CENTER-SURROUND INTERACTIONS IN VISUAL MOTION PROCESSING

By

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Za moga brata Gordana, majku Tonku i oca Juraja

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CHAPTER I

OVERVIEW OF THE DISSERTATION

The main goal of this dissertation is to investigate center-surround interactions in visual motion processing. To advance the understanding of center-surround interactions, I designed a series of experiments that utilized a variety of established and novel psychophysical methods. Such diverse approach was favored because of its potential to generate converging evidence about various properties of center-surround interactions.

The dissertation begins (Chapter II) with a review of psychophysical and neurophysiological characteristics of center-surround interactions in motion processing. This chapter also discusses possible functional roles of center-surround antagonism.

Following the literature review, Chapters III through VII describe the experimental results. Chapter III describes the initial set of experiments that constituted the first direct psychophysical demonstration of contrast-dependent center-surround antagonism in visual motion processing. In Chapter IV, the existence of the optimal size for perceiving motion is demonstrated and its dependency on contrast is quantified. Use of the motion after-effect (MAE) to measure surround suppression is described in Chapter V. Chapter V also documents MAE experiments suggesting that the perceived 3D surface layout modulates surround suppression. In Chapter VI, I describe a novel psychophysical adaptation of the temporal reverse correlation method and demonstrate its usefulness for investigating the temporal properties of center-surround interactions. In the final experimental chapter, I describe a potential functional implication of center-surround interactions in motion-based figure-ground discrimination.

To improve the readability of the dissertation as a whole, I attempted to decrease the redundancy between experimental chapters. Most of the general issues regarding center-surround interactions are described in Chapter II and are not repeated in the introduction sections of the experimental chapters. The introductions of experimental chapters focus solely on the background research directly relevant to the specific chapter. Some overlap remains so that the individual chapters can be understood without reading the entire dissertation. Furthermore, several chapters have been adapted from published or submitted manuscripts. This is indicated at the beginning of those chapters.

I started this line of research three years ago, inspired by neurophysiological work on center-surround interactions in the visual cortex. As this work progressed, neurophysiology continued to be a main driving force behind the experimental design. Furthermore, when interpreting the results of the experiments in this dissertation, I was often tempted to make inferences about the relevant neural mechanisms. Of course, making such conclusions from psychophysical data is often logically difficult and sometimes simply incorrect. The concluding chapter will discuss logical and practical issues regarding the link between neurophysiology and the work described in this dissertation.

CHAPTER II

CENTER-SURROUND INTERACTIONS IN VISUAL MOTION PROCESSING

Adapted from Tadin, D., & Lappin, J. S. (in press). Linking psychophysics and physiology of center-surround interactions in visual motion processing. In L. R. Harris & M. Jenkin (Eds). *On seeing spatial form*. Oxford University Press

Center-surround receptive field organization is a ubiquitous property of visual neurons (Allman, Meizin & McGuiness, 1985a). Such mechanisms are well suited for extracting information about the spatial organization of retinal images. They amplify responses to spatial differences in properties such as luminance, and suppress responses to uniform image regions. The spatial organization of image variations usually is more informative about the structure of the environment than the uniform properties of retinal images.

Given the computational demands of visual motion processing, center-surround mechanisms may play an important role in motion perception. Spatial variations in image motion carry important visual information about the relative locations, orientations, and shapes of surfaces, about the trajectories of moving objects, and about the observer's locomotion through the world (Nakayama, 1985; Braddick, 1993; Regan, 2000; Lappin & Craft, 2000). Uniform motion fields, however, are often caused by eye or body movements and, as such, can make the perception of object motion more difficult. Center-surround mechanisms are well suited for extracting information about the spatial structure of moving fields and for suppressing information about uniform motions.

Center-surround mechanisms found in MT and elsewhere

Center-surround interactions are frequently observed in the neural areas sensitive to motion (e.g., Ölveczky, Baccus & Meister, 2003; Frost & Nakayama, 1983; Kastner, Nothdruft & Pigarev, 1999; Mandl, 1985; Davidson & Bender, 1991). In the primate cortex, center-surround receptive field organization has been observed in the primary visual cortex (V1) (Jones, Grieve, Wang & Sillito, 2001), MT (Allman, Meizin & McGuiness, 1985b), and lateral MST

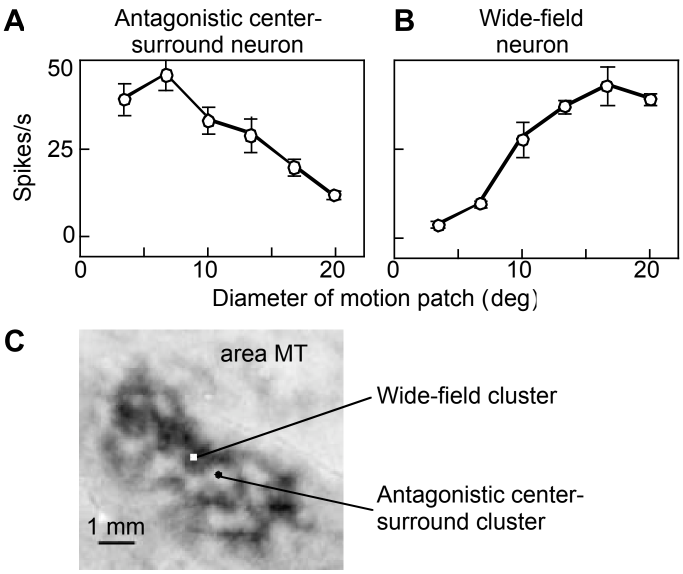

Figure 1. Responses of a typical center-surround (A) and wide-field neuron (B) to random-dot motion of increasing patch size. Patchy 2-deoxyglucose uptake in MT (C) was obtained by presenting a large pattern of random-dot motion to a macaque monkey (Born, 2000). Dark areas show clusters of wide-field neurons. Illustrations courtesy of Richard T. Born.

(Eifuku & Wurtz, 1998). Among these motion-sensitive areas, center-surround mechanisms have been described in most detail in MT (Allman et al., 1985b; Tanaka et al., 1986; Born & Tootell, 1992; Lagae, Gulyas, Raiguel & Orban, 1989; Raiguel, Van Hulle, Xiao, Marcar & Orban, 1995; Bradley & Andersen, 1998; Born, 2000; Borghuis et al., 2003). The function of these mechanisms has been studied both neurophysiologically (Xiao et al., 1995, 1997a, 1997b, 1998; Bradley & Andersen, 1998; Born, Groh, Zhao & Lukasewycz, 2000) and by computational modeling (Nakayama & Loomis, 1974; Buracas & Albright, 1996; Liu & Van Hulle, 1998; Gautama & Van Hulle, 2001). This substantial literature provides a foundation for describing probable perceptual roles of MT center-surround mechanisms.

Allman et al. (1985b) found that responses of most neurons in owl monkey MT were modulated by stimulation in the region surrounding the classical receptive field (Figure 1a). The surround regions are often described as “silent”, because stimulation of the surround alone does not affect the neuron’s response. Most of the observed interactions were antagonistic: The firing rate to motion in the preferred direction in the center region was reduced when the motion pattern was expanded into the surround region. That is, center-surround neurons responded poorly to large fields of uniform motion. If the motion in the surround was in the anti-preferred direction, its suppressive effect diminished, and for some neurons the response was facilitated.

Center-surround neurons are found in all layers of MT, but are less common in layer IV (Raiguel et al., 1995; Born, 2000), suggesting that surround inhibition is probably mediated via intrinsic MT connections. The spatial extent of the surround is usually three to five times larger than the extent of the center region (Tanaka et al., 1986; Raiguel et al., 1995) and the directional tuning of the surround is broader than that of the center (Born, 2000). Initial reports described surrounds as encircling the central region of the receptive fields (Allman et al., 1985b; Tanaka et al., 1986). Subsequent explorations, however, found that the spatial extent of most MT surrounds is non-uniform (Xiao et al., 1995, 1997a, 1997b, 1998), suggesting that such surrounds may have important computational properties.

In addition to neurons with such center-surround antagonism (sometimes called "local motion" neurons), some MT neurons prefer large moving fields and show no surround suppression ("wide-field" neurons) (Figure 1b, Allman et al., 1985b; Born & Tootell, 1992; Raiguel et al., 1995). These two types of neurons are clustered anatomically (Figure 1c; Born & Tootell, 1992) and make different efferent connections, with wide-field neurons projecting to ventral MST and center-surround neurons projecting to dorsal MST (Berezovskii & Born, 2000). These two types are also believed to have different functions, with center-surround neurons coding object motion and wide-field neurons signaling background motion (Born et al., 2000).

Currently available descriptions of center-surround interactions in primate MT have been generally consistent. The stimulus patterns used to characterize these receptive fields, however, have been almost exclusively high-contrast random-dot patterns. As we shall see, this restriction of the methods also restricts the description of these receptive fields. For example, the spatial organization of receptive fields in primate V1 has been found to vary with both contrast (Sceniak, Ringach, Hawken & Shapley, 1999) and color (Solomon, Peirce & Lennie, 2004). Pack and Born (personal communication) found recently that center-surround antagonism in MT neurons substantially decreases or disappears at low contrast.

