Contextual modulations of center-surround interactions in motion revealed with the motion aftereffect

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Segregation of objects from their backgrounds is one of vision’s most important tasks and one that is accomplished with ease. It is often hypothesized that suppressive center-surround receptive field interactions represent a key neural substrate underlying efficient figure–ground segregation, yet this intuitively appealing hypothesis has received very little experimental support. Using the motion aftereffect as an experimental tool, we explored this hypothesis by examining how surround suppression was affected by contextual manipulations that altered the perceived figure–ground relations but kept local motion signals unchanged. The results demonstrated that surround suppression was strong when the visual context implied a large moving field. On the other hand, when the contextual interpretation was consistent with a smaller moving object, surround suppression was greatly reduced. These findings are consistent with the notion that center-surround interactions play a role in segregating moving objects from backgrounds.

Keywords: motion-2D, perceptual organization, depth, receptive fields


Introduction

For objects to be processed and perceived as separate visual entities, the visual system must segregate objects from one another and from their backgrounds. This essential step in visual processing, termed figure–ground segregation, was first systematically investigated by Rubin (1915) and, shortly thereafter, by the Gestalt psychologists (e.g., Koffka, 1935) who identified important figure–ground grouping principles such as proximity, good continuation, and common fate. A particularly rich source of information for figure–ground segregation is visual motion (Regan, 2000). Indeed, human vision is remarkably good at detecting relative motion and at segregating moving objects from their backgrounds (e.g., Braddick, 1993; Lappin, Donnelly, & Kojima, 2001; Nawrot, Shannon, & Rizzo, 1996; Regan, 1989). Several decades ago Nakayama and Loomis (1974) suggested that motion-based figure–ground segregation could be supported by neurons with center-surround receptive fields.

A large fraction of the neurons selectively responsive to visual motion, indeed, have a center-surround receptive field organization, which is typically characterized by suppression of neural responses to large stimuli (Tadin & Lappin, 2005a). Center-surround interactions are especially prominent in cortical area MT (Allman, Miezin, & McGuinness, 1985a; Born & Tootell, 1992), a brain region intimately involved in motion processing (Born & Bradley, 2005; Salzman, Britten, & Newsome, 1990). A typical center-surround neuron responds strongly when its receptive field center is stimulated with motion in its preferred direction (Allman et al., 1985a; Born & Tootell, 1992; Cao & Schiller, 2003; Jones, Grieve, Wang, & Sillito, 2001). However, when the spatial extent of stimulation is enlarged to include the surround region of the receptive field, the neuron’s response is suppressed. Moreover, some center-surround neurons are facilitated when the preferred stimulation of the receptive field center is combined with anti-preferred motion in the surround (Allman et al., 1985a; Tanaka et al., 1986). Thus, center-surround neurons respond well to small moving stimuli...
but are suppressed when stimulated by wide-field, uniform motion. This response property has led to the hypothesis that center-surround interactions are directly involved in the segmentation of moving figures from their backgrounds (Allman et al., 1985a; Born & Tootell, 1992; Cao & Schiller, 2003; Gautama & Van Hulle, 2001; Nakayama & Loomis, 1974). This hypothesis suggests that center-surround suppression might occur because vision tends to suppress motion signals arising from background motion and enhance signals that likely correspond to object motion.

Psychophysically, we and others have provided evidence for center-surround suppression from experiments involving motion direction discrimination (Betts, Taylor, Sekuler, & Bennett, 2005; Tadin & Lappin, 2005b; Tadin, Lappin, Gilroy, & Blake, 2003), motion aftereffect (MAE: Falkenberg & Bex, 2007; Tadin et al., 2003), reverse correlation (Tadin, Lappin, & Blake, 2006b), and binocular rivalry (Paffen, Tadin, te Pas, Blake, & Verstraten, 2006; Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004). Behaviorally, center-surround suppression is evident as the reduced ability to discriminate motion direction of a large moving stimulus—a result likely due to the decreased neural activity of center-surround neurons responding to a large moving stimulus. While the exact nature of the link between these findings and the physiology of center-surround receptive fields is still unclear, behavioral and neurophysiological findings share several important characteristics. Specifically, both exhibit inhibition associated with large moving stimuli, are characterised by the release of inhibition at low contrast, and show similar dependency on the stimulus size (Pack, Hunter, & Born, 2005; Paffen, van der Smagt, te Pas, & Verstraten, 2005; Tadin et al., 2003)—suggesting that psychophysically observed surround suppression in motion might be, in part, a perceptual correlate of neural center-surround mechanisms.

