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The magnitude and dynamics of interocular suppression affected by monocular boundary contour and conflicting local features

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ABSTRACT

A monocular boundary contour (MBC) rivalry stimulus has two half-images, a homogeneous grating and the same homogeneous grating with an additional disc region. The outline/frame of the MBC disc is created by relative phase-shift, or orientation-difference. We found the increment contrast threshold and reaction time to detect a monocular Gabor probe elevated on the homogeneous half-image pedestal. The interocular suppression begins as early as 80 ms upon stimulus onset. Moreover, the suppression magnitude is larger when the MBC disc is defined by orientation-difference rather than phase-shift, revealing the suppression caused by competing local features in addition to MBC.

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1. Introduction

When the two eyes view dissimilar stimuli (half-images) such as the orthogonal gratings in Fig. 1a, one perceives an alternation between the images of the two stimuli. In this phenomenon of binocular rivalry, the stimulus whose image is momentarily perceived is referred to as the dominant stimulus, while the stimulus whose image is not perceived the suppressed stimulus. One approach to revealing the fate of the suppressed image, which is not consciously perceived, is by measuring the effect of the suppression on the detection threshold of a monocular probe. The probe detection protocol has been used by various laboratories in the past (e.g., Blake & Camisa, 1979; Fox & Check, 1972; Li, Freeman, & Alais, 2005; Makous & Sanders, 1978; Nguyen, Freeman, & Wenderoth, 2001; Norman, Norman, & Bilotta, 2000; Ooi & Loop, 1994; Paffen, Alais, & Verstraten, 2005; Smith, Levi, Manny, Harwerth & White, 1985; Su, He, & Ooi, 2009; Wales & Fox, 1970; Watanabe, Paik, & Blake, 2004). Collectively, it is found that during binocular rivalry, the detection threshold of a probe presented to the suppressed eye is higher than that presented to the dominant eye. The elevation of the detection threshold in the suppressed eye is thought to be caused by an interocular inhibitory mechanism that inhibits signals from the suppressed eye before they reach the site(s) of visual awareness (Blake, 1989; Wilson, 2003). Depending on the property

of the probe and binocular rivalry stimulus, the probe detection protocol can reveal either the general, or feature specific, characteristics of interocular suppression (e.g., Alais & Parker, 2006; Blake, 2001; Nguyen et al., 2001; O'Shea & Crassini, 1981; Ooi & Loop, 1994; Smith, Levi, Harwerth, & White, 1982; Stuit, Cass, Paffen, & Alais, 2009).

The current paper uses the probe detection protocol to extend our investigation of binocular rivalry involving monocular boundary contour (MBC) (Fig. 1b). The left half-image of the binocular rivalry stimulus has a homogeneous horizontal grating while the right half-image has a vertical grating disc surrounded by horizontal grating. With free-fusion, one perceives a stable vertical grating disc floating in front of the horizontal grating (Frisby & Mayhew, 1978) rather than the typical binocular rivalry alternation. Psychophysical studies from our laboratory have revealed that the MBC formed between the vertical grating disc and the surrounding horizontal grating in the right half-image leads to a high predominance (about 90%) of perceiving the vertical grating disc (Ooi & He, 2005, 2006). Accordingly, we call the display in Fig. 1b an *MBC rivalry* stimulus to distinguish it from the more typical binocular rivalry stimulus such as the one in Fig. 1a, which we refer to as a *binocular boundary contour (BBC) rivalry* stimulus, since the boundary contours of the two half-images have the same shape and size.

The MBC rivalry stimulus provides a unique opportunity to investigate the contribution of the boundary contour (BC) to binocular rivalry, and its relationship to binocular surface perception (Ooi & He, 2005, 2006; Su et al., 2009; van Bogaert, Ooi, & He,

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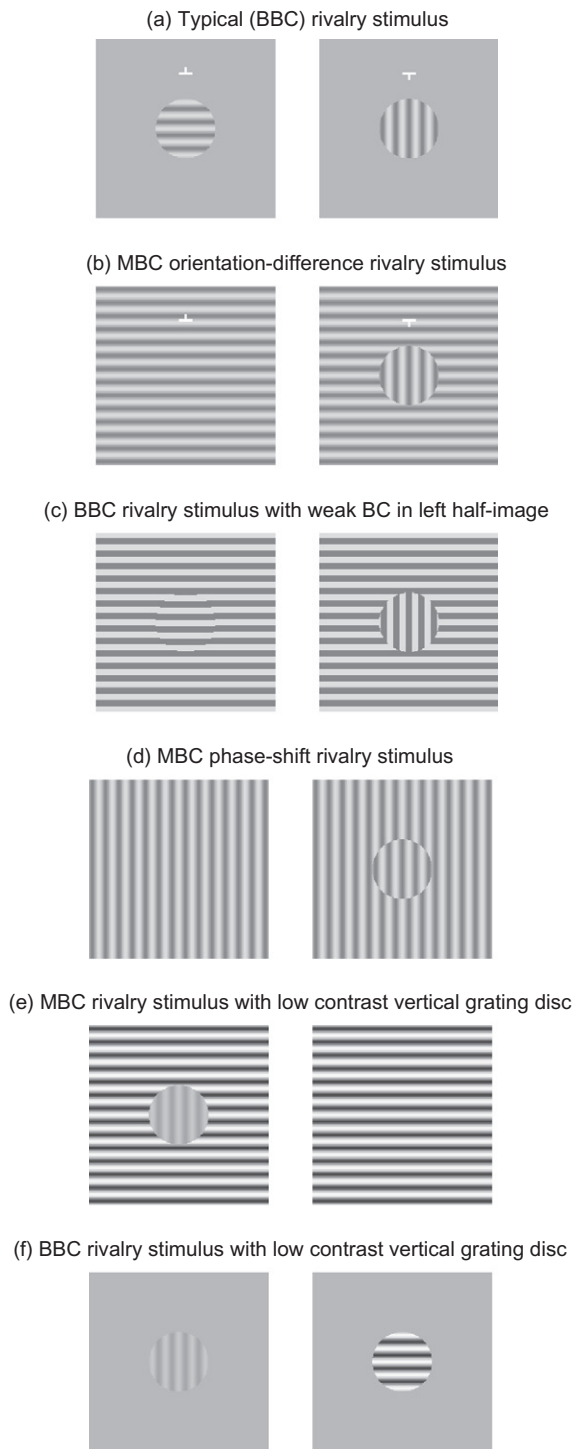


Fig. 1. (a) A typical binocular rivalry stimulus that stimulates the two eyes with grating discs comprising of orthogonal orientation. We refer to this stimulus as the binocular boundary contour (BBC) rivalry stimulus because the boundary contour of each disc corresponds in the two eyes. (b) An MBC orientation-difference rivalry stimulus in which only one half-image carries the monocular boundary contour (grating disc). The vertical grating disc corresponds to a retinal area in the fellow eye receiving the homogeneous horizontal grating. Yet, when free-fused, one seldom experiences the alternation of binocular rivalry as in (a) above, but a relatively stable percept of the vertical grating disc. (c) A BBC rivalry stimulus with a weak boundary contour (horizontal grating disc) in the left half-image, which is created by phase-shifting the central and surround horizontal grating by 36° . The vertical grating disc with the strong boundary contour predominates in perception. (d) An MBC phase-shift rivalry stimulus, created with 180° phase-shift. (e) MBC orientation-difference rivalry stimulus. The vertical grating within the disc has a low contrast. (f) BBC rivalry stimulus. The vertical grating within the disc also has a low contrast. Yet, when compared between (e) and (f), the vertical grating disc predominates in (e) but not (f).