Perceptual correlates of center-surround antagonism

If center-surround antagonism is indeed an integral part of motion processing, we might expect to see the perceptual signature of this antagonism in the form of impaired motion visibility with increasing stimulus size. Existing evidence, however, shows that increasing the size of a low-contrast moving stimulus enhances its visibility, presumably owing to spatial summation. Such psychophysical estimations of the spatial properties of motion mechanisms tend to be based on low-contrast (Anderson & Burr, 1991; Watson & Turano, 1995) or noisy stimuli (Lappin & Bell, 1976), while physiological descriptions of center-surround neurons have been obtained with high-contrast patterns. Several physiological studies of visual cortex have found that center-surround interactions depend on contrast, with surround suppression stronger at high contrast and spatial summation more pronounced at low contrast (Kapadia, Westheimer & Gilbert, 1999, Levitt & Lund, 1997; Sceniak et al., 1999). Thus, contrast thresholds may not fully describe the spatial properties of human motion mechanisms, especially at high contrast.

Psychophysical experiments have often measured motion discriminations near threshold values of contrast or statistical coherence. Such impoverished motion signals probably promote spatial summation, precluding observations of surround suppression. Whatever hints of surround suppression might be found in the literature are likely to be found in experiments using large high-contrast patterns.

Indeed, Verghese and Stone (1996) found that when a large high-contrast pattern was divided into smaller parts, speed discriminations actually improved. The authors suggested that surround suppression was one possible explanation. Murakami and Shimojo (1993) studied induced motion in stationary test stimuli presented within a large patch of moving dots. They found that induced motion was replaced by motion assimilation when the test stimulus was small, low contrast, or presented in the visual periphery — suggesting that motion antagonism changes to motion summation under these conditions. Surround suppression is also suggested by findings in several MAE studies in which large high-contrast adaptation patterns produced relatively small MAEs (Sachtler & Zaidi, 1993; Murakami & Shimojo, 1995; Tadin et al., 2003).

Perhaps a related result was found by Nawrot and Sekuler (1990), who investigated how high-contrast motion at one location influences the perception of adjacent incoherent random motion. Stripes of coherently moving random-dot patterns alternated with stripes of random motion. When the stripes were narrow, the perceived motion of the random stripes was assimilated to the direction of the coherent stripes, and the whole pattern appeared to move in the same direction. When the stripes were wide, the random stripes appeared to move in the opposite direction from the coherent stripes.

Kim and Wilson (1997) found that when the directions of motion in center and surround differed by 45°, the perceived direction of the central motion could shift 30°-40° away from the surround direction. Like most of the results above, these directional interactions increased with the size and contrast of the surround. The perceived shift in the direction of the center stimulus might be a result of selective inhibition of neurons tuned to directions similar to the surround. Broad directional tuning of surround suppression (Born, 2000) may be the cause behind this rather large perceived directional shift.

Center-surround antagonism in motion processing has been found in a diverse set of both physiological and psychophysical studies. Describing these center-surround mechanisms and the conditions in which they operate is important, but it is only half the story. Understanding their functional contribution to vision is arguably more important.

Psychophysics of motion-based figure-ground segregation

An important early step in visual processing is to organize the retinal image into surfaces and objects, segregating figure from ground. Objects can differ from their backgrounds in a variety of physical properties — including luminance, texture, color, motion, temporal synchrony, and binocular disparity (Regan, 2000; Lee & Blake, 1999). The extensive use of camouflage in the animal world (e.g., Théry & Casas, 2002) indicates the crucial visual role of figure-ground segregation. Even the best camouflage, however, breaks down when an animal is moving. Motion discontinuities between object and background provides important additional information for segregating images into separate surfaces (Nakayama & Loomis, 1974; Braddick, 1993; Regan, 2000).

Everyday experience suggests that we are very good at detecting objects moving against a background. We wave our arms when we want to be seen, and we stand still when we want to hide. Psychophysical observations accord with our intuitions. Evidence suggests that motion can be as good (Regan, 1989) and sometimes even better (Nawrot, Shannon & Rizzo, 1996) than other visual cues in segregating figure from ground. Regan and his colleagues have extensively studied the perception of motion-defined form over the past two decades (reviewed in Regan, 2000). A general conclusion from Regan's research is that vision is very efficient in detecting, discriminating, and recognizing motion-defined objects.

Highlighting differences between local motion signals, however, is not always adaptive. Different local motion signals often belong to the same object, and should be integrated rather than differentiated. How does vision determine which local motion signals should be integrated and which motion signals should be differentiated?

Integration and segregation of motion signals can be guided by other visual cues (Rivest & Cavanagh, 1996; Croner & Albright, 1997, 1998) and even form information (Lorenceau & Alais, 2001). Another solution that is independent of other visual sub-modalities may be to determine the spatial extent of motion integration based on the local motion signals. The strength and quality of motion signals can be substantially reduced at low contrast, by noise, or when defined by color. Apparent differences in the direction and velocity of local motion signals may be caused by noise, and the spatial segregation of such signals may lead to incorrect perception. Moreover, under such low-visibility conditions, motion patterns might *require* spatial integration just to be perceived at all. On the other hand, when motion signals are strong, spatial variations in the directions and speeds detected by local mechanisms are more likely to reflect the "true" motion pattern. Under conditions of good visibility, spatial differentiation should be favored.

If the spatial organization of motion signals is adapted in this way to the visibility conditions, then it may also fail under some conditions. Lorenceau and Shiffrar (1992, 1999) have shown that the perceptual integration of moving contours belonging to a single rigid form seen through separate apertures is more likely under low contrast, eccentric viewing, isoluminant, and noisy conditions. Correspondingly, however, such moving contours are *less likely* to be correctly integrated when the local visibility increases. Moreover, vision also makes the complementary error of failing to segregate motion signals from different objects. Regan and Beverley (1984) and Regan (1989) found that motion-defined form discrimination is impaired when the strength of the motion signals is degraded, even when motion sensitivity is relatively unaffected.

The visual ability to accurately perceive motion-defined forms may seem surprising in relation to the supposed physiological separation between mechanisms for form and motion processing. The fact that motion-defined forms pop out from the background and attract attention (typical dorsal stream functions) does not imply that shape characteristics such as orientation and aspect ratio will be accurately perceived. The finding that motion cues are sufficient for perceiving both 2D and 3D shape is remarkable and suggests an interesting interaction between motion processing and ventral stream functions. The visual complexity and diverse phenomenology of motion-based form perception all but guarantees that its neural correlates will involve multiple neural mechanisms in multiple visual areas.

Evidently, vision is very good at detecting relative motion and segregating surfaces, but it is an open question whether these visual abilities derive from center-surround mechanisms. Intuitively, center-surround mechanisms seem likely to be involved in motion-based figure-ground segregation, but this link needs experimental support.

Neurophysiology of motion-based figure-ground segregation

Given the visual sensitivity to relative motion and motion-defined forms, specialized neural mechanisms probably operate to detect differences in the spatial distribution of motion signals. Because of the high proportion of center-surround neurons in MT, and because of its central location within anatomical pathways of motion perception, MT seems likely to be involved in segregating figure from ground and perceiving motion-defined form. As will be discussed below, MT is well equipped for segregating figure from ground, but lacks mechanisms to *directly* extract detailed 2D shape of motion-defined forms. This distinction is in agreement with clinical evidence demonstrating that the detection of motion-defined forms can remain intact even when the identification of such forms is severely impaired (Regan, Giaschi, Sharpe & Hong, 1992; Schenk & Zihl, 1997; Cowey & Vaina, 2000). Neural mechanisms for figure-ground segregation of moving forms are discussed first, followed by a discussion of how the 2D shape of such forms may be extracted.

Moving objects must first be detected and their motion estimated. In principle, this can be done with little regard for detailed 2D shape. Once a moving object is detected and foveated, usually it can be recognized based on cues other than motion, as most objects are not perfectly camouflaged. The responses of center-surround MT neurons amplify the neural signature of objects moving relative to their background. The question, however, is whether such a simple mechanism is sufficient to support our ability to effortlessly segregate moving objects from the background. Presumably, suppression occurs when the center and surround are stimulated by the motion of a relatively large visual feature. For this mechanism to be efficient, it should not be inhibited when *different* visual features stimulate the surround and center regions even if they are moving in the same direction. This may occur, for example, when two objects at different depths move with the same angular velocity.

In such cases, center and surround regions of some MT neurons will be stimulated by similar motion arising from different objects, resulting in response suppression. Because this suppression would be caused by object motion, it would somewhat diminish the ability of MT neurons to contribute to figure-ground segregation. Most MT cells, however, are disparity selective (Maunsell & Van Essen, 1983; DeAngelis and Newsome, 1999), a tuning property that may be exploited for 'inhibiting' surround suppression if center and surround motions are at different depths. This hypothesis was investigated by Bradley and Andersen (1998) who found that the disparity tuning of center and surround regions tend to be different. That is, 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 depths. Surround suppression increased as either surround motion or its depth became more similar to motion in the center. The disparity dependence of 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. This 'elaborated' surround suppression improves the ability of MT neurons to efficiently segregate moving objects from the background.

