

Brief communication

Adaptive center-surround interactions in human vision revealed during binocular rivalry

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Received 9 March 2005; received in revised form 19 May 2005

Abstract

We used binocular rivalry as a psychophysical probe to explore center-surround interactions in orientation, motion and color processing. Addition of the surround matching one of the rival targets dramatically altered rivalry dynamics. For all visual sub-modalities tested, predominance of the high-contrast rival target matched to the surround was greatly reduced—a result that disappeared at low contrast. At low contrast, addition of the surround boosted dominance of orientation and motion targets matched to the surround. This contrast-dependent modulation of center-surround interactions seems to be a general property of the visual system and may reflect an adaptive balance between surround suppression and spatial summation.

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Keywords: Center-surround interactions; Binocular rivalry

1. Introduction

The response of a neuron to a specific stimulus feature presented to its classical receptive field is often affected by presenting the same feature to its (non-classical) surround (Allman, Miezin, & McGuinness, 1985; Born & Tootell, 1992; Tanaka et al., 1986). The nature of these surround interactions is often inhibitory: presenting same direction motion to the surround of a neuron's receptive field typically reduces the response to motion presented to the center. It has been argued that such surround inhibition is implicated in figure-ground segregation (Born, Groh, Zhao, & Lukasewycz, 2000), optimizing information transmission (Vinje & Gallant, 2000) and perception of surface shape (Buracas & Albright, 1996). However, surround suppression might become problematic when neural response to a stimulus

is already weak, for example when stimulus visibility is low. Recent research indicates that this potential problem can be circumvented by reducing surround suppression and/or increasing spatial summation at low contrast (Pack, Hunter, & Born, 2005; Sceniak, Ringach, Hawken, & Shapley, 1999; Tadin, Lappin, Gilroy, & Blake, 2003). For example, in area MT, the suppressive influence of the surround is abolished or greatly attenuated at low contrast (Pack et al., 2005). Does this flexibility at the single neuron level reveal itself at the level of perception? Moreover, are such adaptive surround interactions a general property of visual processing?

Using binocular rivalry as a tool, we addressed these questions by studying contrast-dependency of center-surround interactions in motion, orientation and color processing (Fig. 1). Binocular rivalry was chosen for several reasons: the dynamics of perceptual alternations during binocular rivalry are indicative of the relative perceptual strengths of the rivaling stimuli (Levelt, 1965). Moreover, binocular rivalry is affected

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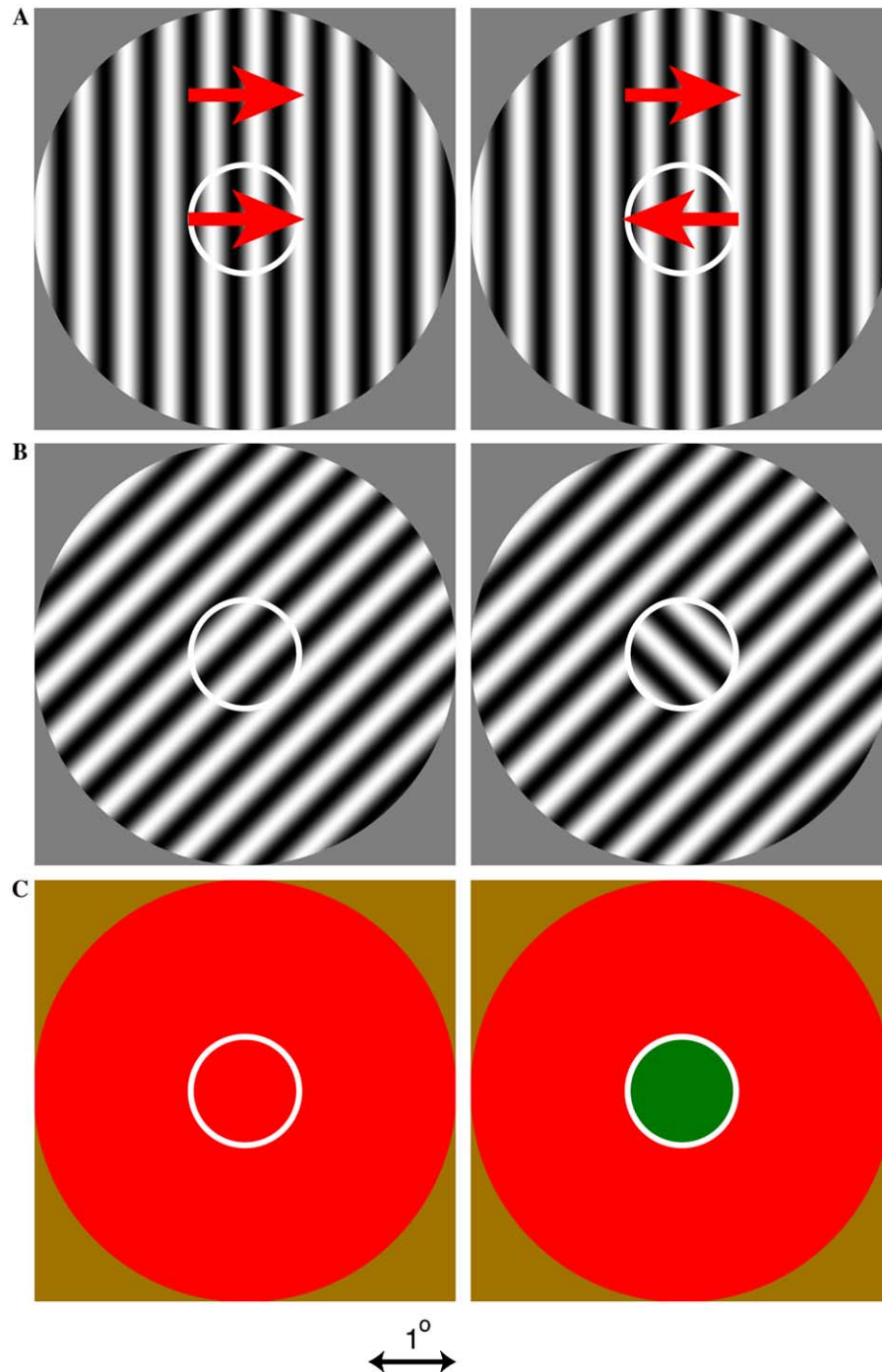


