Center–surround inhibition deepens binocular rivalry suppression

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Abstract

When dissimilar stimuli are presented to each eye, perception alternates between both images—a phenomenon known as binocular rivalry. It has been shown that stimuli presented in proximity of rival targets modulate the time each target is perceptually dominant. For example, presenting motion to the region surrounding the rival targets decreases the predominance of the same-direction target. Here, using a stationary concentric grating rivaling with a drifting grating, we show that a drifting surround grating also increases the depth of binocular rivalry suppression, as measured by sensitivity to a speed discrimination probe on the rival grating. This was especially so when the surround moved in the same direction as the grating, and was slightly weaker for opposed directions. Suppression in both cases was deeper than a no-surround control condition. We hypothesize that surround suppression often observed in area MT (V5)—a visual area implicated in visual motion perception—is responsible for this increase in suppression. In support of this hypothesis, monocular and binocular surrounds were both effective in increasing suppression depth, as were surrounds contralateral to the probed eye. Static and orthogonal motion surrounds failed to add to the depth of rivalry suppression. These results implicate a higher-level, fully binocular area whose surround inhibition provides an additional source of suppression which sums with rivalry suppression to effectively deepen suppression of an unseen rival target.
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1. Introduction

When a dissimilar stimulus is presented to each eye, an observer's perception alternates between both images, a phenomenon known as binocular rivalry (Alais & Blake, 2005). Two aspects of this phenomenon have intrigued visual neuroscientists: the fact that the conflict is resolved by an alternation between the competing monocular images (rather than, for example, resulting in transparency, or a summation), and the fate of the unseen image, which is removed from consciousness despite being physically present on the retina. A thorough knowledge of both aspects of rivalry is necessary if the mechanisms underlying the phenomenon are

to be understood. This paper focuses on the second issue, suppression depth.

Rivalry alternations are irregular and typically occur at a rate averaging about 0.5–1 Hz. A variety of spatial and temporal factors have been shown to influence the rate of rivalry alternations. Breese (1899) observed that the predominance of one image over another in rivalry was markedly enhanced as the luminance intensity of that image increased. Levelt (1965) showed that increasing the stimulus strength of the rival images produces an increase in alternation rate, where stimulus strength is defined in terms of luminance and contour density. Temporal factors can also influence rivalry. The incidence of rivalry between two motion stimuli becomes less likely as temporal frequency increases and the alternation rate increases (Carlson & He, 2000).

Top-down factors have also been shown to influence rivalry alternations. Lack (1978) showed in a series of

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experiments that naïve observers could voluntarily exert some control over rivalry alternation rate. This was especially so after a period of training, although, importantly, none of Lack's observers were able to completely stop rivalry alternations. Lack also ruled out a role for peripheral mechanisms in alternation rate, such as changing pupil size, accommodation, or blink rate and concluded that a central 'switching' mechanism controlled rivalry. Top-down influences have also been shown to exert an influence on the reversal rate of other forms of perceptual bistability (Strüber & Stadler, 1999).

Factors that alter rivalry rate and dominance duration are generally those that involve the parameters of the rival stimuli themselves (e.g., contrast, spatial frequency, etc.). There are, however, some top-down influences which provide interesting exceptions to this rule. One example comes from Kovacs, Papathomas, Yang, and Feher (1996) who showed that coherent images mixed between the eyes were capable of becoming dominant as coherent whole images, presumably driven by a top-down Gestalt influence. This process of interocular grouping was first reported by Diaz-Caneja in 1928 (translation: Alais, O'Shea, Mesana-Alais, & Wilson, 2000). Alais and Blake (1998) investigated a similar issue of stimulus context. They observed that if two elements are engaged in rivalry (drifting gratings), but one forms part of a larger global stimulus (a globally coherent, multi-aperture motion stimulus), then that element was less likely to be suppressed by the single grating rivaling with it. It was proposed that higher-level areas involved in signaling global motion coherence exerted a modulatory feedback influence over the rivalry process at a lower level between the two local gratings, strengthening the signal of the grating belonging to the global stimulus.