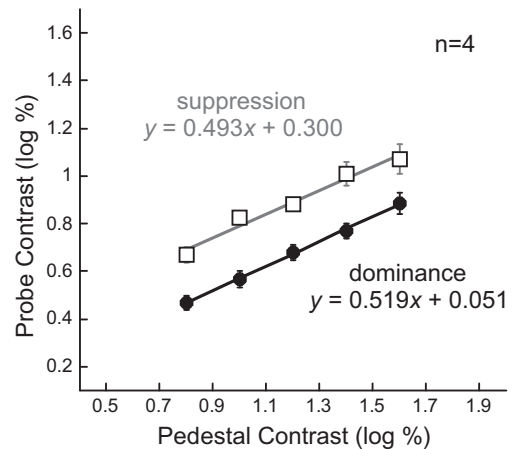


Fig. 2. Data of dominance and suppression TvC functions obtained with the MBC phase-shift rivalry stimulus. The graph is redrawn from a study reported in Su et al. (2009).

2008; Xu, He, & Ooi, 2010). For example, Xu et al. (2010) modified the MBC rivalry stimulus into a BBC rivalry stimulus by inserting a relative phase-shift between the central and surrounding square wave gratings in the left half-image (Fig. 1c, 36° phase-shift) to create a horizontal grating disc with BC. It was found that increasing the phase-shift, which mainly enhances the BC strength of the horizontal grating disc, increases the predominance of seeing the horizontal grating disc. Then in a subsequent experiment Xu et al. (2010) added a circular ring with fixed luminance (same mean luminance as the grating disc) between the horizontal grating disc and surrounding horizontal grating. This time they found that changing the relative phase-shift did not affect the predominance of the horizontal grating disc. This is because the (constant luminance) ring now served as the BC of the horizontal grating disc. Thus, this second experiment shows that the effect of phase-shift in their main experiment (Fig. 1c) is mainly due to the modulation of BC strength caused by the phase-shift, rather than the phase-shift triggering the center-surround interaction (e.g., Alais & Blake, 1998; Fukuda & Blake, 1992; Ooi & He, 2006; Paffen et al., 2005). This result supports an earlier finding by Ooi and He (2006) that the center-surround suppression factor contributes less to binocular rivalry induced by the MBC rivalry stimulus than the BC factor.

Recently, we used a threshold detection method similar to that used by Watanabe et al. (2004) to investigate whether an MBC alone can trigger the interocular inhibitory mechanism to suppress the image in the fellow eye (Su et al., 2009). Our experiments employed an MBC phase-shift rivalry stimulus similar to that in Fig. 1d, where the two half-images have the same vertical grating (i.e., no conflicting local features) and additionally, the right half-image has an MBC grating disc created by the phase-shift. We measured the increment threshold of detecting a monocular Gabor probe on either half-image (pedestal) as a function of the grating contrast to obtain the threshold vs. contrast (TvC) function. We found the TvC function is significantly elevated when measured on the homogeneous grating than on the MBC disc, indicating suppression of the homogeneous grating (the results are reproduced in Fig. 2). This finding indicates that the MBC alone can initiate interocular inhibition. Additionally, we found that the TvC functions measured on both half-images can be fitted by linear functions with similar slopes, suggesting that the contrast gain control mechanism is not affected by the interocular inhibitory mechanism (Watanabe et al., 2004).

The MBC rivalry stimulus, with either orientation-difference or phase-shifted grating, is also useful for investigating the distributed cortical processes involved in binocular rivalry. It is recog-

nized that the cortical representation of visual surfaces includes at least two critical stages: registering surface BCs and spreading-in of the interior surface features (texture and color) within the BCs (e.g., Caputo, 1998; Grossberg & Mingolla, 1985; Nakayama, He, & Shimojo, 1995; Paradiso & Nakayama, 1991; van Bogaert et al., 2008; von der Heydt, Friedman, & Zhou, 2003; Su, Ooi, & He, 2007). Since the boundary contour (BC) information that is responsible for surface image segmentation is largely extracted in cortical area V2 (e.g., Bakin, Nakayama, & Gilbert, 2000; Qiu & von der Heydt, 2005; Zhou, Friedman, & von der Heydt, 2000), it is likely that the MBC initiated interocular inhibitory mechanism resides in area V2. Presumably, once triggered, the interocular inhibition could directly, or via feedback to V1, cause suppression of the image representation from the other eye. But for the MBC orientation-difference rivalry stimulus (Fig. 1b), it is likely that the conflicting local features activate the interocular inhibitory mechanism in area V1, in addition to the MBC triggered interocular inhibitory mechanism in area V2. On the other hand, with either the MBC orientation-difference or MBC phase-shift rivalry stimulus, it is the MBC half-image that contributes substantially to the dominant percept (Ooi & He, 2005, 2006; Su et al., 2009). This notion is reinforced in Fig. 1e, where the low contrast MBC vertical grating disc is predominantly perceived over the high contrast horizontal grating half-image. In contrast, with the BBC rivalry stimulus in Fig. 1f it is the high contrast horizontal disc that is predominantly perceived. Such an observation can lead to the argument that the interocular inhibitory mechanism in area V1, which is activated by conflicting local features, contributes little to interocular inhibition in the MBC rivalry stimulus. If this is true, we will expect the threshold elevation in the suppressed eye (homogeneous grating) to be similar when tested with either the MBC orientation-difference or MBC phase-shift rivalry stimulus. To explore this possibility, our first experiment measured the TvC functions of the MBC orientation-difference rivalry stimulus (Fig. 1b) using the same method and observers as in our earlier study with the MBC phase-shift stimulus (Su et al., 2009).

Our first experiment reveals that the threshold elevation due to the MBC orientation-difference rivalry stimulus is significantly higher than that with the MBC phase-shift rivalry stimulus. This indicates the contributions of both conflicting local features and MBC to interocular suppression. Then to further explore the interocular inhibition in the MBC rivalry stimulus, our second experiment tested whether the magnitude of suppression is independent of the strength of the stimulus in the dominant eye. To do so, we measured the TvC functions of the MBC orientation-difference rivalry stimulus in which the contrast of the homogeneous grating (suppression condition) was fixed while the contrast of MBC disc (dominance condition) varied.

Our third and fourth experiments measured performance of detecting a suprathreshold Gabor probe, respectively in the MBC orientation-difference stimulus and the MBC phase-shift stimulus, at various stimulus onset asynchrony (SOA) (80–410 ms) to investigate the early dynamics of interocular inhibition. Our goal is to reveal that the interocular inhibition triggered by the MBC becomes effective before 150 ms, unlike that with a BBC rivalry stimulus (Su, He, & Ooi, 2006; Wolfe, 1983).

2. Experiment 1: the dominance and suppression TvC functions with the MBC orientation-difference rivalry stimulus

We measured the contrast increment threshold of seeing a monocular Gabor probe presented on the MBC orientation-difference rivalry stimulus (Fig. 3). The luminance contrast of the MBC rivalry stimulus was set at one of six contrast levels (5.01–50.12%). For each contrast level tested, both the right and left

half-images always had the same contrast specification (see Fig. 4, top). This allows us to determine the threshold vs. contrast (TvC) function in the dominance and suppression conditions.

2.1. Methods

2.1.1. Observers

One author, and three observers who were naïve to the purpose of the study, participated in the experiment. For all experiments in this paper, the observers had normal or corrected-to-normal visual acuity and a stereoscopic resolution of 20 s of arc or better. Informed consent was obtained from the naïve observers before commencing the experiment.

2.1.2. Stimuli

A Macintosh G4 computer using MATLAB and Psychophysics Toolbox software generated the stimuli (Brainard, 1997; Pelli, 1997). The images were displayed on a 19-in. flat cathode ray tube (CRT) screen with a 100 Hz vertical scanning rate. The stimuli were viewed with a mirror haploscopic system attached to a head-and-chin rest from a viewing distance of 75 cm.

