, we sought to measure what it takes for the contrast difference to account for the observed asymmetry of the rate of rivalry. In other words, we measured how much the contrasts have to be lowered to reduce the switch rates in the right and lower visual fields to match those in the left and upper fields respectively in a right-handed observer. Two 1.5° gratings at the eccentricity of 1.0° were used. The data in Fig. 4a show that in order to have the same rivalry rate between the upper and lower, or the left and right visual fields, the contrast of stimuli in the lower or right visual field had to be lowered to less than half of the contrast of the stimuli in the upper and left visual

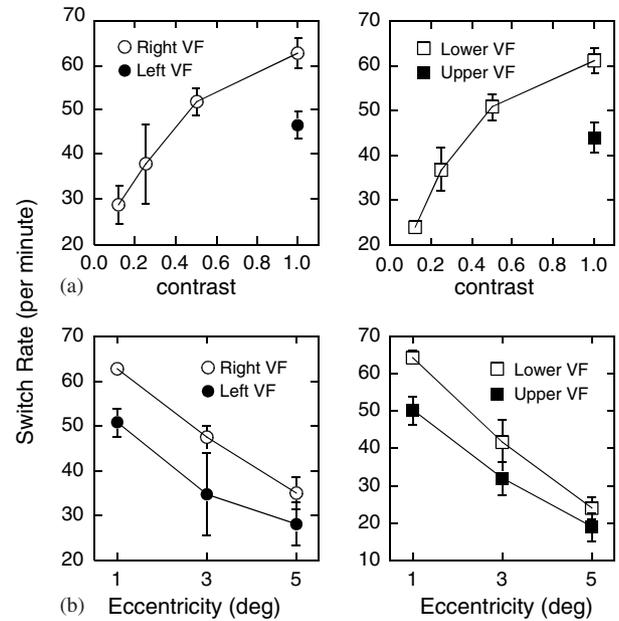


Fig. 4. Contrast and eccentricity dependence of the switch rate for one right-handed observer. (a) To match the switch rates in the right and left, or lower and upper visual fields (VFs), the contrast of the stimuli in the right or lower VF had to be decreased to around 40%, given the contrast of the stimuli in the left or upper VF as 100%. (b) The switch rate decreased with the increased eccentricity, but the difference between the right and left, or lower and upper VFs remained. Error bars are ± 1 s.d.

fields. The need of such a large contrast difference to account for the rate difference together with the insignificant difference in contrast sensitivity between visual fields suggest that the contrast sensitivity does not play a significant role in the observed visual field asymmetry.

We also tested whether the switch rate asymmetry only exists at a particular eccentricity. On three of the right-handed observers who participated in the previous experiments, the switch rates were measured at the eccentricities of 1.0°, 3.0° and 5.0° from the fixation point. To compensate for the loss of visual acuity, the size of the stimuli were increased linearly as a function of eccentricity. The diameters of the stimuli were 1.5, 2.0 and 2.5 corresponding to the three eccentricities tested. Results confirm that the asymmetry is not unique to a particular retinal eccentricity (Fig. 4b). Although the switch rate decreased dramatically with increasing eccentricity, the asymmetry between the left and right visual fields and that between the lower and upper visual fields remained significant at all eccentricities tested.

3.3. Nasal retina vs. temporal retina

The data plotted in Fig. 3 are pooled across the two eyes, showing the difference between different parts of the visual field. When we analyzed the data separately in the two eyes, a rather unexpected pattern emerged in the

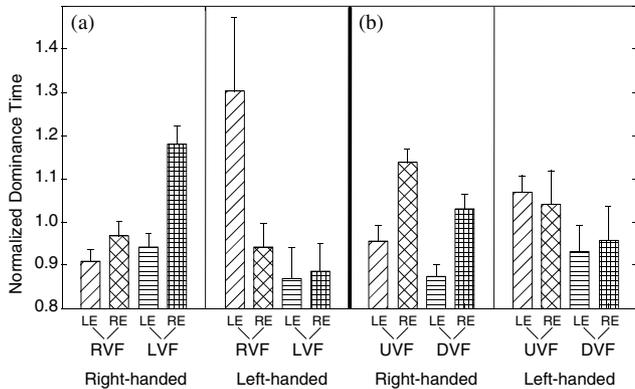


Fig. 5. Normalized mean dominance times of 16 right-handed and 8 left-handed observers plotted separately for the two eyes viewing the stimuli in the right and left (a), lower and upper (b) visual fields (VFs). LE: left eye, RE: right eye. RVF: right VF, LVF: left VF, UVF: upper VF, DVF: lower VF.