Fig. 1. Examples of the stimuli used in Experiment 1. (A) Rival targets moving horizontally in opposite directions were surrounded by annuli containing gratings moving in the same direction as one of the targets. (B) Rival targets differing in orientation were surrounded by annuli containing gratings with the same orientation as one of the targets. (C) Red and green rival targets were surrounded by annuli containing the same color as one of the two targets.

by changes in the surrounding visual context (Alais & Blake, 1998; Carter, Campbell, Liu, & Wallis, 2004; Fukuda & Blake, 1992; Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004; Sobel & Blake, 2002), in a manner that is generally in accord with known neurophysiology of contextual modulations. For example, several studies found that binocularly presented sur-

round can modulate rivalry dynamics of center rival targets (Carter et al., 2004; Fukuda & Blake, 1992; Paffen et al., 2004). We capitalize on this contextual susceptibility of binocular rivalry in our effort to investigate adaptive center-surround interactions in three key attributes in human vision. Thus, by measuring changes in binocular rivalry when the surrounding stimulus was present,

we seek to reveal the nature of center-surround interactions for different visual stimuli. Moreover, the use of binocular rivalry as an investigational tool allows us to employ equivalent experimental designs in different visual sub-modalities.

2. Method

Stimuli (Fig. 1) were generated in MATLAB using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). All rival targets were 1.2° in diameter. Surround annuli were presented binocularly and were 1.7° wide. A 0.1° gap separated center and surround. With the exception of the low-contrast color condition, the background was iso-luminant to the mean luminance of targets and surrounds. Mean luminance was 29 cd/m^2 for the motion experiment and 33 cd/m^2 for the orientation and color experiments. For the low-contrast color condition, the background was uniform black, to prevent color induction in the surround.

Motion stimuli (Fig. 1A) were horizontally drifting sinusoidal gratings (spatial frequency = $2.0 \text{ cycles/}^\circ$, temporal frequency = 2.5 Hz). Contrast was either 100% or 1.5% (Michelson). Center rival targets contained motion in opposite directions and the binocularly presented surround contained motion in the same direction as one of the targets. Oriented stimuli (Fig. 1B) had a spatial frequency of $2.0 \text{ cycles/}^\circ$ and were slowly counterphasing (1 Hz) to prevent Troxler fading (Troxler, 1804). Contrast was either 100% or 1.7%. Center rival targets had orthogonal orientations (-45° and 45° from vertical). Surround orientation matched one of the rival targets. Chromatic targets and surrounds were red and green patches presented at perceptual iso-luminance (Fig. 1C). Iso-luminance was achieved by running a flicker-matching procedure at 12.5 Hz before each session. Center and surround were presented either at high color contrast (36% Michelson in xy color space (Vos, 1978)), or at low color contrast (2%). At high color contrast, the surrounds had the same chromaticity as one of the two targets. For low contrast conditions of all experiments, we checked whether observers were able to discriminate between the two rival targets by running several discrimination-threshold staircases. Discrimination thresholds of all observers were well below the contrast values used in the rivalry experiments.

