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The monocular boundary contour mechanism in binocular surface representation and suppression

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Abstract

Boundary contours are important for representing binocular surfaces, including those in binocular rivalry. Ooi & He (2006) showed that a half-image with a boundary contour defined by abutting gratings predominates in binocular rivalry. The present study investigates the monocular-boundary-contour mechanism using Kanizsa square-like rivalry displays. In Experiment 1, the left half-image had a vertical illusory contour on the right edge while the right half-image had a vertical illusory contour on the left edge. The Kanizsa-elements (discs and pacmen) were filled with 135deg-grating and placed on a 45deg-grating background. When fused, observers experienced a strong predominance for perceiving an illusory rectangle in front of four discs. But this percept was replaced by robust rivalry alternations when the stimulus was manipulated by (i) switching the half-images between eyes, (ii) relocating the pacmen in each half-image to form horizontal illusory contours, or (iii) placing the pacmen diagonally (thus eliminating each monocular illusory contour). Such robust rivalry alternations were similar to those experienced when a 135deg-grating disc rivaled with a 135deg-grating pacman alone on the 45deg-grating background (Experiment 2). Experiment 3 showed that the relatively stable illusory rectangle percept in Experiment 1 is affected by the alignment of the images in the two eyes, in a manner consistent with an adherence to the occlusion constraint in binocular surface formation.

1 Introduction

Binocular disparity information, besides affording fine stereopsis (McKee, 1983), plays an important role in representing surface layout (Nakayama, Shimojo, Silverman, 1989; Nakayama & Shimojo, 1990). But even as the visual system is extracting the binocular disparity information from the two different retinal images, it has to construct a single, instead of two, 3-D surface representation. This process involves the mechanism of interocular inhibition that suppresses the false matches from the two eyes. One way to revealing the workings of the interocular inhibitory mechanism is to investigate visual perception under the stimulus condition where the visual system fails to construct a stable surface representation, which results in binocular rivalry alternation between the visual images.

Traditionally, most studies of binocular rivalry employ a pair of gratings with orthogonal orientations as the rivaling stimulus (e.g., figure 1a) to induce a vigorous perceptual alternation of the dissimilar gratings viewed by the two eyes (Blake, 1989). However, a potential concern of using such a traditional rivalry stimulus is that it is unnatural for our visual system, since we seldom encounter two different images with the same overall size and shape on

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corresponding retinal areas. This concern raises the question whether the findings using the typical binocular rivalry stimulus could be generalized. On the other hand, one could argue from an ecological basis that the rivalry findings reveal insights into the interocular suppression mechanism underlying binocular surface representation. He & Ooi (2001) and Ooi & He (2005, 2006) suggest that the retinal projections of the traditional binocular rivalry stimulus are equivalent to the 3-D surface layout illustrated in figure 1b, where the two eyes view two different surfaces (with orthogonal grating textures) behind a circular aperture. [Hering (1964) was perhaps one of the earliest to consider binocular rivalry stimulation with respect to 3-D depth layout.] This ecological consideration of the traditional rivalry stimulus (figure 1) leads us to propose that the binocular boundary contours that define the aperture have a significant role in determining the rivalry percept. Supporting this proposal, research from our laboratory has shown, for instance, that increasing the strength of the boundary contour in one eye enhances its predominance in binocular rivalry (Ooi & He, 2005; 2006; Xu, He & Ooi, 2006).

Clearly, to substantiate the ecological approach based on 3-D surface-layout, it is important to consider other kinds of 3-D surface layouts that cause binocular corresponding retinal areas to receive different images, which could trigger binocular rivalry (e.g., Shimojo & Nakayama, 1990; Ooi & He, 2003a, 2005, 2006). Ooi & He (2005, 2006) investigated the perception induced by the rivalry display shown in figure 2a. When the display is free-fused convergently, the green grating disc surrounded by a larger red grating background is seen by the left eye while the right eye sees only the red grating background. But rather than experiencing the robust alternating percepts of binocular rivalry, the observer experiences a relatively stable percept of the green grating disc in front of the red grating background (Frisby & Mayhew, 1978; Ooi & He, 2005, 2006). This intriguing percept differs from that induced by the display in figure 1a, even though both displays stimulate binocular corresponding retinal areas with dissimilar images (orthogonal red and green gratings). Evidently, having approximately similar local contrast energy between the orthogonal gratings is not the only factor determining the predominance of a rivaling image. This observation has led to the adoption of the 3-D surface-layout approach, and the proposal that the rivalry display in figure 2a simulates a 3-D surface layout where the green grating disc is located so close to the left eye that it is excluded from the view of the right eye (figure 2b) (Ooi & He, 2005, 2006). But what mechanism linked to the 3-D surface-layout determines the predominance of the image (green grating disc in figure 2) seen by one eye and not the other?

Two candidate-mechanisms could be responsible for the perceptual dominance of the monocular grating disc in figure 2a. The first, figure-selection mechanism hypothesis, proposes that the visual system selects the representation of a monocular figure over the representation of a homogenous region (figureless) in the fellow eye for perceptual dominance. The second, boundary contour mechanism hypothesis, proposes that the visual system has a preference for selecting the image defined by a monocular boundary contour (the frame of the green grating disc in figure 2) for conscious perception. This preference can be traced to the likelihood of the monocular boundary contour being treated as a part of an occluding surface. And, after selecting the monocular boundary contour, the visual system uses the boundary contour as an anchor from which the surface is represented. The image property of the surface is filled-in by extrapolation from the right and left sides of the monocular boundary contour. When the texture property of the extrapolated surface representation from both sides of the boundary contour is the same (as in the green grating in figure 2c), both representations integrate into a unique surface representation. Thus far, there is some empirical support for the boundary contour mechanism hypothesis (Ooi & He, 2006).

