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Center–surround interactions in visual motion processing during binocular rivalry

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Abstract

When each eye is confronted with a dissimilar stimulus, the percept will generally alternate between the two. This phenomenon is known as binocular rivalry. Although binocular rivalry occurs at locations where targets overlap spatially, the area surrounding rivalrous targets can modulate their dominance. Here we show that during binocular rivalry of oppositely moving gratings, a surrounding grating moving in the same direction as one of the two leads to increased dominance of the opposite direction of motion in the center. This increased dominance of the opposite direction in the center was observed irrespective of the eye to which the surround was presented. Inspection of the results for different conditions reveals that the preference for the opposite direction of motion cannot be explained by a single mechanism operating beyond binocular fusion. We therefore suggest that this phenomenon is the outcome of center–surround interactions at multiple levels along the pathway of visual motion processing.
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1. Introduction

When dissimilar stimuli are presented at overlapping retinal locations of the two eyes, the percept periodically switches between the two. This phenomenon is known as binocular rivalry. Binocular rivalry has been proposed to occur between monocular representations of both eyes at overlapping retinal locations within spatially limited zones (Blake, 1989). This is illustrated by the fact that large dissimilar stimuli lead to patch-like rivalry, whereas small dissimilar stimuli lead to periods of exclusive dominance of one entire stimulus (Blake, O'Shea, & Mueller, 1992).

It is known that the area surrounding one of two rivalrous targets can modulate the dominance of the targets. The first systematic investigation of spatial interactions between central rivalrous stimuli and surrounding areas was performed by Levelt (1965). Levelt presented a black disc to one eye and a white disc to the

other eye, resulting in rivalry. In one condition, a white ring was added to the black disc. Levelt's rationale was that adding a ring would increase the 'stimulus strength' of the rival disc it surrounded, leading to increased dominance of this disc. Levelt found that the predominance of the target surrounded by the ring increased, although this increase was not statistically significant. The absence of a significant effect in Levelt's study might be due to the size of the ring used; its width was only 0.5 deg, while the radius of the total stimulus was 3 deg. Later studies, however, *did* show that the area surrounding rivalrous targets could modulate rivalry significantly (Fukuda & Blake, 1992; Ichihara & Goryo, 1978; Mapperson & Lovegrove, 1991). For example, Fukuda and Blake (1992) presented two patches containing orthogonally oriented bars that were both surrounded by an annulus containing bars with the same orientation as one of the two patches. In this condition, the patch containing bars with the orientation orthogonal to the surround was more dominant.

The latter finding relates to results from physiological studies in cats and monkeys, which show that the response to an optimally oriented stimulus presented to a neuron's classical receptive field (CRF) in primary visual

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cortex can be inhibited by presenting a stimulus with the same orientation to its surround (e.g. Blakemore & Tobin, 1972; Knierim & van Essen, 1992). In Fukuda and Blake's (1992) experiment, the response to the center stimulus with the same orientation as the surround is expected to be inhibited. This would lead to relatively higher 'stimulus strength' of the center bars surrounded by the orthogonally oriented surround, which would result in increased perceptual dominance of this center stimulus.

In motion sensitive neurons in middle temporal area (MT), center–surround interactions have also been described (e.g. Allman, Miezin, & McGuinness, 1985). These interactions are often antagonistic, meaning that the response to motion in the preferred direction of the CRF is inhibited by surround motion in the same direction (e.g. Allman et al., 1985; Born & Tootell, 1992). Recently, Tadin, Lappin, Gilroy, and Blake (2003) reported perceptual correlates of these center–surround interactions. They showed that thresholds for detecting the direction of motion of a high-contrast Gabor increased with its size. This increase in threshold was proposed to be the perceptual manifestation of center-surround inhibition, presumably located within motion-sensitive area MT/V5. Moreover, center–surround mechanisms have been proposed to be involved in the detection of motion boundaries (Sachtler & Zaidi, 1995) and in induced motion (or motion contrast), where a stationary stimulus is perceived to move in a direction opposite to the surround (Duncker, 1929/1938; Murakami & Shimojo, 1996; Reinhardt-Rutland, 1988).

The goal of the present study was to investigate in what way center–surround interactions modulate binocular rivalry of moving stimuli. We used two center gratings moving in opposite directions that were surrounded by an annulus containing a grating moving in the same direction as one of the two. Based on the findings on center–surround interactions in visual motion processing, we predict that presenting the annulus leads to increased stimulus strength of the center stimulus with the opposite direction of motion, which in turn leads to increased perceptual dominance of this direction.

