Center-surround inhibition and facilitation as a function of size and contrast at multiple levels of visual motion processing

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Visual context often plays a crucial role in visual processing. In the domain of visual motion processing, the response to a stimulus presented to a neuron's classical receptive field can be modulated by presenting stimuli to its surround. The nature of these center-surround interactions is often inhibitory; the neural response decreases when the same direction of motion is presented to center and surround. Here we use binocular rivalry as a tool to study center-surround interactions. We show that magnitude of surround suppression varies as a function of luminance contrast and surround width. Increasing the size of surround motion increased surround suppression at high contrast. Furthermore, large, high-contrast surrounds facilitated opposite-direction motion in the center. For stimuli presented at low contrast, surround suppression peaked at a smaller surround width. In addition, we provide evidence that surround inhibition occurs at multiple levels of visual processing: Surround inhibition in motion processing is likely to originate from both monocular and binocular processing stages.

Keywords: binocular rivalry, center-surround interactions, motion perception

Introduction

Since the pioneering work of Hubel and Wiesel (e.g., 1968), it is generally acknowledged that visual processing neurons respond selectively to specific stimulus features presented to their receptive fields. According to the classical concept of a receptive field, a neuron responds within a spatially restricted representation of the visual field (Hartline & Graham, 1932). However, many studies have shown that the response of such neurons can be affected by simultaneously presenting stimuli outside its classical receptive field (e.g., Allman, Miezin, & McGuinness, 1985; Gilbert & Wiesel, 1990).

Center-surround interactions have been studied extensively in the domain of visual motion processing. The predominant nature of these center-surround interactions is inhibitory; the response to motion presented to the center of a neuron's classical receptive field decreases when the same direction of motion is presented to its non-classical surround (e.g., Allman et al., 1985; Raiguel, van Hulle, Xiao, Marcar, & Orban, 1995). In addition, facilitation of the neural response has also been reported (Allman et al., 1985; Born & Tootell, 1992). In this case, the neural re-

sponse to center motion increases when motion is presented to the surround. The difference between the natures of surround interactions (inhibition vs. facilitation) might lie in the fact that different cells in MT show different behavior. As pointed out by Born and Tootell (1992), depending on where the cells are located, some cells show facilitation of their response, others inhibition.

At the neuroanatomical level, surround interactions are often associated with motion selective area MT/V5 (e.g., Allman et al., 1985; Raiguel et al., 1995), although they are also observed at other levels involved in visual motion processing, such as V1 and MST (Jones, Grieve, Wang, & Sillito, 2001; Eifuku & Wurtz, 1998).

Several authors have proposed a functional role for center-surround interactions. Nakayama and Loomis (1974) predicted that center-surround interactions in motion processing play an important role in the detection of motion discontinuities or motion boundaries. In addition, these interactions have been implicated in figure/ground segregation (Allman et al., 1985; Lamme, 1995), computation of self-motion during eye movements (Warren, 1995), and the construction of three-dimensional object shape (Koenderink & van Doorn, 1992).

Here we use binocular rivalry as a tool to study surround interactions. During binocular rivalry, dissimilar stimuli presented dichoptically compete for perceptual dominance (for reviews, see Alais & Blake, 2005, or Blake & Logothetis, 2002). Recently, we have reported evidence for center-surround interactions in motion processing during binocular rivalry (Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004). We dichoptically presented targets moving in opposite directions, which could each be surrounded by motion in the same direction as one of the two. Presenting surround motion increased the dominance of the center target containing the opposite direction of motion. Hypothetically, the increased dominance of the opposite direction of motion could be the result of surround facilitation of the opposite direction of motion, surround inhibition of the same direction, or a combination of both. However, because the center targets moved either in the same or in the opposite direction as the surround in that experiment, it was not possible to disentangle surround inhibition from surround facilitation.