In addition to detecting moving objects, our visual system must correctly estimate object speed and trajectory. This is critical, for example, in accurately foveating the moving object and controlling subsequent pursuit eye movements — skills essential in sports like baseball and cricket. Center-surround neurons may signal the presence of a moving object, but cannot also signal its velocity because the responses of center-surround neurons are also influenced by the background speed and direction (Allman et al., 1985b). The responses of center-surround neurons, however, might be disambiguated by the neural signal representing the speed and the direction of background motion — information encoded by wide-field MT neurons (Figure 1b).

The hypothesis that center-surround and wide-field neurons jointly code object motion has received direct support from recent microstimulation experiments (Born et al., 2000). The authors have exploited the fact that center-surround and wide-field neurons are anatomically segregated (Figure 1c, Born & Tootell, 1992) and can be separately stimulated. Monkeys were trained to fixate a stationary target. A moving target then appeared in the periphery and the animal's task was to make a foveating saccade and visually pursue the target. On half of the trials, microstimulation was applied while the animal was estimating the direction and speed of the moving target. Microstimulation of MT sites with the center-surround neurons shifted pursuit eye movements in the direction similar to the preferred direction of the stimulated clusters of neurons. In contrast, microstimulation of the MT sites with wide-field neurons shifted pursuit eye movements in the direction *opposite* to the preferred direction of the stimulated neurons. These results suggest that the activity of center-surround MT neurons represents object motion whereas the activity of wide-field neurons signals background motion. Importantly, replacing microstimulation with large background motion had an effect similar to that of stimulating wide-field neurons.

Once a moving object is detected and visually segregated from its background, motion information can be used to perceive its 2D shape (Regan, 2000). Detailed motion-defined shape is conveyed by kinetic (motion-defined) boundaries — a building block (akin to edges) of motion-defined objects. One strategy for investigating neural mechanisms involved in perceiving the shapes of motion-defined objects is to look for neurons and brain areas with selectivity for kinetic boundaries.

Brain imaging studies have found that MT responds strongly to kinetic boundaries, but this response does not differ from MT's response to uniform motion (Reppas, Niyogi, Dale, Sereno & Tootell, 1997; Van Oostende, Sunaret, Van Heckem Narchal & Orban, 1997; Dupont et al., 1997; for an exception see Shulman, Schwarz, Miezin & Petersen, 1998). Orban and colleagues have suggested that the kinetic occipital area (KO) is an area specialized for processing of kinetic boundaries (Van Oostende et al., 1997; Dupont et al., 1997). Recently, however, KO has been shown to respond to boundaries defined by cues other than motion (Zeki, Perry & Bartels, 2003). So far then, imaging studies have not revealed whether MT or other cortical areas are specialized for processing kinetic boundaries.

Surgical lesions of area MT (and adjacent regions) in non-human primates have produced conflicting results about the importance of MT in processing kinetic boundaries, with post-lesion impairments ranging form mild (Schiller, 1993; Lauwers, Saunders, Vogels, Vandenbussche &

Orban, 2000) to severe (Marcar & Cowey, 1992). Single cell results, however, are more consistent and find that single MT neurons are not selective for the orientation or location of kinetic boundaries (Marcar, Xiao, Raiguel, Maes & Orban, 1995). MT neurons generally respond very poorly to kinetic boundaries. In fact, MT neurons respond as weakly to kinetic boundaries as they do to transparent motion (Snowden, Treue, Erickson & Andersen, 1991; Bradley, Qian & Andersen, 1995).

It should be emphasized, however, that neurons in other visual areas (primarily V2) are selective for the orientation of motion-defined boundaries (Marcar, Raiguel, Xiao & Orban, 2000; Leventhal, Wang, Schmolesky & Zhou, 1998). V2 neurons tuned to the orientation of kinetic boundaries often exhibited similar orientation tuning to luminance edges, resulting in cue-invariant responses to visual boundaries (Marcar et al., 2000). Notably, the response to kinetic boundaries was delayed by about 40 ms (relative to the luminance boundary response), suggesting the role of cortical feedback. One possibility is that this feedback may arise from neural mechanisms sensitive to the coarse 2D shape of moving objects. One speculation is that the initial region-based segmentation of the moving image in MT may provide guidance (through cortical feedback) for the more detailed edge-based analysis elsewhere (e.g., V2). Interestingly, the response latencies of V2 neurons tuned to the orientations of the kinetic boundaries (Marcar et al., 2000) are about 30 ms longer than the latencies of the antagonistic center-surround neurons in MT (Raiguel , Xiao, Marcar & Orban, 1999).

In general, center-surround antagonism in MT neurons seems to yield enhanced visual sensitivity to relative motion. Diverse experimental evidence suggests that surround suppression is the essential part of the remarkably effective neural mechanisms for motion-based figure-ground segregation. MT center-surround neurons can appear to behave ‘intelligently’ by employing suppressive interactions only in situations when motion stimulating their surrounds is likely to belong to the same surface (Bradley & Andersen, 1998) and by reducing surround inhibition when the visibility is low (Pack & Born, personal communication).

The precise role of MT in figure-ground segregation remains an open question, but MT mechanisms seem to be involved in the spatially crude aspects of motion-based figure-ground segregation, especially in detection and trajectory estimation (Born et al., 2000). Quite possibly, some coarse spatial analysis also occurs in MT. Detailed analysis of motion-defined forms, however, seems to rely on visual areas other than MT, although such mechanisms may partially depend on the MT output for information. Connections between visual areas, indeed, seem to play an important role in the perception of motion-define form — a hypothesis supported by the observation that patients with multiple sclerosis, a demyelinating disease of white matter, are often impaired at perceiving motion-defined forms (Regan, Kothe & Sarpe, 1991; Giaschi, Regan, Kothe, Hong & Sharpe, 1992).

CHAPTER III

PERCEPTUAL CONSEQUENCES OF CENTER-SURROUND ANTAGONISM IN VISUAL MOTION PROCESSING

Adapted from Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of centre-surround antagonism in visual motion processing. *Nature*, *424*, 312-315.

Introduction

Motivated by the neurophysiological importance and ubiquity of center-surround interactions in motion processing, we conducted a series of experiments to document possible perceptual correlates of such interactions. By analogy with other aspects of vision (Westheimer, 1967), if centre-surround antagonism is an integral part of motion processing, we should expect to see a perceptual signature of this antagonism in the form of impaired motion visibility with increasing stimulus size. Existing evidence, however, shows that increasing the size of a low-contrast moving stimulus enhances its visibility (Anderson & Burr, 1991; Watson & Turano, 1995), presumably owing to spatial summation. Such psychophysical estimations of the spatial properties of motion mechanisms tend to be based on low-contrast or noisy stimuli, while physiological descriptions of centre-surround motion neurons have been obtained with high-contrast motion. Moreover, in visual cortex, the nature of centre-surround interactions is often dependent on contrast, with surround suppression stronger at high contrast and spatial summation more pronounced at low contrast (Levitt & Lund, 1997; Sceniak et al., 1999; Kapadia et al., 1999; Cavanaugh, Bair & Movshon, 2002). Thus, threshold contrast measurements may not fully describe the spatial properties of human motion perception, especially at high contrast. The described experiments tested this hypothesis by examining observers' abilities to correctly perceive the direction of motion at a range of contrasts and sizes.

Methods

General Methods

Stimulus patterns were created in MatLab with the Psychophysics Toolbox (Brainard, 1997) and Video Toolbox (Pelli, 1997) and shown on a linearized monitor (800 x 600 resolution, 120 Hz). Main results were confirmed at 160 and 200 Hz. Viewing was binocular at 83 cm (yielding 2 x 2 arcmin per pixel). Ambient illumination was 4.8 cd/m^2. Background luminance was 60.5 cd/m^2.

Unless noted otherwise, stimuli were moving Gabor patches: drifting sinewave gratings presented in a spatial Gaussian envelope. The size was defined as the 2σ width of a Gabor patch. To allow presentation of brief motion stimuli, stimulus contrast was ramped on and off with a temporal Gaussian envelope (duration is defined as 2σ of the temporal Gaussian). With 120Hz refresh rate duration thresholds as low as 8-10 ms can be measured.

Duration thresholds (82%) were estimated by interleaved Quest staircases. For each condition, five observers ran four pairs of interleaved staircases, with the first pair discarded as practice. Feedback was provided. All experiments complied with institutionally reviewed procedures for human subjects.

Effects of size and contrast on motion discriminations: duration threshold experiment

Threshold exposure duration required for human observers to accurately identify the motion direction of a drifting Gabor patch was measured. On each trial, a drifting Gabor patch was presented foveally and observers indicated the perceived direction (left or right) by a key press. In separate conditions, observers viewed foveally presented Gabor patches of various sizes (0.67° – 5°) and contrasts (2.9% - 92%), yielding 30 different conditions. Spatial frequency and speed were fixed at 1 cycle/° and 2°/s, respectively.

Additive noise experiment

Effective stimulus contrast was manipulated by adding variable amounts of noise to a fixed-contrast Gabor patch. Duration thresholds for discriminating motion direction were measured for a high-contrast Gabor patch (46%) embedded in a 20° by 20° dynamic noise pattern. The noise pattern consisted of 480 x 480 dark and light pixels randomly regenerated at

120 Hz. This noise mask was combined additively with a foveally presented Gabor patch. Three levels of noise contrast were used (0%, 16%, and 46%) at four different sizes (1° – 4°).