The MBC orientation-difference rivalry stimulus ($6^\circ \times 6^\circ$) was presented upon a gray background with the same mean luminance (87 cd/m^2). One half-image had a homogeneous sinusoidal grating (3 cpd). The other half-image also had the same sinusoidal grating but with an additional 2° sinusoidal grating disc (3 cpd) with an orthogonal orientation (vertical vs. horizontal). A white nonius fixation target ($0.4^\circ \times 0.4^\circ$) was located 0.85° above the grating disc and its corresponding region in the other half-image. The luminance contrast of the MBC rivalry stimulus was set at one of six levels: 5.01%, 7.94%, 12.59%, 19.95%, 31.62% and 50.12% (equivalent log% contrast levels of 0.7, 0.9, 1.1, 1.3, 1.5 and 1.7, respectively).

During each trial, a Gabor probe was presented either on the center of the grating disc of one half-image (dominance condition; see example in Fig. 2a), or on the center of the homogeneous grating of the other half-image (suppression condition; see example in Fig. 2b). The probe was specified by the following formula:

$$L(x, y) = L_m \left\{ 1 + c \cdot \sin(2\pi\omega x) \cdot \left[1 + a \cdot \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right) \right] \right\}$$

In the formula, $L(x, y)$ represents the luminance at a specified location (x, y) . The x -axis is orthogonal to the orientation of the probe's pedestal grating while the y -axis is parallel with the grating orientation; the origin overlaps the center of the probe. L_m is the mean luminance (87 cd/m^2); c is the contrast of the grating; a is the peak contrast increment ratio of the probe; ω is the spatial frequency of the grating (3 cpd); and σ is the standard deviation of the Gaussian function in the Gabor kernel (set to 0.42°). The trial ended with the presentation of a binocular checkerboard mask. The spatial frequency of the mask was 3 cpd; its mean luminance was 87 cd/m^2 and its contrast was 96.5%.

2.1.3. Procedures

The dominance condition was tested with the probe presented on the half-image with the grating disc (pedestal), while the suppression condition was tested with the probe presented on the half-image with the homogeneous grating (pedestal). The probe was always presented to the observer's dominant eye. To control for the effect of orientation, the orientation of the disc and homogeneous grating square were counter-balanced (vertical vs. horizontal). Effectively, this gave rise to four stimulus combinations. Fig. 3a and b illustrate two of the four stimulus combinations where the probe was, respectively, presented on the grating disc half-image (dominance condition) and on the homogeneous grating half-image (suppression condition).

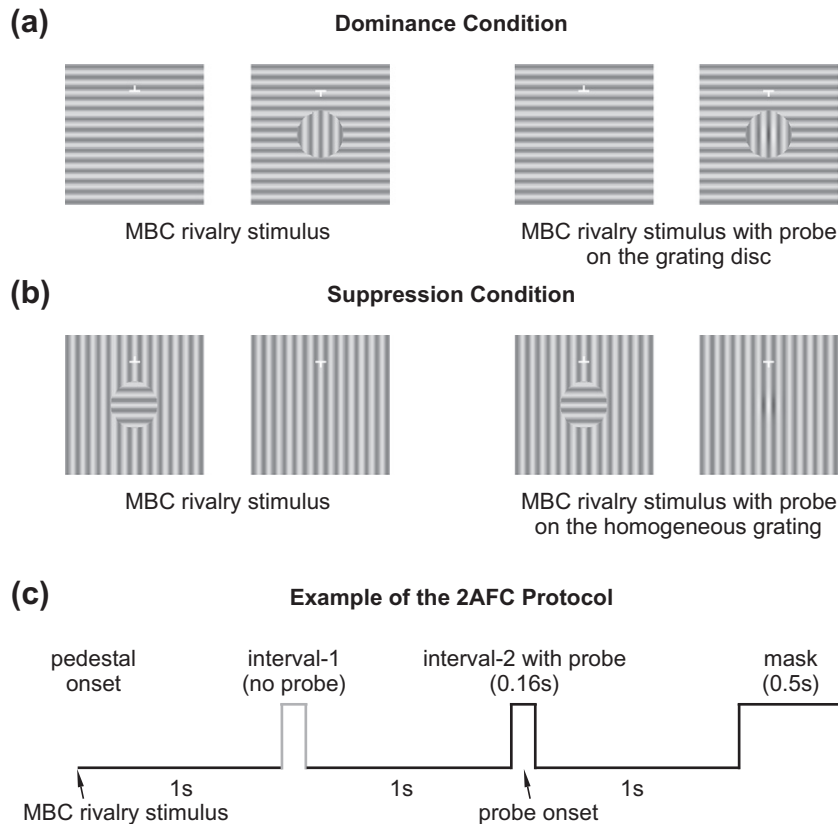


Fig. 3. (a) An example of a dominance condition. Left: the MBC orientation-difference rivalry stimulus with a vertical grating disc in the right half-image and a horizontal grating disc in the left half-image. Right: a Gabor probe is superimposed on the grating disc (pedestal) to measure the contrast threshold for detecting the probe in the dominant eye. (b) An example of the suppression condition. Left: the MBC orientation-difference rivalry stimulus. Right: the Gabor probe is superimposed on the homogeneous grating half-image (pedestal) to measure the contrast threshold for detecting the probe in the suppressed eye. To counterbalance the effect of grating orientation, dominance and suppression thresholds were also tested with horizontal Gabor probe upon a horizontal grating pedestal (not shown). (c) An example of the 2-alternative-forced-choice (2AFC) method. One sec after the onset of the MBC orientation-difference rivalry stimulus (pedestal), a brief tone is presented. This is followed, 1 s later, by another brief tone that is accompanied by the Gabor probe (0.16 s). The trial ended 1 s later with the presentation of a mask (0.5 s). The observer's task was to indicate whether the probe accompanied the first or second tone.

Observers were tested in four separate sessions (2 repeats \times 2 pedestal orientations) with its order counter-balanced. Each session consisted of 12 blocks with the same pedestal orientation, of which six blocks had the grating disc half-image as the pedestal (dominance condition) and the other six blocks had the homogeneous grating half-image as the pedestal (suppression condition). Each block measured the contrast increment threshold for one of the six pedestal contrast levels.

We used a 2AFC-staircase design to determine the contrast threshold of the Gabor probe (Fig. 2c). To begin a trial, the observer steadied himself/herself on a head-and-chin rest and maintained eye alignment on the nonius fixation. He/she then pressed the spacebar on the computer keyboard to present the MBC rivalry stimulus. One sec (interval-1) or 2 s (interval-2) after the onset of the MBC stimulus, a Gabor probe (duration = 0.16 s) was presented on one half-image (pedestal) of the MBC stimulus. Two brief tones, each presented at 1 and 2 s, were used to aid the observers in discriminating between the two separate intervals. The 2AFC trial ended with the presentation of a 0.5 s checkerboard mask. The observer's task was to press one of two keys on the computer keyboard to indicate whether the probe was seen at the first or second interval. No feedback regarding the response accuracy was given to the observer.

Once a trial was completed, the observer would press the spacebar to initiate the next trial. The probe contrast in the subsequent trial was determined based on an adaptive 3-down/1-up rule. At the beginning of each block, the relative intensity (contrast incre-

ment ratio) of the probe was set at 50% (i.e., at its peak, the probe enhanced the contrast of the stimulus by 50%). The step size of the contrast change was 15% after the second reversal and 30% before the second reversal. In the rare event (<1%) where the grating disc of the MBC stimulus was suppressed from perception during the trial, the observer would abort the trial by pressing the down-arrow key. A test block ended after nine reversals. To calculate the contrast increment threshold for data analysis, the probe contrast levels (in log contrast unit) from the last six reversals were averaged.