2. Method

2.1. Observers

Six experienced observers participated in the experiments. Four of the observers were naïve as to the purpose of the experiments. The other two observers (CP and SP) are authors of the current paper. All observers had normal or corrected to normal vision.

2.2. Apparatus and stimuli

The stimuli were generated by an Apple Macintosh dual 867 MHz G4 using the Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on a single luminance linearized 22″ LaCie Blue Electron monitor, at 85 Hz. The viewing distance was 72 cm. Dichoptic presentation was achieved by means of a stereoscope.

The stimuli and conditions are presented in Fig. 1. The stimuli consisted of two circular apertures that could each be surrounded by an annulus. Both center and surround contained sine-wave gratings moving horizontally. The center gratings moved in opposite directions; the surrounding gratings moved in the same direction as one the center gratings. All gratings had a spatial frequency of 1.96 cycles/deg, moved at a constant
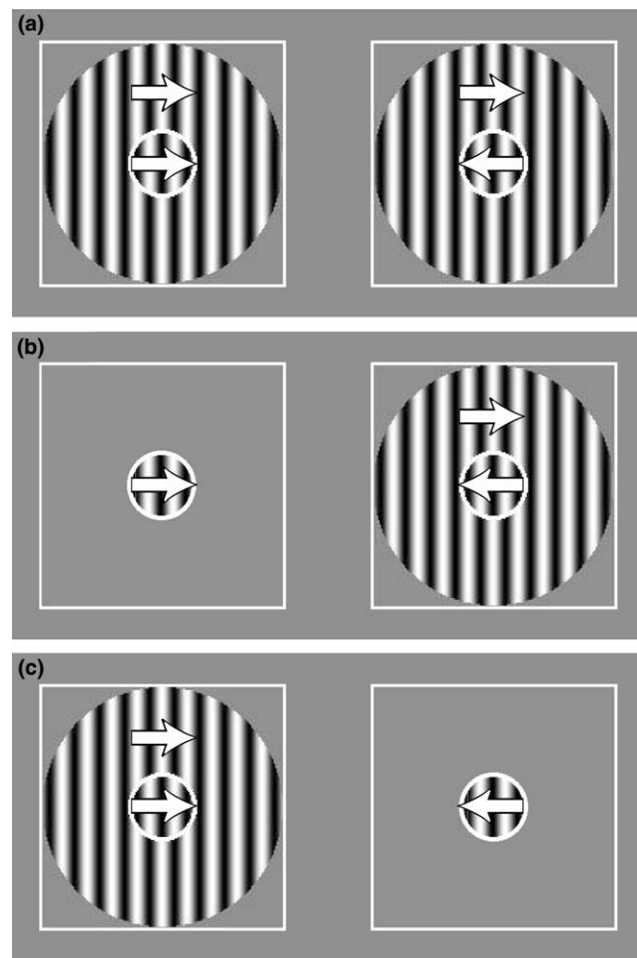

Fig. 1. Stimuli and conditions used in the experiment. The arrows indicate the direction of motion of the gratings. The image on the left was presented to one of the two eyes, the right image to the other eye. (a) The binocular surround (BS) condition. The surround was presented to both eyes. (b) The monocular opposite (MO) condition. The surround was presented around the grating with the opposite direction of motion. (c) The monocular same (MS) condition. The surround was presented around the grating with the same direction of motion. See text for details.

speed of 1.27 deg/s and were presented at 99% contrast. The mean luminance of both the gratings and the background was 50 cd/m^2. The diameter of the center aperture was 1.24 deg; the width of the surrounding annulus was 1.70 deg. There was a gap of 0.09 deg between the center aperture and the annulus. Binocular fusion was aided by a white ring filling the gap between center and surround, a white square drawn around the annulus, and a central fixation point.

The center apertures were presented in all conditions. We varied the positioning of the surround in four conditions:

1. Surrounds around both apertures (binocular surround [BS]).
2. A surround around the aperture with the opposite direction of motion compared to its center (monocular opposite [MO]).
3. A surround around the aperture with the same direction of motion compared to its center (monocular same [MS]).
4. No surround (NS).

For all conditions, the directions of motion within the center apertures were counterbalanced between both eyes. Also, the direction of motion in the surround was counterbalanced between leftward and rightward motion. For the conditions in which the surround was presented to one eye only, the positioning of the surround was counterbalanced between the two eyes. All conditions were presented in random order.