Broadband (random-dot) motion experiment

The stimuli consisted of light and dark pixels (each 3 x 3 arcmin) presented in a spatial Gaussian envelope. From frame to frame of the animation, half of the pixels shifted in one direction (6.2°/s) while the remaining pixels were randomly regenerated (50% correlation), conditions producing vivid motion perception at suprathreshold exposure durations.

This experiment was conducted at high (92%) and low (9%) contrast for a range of stimulus sizes (0.67°, 1.67°, and 4°), yielding 6 conditions. A somewhat higher contrast in the low-contrast condition for random-dot stimuli was required because the contrast sensitivity for such stimuli is worse than the contrast sensitivity for low spatial frequency gratings.

Eccentric presentation experiment

Motion discrimination thresholds were measured for a range of stimulus sizes (1.2° - 7.8°) at different eccentricities (0° - 54°), yielding 24 conditions (contrast was fixed at 92%). Spatial frequency was 0.5 cycles/° and the speed was 4°/s. In this experiment only, motion directions were vertical to avoid potential response biases between motions away and toward the fovea. To present visually larger stimuli within the limited monitor area, a Gaussian spatial envelope was replaced with the two-dimensional raised cosine envelope. For such stimuli, the size was defined as the distance between two diametrically opposing points on the raised cosine envelope where the contrast was 60.7% of the peak contrast (analogous to the 2σ of a Gaussian distribution).

Phase-shift threshold experiment

Observers identified the motion direction of a fixed-contrast Gabor patch that abruptly shifted in phase in the middle of a 100 ms presentation interval. Threshold phase shifts were obtained for a range of contrasts (2.9% - 92%) and sizes (0.67° – 5°) with spatial frequency fixed at 0.5 cycle/°, yielding 30 conditions.

Isoluminant motion experiment

Motion discrimination thresholds were measured for isoluminant (red–green) and luminance contrast (yellow–black) Gabor patches at a range of sizes (1° - 5°), yielding 10 conditions. The spatial frequency was 1 cycle/°.

Both isoluminant and luminance contrast Gabor patches consisted of isoluminant red and green gratings, with the relative phase between the two gratings being the only difference. To present an isoluminant red-green grating, isoluminant red and green gratings were presented spatially in *antiphase*. Presenting the same two gratings *in phase* produced a yellow–black luminance grating. For each observer separately, the red–green isoluminant point was obtained with the minimum motion technique (Cavanagh, MacLeod & Anstis, 1987).

Results

Increasing stimulus contrast dramatically changes the way motion signals are integrated over space (Figure 2). At low contrast (2.8%), duration thresholds decreased with increasing size, reaching a lower asymptote around 40 ms (Figure 2a, c). This result, implying spatial summation of motion signals, is consistent with earlier reports (Anderson & Burr, 1991; Watson & Turano, 1995). At high contrast, however, duration thresholds increased four-fold as the Gabor patch width increased from 0.7˚ to 5˚. In other words, for small Gabors, performance improved with increasing contrast while for large Gabors, performance deteriorated substantially with contrast (Figure 2b). These highly surprising results imply neural processes fundamentally different from spatial summation. Closer examination of the results reveals that duration threshold elevation was greatest for Gabors larger than 2.6˚ in width (arrow in Figure 2b), suggesting the existence of a "critical size." We speculated that surround inhibition might be responsible for the observed decrease in motion sensitivity, leading us to explore this hypothesis in several more experiments.

Similar contrast-dependent size effects were obtained with faster moving stimuli (8˚/s) and with Gabor patches whose spatial bandwidth was held constant by scaling spatial frequency (1 cycle/σ). We also manipulated effective stimulus contrast by adding variable amounts of dynamic noise to a fixed contrast Gabor patch (see Methods). We found evidence for spatial summation when motion appeared within high contrast noise and evidence for spatial suppression when motion appeared within weak noise or when noise was absent altogether

(Figure 3a). In other words, the presence of noise actually improved the visibility of large motion stimuli.

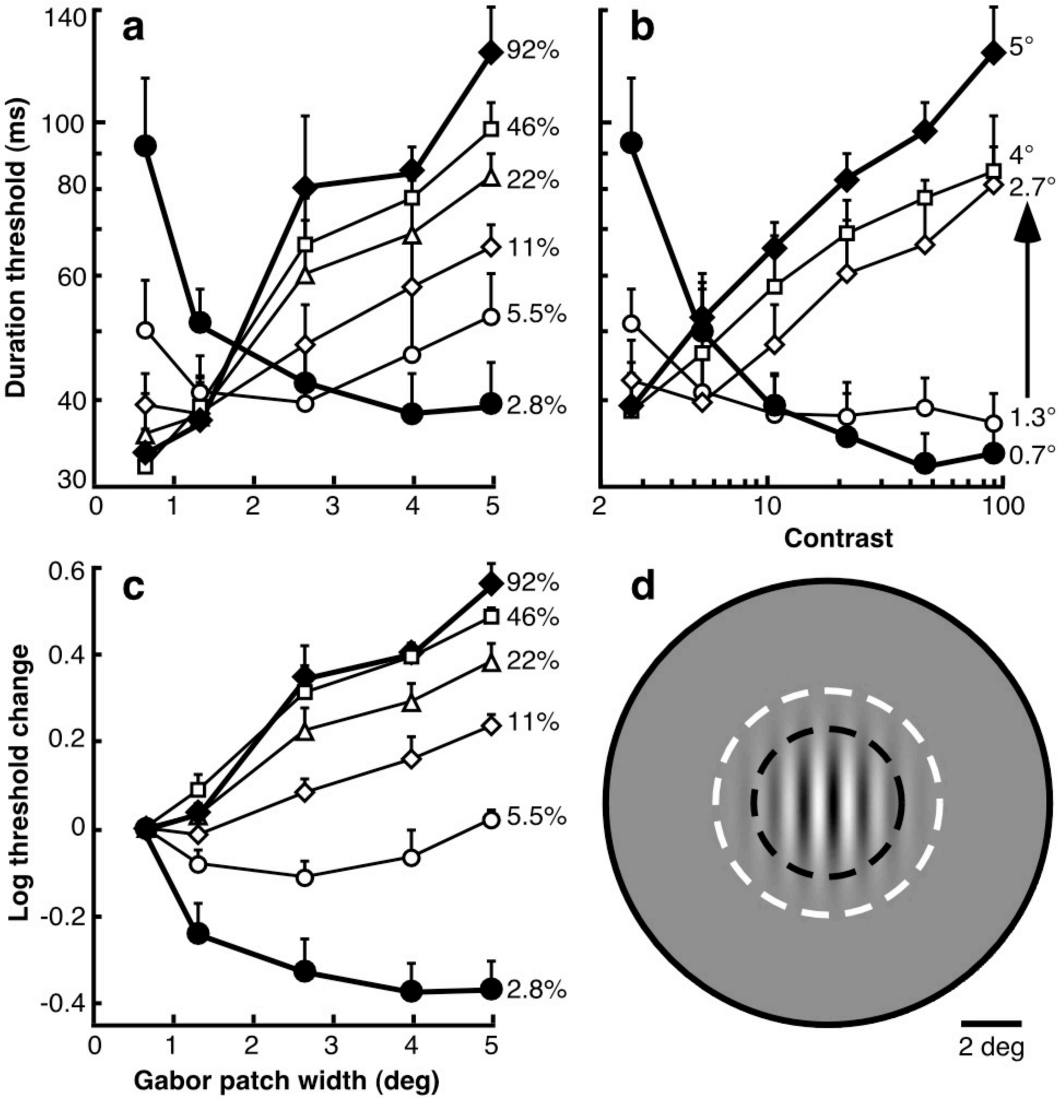

Figure 2. Effects of size and contrast on motion perception. Individual data points are averages for five observers. Error bars are SEM. (a), Duration thresholds as a function of stimulus size at different contrasts. (b), Duration thresholds as a function of contrast for a range of stimulus sizes. (c), Log threshold change as a function of stimulus size at different contrasts. For each observer, log threshold change was calculated relative to the duration threshold for the smallest size (0.7º) at each contrast level. Note that the transition from suppression to summation occurs around 5% contrast, a value which, coincidentally or not, is the contrast where MT neurons attain about 25% of their maximum response on average (Sclar, Maunsell, & Lennie, 1990). (d), A Gabor patch 2.7º wide shown relative to an average foveal macaque MT receptive field. The dashed dark circle illustrates the stimulus size beyond which an average foveal MT center-surround neuron exhibits surround suppression (Raiguel et al., 1995). The radius of the surround is usually about 3 times larger than the center radius, as indicated by the full circle. Full spatial extent of the Gabor patch ($r = 3\sigma = 4$º) is indicated by the light dashed circle.