It should be noted that the threshold measured by this staircase procedure was slightly different from the threshold at 79.4% correct that was usually reported by other studies using the transformed 3-down/1-up staircase method. This is because the step upward (+15%, i.e., 0.0607 log unit) and the step downward (−15%, i.e. −0.0706 log unit) in our experiment was slightly different when analyzed in logarithmic scale. The equilibrium condition (Kaernbach, 1991) for this weighted step size is:

$$S_{\text{down}}p^3 = S_{\text{up}}(1 - p^3)$$

Effectively, we have an S_{down} that equals to 0.0706 log unit and a S_{up} of 0.0607 log unit. Therefore, the threshold reflects the 77.3% correct point on the psychometric function.

2.3.1. Data analysis

The contrast increment threshold data from the dominance and suppression conditions were averaged from those measured on the horizontal and vertical pedestals.

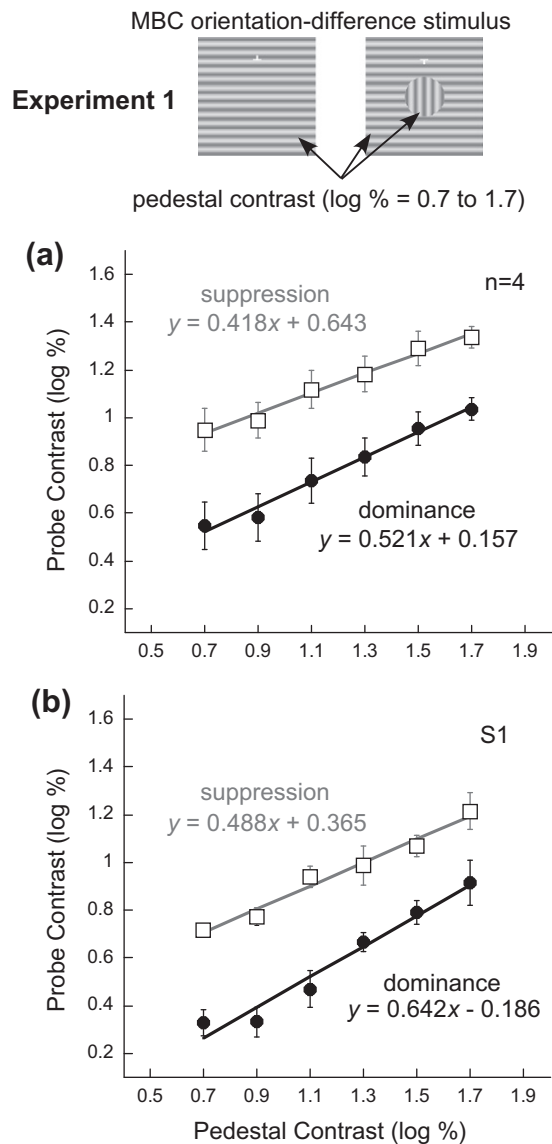


Fig. 4. Results of Experiment 1: the contrast of the MBC orientation-difference rivalry stimulus was set at one of six levels. (a) The average results of all observers in the dominance (circles) and suppression (squares) conditions. While the slopes of the TvC functions for both conditions are not significantly different, the threshold for detecting the Gabor probe is elevated in the suppression condition. The error bars in the graph indicate 1 S.E. (b) The results of a representative naïve observer also show an elevated suppression threshold and no significant difference between the slopes of the TvC functions in the two conditions.

2.4. Results and discussion

We obtained the TvC functions for the dominance (circles) and suppression (squares) conditions by plotting the probe increment contrast threshold versus the pedestal contrast in a log–log coordinate in Fig. 4. Fig. 4a depicts the four observers' average data while Fig. 4b that of a representative naïve observer. By applying a 2-way ANOVA with repeated measures to the average data, we found that the contrast increment thresholds are significantly higher for the suppression condition than for the dominance condition with an average elevation of 0.3–0.4 log unit [$F(1, 3) = 31.734$, $p < 0.025$, 2-way ANOVA with repeated measures]. This indicates there is a meaningful elevation of the contrast increment threshold in the suppression condition compared to that in the dominance condition. Fig. 4 also shows that for both the dominance and suppression conditions, the (log) contrast increment threshold increases signif-

icantly with the pedestal contrast [$F(2.472, 7.416) = 57.837$, $p < 0.001$; with the Greenhouse–Geisser correction], and they have a similar slope (regression line for the dominance condition: $y = 0.521x + 0.157$; regression line for the suppression condition: $y = 0.418x + 0.643$) [$F(2.284, 6.853) = 1.020$, $p = 0.420$; with the Greenhouse–Geisser correction for the interaction effect of dominance/suppression by pedestal-contrast]. This suggests the interocular inhibitory mechanism activated by the conflicting local features and MBC does not have a significant impact on the contrast gain control of the MBC rivalry stimulus. The trend of our current results resembles those found in two previous studies, respectively, by Watanabe et al. (2004) (with typical BBC rivalry) and ourselves (with MBC phase-shift rivalry; Su et al., 2009).

Indeed, the similarity in trend facilitates our comparison between the MBC orientation-difference (Fig. 4) and MBC phase-shift rivalry stimuli (Fig. 2). Overall, the average elevation of the TvC function on the homogeneous grating half-image of the MBC orientation-difference stimulus is larger than that with the MBC phase-shift rivalry stimulus (the same four observers participated in both experiments). Specifically, the average difference in the magnitude of suppression between the two types of MBC rivalry stimuli is about 0.146 log contrast [$F(1, 8) = 74.641$, $p < 0.001$, 2-way ANOVA with repeated measures]. Thus, assuming the MBCs in both stimuli have equal strengths, the larger interocular inhibition in the MBC orientation-difference rivalry stimulus compared to the MBC phase-shift rivalry stimulus is very likely contributed by its local conflicting features (orthogonal gratings).

3. Experiment 2: effect of the contrast of the dominant half-image of the MBC orientation-difference rivalry stimulus on the suppression TvC function

We investigated whether the contrast increment threshold in the suppressed eye is a function of the grating contrast in the dominant eye. Assuming that the increment threshold of the suppressed eye reflects the stimulus strength required for the putative “visual switch” to disengage its selection from the currently dominant image representation to the suppressed one, this experiment will inform whether the selection change depends on the contrast of the stimulus (saliency) in the dominant eye. Experiment 1 above could not reveal this because we varied the grating contrast equally in both the dominant and suppressed half-images (see Fig. 4, top). Therefore, in this experiment we varied only the contrast of the grating disc in the dominant half-image while keeping the contrast of the remaining components of the MBC orientation-difference rivalry stimulus constant (Fig. 5, top).

3.1. Methods

3.1.1. Observers

The same author and three naïve observers participated in the experiment.

3.1.2. Stimuli

We employed the same stimuli as in Experiment 1 except for the manipulation of the contrast of the grating disc in one of five levels (7.94%, 12.59%, 19.95%, 31.62% and 50.12%), while the contrast of the remaining stimulus components was fixed at 19.95%.