In a previous paper (Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004), we investigated related surround effects. We introduced non-rival stimuli in the area surrounding the rival stimuli and demonstrated that stimulation in surround regions influences dominance durations and alternation rates. In these experiments, rival gratings moved in opposite directions and were each surrounded by an annular grating whose direction of motion was the same as one of the rival stimuli. This caused the predominance of the target with the same-direction surround to decrease. That is, the rival stimulus with an opposite-direction surround was more dominant than that with the same-direction surround. It was proposed that the increase in grating predominance when surrounded by an opposed motion resulted from surround inhibition of the kind that has been observed in motion-selective neurons. Surround inhibition refers to the finding that the response of a neuron to its preferred direction of motion decreases when same direction motion is also presented to its non-classical receptive field (Allman, Miezin, & McGuinness, 1985; Born & Tootell, 1992). Thus, a same-direction surround would decrease the stimulus strength of the surrounded rival grating, causing an increase in the predominance of the other grating.

In the present paper, we investigate whether surround motion can also affect the depth of suppression of a surrounded rival target. Depth of suppression refers to the fate of the suppressed stimulus. Despite a suppressed grating being completely absent phenomenally during binocular rivalry, measurements of the neural representation of that grating (as indicated by contrast sensitivity) indicate that it is only suppressed by roughly a factor of 2 relative to the dominant stimulus (Blake & Camisa, 1979; Makous & Sanders, 1978; Nguyen, Freeman, & Wenderoth, 2001). Thus, although rivalry suppression may render a stimulus temporarily invisible, its cortical signal is attenuated rather than eliminated. In order to investigate this question experimentally, we dichoptically presented a horizontally moving grating and a stationary concentric grating. The observer's task was to discriminate a brief speed impulse (an increase or a decrease) in the drifting grating, and sensitivity to the probe triggered during perceptual dominance and suppression is compared. The ratio of dominance-to-suppression thresholds provides a measure of the depth of rivalry suppression. On the basis of center–surround inhibition, we hypothesized that adding a same-direction surround to the grating would add an additional source of suppression, leading to a greater depth of suppression for that grating than would be observed without a surround.

2. General methods

2.1. Observers

Four observers performed in the experiments, authors C.P. and D.A. and two naïve subjects. All had normal or corrected-to-normal vision.