The goals of the first experiment of this study were twofold: (1) to disentangle surround inhibition from facilitation during rivalry and (2) to study the effect of varying size and contrast of both the center and surround on the dominance of rival targets. Recently, both psychophysical (Tadin, Lappin, Gilroy, & Blake, 2003) and physiological (Pack, Hunter, & Born, 2005) studies have shown that magnitude of surround inhibition varies as a function of size and contrast of a motion stimulus. In general, increasing the size and contrast of a motion stimulus increases the magnitude of surround inhibition (Tadin et al., 2003).

In our second experiment, we investigated at what levels of processing center-surround interactions act. As discussed, neurophysiological studies have pointed toward several neuroanatomical loci of center-surround interactions. We used a psychophysical approach to study levels of processing. More specifically, we asked whether processing levels before as well as after binocular fusion are involved in center-surround interactions. Many studies have looked into the contribution of monocular and binocular processing levels to various forms of visual motion processing (e.g., de Weert & Wade, 1984; Georgeson & Shackleton, 1989; Meng, Chen, & Qian, 2004). Here we studied the role of monocular and binocular processing levels in surround interactions.

Experiment 1

The first goal of this experiment was to disentangle surround inhibition from surround facilitation during binocular rivalry. To achieve this, we modified the stimuli used by Paffen et al. (2004). In that experiment, rival targets containing opposite directions of motion were surrounded by motion in the same direction as one of the two. To disen-

tangle surround inhibition and facilitation, we replaced one rival target by a stationary target. The dominance of the stationary target will not depend on the direction of motion of the surround. To study surround inhibition, the targets were surrounded by motion in the *same* direction as the motion target. This manipulation should lead to *decreased* dominance of motion in the center. Absence of surround inhibition should leave dominance of the rival targets unaffected. Likewise, surround facilitation might be observed when both targets are surrounded by a direction of motion *opposite* to the motion target. In this case, the dominance of motion in the center should *increase*. Again, absence of surround facilitation should leave the dominance of the targets unaffected.

Second, to study the effect of size and contrast on surround interactions, we used four surround widths and three contrast levels of center and surround. Based on findings by Tadin et al. (2003) and Pack et al. (2005), we expected surround inhibition to increase with increasing size and contrast.

Method

Observers

Four observers performed in this experiment. Two observers were naive to the purpose of the experiments. The other two were authors. All observers had normal or corrected-to-normal vision.

Apparatus & stimuli

The stimuli were presented with an Apple Macintosh dual 867 MHz G4 using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and a single, luminance-linearized, 22" LaCie Blue Electron monitor at 85 Hz. Viewing distance was 72 cm. Dichoptic presentation was achieved by means of a mirror stereoscope.