Rival targets were presented dichoptically using a mirror stereoscope. Viewing distance was 95 cm for motion conditions and 72 cm for all other conditions. Left- and right-eye stimuli were surrounded by high-contrast guides to promote binocular fusion. Moving and oriented stimuli were presented for 45 s, color stimuli for 30 s. During that time, observers continuously indicated their dominant percept by pressing one of two keys. Six main conditions (3 visual modalities at 2 contrasts) were run

in separate blocks. For each main condition, all possible combinations of center features, surround features and eye presentation were investigated in random order, yielding 16 sub-conditions per observer. Five observers performed in the motion part of the experiment, four in orientation and color parts. In all conditions, three observers were naïve to the purpose of the study.

3. Results

For high-contrast moving rival targets and surrounds (Fig. 2A), predominance of the same direction rival target was greatly reduced. For low contrast targets and surrounds (Fig. 2A, right column), however, the opposite result was observed: the same direction target was predominant most of the time. Examination of predominance percentages (Fig. 2A) reveals that reducing stimulus contrast (while keeping other parameters constant) results in a remarkable 6-fold increase in predominance of the surround-matched target. For stimuli defined by orientation (Fig. 2B), the same orientation rival target was mostly suppressed at high contrast, but exhibited increased predominance at low contrast. In accord with motion and orientation findings, at high color contrast (Fig. 2C), predominance of the target matched to the surround was strongly reduced. When color contrast was reduced, there were no significant biases in predominance (Wilcoxon Signed Ranks test: $T = 777$, $n = 64$, $p = 0.08$). Note that although color results did not “flip” as observed for motion and orientation, the direction of effect was same in all conditions.

The results from the first experiment imply that the presence of high-contrast surrounds reduces the “strength” of the target matching the surround. To test this hypothesis, we performed an experiment in which we varied the contrast of the target *not* matching the defining feature of the surround. If a high contrast surround lowers the strength of a central target with the *same* defining feature as the surround, lowering the strength of the target with the *contrasting* feature (by lowering its contrast) should reduce predominance of the contrasting target. CP and a naïve observer participated in an experiment in which motion and orientation stimuli were used similar to those of the first experiment, except that the contrasting target was presented either at 100%, 50% or 25% luminance contrast.

Predominance of the target matching the defining feature of the surround increased with decreasing luminance contrast of the contrasting target (Fig. 3). In addition, predominance increase was larger for oriented targets than for moving targets. Note that predominance of the same direction motion target is about 30 at 25% contrast of the opposite direction target, whereas predominance of the same orientation target is about 50% at the same contrast level. Thus, in contrast to a