2.2. Apparatus and stimuli

Stimuli and conditions are presented in Fig. 1. Stimuli were generated using Matlab and the Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on a gamma-linearized LaCie Electron 22 in. monitor (75 Hz vertical refresh) connected to an Apple Macintosh G4 and viewed through a mirror stereoscope. Binocular fusion was aided by a white ring filling the gap between center and surround, and by a white square drawn around the annulus. There was also a central fixation point. The rival stimuli consisted of one horizontally moving vertical grating and a stationary concentric ring. The rival targets could each be surrounded by an annulus containing a horizontally moving grating. The grating in the annulus could move in the same or in the opposite direction as the moving central target.
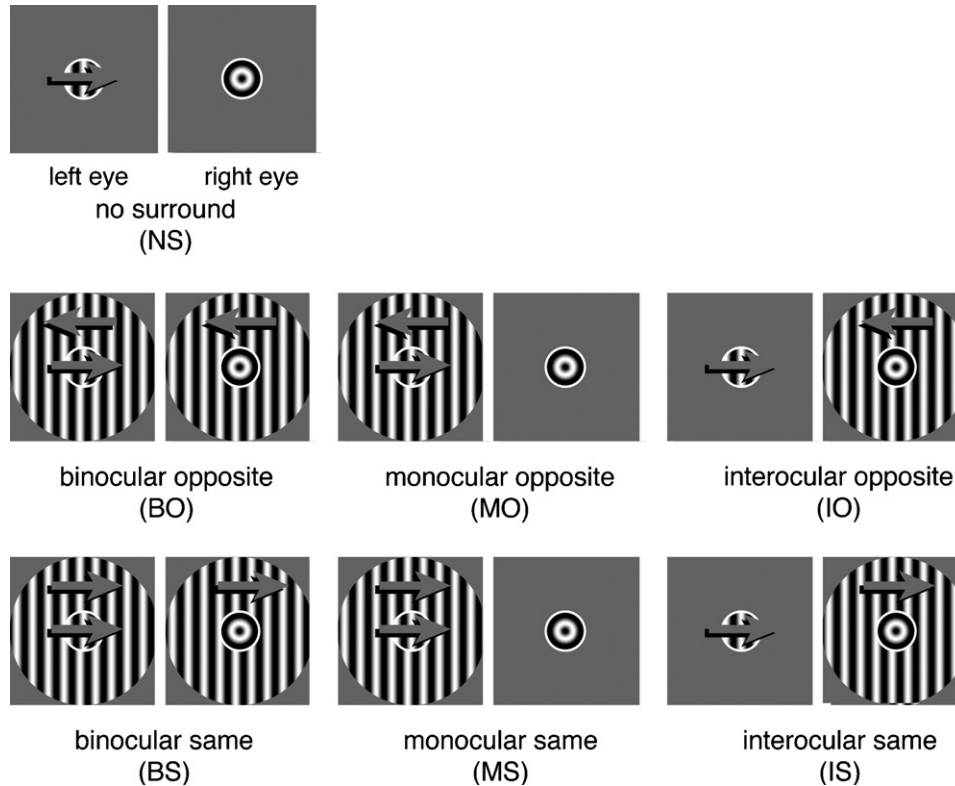
Fig. 1. Stimuli and conditions used in Experiment 1. Pairs of stimuli were presented dichoptically, one stimulus to the left eye and the second one to the other eye. The upper row represents the no-surround condition, the second and third row the different surround conditions. The middle row represents the opposite-direction conditions, the lower row the same-direction conditions. For the surround conditions, the left column represents the binocular condition, the middle column the monocular condition, and the right column the interocular condition.

All gratings had a spatial frequency of 1.96 cycles/deg. Moving stimuli had a speed of 1.27 deg/s and were presented at 99% contrast. The mean luminance of both the gratings and the background was $33\,cd/m^2$. The diameter of the center targets was 1.24 deg; the surrounding annulus was 1.70 deg wide. There was a gap of 0.09 deg between the center aperture and the annulus.

2.3. Procedure

To measure depth of suppression, we compared the observers performance on a discrimination task on the moving target while it was perceptually dominant versus when it was suppressed. Observers were instructed to judge whether a brief speed pulse presented to the moving target was an increment or decrement, according to a method described previously (Nguyen, Freeman, & Alais, 2003). Briefly, the speed of the moving rival grating smoothly increased or decreased according to a raised Gaussian profile, after which it returned to its baseline speed. Because the speed change was multiplicative (speed was either multiplied or divided by the raised Gaussian), the proportionate speed change was the same for increments and decrements. To acquire 75% correct thresholds, the amplitude of the Gaussian speed pulse was varied from trial to trial, using an adaptive staircase method (QUEST: Watson & Pelli, 1983) and subjects had to indicate whether the speed change was an increment or decrement.

Upon initiating a trial, the rival targets appeared. In 'dominance' conditions, observers waited until the moving target was completely dominant, and in 'suppression' conditions, observers waited until the stationary target was dominant. When a given target was dominant, observers pressed the space bar to trigger the brief speed pulse. One hundred and fifty milliseconds after pressing the space bar, the speed pulse appeared, which lasted for 120 ms in total and had a full bandwidth at half-height of 50 ms. One hundred and fifty milliseconds after returning to baseline speed, the trial was terminated and the observer indicated whether the speed pulse was an increase or decrease. If the dominant percept altered before or immediately upon pressing the space bar, the observer could repeat the trial. The repetition of an 'erroneous' trial ensured that pulse discrimination occurred in the respective 'dominance' or 'suppression' condition without exception. Each run consisted of 32 trials, and observers completed at least four runs per condition. The direction of motion of the center target as well as whether the speed pulse was an increment or decrement was randomized from trial to trial.