In the present study, we used the MAE as a psychophysical index of center-surround suppression. The magnitude of the MAE generally increases with the strength of the adapting motion stimulus, where the stimulus strength is typically manipulated using contrast or motion coherence (Alais & Blake, 1999; Keck, Palella, & Pantle, 1976; Nishida, Ashida, & Sato, 1997). When considered along with the abundant evidence showing that neural responsiveness grows with stimulus contrast and with motion coherence (Rees, Friston, & Koch, 2000; Sclar, Maunsell, & Lennie, 1990), this relates the MAE strength with the strength of the associated neural response. Thus, if center-surround suppression weakens neural responses within neurons that reside at or before the locus of neural adaptation underlying the MAE, then strong center-surround suppression should yield a weaker MAE. Here the MAE serves as the “psychologist’s microelectrode” (Frisby, 1979) by presumably revealing the response properties of neural mechanisms activated by adapting stimuli and providing an effective proxy for center-surround interactions (Falkenberg & Bex, 2007; Murakami & Shimojo, 1995; Sachtler & Zaidi, 1993; Tadin et al., 2003). Moreover, the use of the MAE is advantageous because having control over the position and the size of the test stimulus allowed us to restrict psychophysical measurements to a small retinotopic region of interest.

We used the MAE to test the hypothesis suggesting that surround suppression occurs because motion signals arising from backgrounds are suppressed and those likely corresponding to object motion are enhanced. We explored this conjecture by examining how surround suppression is affected by contextual manipulations that altered the perceived figure–ground relations but kept local motion signals unchanged. To manipulate the surrounding context and, consequently, the perceptual appearance of the center stimulus, we employed occlusion and stereoscopic depth-ordering manipulations—two potent cues that define visual context and thus modulate figure–ground relationships (Albright & Stoner, 2002).

The specific hypothesis is that if a contextual manipulation causes a small stimulus to be perceived as a part of a large moving field, then this otherwise small stimulus should be accompanied with strong surround suppression. On the other hand, surround suppression should diminish when that stimulus is perceived as an independent moving object, even when physical differences between the two stimuli are minimal.

### General methods

All stimulus patterns were created in MATLAB with the Psychophysics (Brainard, 1997) and Video (Pelli, 1997) Toolbox routines. All procedures complied with institutionally reviewed guidelines for human subjects. In the experiments using disparity manipulations (Figures 1 and 3), stimuli were shown on a linearized monitor (1024 × 768 resolution, 60 Hz). Viewing was binocular through a stereoscope at 95 cm (yielding 1.35 × 1.35 arcm per pixel). The field of view of the stereoscope was about 9° in diameter. Ambient illumination was 0.01 cd/m². Background luminance was 30.0 cd/m². In the remaining experiment (Figure 2), stimuli were shown on a linearized monitor (800 × 600 resolution, 120 Hz). Viewing was binocular at 83 cm (yielding 2 × 2 arcm per pixel). Ambient illumination was 4.8 cd/m². Background luminance was 60.5 cd/m². In all experiments, observers were instructed to fixate the center of the display.

In the following three experiments, we measured the strength of surround suppression associated with a small, foveally viewed moving stimulus. The physical characteristics of this center stimulus did not change, but its perceptual appearance differed depending on experimental manipulations of the surrounding stimulus. In some conditions, the center stimulus was perceived as a separate moving object, while in other conditions the center
stimulus was perceived to move together with the surrounding area, appearing as a part of a larger moving field. The aim of these experimental manipulations was to alter whether the center stimulus region appeared as a figure or as a part of the background and to determine whether those manipulations affected the strength of surround suppression, as indexed by the strength of the MAE measured in the center region. All of the statistical analyses were preformed on the pooled subject data. In all experiments, all significant group effects were also significant for each subject, except for one observer in Experiment 3 (comparison between “occluder behind” and “occluder in front” conditions).