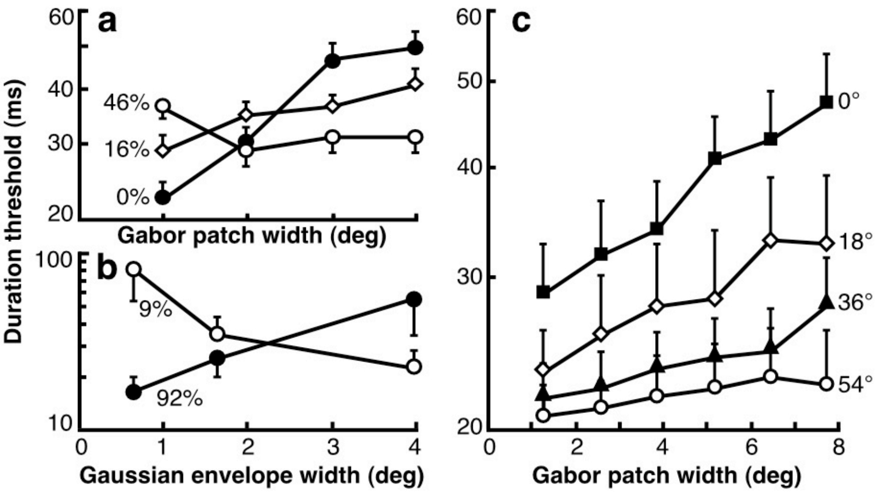

Figure 3. Results from added noise, random-dot and eccentricity experiments. (a), Duration thresholds as a function of stimulus size at different noise contrasts. (b), Duration thresholds as a function of random-dot stimulus size at different contrasts. (c), Duration thresholds as a function of stimulus size at different eccentricities. Error bars are SEM.

Most neurophysiological explorations of center-surround motion neurons have been carried out with spatially broadband random-dot displays. Thus, we also investigated effects of size with random-dot stimuli presented in a spatial Gaussian envelope moving at 6.2˚/s (see Methods). Duration thresholds with these stimuli, too, yielded evidence for spatial summation at low contrast and spatial suppression at high contrast (Figure 3b).

Realizing that the receptive-field sizes of motion-sensitive neurons increase with retinal eccentricity (Raiguel et al., 1995; Albright & Desimone, 1987) we wondered whether the detrimental effect of stimulus size at high contrast would diminish with increasing eccentricity. Accordingly, we manipulated display size for a range of eccentricities with contrast fixed at 92% (see Methods). Once again, foveal presentation yielded evidence for surround suppression (Figure 3c). As eccentricity increased, duration thresholds dropped for all sizes. More importantly, the size dependency of duration thresholds systematically changed with eccentricity, with almost no effect at the largest eccentricity tested.

The motion strength of a periodic Gabor patch can also be varied by adjusting the magnitude of an abrupt phase shift (Nakayama & Silverman, 1985): increasing phase shifts from 0˚ to 90˚ enhances the visibility of motion. We conducted an experiment in which observers identified the motion direction of a fixed contrast Gabor patch that abruptly shifted in phase (see

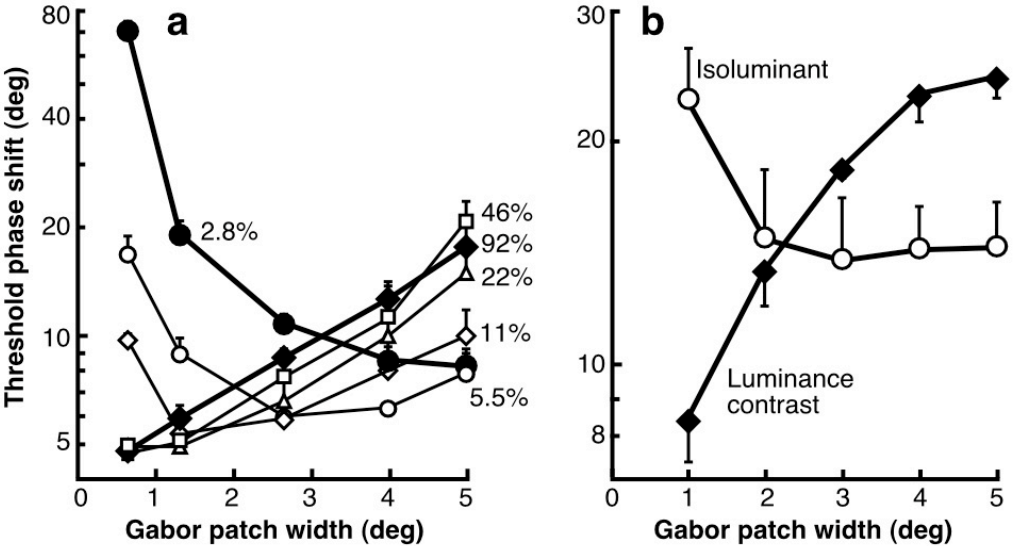

Figure 4. Results from phase shift and isoluminant motion experiments. (a), Phase shift thresholds as a function of stimulus size at different contrasts. (b), Phase shift thresholds as a function of stimulus size for luminance contrast and isoluminant stimuli. Error bars are SEM.

Methods). Results (Figure 4a) replicated the duration threshold findings, again demonstrating the spatial suppression of motion signals at high contrast.

Given the reduced visibility of isoluminant moving stimuli and the reduced MT response to such stimuli (e.g., Gegenfurtner et al., 1995), we may expect spatial summation of isoluminant stimuli similar to that observed for low-contrast and noisy stimuli. Using the phase shift procedure from the previous experiment, we compared thresholds for isoluminant (red-green) and high luminance contrast (yellow-black) Gabor patches (see Methods). Once again, luminance contrast stimuli exhibited surround suppression (Figure 4b). Thresholds for isoluminant stimuli, however, decreased with increasing size, exhibiting spatial summation. This result is surprising in that colour-defined motion with large stimuli was actually perceived more accurately than luminance-defined motion, presumably because the latter is affected by surround suppression.

Discussion

The present study reveals that large-sized objects detrimentally affect human motion perception, which contradicts intuition and challenges accepted ideas about spatial properties of motion perception. In psychophysics, spatial summation has often been assumed as a basic characteristic of motion processing (Anderson & Burr, 1991; Watson & Turano, 1995), but we show that this holds only for low visibility conditions. In addition, our results corroborate and help explain some earlier findings. Verghese and Stone found that dividing a large high-contrast object into smaller parts actually improved performance in a speed discrimination task, leading them to suggest surround suppression as one possible explanation (Verghese & Stone, 1996). Derrington and Goddard (1989) reported that increasing the contrast of a briefly presented, large drifting grating reduced performance, agreeing with a portion of our findings (filled diamonds in Figure 2b). They speculated that brief motion stimuli, by virtue of their broad temporal frequency spectrum, may stimulate motion filters tuned to opposing directions of motion. At high contrast, these paired filters could saturate impairing direction identification. This account fails, however, to explain the effects of size that are central to this paper.

For several reasons, we believe that our results may reflect receptive field properties of center-surround neurons in MT.

- Impaired visual performance with larger stimuli has been construed as the perceptual signature expected from antagonistic center-surround mechanisms (Westheimer, 1967).
- The "critical size" at which we begin to observe strong surround suppression (Figure 2b) is large enough to impinge on the surrounds of MT neurons with foveal receptive fields (Figure 2d). This critical size, however, is much larger than V1 receptive fields and much smaller than MSTl receptive fields, cortical areas other than MT containing center-surround motion neurons (Jones et al., 2001; Eifuku & Wurtz, 1998).
- The detrimental effect of stimulus size diminishes in the visual periphery, consistent with the increase of MT receptive field sizes with eccentricity (Raiguel et al., 1995; Albright & Desimone, 1987).
- Finally, MT neurons respond more weakly to motion of isoluminant gratings than to motion of luminance gratings (Gegenfurtner et al., 1995), a property that dovetails nicely with the failure of isoluminant motion to produce surround suppression.

It is important to emphasize that our conclusion rests on several assumptions, which are not unreasonable given existing evidence:

- We assume that the quality of motion perception covaries with underlying neuronal firing rate — a reasonable assumption for MT neurons (Britten et al., 1992).
- We also assume that the strength of surround suppression induced by a large, moving object is not substantially altered because of the variations in receptive field size and eccentricity. At any given eccentricity in MT, there is about a ten-fold range of receptive field sizes (Raiguel et al., 1995). Thus, surrounds of some neurons will be only partially stimulated, particularly those with receptive-field centers aligned along the stimulus border. But because the border of our stimuli is blurred and low contrast (Figure 2d), these "border neurons" too will be affected by surround suppression, as their partially stimulated surrounds will receive higher contrast stimulation than their centers. Indeed, replication of the current experiment with hardedge circular gratings (i.e., stimuli without a blurred edge) results in greatly diminished surround suppression (P. Bennett, personal communication, May 2004).
- Use of duration thresholds was based on the assumption that if the neural response to a stimulus is weak and/or noisy, then longer stimulus exposure will be required for correct perception. More specifically, deciding whether an object is moving in one of two possible directions can be conceptualized as a process involving accumulation of sensory evidence over time (Roitman & Shadlen, 2002; Gold & Shadlen, 2000). When neuronal responses are noisy or attenuated, as with a highly suppressed motion stimulus, sensory evidence accumulates more slowly and a correct decision thus may require longer exposure duration (Roitman & Shadlen, 2002).
- By comparing our psychophysical results with the receptive field sizes in macaque MT we assume that the properties of human and macaque MT are comparable (Rees, Friston, & Koch, 2000), and that the receptive field sizes are similar for the two species (Kastner et al., 2001).
- Finally, we assume our results arise from center-surround neurons, and not the so-called "wide-field" MT neurons that show no surround suppression (Born & Tootell, 1992). Center-surround and wide-field neurons are anatomically segregated (Born & Tootell, 1992; Raiguel et al., 1995) and produce different behavioural effects when artificially stimulated,

suggesting the conclusion that wide-field neurons may not be directly involved in signalling object motion (Born et al., 2000).