2.4. Conditions

Our experiments examined the influence of surround motion on depth of rivalry suppression of the drifting rival target. There was a no-surround baseline condition (NS), in which the rival stimuli were presented alone (a drifting grating to one eye, a stationary target to the other), and a total of six surround conditions (see Fig. 1):

1. binocular surround, same direction (BS),
2. monocular surround, same direction (MS),
3. interocular surround (i.e., monocular but other eye), same direction (IS),
4. binocular surround, opposite direction (BO),
5. monocular surround, opposite direction (MO),
6. interocular surround, opposite direction (IO).

Since each surround condition included a 'dominance' and a 'suppression' block, there were 14 conditions in total, including the baselines. Each condition was repeated at least four times per observer. The experiment was preceded by several practice blocks whose data were not analyzed. The total duration of the experiment was about 6 h.

3. Experiment 1

With surround stimuli shown to alter the predominance of a central rival target (Paffen et al., 2004), Experiment 1 investigates whether a complementary effect of surround motion on the suppression depth of a rival target can be observed. If such an effect does exist, it will be demonstrated by greater suppression for the six surround conditions relative to the no-surround baseline condition. More specifically, the known physiological effects of center–surround inhibition indicate that same-direction surrounds should produce greater suppression in the central grating than would be observed with opposite-direction surrounds.

4. Results

Fig. 2A shows the mean speed discrimination thresholds for four observers measured during dominance and suppression for the no-surround baseline condition and the six surround conditions. For all conditions, thresholds measured during suppression were significantly higher than those measured during dominance. Even the condition yielding the smallest t score (the no-surround condition) was highly significant with $t > 3.4$ and $p < .003$.

To calculate the suppression depth associated with each of the surround conditions, we divided the dominance thresholds by the suppression thresholds to
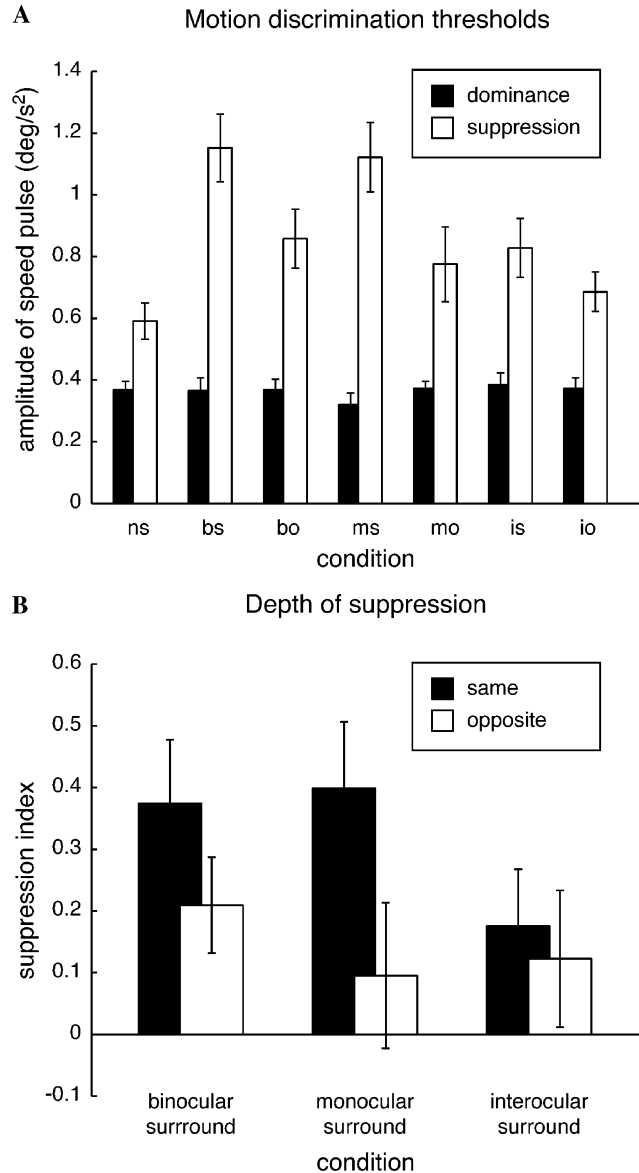