The basic stimuli are presented in Figure 1. The stimuli consisted of two circular apertures that could each be surrounded by an annulus. Because a surround containing motion can possibly inhibit the response to a stationary target with the same orientation, we used a circular stationary concentric target instead. This target contained no motion or orientation information, enabling us to look at the effect of same- and opposite-direction surround motion on the motion rival target only. Although a motion surround is expected to modulate dominance duration of the motion as well as the static target, the source of this modulation will be the surround interactions between the motion surround and motion target. Thus, rivalry was instigated between a motion and a stationary target. The spatial frequency of the stationary target was matched to that of the motion target. The rival targets were each surrounded by an annulus containing a grating moving horizontally in the same or in the opposite direction as the motion target. The gratings had a spatial frequency of 1.96 cycles/deg and
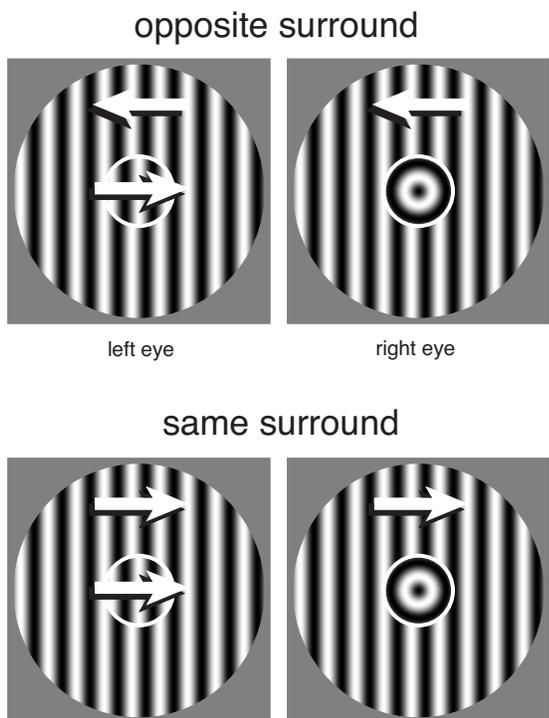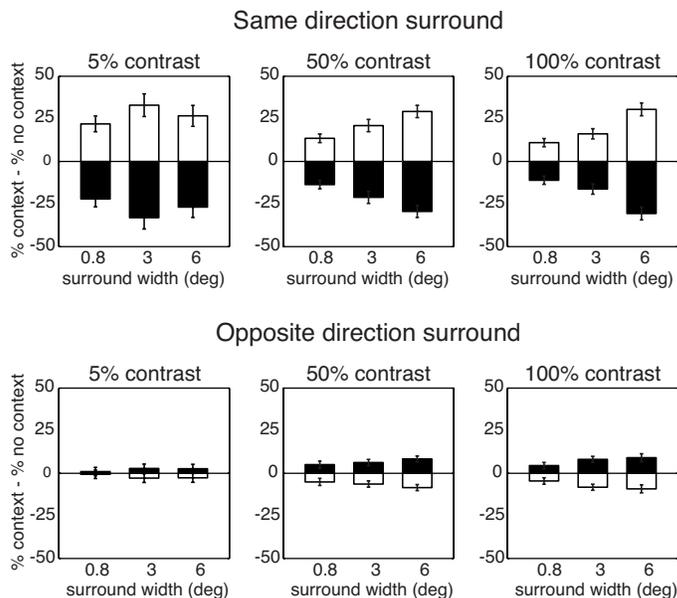
Figure 1. Typical stimuli used in Experiment 1. The stimulus on the left was presented to the left eye, and the one on the right was presented to the right eye. Arrows indicate the direction of motion of the grating.

moved at a constant speed of 1.27 deg/s. 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 surround could have one of three widths (0.8, 3, or 6 deg) or could be absent. There was a gap of 0.09 deg between the center aperture and the annulus. Michelson contrast of both center and surround was 5.0, 49.8, or 99.7%. Binocular fusion was aided by fusion guides consisting of a white ring filling the gap between center and surround, a white square drawn around the annulus, and a central fixation marker.

Results

The results are presented in Figure 2. Because we expressed cumulative dominance of rival targets as percentages of total presentation time, we performed an arc-sine transformation on percentages to approximate normally distributed data. Next we subtracted cumulative dominance of the motion target in the no-surround condition from its cumulative dominance in each of the surround conditions. As a result, negative values indicate a decrease and positive values indicate an increase in predominance of the motion target. Note that the data for the stationary rival targets are symmetrical—performing the same transformation on cumulative dominance of the static target (arc-sinus transformation followed by no-surround subtraction) gives the same data, but with opposite sign.
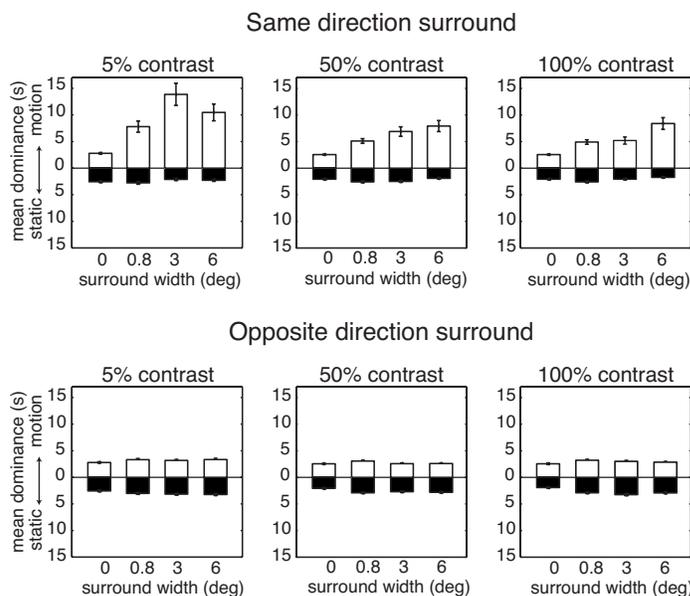