3.1.3. Procedures

The test procedures were similar to that of the first experiment except for a minor adjustment to the staircase protocol. We adjusted the step size of the probe contrast change in the staircase to 0.0667 log unit after the second reversal, and 0.1333 log unit before the second reversal. This led to a theoretical threshold at 79.3%

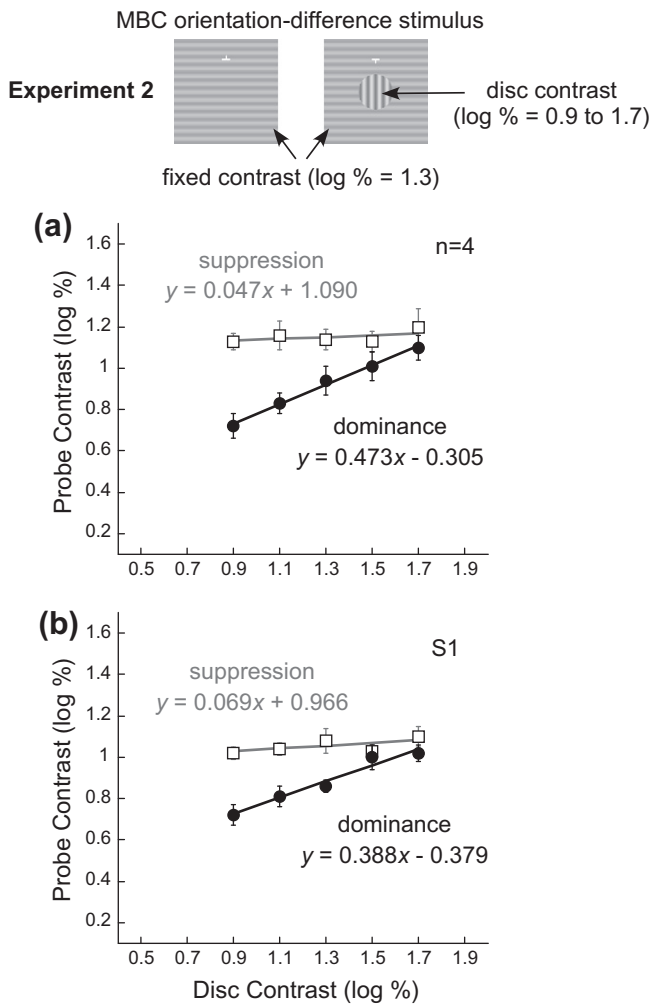


Fig. 5. Results of Experiment 2: the contrast of the grating disc was set at one of five different levels while the remaining components of the MBC orientation-difference rivalry stimulus was fixed at 19.19% contrast level. (a) The average results of all observers in the dominance (circles) and suppression (squares) conditions. The slope of the TvC function for the suppression condition is almost flat, while the slope of the dominance condition is steep. The error bars in the graph indicate 1 S.E. (b) The results of the same representative naïve observer whose data are shown in Experiment 1.

correct, which was slightly different from that of the first experiment (77.3%).

3.2. Results & discussion

Similar to Experiment 1, we plotted the data of the dominance (circles) and suppression (squares) conditions as TvC functions in a log–log coordinate. Fig. 5a shows the average data of the four observers and Fig. 5b the data of the same naïve observer whose data were shown in Fig. 4b (Experiment 1). Clearly, the dominant TvC function has a similar trend to that of the dominance condition in Experiment 1 (regression line: $y = 0.473x + 0.305$) [$F(4, 15) = 5.48$, $p < 0.01$, one way ANOVA with repeated measures]. However, the suppression TvC function does not change significantly with the contrast of the grating disc (regression line: $y = 0.047x + 1.090$) [$F(4, 15) = 0.19$, $p > 0.9$, one way ANOVA with repeated measures]. This finding indicates that the contrast increment threshold of the suppressed eye depends only on the contrast of the half-image stimulating it, and not on the contrast of the half-image (MBC disc) stimulating the fellow eye. In other words, changing the contrast of the MBC grating disc to vary both the strength of the MBC and the local feature within the disc (grating) in the dominant half-image, has little impact on the

suppression threshold in the contralateral half-image. This finding has a significant implication. Suppose that the contrast increment threshold of the suppressed eye reflects the minimal strength of the probe stimulus in the suppressed eye required for the visual process to switch its selection from the currently dominant image representation to the suppressed one. In this regard, our finding (Fig. 5) suggests that no matter how salient the dominant half-image is during binocular rivalry, it is the saliency of the perturbing signals (probe) in the suppressed eye that modulates the putative visual switch. On the other hand, a transient probe that augments the signals of the dominant image representation can prevent it from being unselected (Chong & Blake, 2006; Hering, 1879/1942; Kamphuisen, van Wezel, & van Ee, 2007; Lack, 1978; Levelt, 1965; Mitchell, Stoner, & Reynolds, 2004; Ooi & He, 1999; von Helmholtz, 1909; Walker, 1978).

Our finding with the MBC rivalry stimulus parallels that with the BBC rivalry stimulus. For example, Blake and Camisa (1979) conducted a similar study with the typical BBC rivalry stimulus (conflicting local features only). In their experiment, they presented a circular flash of light (probe) with fixed intensity on a grating half-image. They found that when the grating half-image was suppressed, the percentage correct in detecting the probe did not vary with the contrast of the half-image in the fellow (dominant) eye. Although their study measured the percentage correct performance, rather than threshold, it is gratifying that both studies arrive at the same conclusion.

4. Experiment 3: the effect of SOA on probe detection with the MBC orientation-difference rivalry stimulus

Wolfe (1983) made an intriguing discovery of the effect of presentation duration on the perception of the typical binocular rivalry (BBC) stimulus with vertical and horizontal gratings. His observers reported seeing the gratings as plaid/checkerboard or piecemeal when the stimulus duration was shorter than 150 ms. But beyond 150 ms, the observers saw global dominance of either vertical or horizontal grating. This led to the conclusion that interocular inhibition takes longer than 150 ms to fully assert its influence (Wolfe, 1983). We used a similar method to investigate whether interocular inhibition requires the same duration to assert its influence on the MBC orientation-difference rivalry stimulus (Su et al., 2007). We found that, consistent with Wolfe (1983), observers rarely saw global dominance with presentation durations shorter than 150 ms for the typical BBC rivalry stimulus. With the MBC rivalry stimulus, however, our observers perceived the MBC grating disc, i.e., global dominance percept, for stimulus durations shorter than 150 ms.

To further investigate our finding with the MBC rivalry stimuli, we tested observers' performance in detecting a suprathreshold monocular Gabor probe in Experiments 3 and 4 below. If the interocular inhibitory mechanism is effective before 150 ms (after the onset of the MBC rivalry stimulus), we should expect the rate of detecting a monocular probe on the MBC grating disc (dominance condition) to be higher than that on the homogeneous grating (suppression condition). We tested this prediction by measuring both the percentage correct and response time, in detecting a monocular Gabor probe at various SOAs between the probe and the MBC rivalry stimulus. Experiment 3 tested with the MBC orientation-difference rivalry stimulus and Experiment 4 tested with the MBC phase-shift rivalry stimulus.

4.1. Methods

4.1.1. Observers

One author and four new naïve observers participated in the experiment.

4.1.2. Stimuli

The apparatus and display settings were the same as in Experiment 1 except for the dimension of the CRT monitor being 21 in. At the beginning of each trial, a white $0.45^\circ \times 0.45^\circ$ nonius fixation cross (73.1 cd/m^2) was presented in the middle of a $5^\circ \times 5^\circ$ black frame fusion lock (5 cd/m^2). The MBC orientation-difference rivalry stimulus (Fig. 6) was modified after the one used in Experiment 1 as follows: (i) the mean luminance of the stimulus and gray background was 63.1 cd/m^2 ; (ii) the luminance contrast of the grating was fixed at 39.8%; (iii) the overall size of the MBC rivalry stimulus was $4.5^\circ \times 4.5^\circ$ while and the MBC disc diameter was 1.5° . During a trial, a monocular Gabor probe ($L_m = 63.1 \text{ cd/m}^2$, $c = 39.8\%$, $\sigma = 0.24^\circ$) was presented either in the center of the MBC grating disc (dominance condition), or in the center of the homogeneous grating half-image (suppression condition). The probe was always pre-

sented to the dominant eye. Each trial terminated with a $4.5^\circ \times 4.5^\circ$ black-and-white random-dot mask (dot size = $0.1^\circ \times 0.1^\circ$; contrast = 95%).