Fig. 2. Results of Experiment 1. Error bars represent standard errors of the mean. Results are pooled for all four observers. (A) Motion discrimination thresholds for dominance and suppression trials for all conditions in $\deg/s^2$ (ns, no surround; bs, binocular same; bo, binocular opposite; ms, monocular same; mo, monocular opposite; is, interocular same; and io, interocular opposite). Black bars represent thresholds for dominance trials, white bars represent thresholds for suppression trials. (B) Depth of suppression. Following common practice, depth of suppression indices were calculated by dividing thresholds from dominance trials by thresholds from suppression trials. Next, the resulting ratio for the no-surround condition was subtracted from those of the surround condition, to show only the additional effect due to surround suppression. These indices of depth of suppression are plotted for the three different surrounds (binocular, monocular and interocular). The black bars represent indices for same-direction surrounds, the white bars indices for the opposite-direction surround.

produce a suppression index. This index would have a value of 1.0 if there were no suppression, as thresholds in both dominance and suppression would be identical. Given that thresholds during suppression are all higher

than those for dominance, the suppression indices will be all less than 1.0 by an amount that quantifies suppression depth. Before plotting these suppression indices, the suppression index for the no-surround condition was subtracted from those for the six surround conditions. Thus, the suppression indices shown in Fig. 2B plot the additional contribution made to rivalry suppression due to the suppressive effect of the surround stimuli. Values greater than zero indicate that surround stimuli increase the depth of rivalry suppression of the central target. Overall, adding a surround significantly increased suppression: depth of suppression in surround conditions was significantly larger than in the no-surround condition ($t = 5.4$, $p < .001$).

A two-way ANOVA was conducted on the suppression indices with the factors being the direction of motion of the surround (same versus opposite) and the type of surround (binocular, monocular or interocular). This analysis revealed significant main effects of both factors: direction of surround motion ($F = 10.8$; $p = .01$) and surround type ($F = 5.7$; $p = .04$). No significant interaction between the factors was observed (motion × surround: $F = 1.8$; $p = .2$). As can be seen in Fig. 2B, the significant main effect of surround motion arises because there is greater suppression depth when the surround moves in the same direction as the central rival target compared to when the surround moves in the opposite direction. The main effect of surround type indicates differential effects of surround on suppression depth depending on whether it was a binocular, monocular or interocular surround. Binocular surrounds lead to the largest increase in suppression depth, interocular surround to the smallest increase. This order of effect sizes is supported by a linear regression across these conditions that showed a significant linear trend ($F = 10.3$; $p = .007$). However, post hoc pairwise testing revealed a significant difference only between the binocular and interocular surround conditions ($t = 2.7$, $p = .007$). Thus, although suppression depth increases linearly from interocular, via monocular to binocular surrounds, the increase between successive pairs is not significant.

5. Experiment 2

It might be argued that the increased suppression depth we observed with the six motion surrounds was mainly due to the fact that there was a surround present at all, independent of whether or not the surround moved. Also, the six surround conditions in Experiment 1 contained motions that were either iso-directional or anti-directional. For these reasons, we repeated our speed sensitivity measurements under three new conditions. Depth of suppression was measured using a surround moving orthogonally to the central rival target. In addition, two kinds of stationary surrounds were tested;

collinear and orthogonal. Fig. 3A illustrates the three conditions. Since the results of Experiment 1 showed that binocular surrounds exert the greatest additional suppressive effect on the central rival target, the three conditions were run using only binocular surrounds. The rival targets and all methodological details were the same as used in Experiment 1. Three of the observers that performed in Experiment 1 also took part in this experiment.