The current paper further investigates the boundary contour mechanism hypothesis by employing a binocular rivalry display with a monocular boundary contour in each eye to induce

interocular grouping. Such a stimulus design, albeit used for testing a different hypothesis, is similar to the stimuli designs employed by others in the past (Alais & Blake, 1999; Kovacs, Papathomas, Yang, Feher, 1996; Knapen, Paffen, Kanai, van Ee, 2007; Lee & Blake, 2004; Ooi & He, 2003b). As shown in figure 3a, the left eye's half-image has two green grating discs and two green grating pacmen on a red grating background. The discs and pacmen are arranged in a rectangular formation with the two pacmen vertically aligned on the right side of the display to form a vertical illusory contour. The right eye's half-image is the mirror image, with the pacmen forming a vertical illusory contour on the left of the display, which corresponds to an area in the left half-image without the vertical illusory contour. According to the boundary contour mechanism hypothesis, the visual system selects the monocular illusory contour in each eye as a part of an occluding surface for the binocular percept. From each monocular illusory contour, surface representation is extrapolated and spreads inward to the middle of the display. Since both spreading surface representations carry the same surface feature (red grating), the visual system forms a rectangular illusory surface with red grating that is defined by the two monocular illusory vertical contours. As in the MBC display in figure 2, the visual system renders the illusory rectangle as an occluding surface in front. One can confirm the prediction of the boundary contour mechanism hypothesis by free fusing the rivalry display in figure 3a, and perceiving a relatively stable red grating rectangular surface in front of four green grating discs (as sketched in figure 3b). (Convergent fusers should fuse the left and middle half-images, while divergent fusers the middle and right half-images.)

There is a critical difference between the rivalry displays in figure 3a and figure 2a. The perceived illusory rectangle in figure 3a is due to the two monocular vertical illusory contours that originate from different eyes. In other words, the perceived rectangle is not a monocular figure. This is unlike the perceived disc in figure 2a, which is a monocular figure. As such, the observation from figure 3a supports the boundary contour mechanism hypothesis and rejects the figure-selection mechanism hypothesis. As indicated above, the rivalry display in figure 3a can be caused by a 3-D surface layout where a rectangular surface with a homogeneous texture (red grating) is placed in front of four green grating discs (figure 3b). The front-depth location of the rectangle causes it to occlude the two left discs from the view of the right eye, and the two right discs from the view of the left eye.

Our first experiment measured the observers' rivalry percepts to confirm the phenomenological observation above (figure 3 and figure 4a: occlusion valid condition). In addition, we tested three variants of the stimulus design to further investigate the boundary contour mechanism (see figure 4b–d: occlusion-invalid, diagonal, and horizontal conditions). By comparing the percepts from the occlusion-valid display and the occlusion-invalid display, we will learn whether the occlusion constraint applies to monocular boundary contours (Nakayama & Shimojo, 1990; Shimojo & Nakayama, 1990; Ooi & He 2005, 2006). The fact that the observer can perceive an illusory rectangle occluding the four discs in the occlusion-valid condition (figure 4a or figure 3a) suggests that the visual system utilizes the occlusion constraint. That is, the occlusion-valid display is visually interpreted as a rectangular surface partially occluding the two left discs from the right eye's perspective and the two right discs from the left eye's perspective (figure 3b). In other words, the pacman is interpreted as a disc occluded by the opaque rectangular surface. This occlusion relationship does not hold in the occlusion-invalid condition (figure 4b) where the display is generated by switching the left and right half-images of the occlusion-valid display (Nakayama and Shimojo, 1990). Switching the half-images renders the perceptual interpretation of the pacmen as partially occluded discs impossible. For example, consider the left half-image of the display in figure 4b (occlusion-invalid) with two pacmen on the left, and the right half-image with two discs on the left. Is it possible that the retinal images of this display correspond to a 3-D scene where an (illusory) opaque rectangular surface is seen in front of two discs (on the left of the rectangle) viewed by the right eye, even as it partially occludes the two discs viewed by the left eye (portrayed by the pacmen images)?

No. According to projection geometry, if a front square occludes the left side of the discs viewed by the left eye, then the square must also occlude (at least in part) the leftmost discs viewed by the right eye. But this is not true in figure 4b, as the leftmost discs viewed by the right eye are intact. As such, the display of figure 4b is described as occlusion-invalid.

One can confirm that the visual system applies the occlusion constraint to the monocular boundary contours in determining rivalry dominance by employing stimulus designs that violate the occlusion constraint. (Convergent fusers should fuse the left and middle half-images, while divergent fusers the middle and right half-images.) For instance, by free fusing the abovementioned occlusion-invalid display in figure 4b, one is very likely to experience strong local rivalry alternation between the pacman and disc at each of the four corners, instead of perceiving a relatively stable illusory rectangle as in the occlusion-valid condition (figure 4a). A similar, local and robust rivalry alternation is experienced in the display with the horizontal monocular boundary contours in figure 4d. This can be attributed to the fact that the visual system does not treat horizontal illusory contours as occluding contours during binocular viewing. Owing to the lateral separation of the two eyes, half-occlusion during binocular viewing only occurs for surfaces with vertical boundary contours, or with the vertical vector components of oblique boundary contours, and not with the horizontal boundary contours.