Our results generate testable predictions. For one, they predict that response strength in MT to isoluminant motion stimuli, albeit weak, should increase with stimulus size. For another, the observed contrast dependence of the spatial integration of motion signals is particularly interesting. It predicts contrast-dependent changes in receptive field properties of MT neurons similar to those observed in V1 (Levitt & Lund, 1997; Sceniak et al., 1999; Kapadia et al., 1999; Cavanaugh et al., 2002), which should be measurable using neurophysiological and neuro-imaging techniques. Indeed, recent neurophysiological results (Born et al., personal communication) indicate that MT neurons do not show surround suppression at low contrast.

But why is the nature of center-surround interactions in motion perception so dramatically affected by contrast? At high contrast, the computational benefits of surround suppression (Born et al., 2000; Nakayama & Loomis, 1974; Gautama & Van Hulle, 2001; Buracas. & Albright, 1996) probably outweigh the obligatory decrease in neuronal activity and reduced sensitivity. At low contrast, high sensitivity is essential, so it makes functional sense that receptive field organization shifts from surround suppression to spatial summation. The integration of motion signals over space, then, is an adaptive process that enables the visual system to more efficiently process moving stimuli by employing computationally important suppressive mechanisms only when the sensory input is sufficiently strong to guarantee visibility.

CHAPTER IV

THE SIZE OF THE OPTIMAL MOTION STIMULUS DEPENDS ON CONTRAST

Adapted from Tadin, D & Lappin, J. S. (submitted). The size of the optimal motion stimulus depends on contrast. *Vision Research*.

Introduction

The bulk of our psychophysical knowledge about the spatial properties of motion mechanisms comes from threshold experiments, usually contrast or motion coherence thresholds. Several studies have described the effect of increasing stimulus size on contrast thresholds, and have found that thresholds first improve rapidly with increasing size, and then level off or improve at a slower rate (Anderson & Burr, 1987, 1991; Gorea, 1985; Watson & Turano, 1995). The initial rapid improvement is usually attributed to spatial summation within a single neural mechanism; and gradual improvement at larger sizes indicates probability summation over multiple mechanisms. These experiments assume that the spatial properties of the underlying neural mechanisms are independent of stimulus contrast.

At the time, this contrast-invariance assumption agreed with the physiological conception of a receptive field as a fixed property of a neuron. Recent studies, however, have found that spatial properties of the receptive field are dynamic and depend on the stimulus and the visual context (Levitt & Lund, 1997; Sceniak et al., 1999; Dragoi & Sur, 2000; Kapadia et al., 1999; Cavanaugh et al., 2002). Many of the observed changes in the receptive field physiology are believed to result from contrast-dependent interactions between excitatory and inhibitory processes. Specifically, spatial summation has been found to increase with decreasing contrast (Sceniak et al., 1999). Moreover, surround suppression often becomes more pronounced at high contrast (Cavanaugh et al., 2002). Such adaptive receptive fields make functional sense: At low contrast, sensitivity can be improved by increased spatial summation and reduced surround suppression. When visibility is well above threshold, however, spatial resolution can be improved by reducing spatial summation and taking advantage of center-surround antagonism to differentiate spatial patterns.

These recent physiological findings about the effects of contrast on the spatial properties of cortical receptive fields suggest that psychophysically described motion mechanisms may also change with contrast. Indeed, Tadin et al. (2003) found that the "sign" of spatial interactions changes with contrast: with spatial summation at low contrast and spatial suppression at high contrast. Spatial suppression was manifested by increases in motion discrimination thresholds as the size of the pattern increased. This result was observed at all but the lowest contrasts. Thus, direction discriminations at high contrast were improved by reducing the size of the motion pattern. This relation between size and discrimination thresholds of high-contrast patterns should be U-shaped, however: Further reductions in size below some optimal value should yield reduced discriminations. This minimum-threshold size may be taken to indicate the size at which spatial summation and suppression are optimally balanced.

A general aim of the present study was to demonstrate the existence of the optimal size for perceiving motion. A more specific question was whether this optimal size varies with stimulus contrast. One possibility is that the balance between spatial summation and suppression does not depend on contrast, resulting in a fixed optimal size. (Note that an "optimal size" concept only applies for medium and high contrasts that show significant surround suppression). Another possibility is that the optimal size changes with contrast — possibly decreasing as contrast increases. The results of Tadin et al. (2003) do not distinguish between these two alternatives because they focused on relatively large stimulus sizes. We investigated this issue by measuring duration thresholds for a range of sizes and contrasts.

Methods

Stimulus patterns were created in MatLab with the Psychophysics Toolbox (Brainard, 1997) and Video Toolbox (Pelli, 1997) and shown on a linearized monitor (1024 x 768 pixels resolution, 120 Hz). Viewing was binocular at 83 cm. The ambient illumination was 4.8 cd/m^2 and the background luminance was 60.5 cd/m^2. To allow presentation of brief motion stimuli, the contrast of a stimulus was ramped on and off with a temporal Gaussian envelope (duration was defined as two standard deviations (2σ) of the temporal Gaussian). Thresholds (82%) were estimated by interleaved Quest staircases. For each condition, four pairs of interleaved staircases were completed with the first pair discarded as practice. All experiments complied with institutionally reviewed procedures for human subjects. Four naïve and well-practiced observers participated in the study.

The stimuli were random-dot motion patterns made up of light and dark pixels (each 3.1 x 3.1 arcmin) presented in a spatial Gaussian envelope. Size was defined as 2σ of the spatial Gaussian. Contrast was defined as the peak contrast of the spatial Gaussian. From frame to frame of the animation, half of the pixels shifted in one direction (6.2°/s) while the remaining pixels were randomly regenerated (50% correlation) — conditions producing vivid motion perception at suprathreshold exposure durations. One subject had difficulty with 50% correlated stimuli (thresholds were high and very variable), thus she completed the experiment with 100% correlated motion. Her results at 100% correlation were qualitatively identical to those of other subjects at 50% correlation, but were not included in the average data.

We measured the threshold exposure duration required for observers to accurately identify the motion direction. On each trial, a moving stimulus was presented foveally and observers indicated the perceived direction (left or right) by a key press. Feedback was provided. In separate conditions, observers viewed foveally presented random-dot motion stimuli of eight different sizes (0.25° – 6°) and four contrasts (9% - 92%), yielding 32 conditions.

Results

Increasing the size of a low-contrast moving stimulus resulted in improved performance, whereas the same size increase for high-contrast stimuli ultimately resulted in decreasing performance – suggesting surround suppression (Figure 5a). This replicates the main result of Tadin et al. (2003). Furthermore, at each contrast where surround suppression was observed (20%, 42%, 92%) we observed an optimal size – an intermediate size at which the threshold was the lowest. More notably, this optimal size decreased with increasing contrast: At 92% contrast, the optimal size was about 2.5 times smaller than at 20% contrast. This contrast-dependency of the optimal size is clearly visible when the data are repotted in an area graph (Figure 5b). The optimal size seems to depend on contrast in log-linear manner. Furthermore, the overall shape of the effect of size at high contrasts is similar. That is, the fitted curves for three high contrasts in Figure 5a are very similar except for horizontal and vertical translations, which is apparent in approximately parallel contour lines in Figure 5b. This overall pattern of results was observed for all subjects.

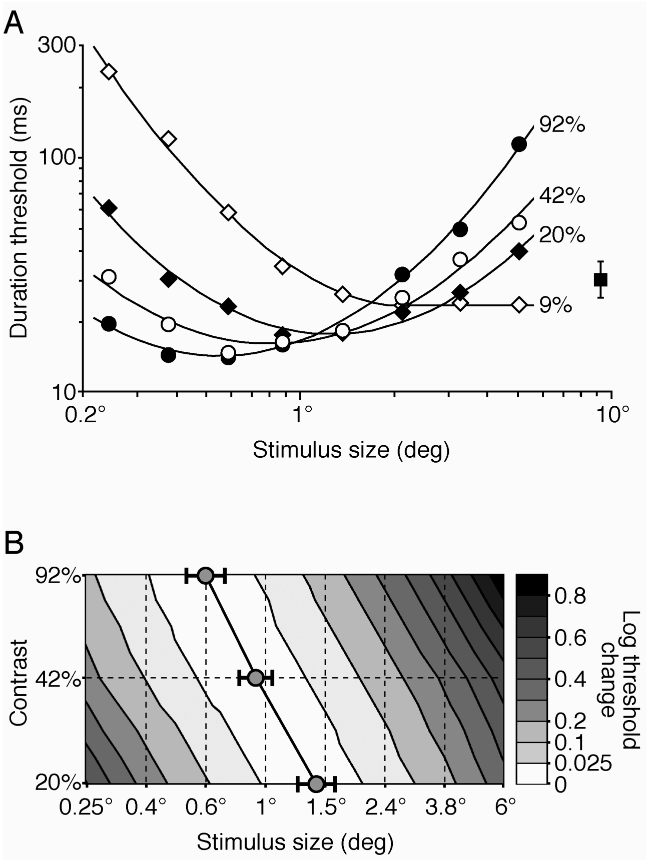

Figure 5. Motion discriminations as a function of stimulus size at different contrasts. (A) Average thresholds for three subjects. To find the size with the lowest threshold, data for three high contrasts were fitted with quadratic functions whose minima were taken as the optimal size (9% contrast was fitted with a quadratic and a horizontal line). Quadratic functions were used simply as a convenient way to estimate the optimal size (mean $r^2 = 0.982$). For clarity, only the average between subject SEM of all data points is shown (filled square). (B) Log threshold change relative to the optimal size at three high contrasts. At each contrast, the fitted quadratic from (A) was normalized relative to its minimum (log threshold change = $\log(f(x)) - \log(\min(f))$. This contour plot was created by 2D linear interpolation of three normalized quadratic fits. Colorbar on the right indicates levels of log threshold change relative to the minimum threshold. Slanted contour lines indicate that the optimal size increases with decreasing contrast. Optimal sizes were also computed for each observer separately by fitting the quadratic to each observer's data. The average optimal size (±SEM) for three subjects is indicated by filled circles.