6. Results

Speed sensitivity thresholds for the three surround conditions were measured during dominance and during suppression. The ratio of dominance to suppression thresholds was calculated to find suppression depth, and the suppression depth obtained from the no-surround baseline in Experiment 1 was subtracted in order to show the suppressive effect of the surround stimuli alone. The results (averaged across the three observers) are presented in Fig. 3B. There are two key findings: (i) Results from an ANOVA revealed that the difference between the three surround conditions is not significant ($F = 1.4$; $p = .3$), and (ii) none of the three conditions lead to a significant increase in suppression beyond the level obtained with the no-surround baseline (one-sample t tests: $t < 0.7$ (largest t); $p > .24$ (smallest p)). Thus, stationary surrounds of either orientation do not affect depth of suppression and nor do translating surrounds if their direction is orthogonal to that of the moving rival target.

7. Discussion

We find that rivalry suppression is deepened by the presence of a drifting grating surrounding a moving rival stimulus. Thus, the attenuation of a suppressed image's signal, typically by about a factor of 2 (Blake & Camisa, 1979; Makous & Sanders, 1978; Nguyen et al., 2001), appears to be further attenuated by the presence of the surround motion. This is consistent with our predictions based on the surround inhibition hypothesis that adding surround motion around a moving rival grating would cause an additional suppressive influence that would sum with rivalry suppression to deepen the overall level of suppression. This result also extends an earlier finding that surround stimuli altered the predominance of a stimulus in rivalry (Paffen et al., 2004) in ways that were consistent with surround suppression.

The additional suppressive component to rivalry suppression produced by surround inhibition appears to be a rather general one since all surrounds effectively increased suppression depth compared to a no-surround baseline (see Fig. 2A). This is consistent with data from single-unit recordings in area MT which show that the classical receptive fields of the vast majority of cells have
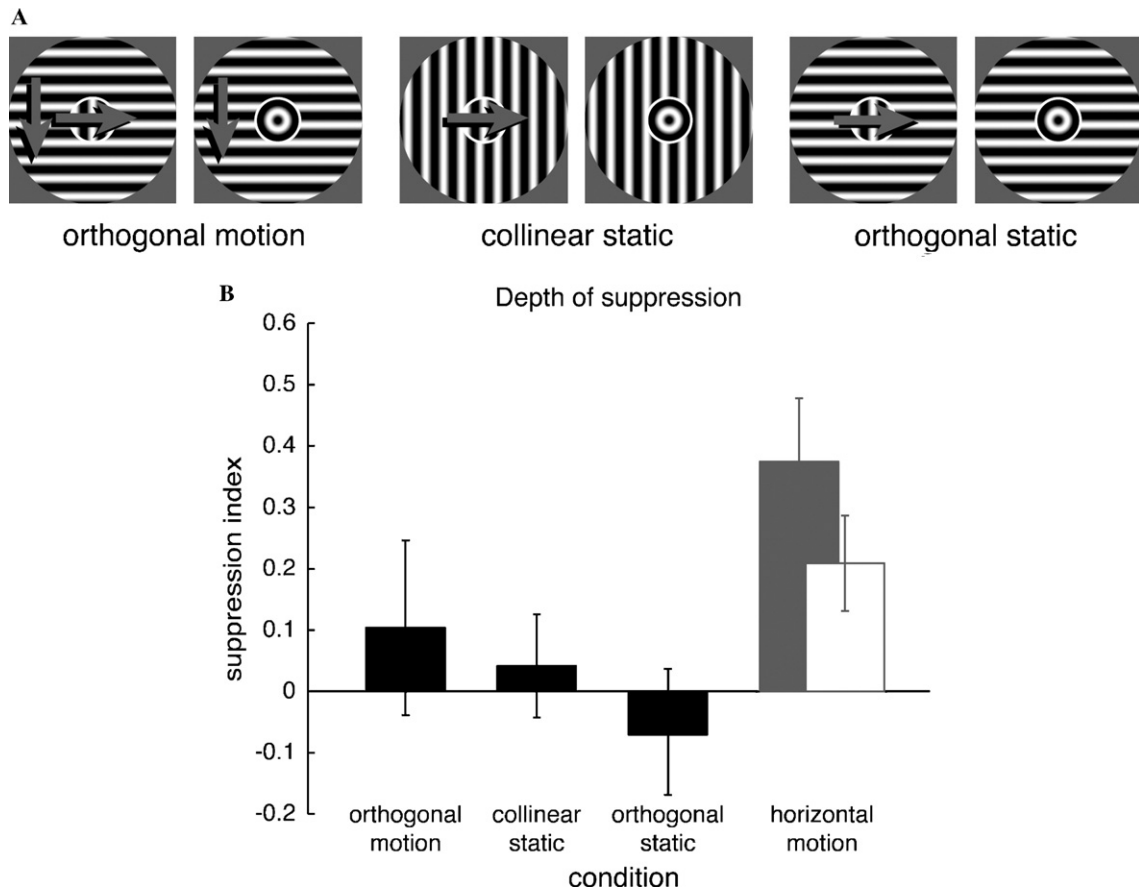
Fig. 3. Stimuli and results of the control experiment. (A) Stimuli: The center targets were the same as in Experiment 1. For all conditions, surrounds were presented to both eyes. In the orthogonal motion condition, a horizontal grating moved orthogonally to the moving target. In the collinear static condition, a static surround was presented with an orientation collinear to the moving center target. In the orthogonal static condition, the surround contained an orientation orthogonal to the center target. (B) Results: The suppression depth indices were calculated in the same manner as for Experiment 1 so that only the additional suppression due to the surround stimulus is plotted. For all three surround conditions, the suppression depth indices are not significantly different from zero. For comparison, the results from Experiment 1 of the binocular same-direction and binocular opposite-direction surround conditions are plotted (the dimmed gray and white bars, respectively). Error bars represent standard errors of the mean.