As another control, our first experiment also measured the observers' percepts of the rivalry display in figure 4c (diagonal condition) where the pacmen are located at the diagonal corners of the square formation. Doing so prevents the formation of any monocular illusory contours. Thus, when one free fuses the display, one experiences robust local rivalry alternation rather than perceive a relatively stable illusory rectangle. The rivalry perception induced by this display in figure 4c is also interesting, given a previous finding by Ooi & He (2003b) that showed an interocular grouping tendency to form illusory surfaces during binocular rivalry. If interocular grouping of the pacmen had occurred in figure 4c, one would have observed a relatively stable illusory rectangle instead of local rivalry alternation. This suggests that the tendency for interocular grouping of the pacmen in figure 4c is not sufficiently strong.

The foregoing analysis and qualitative examination of the displays in figure 4 reveal two interdependent factors for monocular illusory boundary contours to affect binocular rivalry. Specifically, for the monocular illusory boundary contours to be grouped interocularly as a stable illusory rectangle, they need to be both vertical and occlusion-valid (as in figure 4a). Otherwise, robust local rivalry alternation will be experienced (as in the three control conditions in figures 4b–d). As will be shown, the data of our first experiment verify this analysis.

Our second experiment served as an additional control for the first experiment by measuring the perception of binocular rivalry with a display that consisted of a single disc and pacman. This display (figure 6), which is modified from the test display of experiment 1 (figure 4a), eliminates the monocular illusory contour while preserving a remnant of the occlusion constraint. Our third experiment added a nonius fixation target in the test display of experiment 1 to control for the alignment of the retinal images in the two eyes (figure 8). This allowed us to investigate how eye alignment affects binocular rivalry with monocular boundary contours, and to provide further support for the interactive roles of monocular boundary contours and occlusion constraint in binocular rivalry.

2 Experiment 1: The boundary contour mechanism

2.1 Methods

2.1.1 Stimuli—For all experiments reported in the current paper, the rivalry stimuli were presented on a 20 inch flat-screen CRT monitor at a viewing distance of 75 cm. Observers

achieved fusion of the left and right half-images on the monitor screen using a haploscopic mirror system. A chin-and-head rest was used to help stabilize the observer's view.

The two half-images were displayed against a dark (luminance = 2.8 cd/m²) background that encompassed the entire screen. The grating had a line-width of 1.83 min, with the width between two lines of 6.42 min. The grating was oriented either at 45° or 135°. The lines were either red or green against a black background with an average luminance of 10.5 cd/m² for the red grating or 21.5 cd/m² for the green. (These luminance levels were employed for the stimuli because they yielded about equal rivalry predominance. See Results and Discussion below). In each trial the grating discs and pacmen were either red or green, while the background grating (3.2×3.2 deg) was orthogonal to that of the discs/pacmen and had the opposite color (green or red). Each disc had a diameter of 0.8 deg and was spaced at 0.8 deg from each other and 0.4 deg from the edge of the background grating. Two of the discs in each half-image had one quadrant filled with the background grating (pacman). A pair of 0.5×0.5 deg nonius fixation lines seen before the onset of the test stimulus had an average luminance of 55.4 cd/m².

2.1.2 Observers—One author and four observers who were naïve to the purpose of the study participated in all three experiments reported in this paper. All observers had normal or corrected to normal visual acuity, normal color vision, and a stereoscopic resolution of 40 arc seconds or better. All observers except one showed clinically acceptable performance on the Keystone Vision Screener and fixation disparity test. The singular observer exhibited a minor convergence error on the Keystone Vision Screener; however, she showed a similar trend in her data as other observers.

2.1.3 Procedure—The observer began each trial by viewing the nonius fixation target and pressing a key when he/she had obtained proper fusion and alignment. Doing so removed the fixation target and triggered a 30 second presentation of the rivalry stimulus on the CRT monitor. During this viewing period, the observer tracked the course of the rivalry by pressing one of three keys when his/her instantaneous percept changed from one criterion to another. The three possible criteria were perceiving four partially occluded discs (rectangle), four whole discs, or a mixture of occluded (pacmen) and whole discs. A 1 second blank screen followed each trial.

All three-display types (occlusion valid and invalid as one type, horizontal and diagonal) were tested in a test block for a total of 36 test trials [3 (repeats) × 3 (display types) × 2 (left versus right eye half-image pairing) × 2 (red versus green grating discs)], and the trials were presented in a random order. Two blocks were run in each session with a 5 to 10 minute break between blocks and a short (< 2 minute) break after every 12 trials. All observers were tested in two sessions on separate days.

2.2 Results and Discussion

The four graphs in figure 5 plot the average results of the five observers. Since the observers were tested with two differently colored stimuli, i.e., red disc/pacman on green background and green disc/pacman on red background, we first examined the differences in rivalry predominance that resulted from the two differently colored stimuli. We found that for all percepts and display conditions, the average predominance differences between the two colored stimuli are smaller than 10%, and none of them reach the statistically significant level of 0.05 (ANOVA with repeated measures). This finding allows us to pool the data from the two colored stimuli together for further data analysis. The data are analyzed to reveal the predominance, frequency, dominance duration, and suppression duration of the various percepts induced by the four rivalry displays in figure 4. The performances in the main

condition (occlusion-valid) and three control conditions (occlusion-invalid, diagonal and horizontal) were compared.