The stimulus sizes were selected so that the size of small adapting stimuli \( r = 0.88 \) and \( r = 1.25 \) is similar to the average receptive field size in foveal MT. Foveal receptive size estimates for macaque MT range from radius of 0.6° (Albright & Desimone, 1987) to radius of 2.6° (Raiguel, Van Hulle, Xiao, Marcar, & Orban, 1995). The large adapting stimuli \( r = 4 \) and \( r = 7.5 \) should stimulate the surrounds of most foveal center-surround neurons in MT. Of course, this link assumes that the properties of human and macaque MT are comparable (Rees et al., 2000) and that the receptive field sizes are similar for two species (Kastner et al., 2001). The stimulus sizes in this study are also consistent with the psychophysical measurements of critical stimulus sizes required to yield strong surround suppression (Tadin et al., 2003).

### Experiment 1

#### Methods

In the first experiment (Figure 1), adapting stimuli were moving random-texture patterns. The size of each texture element was 5.4 × 5.4 arcmin, speed was 3.17°/s, and Michelson contrast was 99.9%. Three observers participated in the experiment (one naive). High contrast “fusers” were present in all conditions to promote accurate binocular alignment and to provide a reference frame for stereoscopic depth. Four different adapting conditions were used, with two critical conditions illustrated in Figure 1A. The small (radius = 1.25°) and large (radius = 4°) random-texture disks were used in adapting conditions to yield experimental baselines. The size of the large stimuli was limited by the ~10° viewing area of our stereoscope. In the “surround in front” condition, the adapting stimulus consisted of a center and a surround region, both moving in the same direction. The center region was identical to the small adapting pattern condition (i.e., diameter = 2.5°) and was presented at zero disparity. The surround region was 2.75° wide and encircled the center region. The critical manipulation was that the surround was presented at crossed disparity of 5.4 arcmin, thus appearing closer to the observer. The “surround behind” condition was identical to the “surround in front” condition except that the surround was presented at uncrossed disparity (5.4 arcmin), thus appearing farther from the observer. Note that the central region (i.e., the region where the MAE was measured) was identical in all four conditions.

It is important to note that the perceived spatial extent of the center stimulus was similar in the two critical conditions. That is, in the “surround in front” condition,

![Figure 1](http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933536/)
no amodal completion was reported—the center region did not appear a part of a large moving field viewed through an aperture defined by the surround. Instead, the center region was perceived as a small moving stimulus, possibly because surround was not stationary, but moving at the same speed as the center stimulus.

The initial period of adaptation lasted 40 s (8 s “top-off” adaptation after the first trial), followed by a 0.3-s blank screen and a 1-s test stimulus. The test stimulus was a partially correlated random-texture pattern, where a portion of the texture elements was moving in the opposite direction from the adapting pattern while the remaining elements were randomly regenerated. The test stimulus radius was 1.13° (slightly smaller then the small adapting pattern) to minimize the effects of fixational eye movements (cf. Murakami & Shimojo, 1995). After viewing the test stimulus, observers indicated the perceived direction of the test stimulus. The motion correlation of the test stimulus was then adjusted under the control of two interleaved “one-up—one-down” staircases until the test stimulus appeared to have no net, global direction of motion, with the motion of the elements being incoherent (Blake & Hiris, 1993). The motion correlation required for MAE nulling was taken as a measure of the MAE strength (higher correlation indicates the stronger MAE). For each condition, four experimental runs were conducted; two with rightward moving and two with leftward moving adapting patterns. This yielded eight MAE strength measurements for each condition.