Presenting the same data as a function of contrast shows that the discriminations of small moving stimuli improved with contrast, while the visibility of large stimuli counterintuitively decreased with increasing contrast (Figure 6a). From this data, we extracted a contrast-dependency index for each size — defined as the log threshold change between the lowest and the highest contrast. Figure 6b shows that the contrast-dependency of motion discrimination

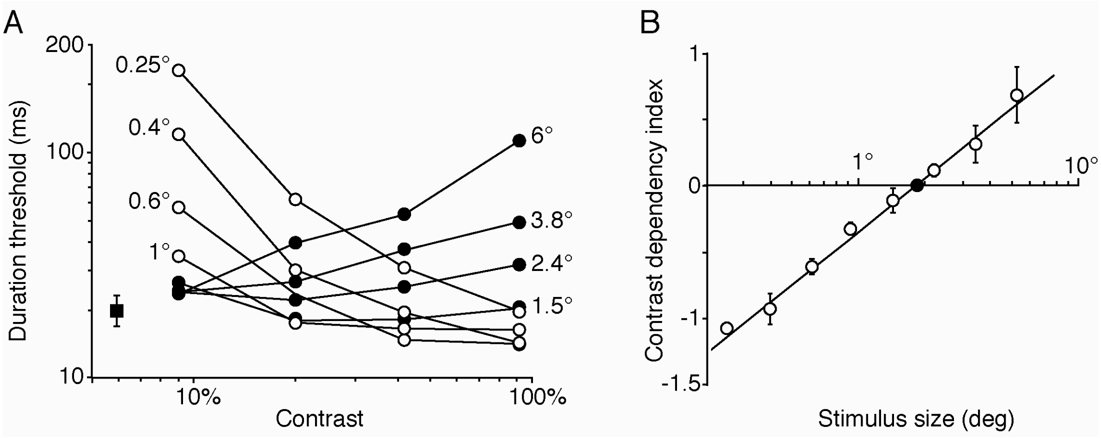

Figure 6. Motion discriminations as a function of contrast at different stimulus sizes. (A) Average thresholds for three subjects. Empty circles indicate stimulus sizes for which increasing contrast improves motion discriminations. Filled circles indicate stimulus sizes for which increasing contrast worsens motion discriminations. For clarity, only the average SEM of all data points is shown (filled square). (B) Contrast dependency index. For each size, a contrast dependency index was calculated as (log threshold at 92% contrast) – (log threshold at 9% contrast). Negative numbers indicate contrast facilitation, while positive numbers show contrast inhibition. To estimate zero crossing (indicated by a filled circle), a linear fit of the data was calculated ($r^2 = 0.994$).

changes in a very orderly manner with increasing size: contrast has a facilitatory effect for small sizes and an inhibitory effect for large sizes. From Figure 6b, we estimated that the intermediate size for which increasing contrast from 9% to 92% has the least effect on motion discrimination is about 2° (114 arcmin).

Discussion

We show that spatial properties of motion perception critically depend on contrast. Specifically, we found that the optimal size for perceiving motion decreases (approx. 2.5-fold) with increasing contrast. This result dovetails nicely with recent reports indicating that the receptive field size in cortical area V1 decreases with contrast, with the magnitude of change between 2-fold and 4-fold (Sceniak et al., 1999; Kapadia et al., 1999; Cavanaugh et al., 2002).

Furthermore, our results raise warning flags about interpreting the previous studies of the receptive field properties of human motion mechanisms (Anderson & Burr, 1987, 1991; Gorea, 1985; Watson & Turano, 1995). Those studies provided important data about basic spatial properties of motion mechanisms operating in low visibility conditions, but such results do not generalize to conditions when visibility of motion is well above threshold.

We speculate that the optimal size for perceiving motion indicates a size at which the inhibitory surround mechanisms prevail over the spatial summation by the excitatory center mechanisms. The contrast dependency of this effect, then, can be accounted for by the asymmetric interactions between excitatory center and inhibitory surround mechanisms. For example, larger receptive field size at low contrast may be a result of the summating center mechanisms whose spatial extent grows with decreasing contrast (Sceniak et al., 1999). Alternatively, a change in the receptive field size can be caused by surround mechanisms with lower contrast gain than the center, with both center and surround being spatially fixed (Somers et al., 1998; Cavanaugh et al., 2002). The consequence of such contrast gain asymmetry will be that the surround effect will remain below threshold at low contrast and, as the contrast increases, will gradually "erode" the spatial summation by the excitatory center. Each of these receptive field models (and their combination) predicts increasing receptive field size with decreasing contrast, and thus can account for our result.

Most investigations of the relationship between receptive field size and contrast have been performed with V1 neurons. Based on our earlier psychophysical results, we hypothesized that the balance between surround suppression and spatial summation in MT will also depend on contrast (Tadin et al., 2003). Unfortunately, virtually all published studies of surround suppression in MT were restricted to high-contrast moving stimuli. Recent unpublished results by C. C. Pack and R. T. Born indicate, however, that MT center-surround antagonism observed at high contrast substantially weakens or even disappears at low contrast (personal communication, August 2003). This finding shows that contrast-dependent pooling of spatially distributed signals is a prominent feature of neural computation in MT.

In summary, we show that the dynamics of the spatial integration of motion signals depend on contrast. This finding is in accord with observations in V1 and MT indicating that the stimulus size evoking the best response decreases with contrast. Finally, we suspect that this result is not specific to contrast, as other stimulus parameters have also been shown to affect the spatial properties of visual neurons (e.g., Lamme, 1995; Kapadia et al., 1999; Ito & Gilbert, 1999; Treue, 2001; Solomon et al., 2004). For example, spatial properties of motion mechanisms might also adjust adaptively to changes in signal/noise ratio, chromatic properties, figure/ground belongingness, and allocated attention.

CHAPTER V

EXPLORATION OF CENTER-SURROUND INTERACTIONS IN MOTION PROCESSING USING MOTION AFTER-EFFECT

Partially adapted from Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of centre-surround antagonism in visual motion processing. *Nature*, *424*, 312-315.

Introduction

In the previous chapters, center-surround interactions in motion were explored with brief moving stimuli and, in most cases, by measuring duration thresholds. Use of brief stimuli allowed us to present highly visible high-contrast stimuli, which were required to demonstrate center-surround suppression and still measure psychophysical thresholds. To extend the generality of psychophysically observed center-surround interactions, however, it is desirable to replicate our main results with longer moving stimuli.

Brief motion stimuli have a very broad temporal frequency spectrum, which may result in such stimuli being processed differently than longer stimuli. This idea was introduced by Derrington and Goddard (1989) who reported that increasing the contrast of a briefly presented, large drifting grating reduced performance. They speculated that brief motion stimuli, by virtue of their broad temporal frequency spectrum, may stimulate motion filters tuned to opposing directions of motion. For example, a very brief rightward moving stimulus will contain most of the energy in the rightward direction but also some energy in the leftward direction. At low contrast, this activation imbalance between motion filters sensitive to opposing directions is sufficiently large and correct direction of motion is perceived. At high contrast, however, these paired filters could saturate, thereby impairing direction identification.

Contrast saturation of opposing motion units as proposed by Derrington and Goddard (1989) provides a plausible explanation for effects of contrast that they and we have found. This interpretation has difficulty, however, accounting for the effects of size that are central to the research reported in the present dissertation. Nevertheless, it is important to investigate whether psychophysically observed center-surround interactions generalize to prolonged presentations, thus ruling out an explanation based on the contrast saturation of opposing motion units.

How can center-surround interactions be demonstrated with longer stimulus durations? Standard psychophysical threshold measurement is not an option as prolonged, large, high-contrast moving stimuli are well over the threshold. One alternative is to use the MAE as a measuring tool.

Use of the MAE — an illusory perception of motion following prolonged exposure to motion — is motivated by the observation that surround inhibition in motion-sensitive neurons decreases neural activity in response to a large moving stimulus (Allman et al., 1985b). This decreased activity may be evident in a weaker adaptation of motion-sensitive center-surround neurons during prolonged exposure to motion. The MAE is thought to reflect the adaptation of motion-sensitive neurons (Huk, Ress, & Heeger, 2001). Given our findings with duration thresholds, we predicted that adapting to a large high-contrast moving stimulus should result in a weaker MAE whereas adaptation to a low-contrast stimulus should not. These hypotheses are investigated in Experiment 1.