Predominance—The average patterns of predominance in the occlusion-valid condition are different from those of the three control conditions [Main effect of percepts: $F(2, 8)=1.653$, $p=0.251$; Main effect of conditions: $F(3,12)=1.833$, $p=0.195$; Percept $\times$ Condition Interaction Effect: $F(6,24)=21.638$, $p<0.001$; 2-way ANOVA with repeated measures]. Specifically, in the occlusion-valid condition the predominance for seeing the illusory rectangle is higher than for seeing the four-discs [$t(4)=5.249$; $p<0.01$] and the mixture [$t(4)=8.313$, $p<0.001$]. This trend is not found in the three control conditions. In addition, the predominance for seeing the illusory rectangle is higher in the occlusion-valid condition than in the three control conditions [$F(3,12)=44.779$, $p<0.001$; one way ANOVA with repeated measures]. Together, these two findings indicate that the boundary contour mechanism selects the monocular illusory contours to form a global surface representation when the occlusion constraint is met. Our data also reveal that the patterns of predominance among the three control conditions are similar [Main effect of the conditions: $F(2,8)=1.714$, $p=0.240$; Percept $\times$ Condition Interaction Effect: $F(4,16)=0.422$, $p=0.791$; 2-way ANOVA with repeated measures analysis]. Unlike the occlusion-valid condition, more incidences of seeing the mixture and the four discs were experienced in the three control conditions. This further reinforces the conclusion of our findings above; as it shows that the integration of the monocular illusory contours from the two eyes cannot occur without both the monocular vertical component of the illusory contours and observance of the occlusion constraint. Without them, perception is largely dictated by robust local rivalry alternation between the disc and pacman at corresponding retinal areas.

Frequency—The average frequencies of experiencing particular percepts in the occlusion-valid condition are different from those of the three control conditions [Main effect of percept: $F(2, 8)=0.548$, $p=0.598$; Main effect of condition: $F(3,12)=3.166$, $p=0.0641$; Percept $\times$ Condition interaction effect: $F(6,24)=9.556$, $p<0.001$; 2-way ANOVA with repeated measures]. In the occlusion-valid condition, the frequency of seeing the illusory rectangle is higher than that of seeing the four-discs [$t(4)=3.174$; $p<0.05$] and the mixture [$t(4)=2.894$, $p<0.05$]. This trend is not exhibited in the three control conditions. But the frequency of seeing the illusory rectangle is similar among all four conditions [$F(3,12)=0.364$, $p=0.780$; one way ANOVA with repeated measures]. This indicates that the higher predominance of the illusory rectangle in the occlusion-valid condition, and not in the three control conditions, is mainly attributable to the longer dominance duration in the former condition (as evidenced in the dominance duration graph). The frequency data among the three control conditions are similar [Main effect of condition: $F(2,8)=1.484$, $p=0.283$; Percept $\times$ Condition Interaction Effect: $F(4,16)=0.260$, $p=0.899$; 2-way ANOVA with repeated measures].

Dominance Duration—The average dominance duration data in the occlusion-valid condition are different from those in the three control conditions [Main effect of the percept: $F(2, 8)=3.372$, $p=0.104$; Main effect of the condition: $F(3,12)=3.678$, $p=0.056$; Percept $\times$ Condition interaction effect: $F(6,24)=5.339$, $p<0.003$; 2-way ANOVA with repeated measures]. In the occlusion-valid condition, the dominance duration of seeing the illusory rectangle is longer than that of seeing the four-discs [$t(4)=3.396$; $p<0.05$] and the mixture [$t(4)=3.302$, $p<0.05$]. Furthermore, the dominance duration of perceiving the illusory rectangle is significantly longer in the occlusion-valid condition than in the three control conditions [$F(3,12)=8.442$, $p<0.005$; one-way ANOVA with repeated measures]. There is no significant difference among the three control conditions in which the dominance duration is longer for seeing the mixture than for seeing the rectangle and the four discs [Main effect of the percept: $F(2, 8)=6.312$, $p<0.025$; Main effect of the condition: $F(2,8)=2.909$, $p=0.112$; Percept $\times$

Condition interaction effect: $F(4,16)=0.481, p=0.749$; 2-way ANOVA with repeated measures].

Suppression Duration—The average suppression duration results have an opposite trend from the average dominance duration results. It is also clear that the average suppression duration data in the occlusion-valid condition are different from those of the three control conditions [Main effect of the percept: $F(2,8)=5.304, p=0.304$; Main effect of the condition: $F(3,12)=5.001, p<0.025$; Percept $\times$ Condition interaction effect: $F(6,24)=8.504, p<0.001$; 2-way ANOVA with repeated measures]. In the occlusion-valid condition, the suppression duration of the illusory rectangle is significantly shorter than that of the four-discs [$t(4)=2.899, p<0.05$] and the mixture [$t(4)=2.860, p<0.05$]. The suppression duration of the occlusion-valid condition is significantly shorter compared to that of the three control conditions [$F(3,12)=9.604, p<0.0025$; one-way ANOVA with repeated measures]. The suppression durations among the three control conditions are similar, with the suppression duration being longer for the rectangle and four discs than for the mixture [Main effect of the percept: $F(2,8)=6.515, p<0.025$; Main effect of condition: $F(2,8)=3.902, p=0.066$; Percept $\times$ Condition Interaction Effect: $F(4,16)=0.876, p=0.500$; 2-way ANOVA with repeated measures].

Taken together, our data support the boundary contour mechanism hypothesis, which predicts that the visual system is capable of extracting the two monocular illusory vertical contours to form an integrated surface representation for perceptual dominance. The current findings also reveal that the underlying boundary contour mechanism utilizes the occlusion constraint.

It should be noted that the binocular rivalry displays used in our experiment above comprised of elements (pacmen and discs) that were surrounded by gratings with an orthogonal orientation (figure 4). Although such a “center-surround” like configuration could affect binocular rivalry (e.g., Fukuda & Blake, 1992; Paffen, Alais, & Verstraten, 2005), its influence does not alter our conclusion. This is because our conclusion is largely based on the performance differences among the four displays with the same center-surround like configuration.