Results

In all conditions, the MAE direction was opposite to the adapting motion. The results (Figure 1B) show that contextual modulations affected the strength of the MAE evoked by the fixed center stimulus ($F(3,92) = 12.9$, $p < 0.001$). Based on the previous results (Falkenberg & Bex, 2007; Tadin et al., 2003), we expected that the MAE measured at the location of the small stimulus should decrease as the size of the adapting stimulus increased. Indeed, adapting to the small moving pattern resulted in a stronger MAE than adapting to the large moving pattern ($t(46) = 5.99$, $p < 0.001$). Moreover, when the surround was presented stereoscopically at a different depth plane (either in front or behind the center), an intermediate MAE was measured, indicating that surround suppression is weakened when the center and surround motions appear at different depths ($t(46) = 3.02, 3.00, p < 0.005$, i.e., are presented at different disparities). In these critical conditions, the stimulus area is identical to the large adapting pattern but the resulting MAE is significantly stronger. The center region in these displays, however, is perceived as a separate, smaller moving object, which evidently reduced surround suppression. Moreover, this result is consistent with neurophysiological observations demonstrating that center-surround antagonism in MT is reduced when the surround is presented at a different disparity from the center stimulus (Bradley & Andersen, 1998).

In the next two experiments, we tested whether similar modulations in the suppressive effects of the surround generalize to displays where the entire adapting stimulus is presented at zero disparity and perceived stimulus size is manipulated using occlusion cues.

### Experiment 2

**Methods**

In the second experiment (Figure 2), adapting stimuli were moving gratings. Spatial frequency and velocity were $1 \text{ cycle/}°$ and $4°$/s, respectively. Michelson contrast was 26%. Three observers participated in the experiment (two naive). Four different adapting conditions were investigated. As in the previous experiment, the central adapting region was identical in all four conditions. The small adapting stimulus was a drifting grating presented in a disk with a radius of 0.88°. The big adapting stimulus was a drifting grating presented in a spatial envelope that consisted of a uniform disk surrounded by a gradually fading border (i.e., with a spatial contrast gradient equal to a half cycle of a raised cosine). The radius of the uniform disk section was 5° and the width of the fading border was 2.5°, resulting in a 7.5° stimulus radius. In the “cut” adapting condition, the stimulus was the same as the big adapting grating except that the stimulus was “cut” as shown in the Figure 2A. The width of the cut sections was 2°. The central grating patch was identical to the small adapting pattern (radius = 0.88°). The stimulus in the “occluded” condition was the same as the “cut” adapting pattern except that the cut sections were filled with a static random-texture pattern (each texture element was $2 \times 2$ arcmin).

The “cut” and “occluded” conditions were compared because the area covered by the moving grating was identical in two conditions, but the extent of the perceived motion differed. In the “cut” condition, observers typically perceived a small central grating moving separately from the surrounding grating patches. In the other critical condition, the large adapting grating was cut in the same way, but now the cut sections were filled with an opaque texture. In this “occluded” condition, the center section is now generally perceived as part of a large grating drifting behind the occluder. This occlusion manipulation is analogous to the well-known Bregman’s letter B demonstration (Bregman, 1981) where the occluded letters are perceived as unrecognizable fragments if the opaque occluder was not visible. The described percepts correspond to what observers perceived about 90% of the time (subjective report). For example, observers reported occasionally perceiving the “cut” stimulus as a large grating.
drifting behind the occluder. Such instances, however, were infrequent and brief.

The test stimulus consisted of two overlapping gratings drifting in opposite directions (i.e., a counterphase flickering grating). The test stimulus parameters were the same as the adapting gratings except for the stimulus radius, which was fixed to 0.79°, and thus was slightly smaller than the small adapting pattern. When the contrasts of two overlapping test gratings are identical, the motion is ambiguous and the test stimulus appears to flicker. Adapting to a motion in one direction effectively decreases motion strength of the grating moving in the adapted direction (von Grünau & Dubé, 1992). As a result, the test stimulus will appear to move in the opposite direction. To restore the perception of counterphase flicker during the experiment, the contrast of the grating moving in the adapted direction was increased, and the contrast of the other grating was decreased. The contrast ratio required to restore flicker perception provided the measure of the MAE strength (higher contrast ratio indicates the stronger MAE).