Figure 2. Results of Experiment 1: dominance of the motion and the static target for same- and opposite-surround motion at different surround sizes and contrasts. Results are pooled data for four observers. White bars represent dominance for the static target and black bars represent dominance for the motion target. The two upper panels plot the net effect in cumulative dominance of adding surround motion to the rival targets (see text). The two lower panels show mean dominance durations. Error bars represent standard errors of the mean.

Next we analyzed whether adding same-direction motion decreased cumulative dominance of the motion target (indicating inhibition), and whether opposite direction increased dominance (indicating facilitation). For all same-direction surrounds, dominance of the motion target was significantly smaller than zero, indicating inhibition (smallest, $T(31) > 4.5$; largest, $p < .001$). For opposite-direction surrounds, only the two largest surround sizes for 50% and 100% contrast led to a significant increase of dominance of the motion target (smallest, $T(31) > 3.4$; largest, $p < .001$).

Next we analyzed the influence of increasing size of surround and contrast of center and surround on predominance of the motion target. Applying a repeated measurements ANOVA with all factors (same- and opposite-direction surround, three surround widths, and three luminance contrasts) resulted in significant main effects of surround motion direction, $F(1,31) = 172.0$, $p < .001$, and surround width, $F(2,30) = 5.5$, $p = .006$, as well as significant interactions between surround motion direction and surround width, $F(2,30) = 14.5$, $p < .001$, and between surround motion direction, luminance contrast, and surround width, $F(4,28) = 3.1$, $p = .02$.

To understand the influence of size and contrast on each surround-motion direction, we analyzed the two motion directions separately. For same-direction surround motion, we observed a significant main effect of surround width, $F(2,30) = 11.1$, $p < .001$, and a significant interaction between luminance contrast and surround width, $F(4,28) = 3.4$, $p = .01$. Figure 2 shows that increasing the size of the surround decreases the dominance of the motion target at 50% and 100% contrast. However, at 5%, contrast dominance durations show a U-shape with increasing size. Note that there is no overall increase in dominance of the motion target with increasing contrast.

For opposite-direction surround motion, a significant main effect of surround width was observed, $F(2,30) = 4.5$, $p = .02$; increasing the width of the surround increases dominance of the motion target.

Discussion

The results of Experiment 1 can be summarized as follows. For large surround widths at high contrast, we find surround facilitation of the opposite direction of motion. At smaller sizes and low contrast, no facilitation of the opposite direction was observed.

For all same-direction surround conditions, we find evidence for inhibition. Increasing surround width decreases dominance of the motion target at 50% and 100% contrast. At the lowest contrast, adding a surround also decreases dominance of the motion target. However, maximum modulation is observed at a surround width of 3 deg. Thus, for the lowest contrast, surround inhibition appears to peak at a smaller size than at higher contrasts of center and surround.

Also, it can be noted that inhibition is generally stronger than facilitation; same-direction motion has a stronger effect on dominance of the rival targets than opposite-direction motion.