3 Experiment 2: Binocular rivalry without boundary contour integration

We found in Experiment 1 that the binocular rivalry perception among the three control conditions (occlusion-invalid, horizontal and diagonal conditions in figure 4) is similar. For example, the predominance of perceiving the illusory rectangle in the three control conditions is smaller than that of perceiving the four discs (figure 5). This suggests the possibility that the visual system either did not integrate, or poorly integrated, the four elements in each of the three control conditions in processing the rivaling information. As such, the rivalry perception is largely dominated by local competition between the pacman and disc at each corresponding retinal location. The current experiment investigated this possibility. To do so, we modified the stimuli in the occlusion-valid and occlusion-invalid conditions from the first experiment above. For the display in each condition from figure 4, we removed three of the four paired rivaling elements so that only the pair at the bottom left corner was used as the rivalry stimulus (figure 6). Eliminating three of the four-paired elements allowed us to test the local outcome of rivalry. For a phenomenological observation, if one free fuses the rivalry displays in figure 6, one is likely to experience frequent rivalry alternation between the pacman and disc in both the occlusion-valid and occlusion-invalid conditions. (For convergent fusers, the left and middle half-images serve as the occlusion-valid display, while the middle and right half-images serve as the occlusion-invalid display. The reverse is true for divergent fusers. (Note: We refer to these stimuli as “occlusion-valid” and “occlusion-invalid” based on the assumption that the image of the pacman stimulus is interpreted by the visual system as part of a disc that is occluded by one corner of an illusory rectangle. Doing so also facilitates the comparison between this and the first experiment above.) That both conditions in figure 6 produce almost similar and

robust rivalry alternation is in contrast to the perception experienced with the corresponding displays in figure 4. This underscores the role of boundary contour integration in the occlusion-valid condition of Experiment 1 (figure 4).

3.1 Methods

3.1.1. Stimuli—The rivalry display consisted of a single pacman and a single disc (figure 6). The diameter of the disc and pacman were both 1.10 deg, and they were each centered on a 2×2 deg grating background. The pacman stimulus was created by filling the upper left quadrant of the disc with the pattern of the background. As in the previous experiment, the stimuli were filled with either a green or red grating oriented at either 45° or 135°, with the color (red or green) and orientation of the grating background being different from the disc and pacman. The stimuli were displayed against a black background and centered on each half of the screen.

3.1.2. Procedure—The two-possible disc/pacman pairs were randomly mixed within a test block of 24 trials [2 (occlusion-valid or occlusion-invalid) × 2 (colors) × 6 (repeats)]. Each trial lasted 30 seconds, and the same response methods from Experiment 1 were used for this experiment, except that the observers were instructed to report a pacman, a single disc, or mixed percept.

3.2. Results and Discussion

The average results of the occlusion-valid and occlusion-invalid conditions are plotted in figure 7. They are analyzed for the predominance, frequency, dominance duration, and suppression duration of the reported percepts.

Predominance—There is no significant difference between the occlusion-valid and occlusion-invalid conditions, or a significant difference among the three percepts [Main effect of percepts: $F(2,8)=0.470$, $p=0.641$; Main effect of conditions: $F(1,4)=1.000$, $p=0.374$; Percept × Condition Interaction Effect: $F(2,8)=2.455$, $p=0.147$; 2-way ANOVA with repeated measures]. It is noteworthy that in the current occlusion-valid condition, the predominance of seeing the pacman and disc is similar, unlike that in the occlusion-valid condition of Experiment 1. This difference lends support to the explanation that in Experiment 1, the strong predominance of seeing the illusory rectangle in the occlusion-valid condition is due to the monocular illusory contours being formed between the two vertically aligned pacmen rather than being due to the local images of the pacmen per se.

Frequency—There is no significant difference between the occlusion-valid and occlusion-invalid conditions, or a significant difference among the reported percepts [Main effect of the percept: $F(2,8)=0.202$, $p=0.821$; Main effect of the condition: $F(1,4)=6.791$, $p=0.060$; Percept × Condition Interaction Effect: $F(2,8)=0.179$, $p=0.839$].

Dominance duration—The dominance durations in the occlusion-valid and occlusion-invalid conditions are similar, as are the dominance durations of the three reported percepts [Main effect of the percept: $F(2,8)=0.448$, $p=0.654$; Main effect of the condition: $F(1,4)=4.350$, $p=0.105$; Percept × Condition interaction effect: $F(2,8)=2.397$, $p=0.153$]. The dominance durations of perceiving the pacman and disc in the current experiment (figure 7) are compatible to those of perceiving the illusory rectangle and four discs in the three control conditions of Experiment 1 (figure 5). They are, however, shorter than that of perceiving the illusory rectangle in the occlusion-valid condition of Experiment 1.

Suppression duration—The suppression duration is slightly longer for the occlusion-valid condition than for the occlusion-invalid condition [Main effect of the percept: $F(2,8)=3.947$, $p=0.064$; Main effect of the condition: $F(1,4)=7.646$, $p=0.051$; Percept × Condition interaction

effect: $F(2,8)=7.049, p=0.017$]. The suppression durations of the pacman and disc in the current experiment (figure 7) are compatible to those of the illusory rectangle and four discs in the three control conditions of Experiment 1 (figure 5).