The initial period of adaptation lasted 30 s (10 s “top-off” adaptation after the first trial), followed by a 0.3-s blank screen and a 1-s test stimulus. After viewing the test stimulus, observers indicated the perceived direction. The contrast ratio of two gratings composing the test stimulus was adjusted under the control of two interleaved “one-up–one-down” staircases. Each staircase was terminated after 6 reversals, with the average of last 4 reversals taken as the MAE strength. Staircase step size was 0.05 log units before the second reversal and 0.025 log units after the second reversal. For each condition, four experimental runs were conducted; two with rightward moving and two with leftward moving adapting patterns. This yielded eight MAE strength measurements for each condition.

Results

Contextual manipulations of the adapting stimulus affected the strength of the MAE evoked by the fixed center stimulus (Figure 2B, $F(3,92) = 4.70, p < 0.005$). The MAE direction was always opposite to the adapting motion. As in the first experiment, the resulting MAE was substantially stronger when the adapting pattern was smaller compared to when the adapting pattern was large ($t(46) = 3.41, p < 0.005$), a result indicating surround suppression. Of significance, the MAE strength for the “cut” and “occluded” conditions differed even though the size of the moving pattern in those conditions did not, with “cut” stimulus yielding a stronger MAE ($t(46) = 1.68, p < 0.05$). Moreover, the MAE for the “cut” condition did not differ from the MAE for the small adapting pattern ($t(46) = 0.30, p = 0.78$). This result is in accord with the observers’ perception of the “cut” pattern, which typically was perceived as a small moving object surrounded by four moving segments. The MAE in the “occluded” condition was weaker, approaching the MAE for the big adapting pattern. This result again corresponded with observers’ subjective descriptions of the display, with the occluded stimulus perceived as a large moving grating moving behind the occluder. These findings show that the strength of surround suppression is not determined solely by the spatial extent of the stimulus pattern. Surround suppression, as measured by the MAE, also depends on whether the moving pattern is perceived as a large object or as disconnected small objects. Specifically, surround
suppression occurs when a large moving stimulus is perceived, but not when the “same” stimulus is perceived as multiple moving fragments.

**Experiment 3**

In the second experiment, we used implied occlusion to manipulate observers’ perception of a drifting pattern. Actual occlusion, of course, entails the presence of a visible, opaque surface situated between the observer and the occluded object, whereas in the previous experiment only the “occluded” condition, not the “cut” condition, contained a large, visible random-texture pattern. To more closely mimic the ecologically natural conditions of occlusion, we performed another experiment that employed stereoscopic occlusion; this manipulation minimizes physical stimulation differences between the conditions being compared.

**Methods**

In the final experiment (Figure 3), adapting stimuli were moving gratings. Spatial frequency and velocity were 1 cycle/° and 4°/s, respectively. Michelson contrast was 99.9%. Three observers participated in the experiment (two naive). Four different adapting conditions were used, with two critical conditions (illustrated in Figure 3A). High contrast “fusers” shown in Figure 3 were present in all conditions. Again, note that the central region (where the MAE was measured) was identical in four conditions. The small (radius = 0.88°) and large (radius = 4°) drifting gratings used to yield experimental baselines. Both stimuli were presented at zero disparity. In the “occluder behind” adapting condition, the stimulus was the same as the big adapting grating except that an occluder with the same luminance as the background was stereoscopically placed at the uncrossed disparity (5.4 arcmin) as shown in Figure 3A. The width of the occluder sections was 2°. The central grating patch was identical to the small adapting pattern (radius = 0.88°). The stimulus in the “occluder in front” condition was the same as in the “occluder behind” condition except that the grating was stereoscopically placed at crossed disparity (5.4 arcmin). These two critical conditions were compared because the area covered by the moving grating was identical in two conditions, but the extent of the perceived motion differed. In the “occluder behind” condition, observers typically perceived a small central grating moving separately from the surrounding grating patches. In the “occluder in front” condition, however, observers generally perceived a large moving grating behind an occluder.