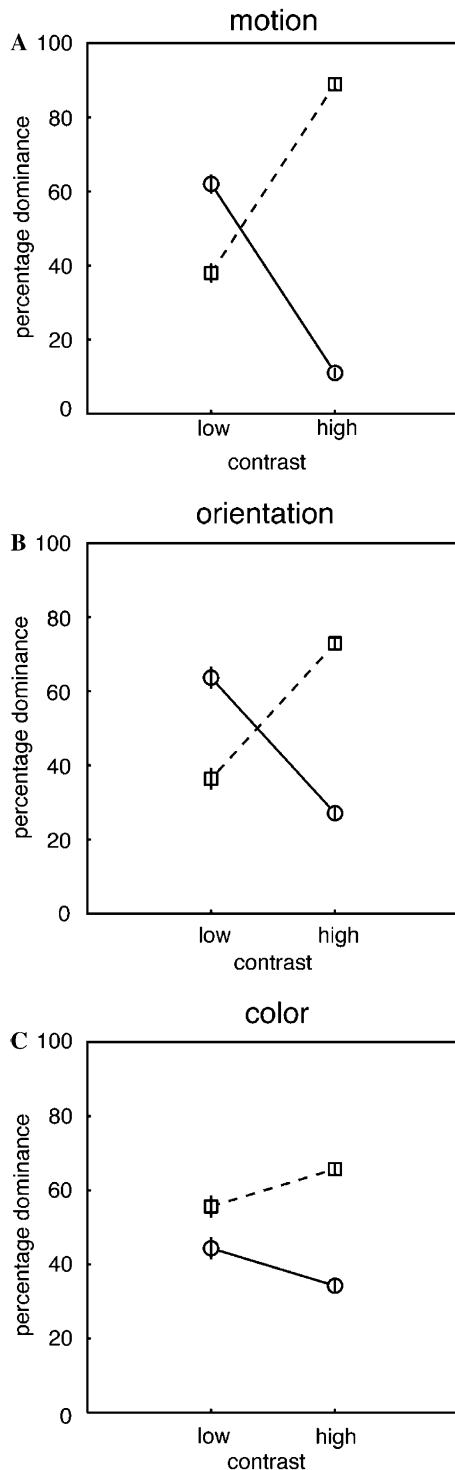


Fig. 2. Results of Experiment 1. Average percentage predominance as a function of contrast is shown for rival targets defined by (A) motion direction, (B) grating orientation, and (C) color. Solid lines and circles show cumulative dominance for the target sharing its defining feature with the surround. Dashed lines and squares show the data for the target with the contrasting feature. Error bars are standard errors of the mean.

same orientation target, surround inhibition of a same direction motion target is still quite strong at 25% luminance contrast, suggesting that surround influence

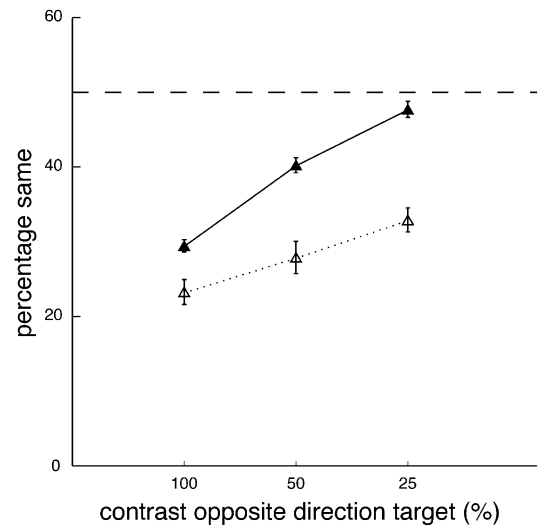


Fig. 3. Results of Experiment 2. Average percentage predominance of the target sharing its defining feature with the surround across several contrasts of the contrasting target. Solid lines and filled triangles represent predominance for orientation targets, dotted lines and open triangles data for motion targets. The dashed line represents the level at which predominance of the rival targets is in balance. Error bars are standard errors of the mean.

is stronger and more resistant for moving targets (also compare motion and orientation conditions of Fig. 2). This observation may stem from the faster contrast saturation of the motion system (Sclar, Maunsell, & Lennie, 1990) and/or the fact that the orientation of the moving rival targets matched the surround orientation (Fig. 1A).

In fact, the surround modulation for motion targets might in part be induced by the iso-oriented surround. To isolate surround interactions solely induced by a moving surround, we conducted an experiment in which rival targets and surrounds were random-pixel arrays¹, which are broadband in terms of orientations present. Two naïve observers and one author (CP) participated in this experiment. Again, the dominance of the target moving in the same direction as the surround was greatly reduced at high contrast (100% Michelson), and boosted at low contrast (3% Michelson) (Fig. 4). The magnitude of the high-contrast effect is less than for the grating motion (Fig. 4 vs. Fig. 2A), which may be due to the iso-oriented surround present in the moving grating stimuli. Interestingly, the influence of the moving random-pixel surround is still stronger than that observed with the static iso-oriented surround (Fig. 4 vs. Fig. 2B).

¹ The size of the rival targets and the surround was same as in Fig. 1. Random-pixel array consisted of densely packed individual pixels ($0.04^\circ \times 0.04^\circ$, dark or light with equal probability) and moved with the same speed as the gratings in Fig. 1A (1.25°/s).