Overall, the results of the current Experiment 2 with single rivaling element (disc versus pacman) displays are more compatible to those of the three control conditions in Experiment 1, than to the occlusion-valid condition in Experiment 1. This is consistent with the explanation that the rivalry mechanism mainly acted locally in the three control conditions of Experiment 1. The current finding of about equal predominance for the single pacman and disc in the display in figure 6 also rules out a possible argument for the main finding in Experiment 1. The argument is that in the occlusion-valid condition in Experiment 1 (figure 3a), each pacman has a higher chance to be dominant over the disc, and with all four pacmen being simultaneously dominant, the visual system integrates them to form a stable illusory rectangle. This alternative operation (argument) leading to the relatively stable percept of the illusory rectangle in the occlusion valid condition of Experiment 1 differs from what we have hypothesized thus far. Namely, we hypothesize that the visual system first creates the vertical illusory boundary contour in each eye, and then forms the illusory rectangle by extending the surface representation from the two monocular boundary contours.

4. Experiment 3: Fixation control and binocular correspondence

We did not use a fixation target to control for the observers' fixation position while they were viewing the rivalry displays in Experiment 1 (figure 4). Thus, it is uncertain which parts of the images in the two eyes stimulated corresponding retinal areas, and how this might have affected binocular rivalry. To investigate this, we added nonius fixation targets at two different depth planes in the occlusion-valid and occlusion-invalid displays (figures 8a and 8b). When the nonius fixation target is placed at the same depth plane as the four green grating discs/pacmen in the occlusion-valid display, the entire discs and pacmen images from each eye fall on corresponding retinal areas (see the aligned condition in figure 8a; convergent fusers should fuse the left and middle half-images while divergent fusers the middle and right half-images). This alignment is illustrated in figure 8c (only the left side of the display is shown). However, when the fixation target is placed at a front depth plane relative to the four discs/pacmen (misaligned condition in figure 8b), only half of each disc image in one eye and half of each pacman image in the other eye fall on corresponding retinal areas (figure 8d). Could this difference in binocular image alignment lead to dissimilar binocular rivalry perception?

This question can be answered in the affirmative by free fusing the displays in figures 8a and 8b and experiencing the different percepts induced. Whereas a strong rivalry alternation between the discs/pacmen is experienced in the aligned condition, a relatively stable percept of an illusory rectangle is perceived in the misaligned condition. The latter percept is very similar to that induced by the occlusion-valid display in Experiment 1 (figure 4) without the fixation target. This observation also suggests an alternative hypothesis for the results of Experiment 1. The alternative hypothesis would claim that the binocular image misalignment in the occlusion-valid condition in Experiment 1 served as the sole factor causing the relatively stable percept of the illusory rectangle. As a consequence, it is possible that in Experiment 1, our observers were somehow able to fixate at the front depth plane in the occlusion-valid condition, which led to a misalignment between the discs and pacmen images in the two eyes (as in figures 8b and 8d). However, they could not bring fixation to the front depth plane in the three control conditions, and thus the discs and pacmen images in the two eyes remained aligned.

To test the alternative hypothesis, we added nonius fixation targets to the occlusion-invalid displays at two different depth planes (see figures 8a and 8b; convergent fusers should fuse the

middle and right half-images while divergent fusers the left and middle half-images). Figures 8e and 8f illustrate the binocular correspondence of the discs/pacmen images in the aligned and misaligned conditions, respectively (only the left side of the display is shown). If the alternative hypothesis were correct, we would expect to experience a relatively stable percept of the illusory rectangle in the misaligned condition. However, after free fusing the displays in figure 8, one is very likely to experience a strong rivalry alternation instead of perceiving a relatively stable illusory rectangle in the misaligned condition. This observation does not support the prediction of the alternative hypothesis. The current experiment measured our observers' rivalry percepts of displays similar to those in figures 8a and 8b to confirm this phenomenological observation.

4.1 Methods

4.1.1 Stimuli—The rivalry stimuli were similar to those in Experiment 1 except for the following changes. The diameter of the disc was 1.1 deg and the spatial separation between the two discs was also 1.1 deg. The dimension of the grating background was increased to 4.4×4.4 deg. The 0.5×0.5 deg white nonius fixation target had the same disparity as the four discs in the aligned condition, and had a 0.55 deg front disparity with respect to the four discs in the misaligned condition. The nonius fixation target was centered between the four pacmen in each eye, and they were presented throughout the trial.

4.1.2. Procedure—The test procedure was similar to Experiment 1, except for one difference. The observers were instructed to fixate at the nonius fixation target and to maintain its alignment during the trial. In the misaligned condition, observers were tested in a block of 32 trials [8 (repeats) × 2 (occlusion valid versus occlusion invalid) × 2 (red versus green grating discs)]. In the aligned condition, besides the occlusion-valid and occlusion-invalid displays (with vertical illusory contours), the observers were also tested in a display with horizontal illusory contours (similar to figure 4d). The observers were tested in three test blocks with 24 test trials each [3 (repeats) × 2 (vertical MBC: occlusion valid versus occlusion invalid) × 2 (horizontal MBC: top MBC versus bottom MBC) × 2 (red versus green grating discs)]. They were given a 5 to 10 minute break between each block and a short (< 2 minute) break between every 12 trials.

4.2 Results and Discussion

For the aligned condition, the differences among the three displays (horizontal, occlusion-valid and occlusion-invalid) did not reach the statistically significant level of 0.05 (2-way ANOVA with repeated measures). However, the data obtained from the horizontal display are not shown in the current paper (figure 9), as the purpose of the current experiment is to make a comparison between the occlusion-valid and occlusion-invalid displays.