The MAE was measured using the counterphase flicker test and adjustment procedure identical to that described for the previous experiment. The test stimulus was slightly smaller than the small adapting pattern (radius = 0.79°) to minimize possible effects of small, unintentional eye movements during fixation.

**Results**

The results (Figure 3B) show that stereoscopic occlusion manipulations affected the strength of the MAE evoked by the center stimulus ($F(3,93) = 9.27, p < 0.001$). Once again, the small adapting pattern yielded a larger MAE than the large adapting pattern ($t(46) = 5.21$, Figure 3. Effects of stereo occlusion and stimulus size on the strength of surround suppression. (A) Single-frame snapshots of the left- and right-eye stimuli in two critical adapting conditions. These illustrations are made for cross-fusing. Top and bottom panels illustrate “occluder in front” and “occluder behind” conditions, respectively. Scale bar is 2°. In separate adapting runs, the grating pattern drifted either leftward or rightward. The borders of the grating patterns were always stationary. (B) Effects of stereo occlusion and stimulus size on the MAE strength for three observers. The MAE strength for the big stimulus condition ranged from 1.11 to 1.53. To average the data, the results from individual observers were normalized relative to the threshold for the big condition and then averaged. Error bars are SEM.
p < 0.001). Moreover, “occluder behind” condition yielded a larger MAE than the “occluder in front” condition ($t(46) = 2.33, p = 0.01$)—a result analogous to the outcome of the previous experiment. The MAE for the “occluder behind” condition was similar to the MAE induced by the small adapting pattern ($t(46) = 0.38, p = 0.71$). In contrast, the MAE for the “occluder in front” condition was substantially smaller ($t(46) = 3.23, p < 0.005$). This result matched observers’ perception of the “occluder in front” stimulus, which was perceived as a large stimulus drifting behind an occluder.

**Discussion**

In three experiments, we found that contextual manipulations of a surround stimulus had strong effects on the MAE induced by an unchanging center stimulus. Moreover, the MAE was strongly affected even though critical experimental manipulations did not involve changes in surround motion signals but rather changes in occlusion and stereo cues. The common finding from all three experiments is that if a visual context implies that the center stimulus is a part of a large moving stimulus, the resulting MAE was weak—a result implying strong surround suppression (Falkenberg & Bex, 2007; Tadin et al., 2003). On the other hand, if the visual context implies that the center stimulus is an object separate from the surrounding moving stimulus, the resulting MAE was strong—a result implying a lack of strong surround suppression. Overall, these findings show that center-surround suppression is modulated by contextual interactions that affect the perceived figure–ground relationships. The modulations reported here only affected the MAE magnitude: the MAE direction was always in the opposite direction from the adapting stimulus.

**Center-surround suppression and figure–ground discrimination**

One of the fundamental requirements for successful visual perception is segregation of objects from their backgrounds. Vision seemingly accomplishes this inherently difficult task with ease, especially if object motion differs from the background (Regan, 2000). Early theoretical work (Nakayama & Loomis, 1974) linked center-surround interactions and motion-based figure–ground discrimination. A defining property of antagonistic center-surround interactions is a better response to a small stimulus differing from its background than to a large uniform visual stimulus. Because of this defining property of surround suppression, neurophysiological explorations of center-surround interactions often postulate figure–ground discrimination as a likely functional role of surround suppression (e.g., Allman et al., 1985a; Allman, Miezin, & McGuinness, 1985b; Born & Tootell, 1992; Jones et al., 2001; Lamme, Supér, & Spekreijse, 1998).