large modulatory surround fields (Bradley & Andersen, 1998; Raiguel, Van Hulle, Xiao, Marcar, & Orban, 1995) whose activation almost always produces a suppression of the classical receptive field response (Allman et al., 1985; Bradley & Andersen, 1998; Xiao, Raiguel, Marcar, Koenderink, & Orban, 1995). Another point worthy of note is that the various surrounds appeared to exert no significant influence on the rival grating during dominance, as thresholds for speed-pulse detection in Fig. 2A are all very similar across the six surround conditions and are not significantly different from the dominance threshold recorded for the no-surround condition.

At first sight, the lack of a surround effect on dominance thresholds appears to be odd. However, this result is not inconsistent with other investigations. For example, in Nguyen et al. (2003), suppression depth deepened across a range of conditions but without any change at all in dominance thresholds. In other words, the suppression-deepening effect was determined solely by how deeply suppressed the 'suppressed' target was, and not by how

'visible' the dominant target was. Nguyen et al.'s results are especially relevant since they also used detection of speed pulses as the task in their threshold measurements.

One of the predictions of the surround inhibition account is that same-direction surrounds should add more to the suppression of the rival target than would opposite-direction surrounds. A number of studies have specifically compared same- and opposite-direction surrounds and found that opposite-direction surrounds were less suppressive of the response in the classical receptive field than were same-direction surrounds (Allman et al., 1985; Bradley & Andersen, 1998; Xiao et al., 1995). Indeed, a minority of cells actually exhibit response facilitation when stimulated by an opposite-direction surround (Tanaka et al., 1986). Consistent with these observations, our suppression depth measurements revealed a significant main effect of surround direction (see Fig. 2B), with same-direction surrounds adding more to rivalry suppression than opposite-direction surrounds.