Our results are in line with Tadin et al. (2003), who used similar stimulus sizes (widths of 1–5 deg) and with Pack et al. (2005), who used stimuli up to 35 deg in diameter. These studies also reported evidence for increase of inhibition for high-contrast stimuli with increasing stimulus size. Our results on the effect of contrast are not as clear-cut. Whereas Tadin et al. (2003) reported increase of duration thresholds and hence an increase in surround inhibition with increasing contrast, we report equal inhibition across several contrasts. On the other hand, the difference between duration thresholds of the two highest contrasts used by Tadin et al. (46% and 92%) was small. Also, as indicated by the significant interaction between surround width and contrast, surround inhibition does not increase for all sizes at the lowest contrast we used. Apart from this, we do not find much difference between magnitude of inhibition and level of luminance contrast. At 5% contrast, surround inhibition still appears to be quite strong. However, inhibition reaches it optimal level at a smaller size than at higher contrasts, which indicates that surround inhibition decreases with size at low contrast. A possible reason for the discrepancy between Tadin et al. (2003) and our data might be that they used a moving Gabor in their experiments, whose luminance contrast peaks at the center and drops in the periphery. The strong inhibition we find at the lowest contrast might be because luminance contrast of our surround is higher than that of Tadin et al. (2003).

Experiment 2

In Experiment 2, we did not use binocular rivalry to study surround interactions. Instead, we presented the center and surround to only one eye. The surround, however, could be presented to the same eye as the center, or to the other eye. In this way, we can disentangle the respective contribution of monocular and binocular levels of processing to center-surround interactions.

We used a center target consisting of oppositely moving gratings with variable contrast ratio for leftward and rightward motion. Based on the results of Experiment 1, we predicted that adding a surround containing leftward or rightward motion would lead to a shift in the perceived direction of the center target toward a direction of motion opposite to that of the surround. In theory, binocular surround interactions can occur for both within- and between-eye presentation. However, monocular surround interactions can only occur for within-eye presentation.

For this experiment, several predictions can be made: If within-eye presentation of center and surround leads to a larger shift than between-eye presentation, it implies the

contribution of monocular levels of processing. On the other hand, if only binocular levels are involved, both conditions should lead to a similar shift in perceived direction. In the extreme case of absence of binocular components, only within-eye presentation should bias the perceived direction of motion in the center.

Method

Observers

Five observers performed in this experiment. Three observers were naive to the purpose of the experiments. All observers had normal or corrected-to-normal vision.

Apparatus & stimuli

The set-up was the same as in Experiment 1. The stimuli and conditions are presented in Figure 3. The center stimulus was produced by adding a leftward and a rightward motion grating with variable contrast ratio. The surround moved either leftward or rightward. The diameter of the center targets was 1.24 deg; the surrounding annulus was 1.70-deg wide. There was a 0.09-deg gap between the center aperture and the annulus. The speed and spatial frequency of component center grating and surrounding gratings were the same as in Experiment 1. The same holds for the mean luminance of stimuli and background. The experiment involved two conditions, a monocular surround condition and an interocular surround condition.

monocular surround (MS)

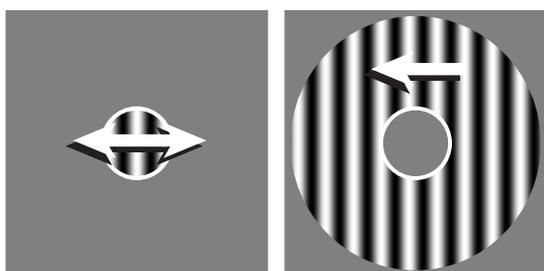left eye   right eye
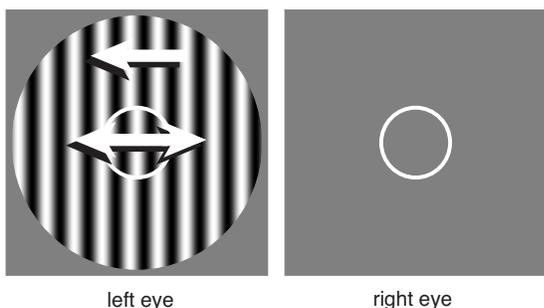
interocular surround (IS)

Figure 3. Stimuli and conditions used in Experiment 2. In each condition, the center and the surround were presented to only one eye. The surround was presented either to the same eye as the center (first row) or to the other eye (second row).