result. Fig. 5 shows the normalized average dominance duration when stimuli were presented in one of the four visual fields (LVF, RVF, UVF, DVF), separately for each eye (LE, RE). For the right-handed observers, there was a clear effect of right eye dominance in that the stimuli presented to the right eye in general had a longer dominance time. This eye dominance effect interacted with the visual field effect that we are reporting in this paper. The right eye dominance was much stronger when the stimuli were presented in the left visual field. Fig. 5a shows that for right-handed observers the longest dominance time occurred for the stimulus presented to the left visual field received by the right eye. For the left-handed observers, there was not a clear left eye dominance, except only in the condition when the stimuli were presented to the right visual field, in which case the left eye had the longest dominance time (see Fig. 5a). In other words, the right eye's temporal retina with an uncrossed pathway to the right hemisphere in the right-handed observers and the left eye's temporal retina with an uncrossed pathway to the left hemisphere in the left-handed observers enjoyed the longest dominance times on average. It appears that the left and right visual field asymmetry is mainly due to the longer dominance times of the temporal retina, right temporal retina for right-handed observers and left temporal retina for left-handed observers.

Functional asymmetries between the nasal and temporal hemi-field have been reported before, which are more noticeable in the far periphery and usually with the nasal hemi-retina superior (Fahle, 1987; Fahle & Schmid, 1988). Consistent with these functional observations, anatomically the nasal hemi-retina has a higher cone density (Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987). However, our experiment showed that the temporal retina, "inferior" in these earlier studies, enjoyed longer dominant periods over the fellow eye's

nasal retina during binocular rivalry. The fact that our finding could not be predicted by the temporal hemi-retina's superiority in these basic visual sensitivity tests suggest that the asymmetry reported here likely reflects a cortical origin.

Recently it was discovered that eye dominance is not a static property but varies with the gaze direction (Carey, 2001; Khan & Crawford, 2001; Khan & Crawford, 2003). More specifically, people with right eye dominance when looked straight ahead will switch to left eye dominance if they look toward the left and vice versa. In our study, observers directed their attention to different parts of the visual field while maintaining fixation, it is not clear whether the direction of attention will have similar effect on eye dominance. In addition, for most observers, the switching of eye dominance occurs when gaze is shifted by more than 10° , while in our study the visual field asymmetry can be observed when stimuli were presented only 1° off the fixation point. These considerations make it very unlikely that the eye dominance in general and the switch of eye dominance due to gaze direction contributed to the observed visual field asymmetry in rivalry rates. Obviously, the asymmetry between the upper and lower visual fields is orthogonal (literally) to the eye dominance. For stimuli presented along the vertical meridian, the right-handed observers showed again a right eye dominance effect in addition to the visual field asymmetry while the left-handed observers only showed a visual field asymmetry without an eye dominance effect (see Fig. 5b).

3.4. Faster rivalry resulting from generally faster neural dynamics in specific retinotopic areas?

Our data concerning the left and right visual field asymmetry can be interpreted in either a narrow or a broad perspective. A narrow interpretation is that binocular competition in the left hemisphere occurs at a faster pace. A broader view would be that the left hemisphere has a generally faster neural dynamics, not restricted to perceptual competition. Additional evidence supports the latter interpretation. It has been reported that the left hemisphere had an advantage in discriminating fast temporal events (Nicholls, 1994). Evoked potential recordings also support that the left hemisphere is the faster one of the two (Rebai, Mecacci, Bagot, & Bonnet, 1986). We also have acquired preliminary data using monocular bi-stable stimuli that showed a faster alternation for the right visual field stimuli in the right-handed observers.

When stimuli were presented at the vertical meridian, both the left- and right-handed observers had longer dominance times for the stimuli presented in the upper visual field, but the right-handed group showed an additional right eye dominance over the left eye (see Fig. 5b). As discussed above, the vertical asymmetry could

not be explained by possible contrast sensitivity differences. Many asymmetries have been reported between the upper and lower visual field (Previc, 1990), including the lower visual field's advantage in spatial attention (He, Cavanagh, & Intriligator, 1996). However, there is no direct evidence linking attention and the rate of binocular rivalry. Here again, it is possible that faster rivalry for stimuli in the lower visual field is resulted from the faster temporal dynamics of the neurons receiving information from the lower visual field. The finding that the lower visual field has a higher temporal sensitivity than the upper visual field (Payne, 1967; Skrandies, 1985; Tyler, 1987) lends support to this idea.

4. Conclusions

The result that rivalry rates are different in different parts of the visual field suggests that the control of rivalry rate is likely a retinotopically local process. This result argues against rivalry models which suggest that the control of rivalry alternations is situated at a level removed from retinotopic-specific neural substrates such as the frontoparietal cortex (Lumer, Friston, & Rees, 1998) or the competition between the two hemispheres (Miller et al., 2000). Our findings support the view that binocular rivalry is the result of local competition of two eye's inputs. Furthermore, the results also suggest that in right-handed people, the left hemisphere is the faster hemisphere, and in both left- and right-handed people, the cortical neurons receiving input from the lower visual field have a faster neural dynamics.

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