2.3. Procedure

During the experiments, observers sat in a dark room while a chin rest supported their head. Observers were instructed to fixate a central marker and to continuously indicate the perceived direction of motion in the center. Before starting the actual experiment, observers were familiarized with the stimuli and the task. At the beginning of each trial, the fusion guides appeared along with a fixation cross which remained present during the trial. The stimuli appeared 0.5 s later. One trial lasted 30 s. After the stimuli disappeared, a dynamic mask was presented for 4.5 s to minimize motion adaptation effects (e.g. Anstis, Verstraten, & Mather, 1998). One session lasted about 10 min. All observers performed 5 sessions, resulting in 20 trials per condition for each observer.

3. Results

The results are presented in Fig. 2. We used two measures to analyze the dominance of the perceived direction of motion in the center compared to the motion in the surround. The first is *cumulative dominance*
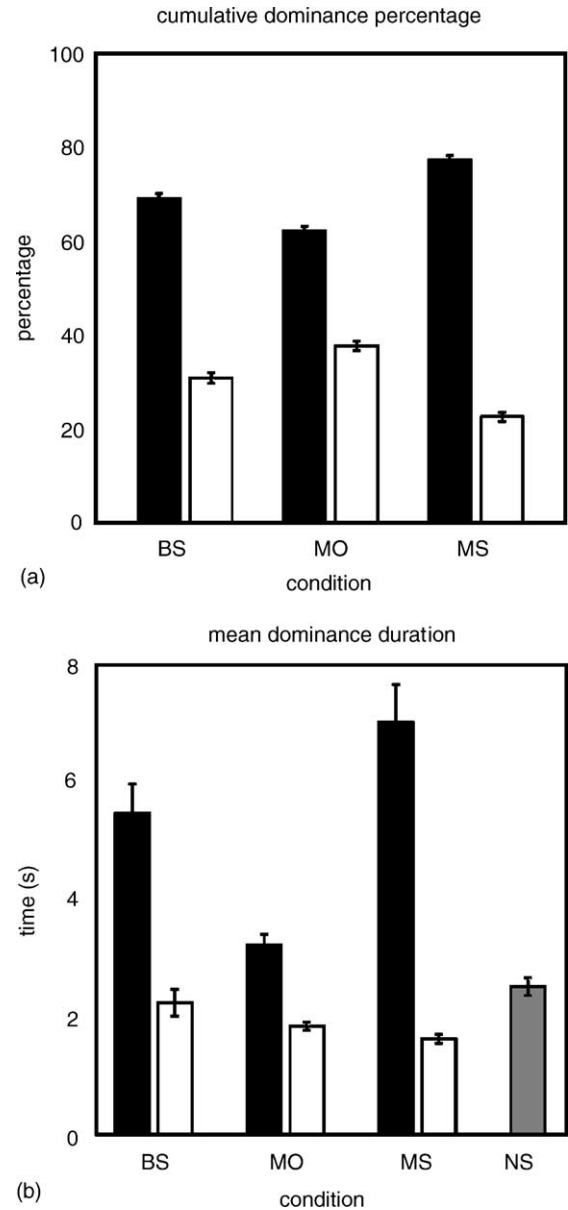

Fig. 2. Results of the experiment. Results are averages of 6 observers. Grouped bars represent the different surround conditions. The black bars represent the dominance of the opposite direction of motion (compared to that of the surround); the white bars the dominance of the same direction. Standard errors of the mean are plotted on top of the bars. (a) Cumulative dominance percentage. (b) Mean dominance duration. The grey bar represents the data for the no surround (NS) condition.

percentage, which represents the mean cumulative durations of both the opposite and same direction responses during one trial, expressed as the percentage of the total presentation time (Fig. 2(a)). This measure is informative about the relative dominance of both the same and the opposite direction of motion. The second measure is *mean dominance duration*, which refers to the mean duration of a single dominant percept for both the opposite and same direction responses (Fig. 2(b)). This

measure can potentially reveal the nature of center–surround interactions. For example, it might reveal that when a surround is presented, the same direction of motion is perceived for shorter durations and the opposite direction for longer durations. For the no surround condition, we analyzed the mean durations of both leftward and rightward responses.