In Experiment 2, we tested motion surrounds with an orthogonal direction relative to the central grating and found little or no addition to rivalry suppression. While most single-unit neurophysiological work on MT surrounds has focussed on preferred versus antipreferred directions in the surround, relative disparity and relative speed (Allman et al., 1985; Bradley & Andersen, 1998; Raiguel et al., 1995; Xiao, Raiguel, Marcar, & Orban, 1998), Tanaka et al. (1986) did measure the directional tuning curve of surround motion suppression. Their finding was that suppression was maximal for same-direction surrounds and steadily declined as the angle between the center and surround motion increased. When the center and surround motion directions differed by 90 deg, there was little or no suppression such that the response to an orthogonal surround was almost identical to the no-surround response. This pattern of results is in close agreement with our orthogonal-direction surround condition (see Fig. 3B) in which little or no additional suppressive effect was observed relative to the no-surround condition.

The ocularity of the surround stimulus was also important in mediating the size of the suppressive surround effect. We found that binocular surrounds were more effective than monocular, which were more effective than interocular surrounds (see Fig. 2B). Presumably binocular surrounds are most effective because binocular summation in the neural surround field would strengthen the surround signal and thereby cause a greater degree of suppression on the units responding to the drifting grating rival target. Consequently, a binocular surround should result in a greater addition to the baseline suppression depth than would a monocular surround, as we observed. Monocular surrounds, however, are still quite effective, but less so if presented interocularly to the other eye.

Presentation of static surrounds appears not to exert a suppressive effect on motion rivalry targets (see Fig. 3B). This is probably explained by the fact that mechanisms in distinct cortical areas are involved in detection static and drifting stimuli, most likely V1 and MT, respectively, which would probably preclude center–surround interactions. Units in area MT, for example, where neurons are highly specialized for the detection of movement, respond only weakly and transiently to static stimuli. Because of this, there would be little or no scope for a suppressive interaction from the static surround on the classical receptive field in MT responding to the motion of the central rival target.

The present experiments can be compared with those of Alais and Blake (1999). In their experiments, facilitative rather than inhibitory effects were reported when a static grating was flanked by another static grating, especially when the gratings were collinear and adjacent. The two paradigms are similar in that adding a flanking grating is not unlike adding a (partial) surround grating.

However, there are important differences between the paradigms. First, in Alais and Blake (1999), the two gratings were horizontally separated by several degrees, making it doubtful that one grating was even within the spatial zone of the other grating's surround field. Second, even if it were, the point remains that the small flanking grating would provide only a partial stimulus for the much larger surround field. These differences may be important, because the pattern of data obtained in Alais and Blake's experiments were also completely different to ours, being primarily facilitative rather than inhibitory. Together, this points to a different substrate underlying the two data sets, and the most likely account of Alais and Blake's data is in terms of lateral intrinsic connections in V1. Supporting this, the level of facilitation they observed dropped when the gratings were oriented in parallel, and dropped again if they were orthogonal, exactly as predicted from patterns of intrinsic connectivity. Thus, the important differences between their flanking experiments and our surround experiments suggest different neural substrates rather than a conflict of data.

In summary, the experiments described above show that a drifting surround stimulus can exert a strong effect on binocular rivalry by deepening the suppression of the surrounded (translating) rival target. Two factors that are important in this effect are the direction of motion of the surround relative to the central stimulus and the ocularity of the surround. First, same-direction surrounds add more to suppression depth than do opposite-direction surrounds, with no effect for orthogonal-direction surrounds. Second, binocular surrounds cause more suppression than monocular and interocular surrounds, respectively. Surrounds that are static or that move orthogonally to the rival target appear not to exert a suppressive effect. We propose these findings are best explained in terms of surround inhibition that has been observed in motion-selective cells in monkey area MT (Allman et al., 1985; Born & Tootell, 1992). Specifically, surround inhibition provides an additional source of suppression which sums with rivalry suppression to effectively deepen the suppression of the unseen rival target.

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