Figure 9a–d plots the average results of the aligned condition for the occlusion-valid and occlusion-invalid conditions (vertical contours). Clearly, there is no preference for seeing the illusory rectangle in the occlusion-valid condition, which is in contrast to the results of Experiment 1 (figure 5) where no fixation target was used. Two-way ANOVA with repeated measures was applied to the predominance, frequency, dominance duration, and suppression duration data. For all four categories, the main effect of stimulus conditions (occlusion-valid vs. occlusion-invalid) and the main effect of the three percepts do not reach the significant level {[Predominance: $F(2, 8)=0.416$, $p=0.673$; $F(1,4)=0.615$, $p=0.477$; $F(2,8)=1.398$, $p=0.302$]; [Frequency: $F(2, 8)=0.788$, $p=0.487$; $F(1,4)=1.021$, $p=0.369$; $F(2,8)=3.037$, $p=0.104$]; [Dominance duration: $F(2, 8)=0.303$, $p=0.747$; $F(1,4)=2.847$, $p=0.167$; $F(2,8)=1.398$, $p=0.302$]; [Suppression Duration: $F(2, 8)=0.286$, $p=0.758$; $F(1,4)=2.944$, $p=0.161$; $F(2,8)=0.115$, $p=0.893$]}.

The average results for the misaligned condition (figure 9e–h) have a similar trend to that in Experiment 1 (figure 5). That is, the data show a strong bias for seeing the illusory rectangle in the occlusion-valid condition but not in the occlusion-invalid condition. Two-way ANOVA with repeated measures reveals a significant main effect of the three percepts and a significant interaction effect between the percepts and stimulus conditions {[Predominance: $F(2,8) = 16.436, p < 0.001$; $F(1,4) = 1.000, p = 0.374$; $F(2,8) = 33.550, p < 0.001$]; [Frequency: $F(2,8) = 5.443, p < 0.05$; $F(1,4) = 7.74, p = 0.050$; $F(2,8) = 10.744, p < 0.005$]; [Dominance duration: $F(2,8) = 16.116, p < 0.005$; $F(1,4) = 10.456, p < 0.05$; $F(2,8) = 20.479, p < 0.001$]; [Suppression Duration: $F(2,8) = 14.260, p < 0.0025$; $F(1,4) = 13.247, p < 0.025$; $F(2,8) = 19.888, p < 0.001$]}.

Overall, the current findings indicate that the alignment between the images of the two eyes due to the manipulation of fixation depth can significantly affect binocular rivalry. Given the fact that the results of the misaligned condition are similar to that of Experiment 1 (without fixation target), it is possible that in Experiment 1, our observers might have fixated at the front depth plane even though they were not instructed to do so. This resulted in the relatively stable percept of the illusory rectangle in the occlusion-valid condition. But the finding of no strong bias for perceiving the illusory rectangle in the occlusion-invalid condition rejects the alternative hypothesis, which claims that image alignment (and hence eye movement) is the sole factor affecting binocular rivalry perception in Experiment 1. All these support the view that the impact of image alignment on binocular rivalry perception is contingent on the observance of the occlusion constraint related to 3-D surface layout.

5 General discussion

Our experiments reveal that the visual system is able to form a stable surface representation (illusory rectangle) by integrating two illusory monocular boundary contours (MBC) from different eyes. Since there is no rectangular figure in the monocular image (e.g., see figure 4a), this finding reinforces the explanation that for the type of binocular rivalry display shown in figure 2a, the strong predominance of the monocular grating disc (as a figure) is attributable to the MBC that defines the monocular grating disc, and not necessarily to the figure representation of the disc. Our experiments also demonstrate that the formation of the stable surface representation from the MBCs respects the occlusion constraint. When the image configuration violates the occlusion constraint, the visual system cannot form a stable surface but reverts instead to strong local rivalry alternation. This finding parallels previous observations that the occlusion constraint affects the perception of binocular rivalry displays with binocular boundary contours (BBC) (Ooi & He, 2005; 2006; Shimojo & Nakayama, 1990). Together they further support the notion that the image properties of 3-D surface layout and the ecological constraints used by the visual system to represent binocular surfaces should also affect the perception of binocular rivalry displays (Ooi & He, 2003a, 2003b, 2005, 2006). Supporting this notion, a number of empirical findings have shown that surface image properties such as illusory surface, occlusion, and transparency have significant impacts on binocular rivalry (e.g., Ooi & He, 2003b, 2005, 2006; Shimojo & Nakayama, 1990; Sobel & Blake 2002; Zwan & Wenderoth, 1994). Such findings are also consistent with the discovery that surface image properties (e.g., occlusion and background surface) can affect binocular depth perception of objects (e.g., Gillam & Sedgwick, 1996; Glennerster & McKee, 1999; He & Ooi, 2000; Mitchison & McKee, 1990; Nakayama & Shimojo, 1990).

Other than external stimulus properties, an observer's internal bias for a perceived depth sign can affect the perception of binocular displays. For example, O'Shea and Blake (1987) used random-dot stereograms with zero disparity surround and a central uncorrelated region and found that their observers reported perceiving the central region to be either at a near or far depth, relative to the correlated surround of the stereograms. The direction of the perceived depth was subjected to individual difference. O'Shea and Blake coined this phenomenon

“rivaldepth”. They further found that the direction of perceived rivaldepth was related to their observers’ fixation disparity; observers with tonic overconvergence (fixation disparity) saw far rivaldepth and vice versa. Altogether, their observations of rivaldepth led them to suggest that the visual system treats uncorrelation as a potentially correlated disparity beyond the fusion limit. Even though we did not utilize random-dot stereograms as our stimuli (O’Shea and Blake pointed out that rivaldepth occurs exclusively with random-dot stereograms), the observations in this paper echo the suggestion that binocular rivalry is related to the 3-D perceptual interpretation of the retinal images.