4.1.3. Determination of the Gabor probe

The contrast increment of the Gabor probe for this and the following experiment was determined separately for each observer. To do so, a monocular vertical grating pedestal ($4.5^\circ \times 4.5^\circ$, 3 cpd, 63.1 cd/m^2 , 39.8% contrast) upon a homogeneous gray background was presented to the eye to be stimulated with the Gabor probe. The fellow eye viewed the same gray background (without the stimulus). This was followed, after a 100 ms SOA, by the Gabor probe (10 ms). The observer reported whether he/she detected the probe. The goal was to find the weakest probe strength (contrast increment) that led to a detection rate of no less than 86.7%. Thus,

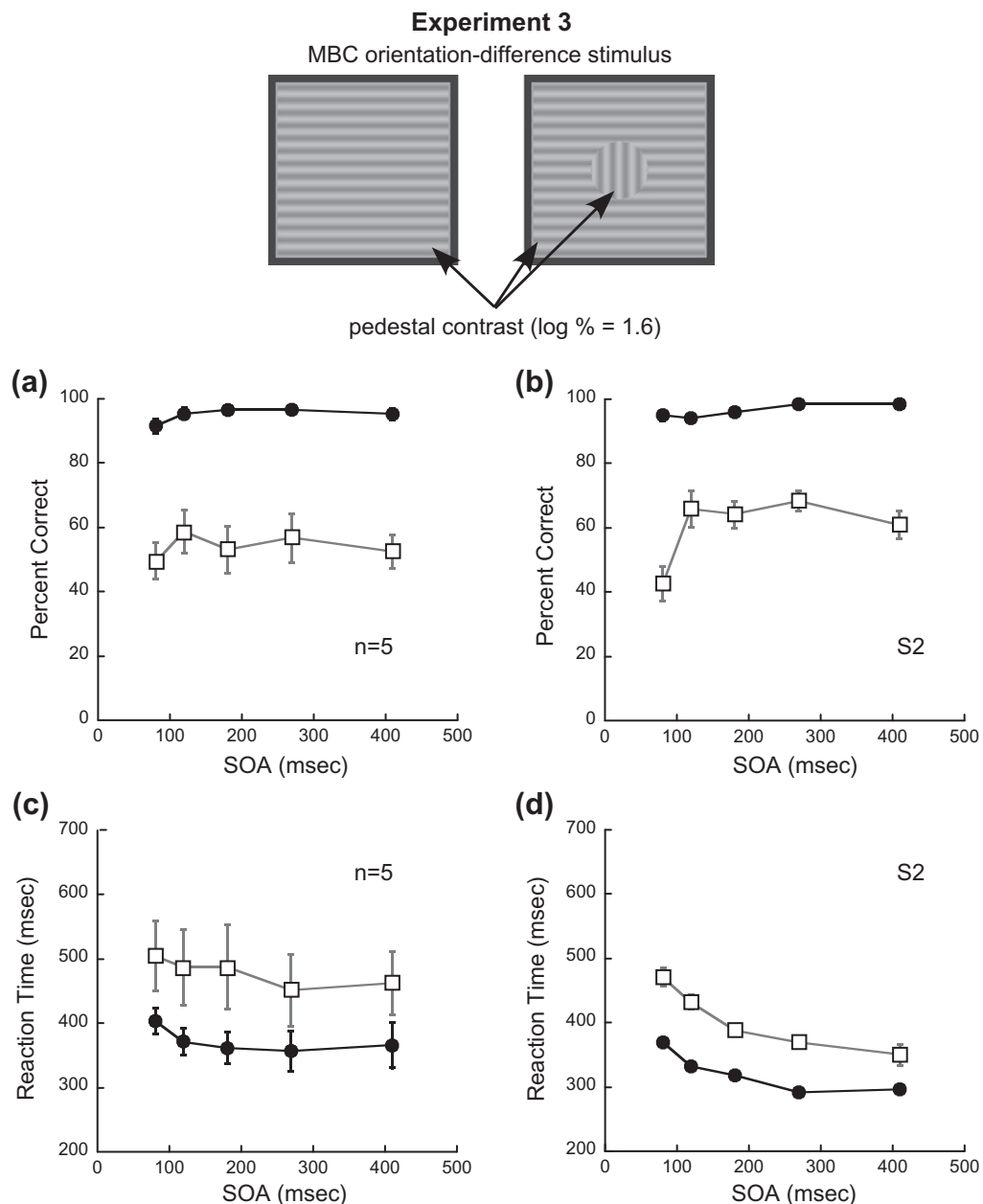


Fig. 6. Results of Experiment 3 with the MBC orientation-difference rivalry stimulus. (a) The average percentage correct detection of all observers is higher in the dominance (circles) than suppression (squares) condition. (b) The detection data of a representative naïve observer show a similar trend. (c) The average reaction time for responding to seeing the Gabor probe is shorter in the dominance (circles) than suppression (squares) condition. (d) The reaction time data of the same representative naïve observer. The error bars in the graphs indicate 1 S.E.

a series of mini-experimental blocks with various probe strengths were run. Each experimental run tested 3–4 blocks of different probe strengths (15 trials per probe strength). The probes were varied by a step of approximately 4%, within a contrast range of 15.92–39.81%. The probe strength that led to a detection rate of at least 13 out of 15 hits (86.7% detection) was used for Experiment 4. Since the suppression with the MBC-orientation-difference rivalry stimulus is significantly larger, we added ~10% higher in increment contrast to the probe for use in the current experiment.

4.1.4. Procedures

The Gabor probe, whose increment contrast level was determined above, was presented on either half-image of the MBC orientation-difference rivalry stimulus. For each test trial, the probe duration was 20 ms and its onset relative to the onset of the MBC orientation-difference rivalry stimulus (SOA) was 80, 120, 180, 270, or 410 ms. This allowed us to measure the detection rate and response time to detect the probe in the dominance and suppression conditions. To check for the reliability of the observer's responses, we also included catch trials in which the MBC orientation-difference rivalry stimulus was presented without the probe. The catch trials and test trials were intermingled within a block of 240 trials {[5 SOAs \times 2 test conditions (dominance and suppression) \times 2 probe orientations (horizontal and vertical) \times 10 repeats] + 40 catch trials}. The trials were semi-randomized with the provision that no more than three consecutive trials had exactly the same combination of test condition and probe orientation. In all, six blocks of trials were conducted over two sessions for each observer.

To begin a trial, the observer aligned his/her eyes with the nonius fixation and pressed the spacebar on a computer keyboard. This led to the removal of the nonius fixation (the surrounding square fusion lock remained) and 250 ms later, the presentation of the MBC rivalry stimulus. Depending on the type of trial (test or catch), the probe could be added at the appropriate SOA. The observer's task was to respond as quickly as possible by pressing the right arrow key of the keyboard if he/she saw the Gabor probe. Once the response was made, the trial terminated with the presentation of the mask (250 ms). If no response was made (because the probe was either not detected or absent), the MBC rivalry stimulus would be removed after 1.5 s and the trial terminated with the presentation of the mask. If no probe was detected, the observer should not press any key.

Several precautionary measures were implemented. In the rare event (<1%) where the MBC disc disappeared (suppressed) during the trial, or had its texture seen in plaid/piecemeal, the observer would abort the trial by pressing the down-arrow key. The trial would then be repeated. Audio feedbacks with different tones were given to convey two possible types of false alarms: (i) responding to a catch trial, and (ii) responding less than 100 ms upon the probe onset (anticipatory response). Trials with anticipatory responses (<0.1%) would be repeated. A third audio feedback accompanied the "regular" test trials where probe detection were made. In this way, the observer could monitor the reliability of his/her responses. For each block of trials, the observer was allowed to make a maximum of four false alarms (10%) when responding to the catch trials. If a fifth false alarm was made, the test program would abort and the observer would have to repeat the entire block of trials. Furthermore, a 1-min rest period was inserted after every 40 trials to reduce the possibility of observer fatigue during the 240-trial block.