As can be seen from Fig. 2(a), the cumulative dominance percentage of the opposite direction of motion is larger than 50% percent in all surround conditions (BS: $t = 17.3$, $p < 0.001$, MO: $t = 12.3$, $p < 0.001$, MS: $t = 27.9$, $p < 0.001$). Also apparent from Fig. 2(a) is that the different conditions yield different effect magnitudes. The preference for the opposite direction of motion is larger for MS than for BS ($t = 5.6$, $p < 0.001$) [1] which in turn is larger than MO ($t = 4.62$, $p < 0.001$). The difference between MS and MO is also significant ($t = 10.8$, $p < 0.001$).

From Fig. 2(b), one can appreciate that the mean dominance times are strongly modulated by the surround. The mean dominance time of the opposite direction of motion is larger than that of the NS condition in all surround conditions (NS versus BS: $t = 5.6$, $p < 0.001$, NS versus MO: $t = 2.9$, $p = 0.01$, NS versus MS: $t = 6.8$, $p < 0.001$). In addition, the mean dominance time for the same direction of motion is decreased compared to that of the NS condition in the MO and the MS conditions (NS versus MO: $t = 4.0$, $p < 0.001$, NS versus MS: $t = 5.2$, $p < 0.001$), but not in the BS condition ($p > 0.05$).

4. Discussion

The present study shows that presenting a surround dramatically affects the dominance of rival targets in the center. Furthermore, presenting surround motion leads to dominance of the opposite direction in the center irrespective of the eye to which the surround is presented. The opposite direction of motion appears to have high 'stimulus strength' during rivalry. This is illustrated by the fact that in some trials, observers exclusively perceived the opposite direction of motion during the entire presentation of 30 s. This implies that a surround strongly modulates the local rivalry process between the center gratings.

A related phenomenon was observed by Blake, Yu, Lokey, and Norman (1998). They presented dots moving either rightward or leftward to the left eye and right eye. In some conditions, the dots were surrounded by an annulus containing dots moving in the same direction, the opposite direction, or in random directions. The results showed that the center stimulus that was surrounded by the annulus became more dominant, irrespective of the direction of motion within the annulus. This means that in Blake et al., dominance was mostly dependent on which eye the surround was presented to. In our study the opposite direction of motion in the center is more dominant irrespective of the eye to which the surround is presented. One possible reason for the discrepancy might be that Blake et al. used sparse dots. Probably, sparse dots activate motion selective neurons less than the high contrast gratings in our study. Consequently, in Blake et al. center–surround interactions would be less prominent than in our study.

Blake and Logothetis (2002) suggested that the same 'neural machinery' is involved during perception of a dominant stimulus under rivalry conditions as in the case of normal, non-rivalrous viewing. Thus, center–surround interactions within visual processing stages under normal (non-rivalrous) viewing conditions are likely candidates to explain the results described here. Based on physiological studies on motion processing, it is tempting to suggest that the observed phenomenon is the result of center–surround interactions at the level of area MT/V5. Since center–surround interactions are often antagonistic, presenting a surround might lower the stimulus strength of a rival target with the same direction of motion in the center by inhibiting the neuronal response to the center. As a result, the opposite direction of motion in the center has higher stimulus strength than its rival, resulting in increased perceptual dominance of this direction of motion.

Most input to MT neurons is binocular (Felleman & Kaas, 1984). Accordingly, center–surround antagonism beyond the site of binocular fusion should be sufficient to explain the results. However, the results show that the preference for the opposite direction of motion is larger in the MS condition as compared to the MO condition. If inhibition of the same direction of motion would occur only after binocular fusion, both conditions should have yielded similar results. In this respect it is interesting to note that center–surround interactions in motion processing in area V1 have been shown to resemble those found in MT/V5 (Jones, Grieve, Wang, & Sillito, 2001). Therefore, it is possible that center–surround interactions before the level of MT/V5 are also involved in the observed effects. This would imply that both monocular as well as binocular center–surround interactions are involved.

Alternatively, facilitation of the opposite direction of motion might be involved. If so, this would mean that, when center and surround have the same direction of motion, the response to the center will be inhibited and when center and surround have an opposite direction of motion, the response to the center will be facilitated. However, this does not explain the differences between the different surround conditions.

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[1] When applicable, *p*-values were Bonferroni corrected for multiple comparisons.

In conclusion, we find a strong preference for motion in a direction opposite to that in the surround during binocular rivalry. This implies that surround motion can modulate local motion rivalry. Although center–surround interactions after binocular fusion at the level of MT are potential candidates to explain the results, we suggest that center–surround interactions at earlier stages of processing are involved as well.

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