There are reasons to believe that the current findings highlight the neural processing in cortical areas V1 and V2. It is likely that the rivaling images (i.e., disc/pacman vs. background with orthogonal grating) at corresponding retinal areas are registered at V1, triggering the local interocular inhibitory mechanism. Meanwhile, the formation of the illusory contours/surfaces may only occur at V2 or beyond. Neurophysiological studies have revealed that neural processes in the primary visual cortex (V1) and extrastriate cortices are involved in representing binocular surfaces (Bakin, Nakayama & Gilbert, 2000; Qiu & von der Heydt, 2005; Sugita, 1999; von der Heydt, Zhou & Friedman, 2000; Zhou, Friedman & von der Heydt, 2000). In particular, Peterhans and von der Heydt (1989) found that more cells in V2 than V1 are excited by the Kanizsa-square-like illusory surface stimulus. Consistent with this finding, more than 50% of the neurons in V2 exhibit a bias to the side of a stimulus image that owns the border, with fewer neurons (18%) in V1 showing the same bias (Zhou et al, 2000). It is well known that the visual system determines the (border) ownership of the boundary contour formed between two surface images in order to extract the depth of a surface from its surrounding (Kanizsa, 1979; Nakayama, He & Shimojo, 1995). With the determination of the border ownership, the visual system is able to determine the surface depth relationship and to form a global surface representation. In this way, the surface image that owns the boundary contour (border) is treated as the occluding surface while the one that does not is treated as the occluded surface. Given that the Kanizsa-square-like illusory surface is perceived as the occluding surface, it is possible that the V2 cells responding to the Kanizsa-square-like stimulus must also carry the border ownership signals. Our current psychophysical findings reveal that when the monocular illusory boundary contours are occlusion-valid, the visual system can form a relatively stable illusory surface in front as the occluding surface; however, when it is occlusion-invalid, local rivalry alternation ensues. With the illusory contour/surface being represented at V2, the visual system either provides a feedback to V1 (Lee & Nguyen, 2001) to resolve the interocular inhibition, or interacts with the interocular inhibitory signals from V1 at V2 to influence the rivalry perception. Future neurophysiological research should be able to clarify which of the two strategies the visual system adopts.

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Figure 1.

(a) A pair of orthogonal grating stimulus that is traditionally used in binocular rivalry research, which induces frequent alternation between the percepts of the two gratings. (b) An illustration of the retinal projections of the traditional binocular rivalry stimulus from a 3-D surface layout.

Figure 2.

(a) A pair of new binocular rivalry stimulus used by Ooi & He (2005, 2006). Unlike the traditional rivalry stimulus, this stimulus induces a relatively stable percept of the green grating disc. Note that the retinal area in the fellow eye corresponding to the green grating disc has an orthogonal red grating. (b) A possible 3-D layout that produces the stimulus in (a). (c) An illustration of the spreading stage of the boundary contour mechanism hypothesis, which proposes that the texture of the grating disc is extrapolated from the monocular boundary contour.

Figure 3.

(a) A binocular rivalry stimulus with an illusory monocular boundary contour in each half-image. For this stimulus, and subsequent stimuli, convergent fusers should free fuse the left and middle half-images (as indicated by the cross-eye symbol below the display), while divergent fusers the middle and right half-images (parallel-eye symbol). (b) An illustration of the fused percept of the stimulus in (a), which induces a relatively stable percept of a red grating rectangular surface in front of four green grating discs.

Figure 4.
The binocular rivalry stimuli (four conditions) used in Experiment 1.

Figure 5.

The data obtained from Experiment 1 are analyzed for their average predominance, frequency of perceiving particular percepts, dominance duration and suppression duration. Overall, the average predominance and dominance duration for perceiving the illusory rectangle (four partially occluded discs) are higher in the occlusion-valid condition than in the three control conditions.

Figure 6.

The binocular rivalry stimuli used in Experiment 2. For convergent fusers, the left and middle half-images constitute the occlusion-valid condition, while the middle and right images constitute the occlusion-invalid condition. The converse is true for divergent fusers. In both conditions, observers are more likely to experience a strong rivalry alternation.

Figure 7.

The data obtained from Experiment 2 are analyzed for their average predominance, frequency of perceiving particular percepts, dominance duration and suppression duration. Overall, there is no significant difference between the two stimuli conditions tested.

Figure 8.

(a and b) The binocular rivalry stimuli used in Experiment 3. A pair of nonius fixation target is inserted in each stimulus display to control for eye alignment and the rivalry images' stimulation of corresponding retinal areas. In the aligned condition (a), the nonius fixation target is placed at the same depth plane as the four green grating discs/pacmen. This results in the entire discs and pacmen falling on corresponding retinal areas, as illustrated in (c) for the occlusion-valid stimulus and (e) for the occlusion-invalid stimulus (only the left half on each half-image is shown). In the illustration, the red dash lines in (c) and (e) indicate the binocular corresponding retinal area. In the misaligned condition (b), the nonius fixation target is placed at a front depth plane relative to the four discs/pacmen. Therefore, only half of each disc image

in one eye and half of each pacman image in the other eye fall on corresponding retinal areas (d and f).

Figure 9.

The data obtained from Experiment 3 are analyzed for their average predominance, frequency of perceiving particular percepts, dominance duration and suppression duration. (a–d) plot the data for the aligned condition and (e–h) the data for the misaligned condition. Unlike the occlusion valid-misaligned condition, there is no preference for seeing the illusory rectangle in the occlusion valid-aligned condition.