Procedure

We varied the contrast ratio of the center stimulus using a constant-stimuli design. For each of the two conditions, we counterbalanced the positioning of the center grating (left eye, right eye) and the direction of motion of the surround grating. The observer initiated a trial by pressing the space bar. After 0.5 s, the stimuli were presented for 0.5 s. The task of the observer was to report the perceived direction of motion in the center. Each observer performed in 4 runs of approximately 10 min, resulting in 20 trials per contrast ratio.

Results

The results are presented in Figure 4 and in Table 1. For each of the conditions, we fitted all "rightward" responses against the log contrast ratio of the center stimulus.
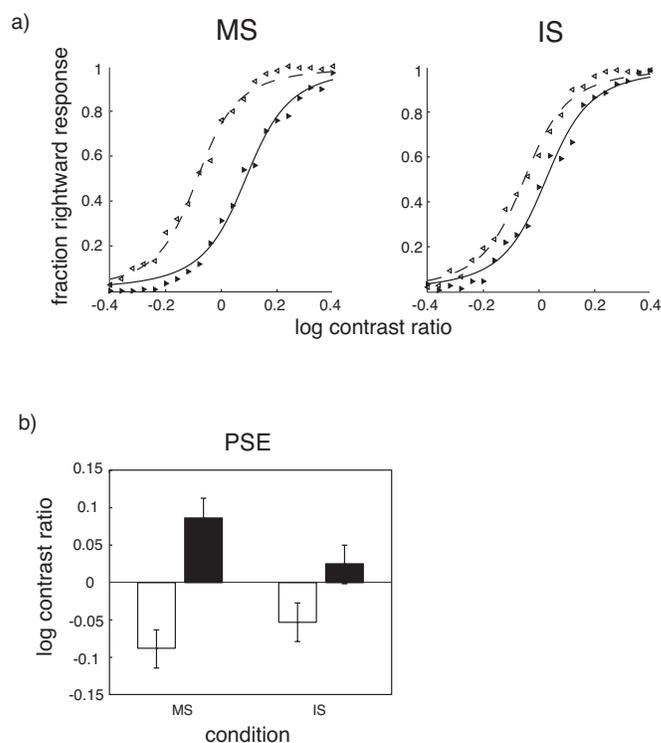

Figure 4. Results of Experiment 3 for pooled data of five observers. Upper panels represent fractions of rightward responses plotted against the log contrast ratio of the center target (left/right). Triangles represent the fraction of right responses for each of the contrast ratios. Lines represent the psychometric curves resulting from fitting the data to a cumulative Gaussian. Filled triangles and solid lines represent the data for a rightward-moving surround. Open triangles and dotted lines represent the data for leftward-surround motion. The left panel represents the monocular surround condition and the right panel represents the interocular surround condition. The lower panel represents points of subjective equality and 95% confidence intervals of each surround condition. MS, monocular surround condition; IS, interocular surround condition. White bars represent PSE's for a rightward motion surround, and black bars represent PSE's for a leftward motion surround.

	MS-l	MS-r	IS-l	IS-r
Cp	-0.04:0.01	0.04:0.08	-0.08:-0.04	-0.04:0.00
Eo	-0.07:-0.02	-0.03:0.02	-0.04:0.01	-0.02:0.03
Mn	-0.10:-0.05	-0.02:0.01	-0.08:-0.01	-0.12:-0.08
Oj	-0.16:-0.11	0.20:0.25	-0.11:-0.06	0.14:0.18
Sp	-0.18:-0.14	0.17:0.22	-0.08:-0.03	0.08:0.13
All	-0.11:-0.06	0.06:0.11	-0.08:-0.02	0.00:0.05

Table 1. The 95% confidence intervals of points of subjective equality for all subjects and the pooled data (all). MS-l and MS-r are the fraction rightward responses in the monocular surround condition for leftward and rightward surround motion, respectively. IS-l and IS-r are the fraction rightward responses in the interocular surround condition for leftward and rightward surround motion, respectively.