Direct behavioral support for this hypothesis has been lacking. Arguably, the best existing link comes from MT recordings by Born, Groh, Zhao, and Lukasewycz (2000). Using a classic step-ramp task, Born et al. showed that microstimulation of antagonistic center-surround neurons just before a monkey made a saccade to a moving peripheral target caused a shift in the ensuing pursuit eye movements in the preferred direction of the stimulated cluster of neurons. This result is consistent with the well-established role of MT neurons in signaling motion direction and confirms that the pursuit velocity just after a saccade reflects motion processing just before the saccade. In addition to antagonistic center-surround neurons, MT also contains wide-field neurons that lack suppressive surrounds and prefer large moving stimuli (Born & Tootell, 1992). However, stimulation of wide-field neurons just before the monkey made a saccade to a moving peripheral target shifted post-saccadic pursuit in the anti-preferred direction. The analogous result was obtained when the microstimulation was replaced with a large moving background stimulus. This observation suggests that the activation of wide-field neurons signals background motion and indicates distinct functional roles of center-surround and wide-field neurons. Thus, using eye movements as an index of motion perception, the Born et al. study points to the involvement of center-surround receptive field interactions in the segmentation of object motion from the background motion.

Correlational evidence for a functional link between center-surround suppression and figure–ground discrimination comes from special population studies. Here the prediction is that abnormal weakening of surround suppression should be associated with reduced ability to discriminate moving objects from their backgrounds. Indeed, elderly observers exhibit reduced center-surround antagonism (Betts et al., 2005) and show impaired discrimination on a motion-based figure–ground task (Wist, Schrauf, & Ehrenstein, 2000). Similarly, patients with schizophrenia evidence both weaker surround suppression (Tadin, Kim, et al., 2006a) and impaired figure–ground segmentation of moving objects (Schwartz, Maron, Evans, & Winstead, 1999).

Our experimental strategy was to psychophysically manipulate the extent to which a moving stimulus was perceived as a figure. We show that psychophysically changing stimulus appearance from a large uniform moving stimulus to several small objects reduces surround suppression, even when local motion signals remain unchanged. A possible interpretation of these results is that a functional role of center-surround mechanisms in motion perception is to enhance segregation of moving objects from the background. Perceptually, center-surround suppression is manifested as a reduced ability to perceive high-contrast motion as the stimulus size increases (Tadin et al., 2003).
Thus, taken at face value, surround suppression appears to hinder rather than enhance vision. Our results, however, imply that this seemingly maladaptive mechanism might have an important visual function.

Given the ubiquity of center-surround interactions in motion and in other aspects of vision, figure–ground segregation is likely just one, nonetheless important, function of center-surround interactions. For example, theoretical work suggested a possible involvement of center-surround interactions in the perception of 3D shape from motion cues (Buracas & Albright, 1996; Xiao, Raiguel, Marcar, Koenderink, & Orban, 1995).

MAE implications

The present results also show that neural mechanisms responsible for the MAE are not strictly local but are modulated by spatial visual context—a conclusion consistent with previous MAE studies (e.g., Bell, Lehmkule, & Westendorf, 1976; Day & Sterlow, 1971; Murakami & Shimojo, 1995; Sachtler & Zaidi, 1993; Wade, Spillmann, & Swanston, 1996). Most of the previous work has aimed at determining the role of relative motion in generation of the MAE: the motion after-effect is markedly reduced in the absence of patterned background (Day & Sterlow, 1971) and enhanced if the background is moving in the opposite direction from the adapted motion (Murikami & Shimojo, 1995). Here we show that the MAE can be modulated even when the surrounding local motion signals are constant and the experimental manipulation rely on non-motion cues. This means, then, that the effects of the surrounding context on the locally measured MAE are not restricted to motion or relative motion manipulations. This is consistent with a study showing that the appropriate depth-ordering of the apertures surrounding an adapting motion stimulus can bias the direction of the resulting MAE (van der Smagt & Stoner, 2002).

It is worth noting that our experiments employed two different types of dynamic test stimuli to measure the MAE, i.e., partially correlated random-texture pattern and counterphase flickering gratings. It is widely believed that both forms of test stimuli tap higher-level motion mechanisms (Culham et al., 1998) not engaged when using a stationary test figure (van de Grind, Lankheet, & Tao, 2003), as so often used in demonstrations of the waterfall effect. Thus, it is conceivable that the effects of surround suppression and context on motion adaptation might express itself differently when tested using the so-called static MAE. It is also noteworthy that surround context affected both the MAE measured with random-texture patterns and the MAE measured with flickering gratings, two types of MAE that themselves are not necessarily identical (van de Grind et al., 2003).