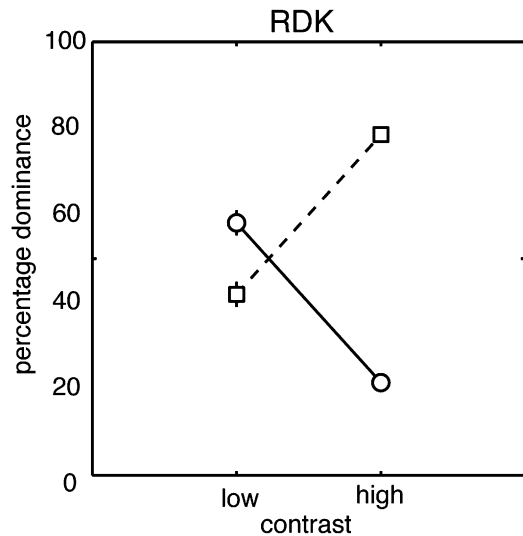


Fig. 4. Results of Experiment 3. Average percentage predominance of random pixel motion as a function of contrast. Solid lines and circles show cumulative dominance for the same direction motion, Dashed lines and squares show the data for opposite direction motion.

4. Discussion

We show that when rival targets are of high contrast, a target matching the surround in the relevant visual attribute is effectively weaker than a target that differs from its surround. In principle, this result could arise from surround facilitation of the target differing from the surround or from surround suppression of the target matching the surround. From the rivalry data alone, we cannot distinguish between these two possibilities as both predict similar changes in predominance. Neurophysiological investigations, however, primarily report strong and widespread suppressive interactions in motion (Born et al., 2000; Born & Tootell, 1992; Tanaka et al., 1986), orientation (Jones, Wang, & Sillito, 2002) and color processing (Solomon, Peirce, & Lennie, 2004). True facilitation (response above the response to the optimal center stimulus alone), however, occurs only in a portion of neurons (Jones, Grieve, Wang, & Sillito, 2001; Jones et al., 2002; Series, Lorenceau, & Fregnac, 2003; Tanaka et al., 1986). Moreover, we have previously shown that surround suppression has pronounced effects on motion perception (Tadin et al., 2003). In addition, we have observed that the effects reported here are reduced if the center and surround gratings in the “same” condition are out of phase (data not shown)—a manipulation that does not change the relationship between the center and the surround in the “opposite” condition. Thus, we are inclined to believe that center-surround interactions in binocular rivalry reported here likely arise from suppressive interactions. Such suppressive interactions may decrease neural response to the target

matching the surround and presumably shift predominance balance in favor of the target differing from the surround.

On the other hand, when rival targets were of low contrast, predominance of the target matched to the surround increased. This contrast-dependent change of rivalry dynamics is consistent with recent work demonstrating that surround inhibition weakens or even changes to spatial summation as the stimulus visibility decreases (Pack et al., 2005; Sceniak et al., 1999; Tadin et al., 2003). Thus, contrast-dependent changes in center-surround interactions at the single neuron level are in accord with the contrast-dependent changes in binocular rivalry reported here. The absence of a boost in dominance for low-contrast color might be due to the fact that the contrast used was relatively high (2% in xy -color space, compared to 1.5% and 1.7% for motion and orientation respectively). However, at lower color contrast, observers were not able to track rivalry alternations.

In addition to demonstrating center-surround interactions, our results add to the evidence pointing to potent contextual modulation of binocular rivalry predominance. Among those sources of evidence are several earlier studies (Alais & Blake, 1998; Carter et al., 2004; Fukuda & Blake, 1992; Paffen et al., 2004; Sobel & Blake, 2002) showing that the global configuration in which a rival target is embedded can influence predominance of that target. None of those earlier studies, however, were conducted in ways that would have revealed the contrast-dependent complexities of the surround effects highlighted in the present study.

The contrast-dependent center-surround interactions modulating binocular rivalry are likely a general property of visual processing, as suggested by our observations in motion, orientation and color processing. Our results are not specific to binocular rivalry, for analogous results are seen in motion perception as indexed by duration thresholds and the motion after-effect strength (Tadin et al., 2003). Such flexible, stimulus-driven processing is clearly adaptive, because computationally powerful surround inhibition is only useful when neural signals are strong enough to withstand suppression. When signals are weak, however, it makes sense to boost those signals by summing interactions. We speculate that these adaptive surround interactions equip the visual system with a powerful tool to process visual information under a variety of visibility conditions.

Acknowledgments

Supported by EY13358 to R.B. and grants from the Netherlands Organization for Scientific Research (NWO). We thank Joseph Lappin for helpful discussions.

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