Values less than zero represent net leftward motion energy (when the log rightward-leftward-motion ratio is smaller than 1); values above zero represent net rightward motion energy. Psychometric functions (Figure 4, top panels) were acquired by fitting the data to a cumulative normal distribution function. From this function, the point of subjective equality (PSE) was acquired. Via a bootstrap procedure, we acquired confidence intervals (CIs) reflecting uncertainty of the fit. Table 1 represents 95% confidence intervals for individual subjects and for the pooled data of all observers. Non-overlapping confidence intervals were taken as a significant difference between conditions. Statistical analysis was performed on the pooled data of all observers.

The surround had a significant effect on the perceived direction of motion in both surround conditions. In the monocular surround condition, the PSE for leftward surround motion was significantly smaller than the PSE for rightward surround motion (MS-l, 95% CI: -0.11:-0.06 vs. MS-r, 95% CI: 0.06:0.11). The same holds for the interocular surround condition: The PSE was significantly smaller for leftward than for rightward surround motion (MS-l, 95% CI: -0.08:-0.02 vs. MS-r, 95% CI: 0.00:0.05).

Next we compared the difference in biases of rightward and leftward surrounds (Figure 4, lower panel) between the monocular and interocular surround conditions using a paired *t* test on the mean PSEs of the five observers. The surround bias is significantly larger for the monocular compared to the interocular condition, $t(4) = 2.8$, $p = .003$.

Discussion

This experiment was designed to investigate whether multiple levels of motion processing are involved in surround inhibition. In both surround conditions, the perceived direction of motion in the center was shifted in a direction opposite to that of the surround. This implies that the observed center-surround interactions are at least partly acting at a binocular level. When center and surround were presented to the same eye, this shift was larger compared to when the surround was in the other eye. This implies that center-surround interactions on monocular levels of processing also contribute.

Quantitatively, the surround modulation was about twice as large when center and surround were presented within one eye compared to when they were presented between both eyes. This suggests that monocular and binocular levels of processing contributed about equally to surround inhibition.

General discussion

In two experiments we studied surround interactions in motion processing. The first experiment revealed that dominance of a rival motion target varies with size and contrast of surround motion. More specifically, increasing the size of surround motion increased the dominance of the rival motion target when it moved in the opposite direction, whereas its dominance was decreased when it moved in the same direction. However, same-direction motion had the largest effect on dominance. Varying luminance contrast of both center and surround had a less pronounced effect on dominance of the rival targets. Only for same-direction motion was an effect of luminance contrast observed: at the lowest contrast, dominance of the motion target first decreased, then increased when the size of the surround increased. In the second experiment we showed that the observed surround interactions are operating on both monocular and binocular levels of processing: Dichoptic presentation of center and surround leads to significant shift of the perceived direction in the center. However, this shift was weaker than when center and surround were presented monocularly.

We carried out these experiments to study surround interactions often observed in neurophysiology. Our results are in line with single-cell recordings. That is, surround interactions (1) are predominantly inhibitory, (2) vary as a function of size and contrast, and (3) involve multiple levels of processing.

Here we discuss our findings and their relation to physiology in greater detail. In physiological studies, observed surround interactions are often inhibitory, although surround facilitation is also observed. For example, Allman et al. (1985) found many neurons whose response was inhibited by presenting same-direction motion to the surround. Only few neurons have been described showing surround facilitation (e.g., Allman et al., 1985; Tanaka et al., 1986). Psychophysical studies have primarily focused on center-surround inhibition as well (e.g., Tadin et al., 2003). To summarize our results and those of single-cell recordings, surround facilitation is observed, but surround inhibition is more prominent.