The data from the six blocks of trials were pooled for analysis of reaction time data. To increase data reliability, responses whose reaction times deviated from the mean by larger than three standard deviations were excluded from analysis. This rarely occurred (<0.1%).

4.2. Results

Fig. 6a and b show, respectively, the average detection data of five observers and the data of a representative naïve observer. The percentage correct in detecting the monocular Gabor probe is plotted as a function of SOA for both conditions. As predicted, detection is significantly higher in the dominance condition (circles) than in the suppression condition (squares) [$F(1, 4) = 57.467, p = 0.002$; 2-way ANOVA with repeated measures]. The percentage correct detection in both conditions does not vary significantly with SOA [SOA main effect: $F(4, 16) = 1.159, p = 0.365$; interaction between condition and SOA: $F(1.885, 7.541) = 0.388, p = 0.680$; with Greenhouse–Geisser correction]. This indicates that interocular inhibition becomes effective as early as 80 ms after the onset of the MBC orientation-difference rivalry stimulus. The tendency of the magnitude of suppression to be largely constant over the various SOAs appears consistent with previous studies using the BBC rivalry stimulus that tested thresholds at longer test durations (Fox & Check, 1972; Norman et al., 2000). For example, Norman et al. (2000) measured the percentage correct of detecting a probe presented to either the dominant or suppressed eye after the observer indicated perceiving global dominance of the BBC rivalry stimulus. They found the reduction of the percentage correct in the suppressed eye was constant.

Our conclusion is also confirmed by the reaction time data in Fig. 6c (average) and d (same naïve observer). The average reaction time is shorter in the dominance condition (circles) than in the suppression condition [$F(1, 4) = 11.821, p = 0.026$; 2-way ANOVA with repeated measures]. Reaction times decrease significantly with SOA [$F(1.657, 6.627) = 7.526, p = 0.022$; with Greenhouse–Geisser correction]. The difference in reaction time between the two conditions does not change significantly with SOA [$F(4, 16) = 0.929, p = 0.472$].

5. Experiment 4: the effect of SOA on probe detection with the MBC phase-shift rivalry stimulus

The results of Experiment 3 reveal effective interocular inhibition of MBC orientation-difference rivalry stimulus as early as 80 ms after its onset. Since interocular suppression in the MBC orientation-difference rivalry stimulus can be contributed by both the local conflicting features and the MBC, it is important to investigate if the interocular inhibition initiated by the MBC alone can be effective earlier than 150 ms. Thus, we used the same method as in Experiment 3 to measure the effect of SOA on the percentage correct and reaction time of detecting the monocular Gabor probe with the MBC phase-shift stimulus (Fig. 7).

5.1. Methods

5.1.1. Observers

One author and three naïve observers, who also participated in Experiment 3, participated in the current experiment. In addition, two new naïve observers were tested.

5.1.2. Stimuli

The stimulus parameters were the same as those in Experiment 3, but with two key exceptions. One, the MBC disc was created by a 90° phase-shift between the central and surrounding vertical grating (MBC phase-shift stimulus) (Fig. 7). Two, unlike Experiment 3 that tested both vertical and horizontal orientation (for the purpose of counterbalancing), we only tested the vertical orientation. The increment contrast of the Gabor probe was determined individually for each observer with the method described in Experiment 3.

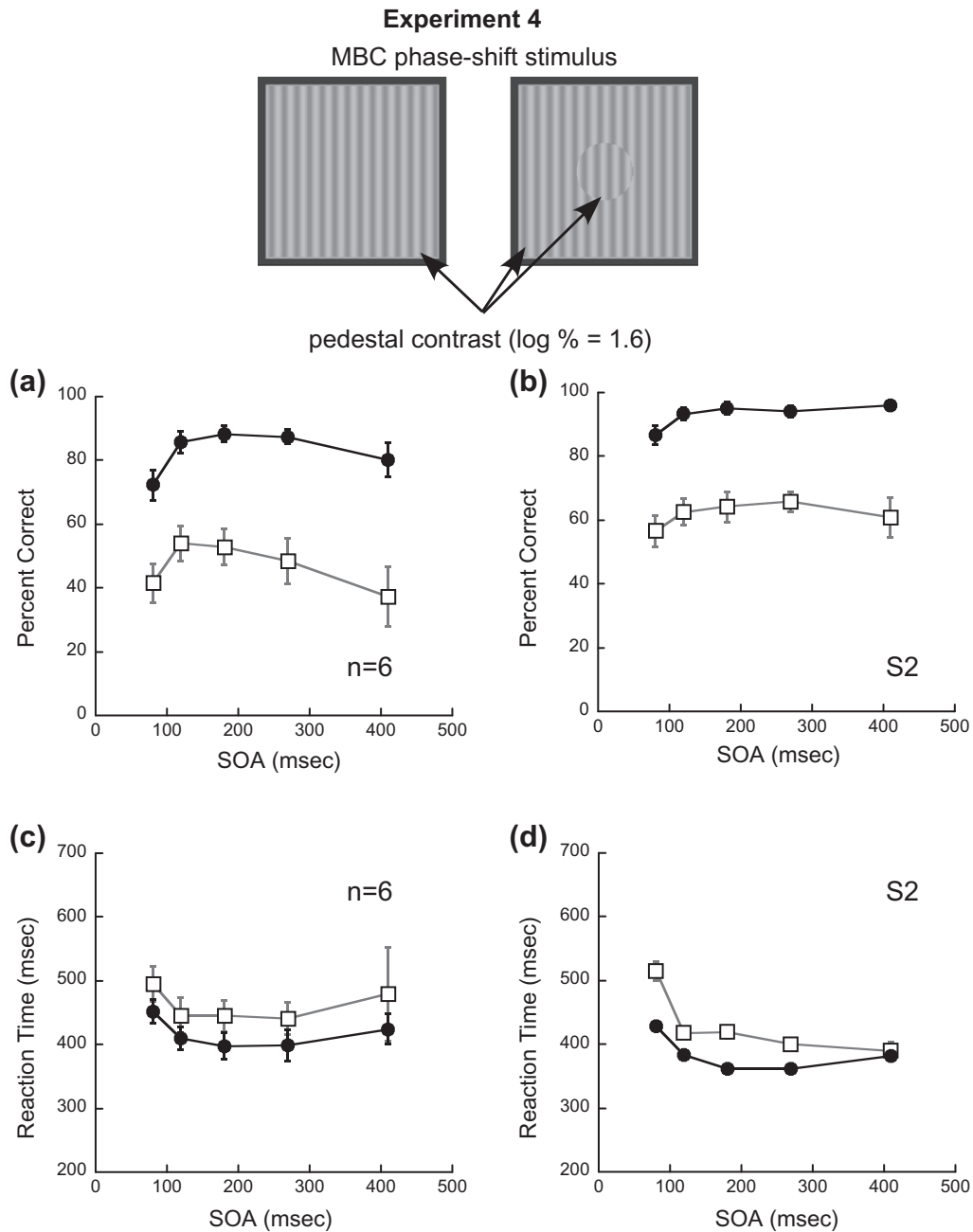


Fig. 7. Results of Experiment 4 with the MBC phase-shift rivalry stimulus. (a) The average percentage correct detection of all observers is higher in the dominance (circles) than suppression (squares) condition. (b) The detection data of the same representative naïve observer tested in Experiment 3 show a similar trend. (c) The average reaction time for responding to seeing the Gabor probe is shorter in the dominance (circles) than suppression (squares) condition. (d) The reaction time data of the same representative naïve observer. The error bars in the graphs indicate 1 S.E.