A possible role of attention should also be considered because of known attentional effects on the MAE strength (Alais & Blake, 1999; Rezec, Krekelberg, & Dobkins, 2004). Our experienced observers were instructed to fixate and to attend to the center of the stimulus. Nevertheless, it is conceivable that even weak spreading of attention away from the center in conditions with a large surround stimulus is sufficient to cause a substantially weaker MAE. If that indeed were the case, we would expect similar effects at low-contrast because the effects of attention on the MAE strength seems to be independent of contrast (Rezec et al., 2004). At low contrast, however, large moving stimuli actually yield stronger MAE measured in the stimulus center (Tadin et al., 2003), suggesting that possible attentional effects cannot account for the large changes in the MAE with changing stimulus size.

Interaction between stereo and motion

In two experiments, we show that stereoscopic experimental manipulations affect center-surround suppression in motion processing. The present result can be added to other findings documenting the interactions between motion perception and stereopsis (e.g., Edwards & Badcock, 2003; Nawrot & Blake, 1991; Sohn & Seiffert, 2006; Tittle & Braunstein, 1993; van Ee & Anderson, 2001; Verstraten, Verlinde, Frederiksen, & van de Grind, 1994). Evidence for this coupling of motion and stereopsis is also found in the visual cortex. For example, placing either transparent or spatially adjacent motions at different depths changes the way MT neurons respond to such stimuli (Bradley & Andersen, 1998; Bradley, Qian, & Andersen, 1995), even though the 2D motion pattern remains unchanged. Thus, it is not surprising that MT neurons are tuned for disparity, though the tuning is relatively coarse (DeAngelis & Newsome, 1999; Maunsell & Van Essen, 1983). Bradley and Andersen (1998) found, however, that disparity tuning of center and surround receptive field regions tend to differ: a neuron that is typically suppressed by a surround moving in its preferred direction becomes unsuppressed if the center and surround motions are at different stereoscopic depths. The disparity dependence of MT surround suppression indicates that MT neurons are modulated by motion fields arising from a single surface but are unaffected by the motions of other surfaces at different depths. These results paint a more general picture of surround suppression in MT. Center-surround antagonism does not blindly suppress a neuron’s response whenever the surround motion moves in the neuron’s preferred direction; instead, surround suppression tends to occur when surround and center motion seem to belong to the same surface (or background)—an observation mirroring our psychophysical findings.

Contextual modulations at low contrast

In this study, we investigated contextual modulations of center-surround interactions at high contrast. Converging
evidence, however, suggests that surround suppression gives way to spatial summation at very low contrast—increasing the size of a low contrast stimulus results in stronger neural activity in MT (Pack et al., 2005) and also in improved motion discriminations and a stronger MAE (Tadin et al., 2003). Thus, at very low contrasts, we should expect a pattern of results opposite to those presented in Figures 1 2 3: We would expect large adapting stimuli and stimuli that appear large to yield the strongest MAE. Replication of our stereo experiments at low contrast, however, is precluded by the fact that stereopsis breaks down at low contrasts (Cormack, Stevenson, & Schor, 1991)—an observation confirmed in pilot experiments. Replication of the Experiment 2 was uninformative because lowering the contrast changed the perceptual appearance of a critical condition. The interior grating edges in the “cut” condition did not appear sharp as in Figure 2A: the cut sections were not visible because they “filled in” with the surrounding grating pattern. These “visual phantoms”, especially prominent for moving stimuli (Tynan & Sekuler, 1975), essentially transformed the “cut” stimulus into a large uniform grating. In pilot explorations, we indeed found that this stimulus yields a strong MAE, similar to the MAE produced by a low-contrast, large moving grating.

Acknowledgments

This work was supported by NIH EY07760 and NIH EY015558. We thank Davis Glasser for help with manuscript preparation.

Commercial relationships: none.

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