As discussed above, magnitude of surround inhibition varies as a function of size and contrast. Tadin et al. (2003) recently showed that duration thresholds and magnitude of the motion aftereffect (MAE) (both assumed to be indicators of magnitude of surround inhibition) (see Anstis, Verstraten, & Mather, 1998) varied with stimulus size and contrast. While duration thresholds increased with increasing

size and contrast of a motion stimulus, the magnitude of the MAE decreased. These findings were supported by a recent study of Pack et al. (2005), who recorded responses of neurons in MT of the macaque. For low-contrast motion, responses kept increasing with increasing size of motion. In contrast, the response to high-contrast motion peaked at a certain stimulus size after which the response dropped. Our results are in line with these findings: Increasing the size of surround motion decreased dominance of a rival motion target. Increasing luminance contrast had a less pronounced effect in our study. Surround inhibition was about equal across several contrasts, although surround inhibition peaked at a smaller surround size at the lowest contrast.

Surround interactions in motion processing have been described in V1, MT, as well as in MST. Most of these studies have focused on area MT. Jones et al. (2001) recently showed that surround suppression in motion processing can also be observed in V1. Interestingly, from anatomical studies it is known that input to MT is largely binocular (Felleman & Kaas, 1984), whereas V1 is subdivided in ocular dominance columns, which receive monocular input (Wiesel, Hubel, & Lam, 1974). In our study, dichoptic (between-eye) presentation of center and surround produced a smaller shift in perceived direction of center motion than within-eye presentation. From this we can infer that the magnitude of surround inhibition was larger for within-eye presentation than for dichoptic presentation. Assuming that our within-eye surround condition involved both monocular and binocular levels and our between-eye condition only binocular levels, we infer that the within-eye surround effect is the result of surround interactions at binocular *as well as* monocular levels of processing. These monocular and binocular components might correlate with surround interactions observed in V1 and MT. A monocular contribution to surround interactions might be mediated by V1 or via feedback connections from MT to V1 (a suggestion put forward by Jones et al., 2001, and supported by Hupé et al., 1998). Although we can only speculate about the anatomical underpinnings of the observed center-surround interactions, we *can* conclude that they occur at monocular and binocular levels of processing.

Our experiments were mainly aimed at studying surround interactions, yet the results of Experiment 1 also add to accumulating evidence of contextual modulation during binocular rivalry (Levelt, 1965; Fukuda & Blake, 1992; Alais & Blake, 1998; Alais & Blake, 1999; Sobel & Blake, 2002; Carter, Campbell, Liu, & Wallis, 2004; Paffen et al., 2004). Although the suggestion of surround interactions during binocular rivalry has been put forward is some of these studies, we have now tested this more directly, by looking at same-direction inhibition and opposite-direction facilitation separately.

The use of binocular rivalry also allows us to explore another aspect of surround interactions: Does surround inhibition have the same effect on center motion as decreasing the center's luminance contrast? For example, it

has been reported that perceived contrast of center motion decreases when surrounded by same-direction motion (Takeuchi & De Valois, 2000). Binocular rivalry can also provide insight into this question. According to Levelt (1965), manipulating the stimulus strength of one target engaged in binocular rivalry changes the time this target will be suppressed, leaving its mean dominance duration unaffected. For example, decreasing the stimulus contrast of one target leads to increased dominance of the other. In this respect, it is informative to look at how the surround motion influenced mean dominance durations of the center targets in Experiment 1. When surrounded by the same direction of motion, the mean dominance duration of the rival motion target decreases somewhat in some conditions. However, the increase in predominance of the rival static target was mainly caused by an increase in mean dominance duration of the static target (Figure 2, lower panels). Thus, adding surround motion mainly modulated the dominance duration of the static target. If we apply Levelt's (1965) concept of stimulus strength, adding a same-direction surround decreases stimulus strength of the rival motion target in a similar manner as decreasing this target's luminance contrast. This implies that surround interactions in motion processing act to modulate effective contrast of motion stimuli.

Acknowledgments

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