5.1.3. Procedures

All aspects of the experimental procedures were similar to those in Experiment 3, except for the following. While each observer was still tested over two experimental sessions, the total number of blocks was 12. This is because each block now comprised 120 trials {[5 SOAs (80, 120, 180, 270, and 410 ms) × 2 test conditions (dominance and suppression) × 10 repeats] + 20 catch trials}. To maintain the same false alarm rate (10%) for penalty (aborting the entire block of trials), the observer was only allowed to make a maximum of two false alarms (responding to catch trials) in each block of trials.

5.2. Results & discussion

Fig. 7a and b, respectively, depict the average detection data of six observers and the data of one representative naïve observer. The percentage correct in detecting the monocular Gabor probe is plotted as a function of SOA. Similar to Experiment 3 (Fig. 6a and b), the detection rate is significantly higher in the dominance condition (circles) than in the suppression condition (squares) [$F(1, 5) = 30.043$, $p = 0.003$, 2-way ANOVA with repeated measures]. The detection rate in the two conditions does not change significantly with SOA [$F(1.680, 8.402) = 2.398$, $p = 0.153$; with

Greenhouse–Geisser correction]. Overall, the finding indicates that the interocular inhibition triggered by the MBC begins as early as 80 ms after the onset of the stimulus.

The reaction time results in Fig. 6c (average) and d (naïve observer) show a similar trend. The average reaction time is shorter in the dominance condition (circle symbols) than in the suppression condition [$F(1, 5) = 9.821, p = 0.026$, 2-way ANOVA with repeated measures]. The difference in reaction time between the two conditions do not change significantly with SOA [$F(1.166, 5.832) = 0.084, p = 0.818$, with Greenhouse–Geisser correction]. Similarly, the reaction time for each condition does not change significantly with SOA [$F(1.181, 5.907) = 2.874, p = 0.143$, with Greenhouse–Geisser correction].

To summarize, this experiment together with Experiment 3, reveal interocular inhibition begins as early as 80 ms when locally measured with a Gabor probe. This finding supports the results of our earlier study with the MBC orientation-difference rivalry stimulus, which found that the global dominance percept can be obtained before 150 ms (Su et al., 2006). But we wish to point out a critical difference between the two studies. That is, measuring local dominance/suppression with the probe method only gauges the event at the probed area of the stimulus. Whereas, measuring global percept gauges the overall event after surface integration of like (dominant) features has occurred. Thus, it is reasonable to assume that it would take a longer time to achieve global dominance than local dominance. As such, it is possible that if measured locally, BBC rivalry stimuli might exhibit interocular inhibition earlier than 150 ms.

6. General discussion

In summary, to understand how the suppressed image of the MBC rivalry stimulus is processed, we first measured the dominance (probe on the MBC grating disc) and suppression (probe on homogeneous grating) TvC functions of the MBC orientation-difference rivalry stimulus. We found the TvC function for the suppression condition is elevated compared to that for the dominance condition, although both functions have similar slopes. While the trend of the TvC functions is similar to that found with the MBC phase-shift rivalry stimulus (Su et al., 2009), the magnitude of suppression with the MBC orientation-difference rivalry stimulus is larger. This comparison allows us to distinguish between the extent of interocular inhibition caused by the MBC alone (Su et al., 2009), and the extent caused by both the MBC and local conflicting features together. Our second experiment showed that for the MBC orientation-difference rivalry stimulus, the contrast increment threshold on the suppressed half-image (the homogeneous grating) is independent of the contrast of the dominant half-image (MBC grating disc). Our third and fourth experiments measured both the percentage correct and reaction time of detecting a monocular Gabor probe and showed that the MBC initiated interocular inhibition becomes effective as early as 80 ms after stimulus onset. In all, the current findings obtained with the probe detection protocol provide a different perspective on the mechanisms underlying the perception of the MBC rivalry stimulus, compared to our previous studies using the perceptual tracking method (Ooi & He, 2005, 2006; van Bogaert et al., 2008).

It is now well established that binocular rivalry is mediated by a distributed cortical neural network (Andrews, Sengpiel, & Blake, 2005; Blake & Logothetis, 2002; Fang & He, 2005; Lee & Blake, 2004; Lee, Blake, & Heeger, 2007; Leopold, Wilke, Maier, & Logothetis, 2005; Nguyen, Freeman, & Alais, 2003; Ooi & He, 1999, 2003; Papathomas, Kovács, & Conway, 2005; Suzuki & Grabowecky, 2002, 2007; Tong & Engel, 2001; Tong, Meng, & Blake, 2006). Along this cortical network, the visual system implements a sequence of actions that include the processing of local features,

surface boundary contours, and surface/object representation. For example, a number of psychophysical studies have demonstrated that image properties that are largely processed in the extrastriate cortices can significantly affect binocular rivalry (e.g., Alais & Blake, 1999; Kovács, Papathomas, Yang, & Fehér, 1996; Ooi & He, 2003, 2006; Paffen et al., 2005; Shimojo & Nakayama, 1990; Sobel & Blake, 2002; Su et al., 2009; van Bogaert et al., 2008; van der Zwan & Wenderoth, 1994; Xu et al., 2010). Binocular rivalry is thus the collective outcomes of these sequential processes that lead to binocular surface representation. Along this line of thinking, Ooi and He (2005), based on the possible projection geometry of the BBC and MBC rivalry stimuli, proposed that the visual system represents a stimulus beginning at the boundary contours, with the interocular inhibitory mechanism playing a role in representing the interior surface.

We further speculate that in natural viewing, the interocular inhibitory mechanism is involved in representing binocular surfaces at, and beyond, the horopter. For surfaces near the horopter, the interocular inhibitory mechanism primarily eliminates the false matches of the retinal images to achieve a single, 3-D surface representation. For surfaces far beyond the horopter (outside the binocular fusional zone), their half-images fall on vastly non-corresponding areas. In other words, corresponding retinal areas receive dissimilar half-images, which largely are unmatchable. Evidently, from the phenomenon of binocular rivalry, we can surmise that the visual system adopts the strategy of selecting one half-image (and suppressing the other) at a time for perception, instead of superimposing the two dissimilar half-images for perception. A possible reason is that sampling one half-image is more informative than sampling a mixture of two half-images. The dynamic characteristics of binocular rivalry ensure that both half-images are alternately sampled over time. What is sampled depends on both bottom-up and top-down visual processes. In this respect, the BC-based, bottom-up mechanism plays a significant role as a pictorial cue. When the (local) corresponding area receives one homogeneous half-image (without BC) and one half-image with BC (i.e., an MBC rivalry stimulus), it is more likely the former is treated as a part of a larger background surface whereas the latter as part of an object surface (i.e., figure). This biases the visual system to select the half-image with the BC for surface representation (hence, dominance). The outcomes of these local interactions will then be integrated for global surface representation (e.g., Alais & Blake, 1999; Kovács et al., 1996; Ooi & He, 2003, 2006; van Bogaert et al., 2008).

Thus, for the MBC rivalry stimulus, the visual system preferentially selects the MBC and the monocular feature attached to the MBC (in the same eye) for representation, leading to the interocular inhibitory mechanism suppressing the feature information from the other eye. On the other hand, for the BBC rivalry stimulus that carries the same boundary contour in each eye, the visual system represents the interior texture images beginning from the boundary contour in each eye. [The 3-D projection geometry of the BBC rivalry stimulus corresponds to a natural scene where the two eyes view two different texture surfaces through an aperture (Ooi & He, 2005).] Consequently, a local competition between the conflicting features (e.g., orthogonal orientation) ensues, with the winning feature being integrated into a global surface (dominant percept). Accordingly, it takes a longer time to achieve a global surface representation (dominance) with the BBC rivalry stimulus than with the MBC rivalry stimulus. Hence, the effect of interocular inhibition can be observed earlier with the MBC rivalry stimulus (<80 ms) than with the BBC rivalry stimulus (>150 ms).

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