One advantage of the MAE over threshold-based measures is that MAE is a measure of the after-effect strength at a specific retinal location defined by the spatial extent of the test stimulus. For example, when measuring duration thresholds, neurons with receptive fields aligned along the border of large stimuli are an issue as observers may base their responses on the activity of less-suppressed "border neurons" (see Chapter 3 for details). Such "border neurons" are not an issue in an MAE study as the after-effect strength is measured only in the small region in the center of the adapting pattern.

This useful property of MAE was exploited to study surround suppression with more complicated stimulus patterns. In Experiments 2 and 3, we explored how surround suppression was affected by visual context cues that varied whether the stimulus was perceived as a large occluded stimulus or as detached small stimuli. The goal of these experiments was to find out whether *perceived* surface layout modulates surround suppression even when the spatial extent of the stimulus is unchanged. Such a finding would suggest that surround suppression is modulated by higher-level visual context.

In Experiment 4, we investigated how the strength of suppression changed when the stimulus surround was at a different disparity than the center. This experiment was motivated by single cell MT data indicating that surround suppression diminishes when center and surround regions are stimulated by motions at different disparities (Bradley & Andersen, 1998).

An implicit hypothesis in these experiments is that surround suppression might occur because vision tends to suppress motion signals arising from background motion. We explored this hypothesis by examining how surround suppression is affected by various "non-motion" manipulations that altered the extent to which a moving pattern appears like a large moving background.

Experiment 1

Methods

In all experiments, stimulus patterns were created in MatLab with the Psychophysics Toolbox (Brainard, 1997) and Video Toolbox (Pelli, 1997). Stimuli were shown on a linearized monitor (800 x 600 resolution, 120 Hz). Viewing was binocular at 83 cm (yielding 2 x 2 arcmin per pixel). Ambient illumination was 4.8 cd/m^2. Background luminance was 60.5 cd/m^2. Stimuli were moving Gabor patches: drifting sinewave gratings presented in a spatial Gaussian envelope. Spatial and temporal frequency were 1 cycle/° and 4°/s, respectively. The size was defined as the 2σ width of a Gabor patch. Three observers participated in the experiment. All procedures complied with institutionally reviewed guidelines for human subjects.

Observers adapted to a Gabor patch centered in fovea. In different conditions, adapting stimuli were varied in size (1°, 2°, and 5°) and contrast (2.8% and 26%). The test stimulus consisted of two overlapping Gabor patches drifting in opposite directions (i.e., a counterphasing grating). The test stimulus parameters were the same as the adapting Gabor patch except for the stimulus width, which was fixed to 1°. When the contrasts of two overlapping Gabor patches were identical, the motion was ambiguous and the test stimulus appeared to flicker. Adapting to a motion in one direction effectively decreased the motion strength of the Gabor patch moving in the adapted direction and the test stimulus appeared to move in the opposite direction. Then, to restore the perception of flicker, the contrast of the Gabor patch moving in the adapted direction was increased and the contrast of the other Gabor patch was decreased. The contrast ratio required to restore flicker perception was taken as a measure of MAE strength (higher contrast ratio indicates stronger MAE).

The initial adaptation was for 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

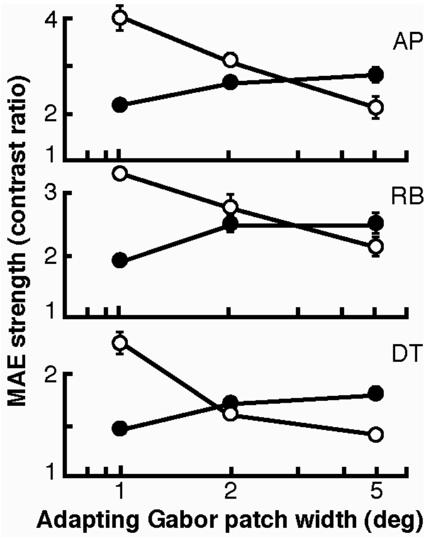

Figure 7. Effects of stimulus size and contrast on the MAE strength for three subjects (Experiment 1). Filled symbols show MAE strength for low-contrast adaptation (2.8%). Empty symbols show results for high-contrast adaptation (26%). Error bars are SEM.

indicated the perceived direction. The contrast ratio of two Gabor patches composing the test stimulus was adjusted under the control of two interleaved 'one-up—one-down' staircases. Each staircase converged 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 and Discussion

As hypothesised, MAE strength decreased with increasing size when observers adapted to a high-contrast Gabor patch, suggesting spatial suppression (Figure 7). This result is consistent with earlier observations (Sachtler & Zaidi, 1993; Murakami & Shimojo, 1995) that were restricted to high-contrast adapting stimuli. On the other hand, as predicted, when a low-contrast adapting stimulus was used, MAE strength increased with increasing size. The low contrast result is also a built-in control showing that the size difference between the large adapting pattern and the small test stimulus is not what is causing the reduced MAE at high contrast as suggested by Sachtler & Zaidi (1993).

These results psychophysically demonstrated surround suppression at high contrast using long duration stimuli. We suggest that the smaller MAE for large high-contrast stimuli is a result of a lower firing rate of motion-sensitive neurons during the adaptation period. Furthermore, given that MAE is often associated with area MT (Huk et al., 2001), the present result is another piece of evidence suggesting that psychophysically observed surround suppression is a perceptual correlate of the antagonistic center-surround neurons in MT.

In the remaining experiments, we used MAE to investigate whether certain contextual manipulations that determine whether a motion stimulus is perceived as a large object or multiple small objects also affect the strength of surround suppression.

Experiment 2

Methods

Stimuli were shown on a linearized monitor (800 x 600 resolution, 120 Hz). Viewing was binocular at 83 cm (yielding 2 x 2 arcmin per pixel). Ambient illumination was 4.8 cd/m^2. Background luminance was 60.5 cd/m^2. Stimuli were moving gratings. Spatial and temporal frequency were 1 cycle/° and 4°/s, respectively. Contrast was 26%. Three observers participated in the experiment. All procedures complied with institutionally reviewed guidelines for human subjects.

Four different adapting conditions were investigated (Figure 8). Note that the central region (i.e., the region where MAE was measured) was identical in four conditions:

- Small adapting pattern. A moving grating was presented in a disk with a diameter of 1.75°.
- Big adapting pattern. A moving grating was 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 diameter of the uniform disk section was 10° and the width of the fading border was 2.5°, resulting in the 15° stimulus diameter.
- “Cut” adapting pattern. Same as the big adapting pattern except that the stimulus was “cut” as shown in the Figure 8. The width of the cut sections was 2°. The central grating patch was identical to the small adapting pattern (diameter = 1.75°).

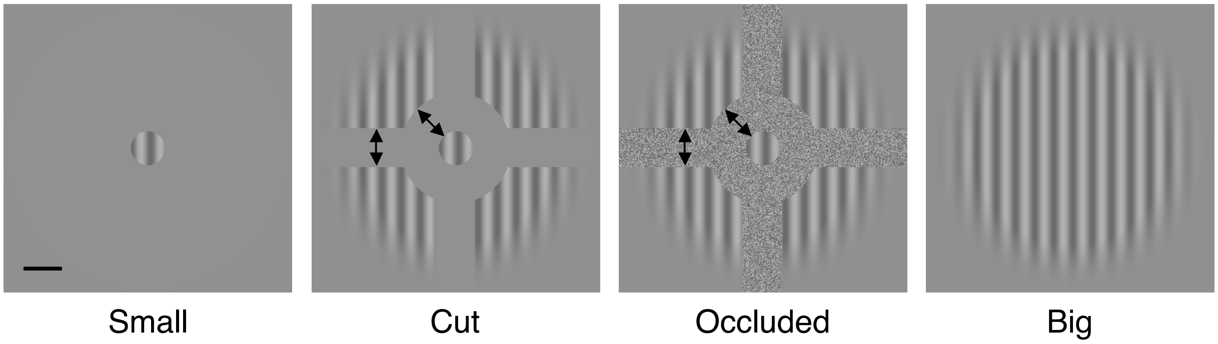

Figure 8. Single-frame snapshots of the stimuli in four Experiment 2 conditions. Scale bar in the bottom left corner and the arrows in the middle panels are 2°. The random-pixel occluder and the cut sections were always stationary. In separate experimental runs, the grating pattern drifted either leftward or rightward.

- "Occluded" adapting pattern. Same as the "cut" adapting pattern except that the cut sections were filled with the random-pixel texture (each texture pixel was 2 x 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 "occluded" condition, however, observers generally perceived a large moving grating behind an opaque occluder.

MAE was measured using the procedure described in Experiment 1. The test stimulus was slightly smaller than the small adapting pattern (diameter = 1.57°) to minimize the effects of fixational eye movements (Murakami & Shimojo, 1995).

Results and Discussion

We found that the smaller adapting pattern yielded larger MAE than the large adapting pattern (Figure 9), replicating the result of Experiment 1. Interestingly, the MAE strength for the "cut" and "occluded" conditions differed even though the size of the moving pattern in those conditions did not. The MAE for the "cut" condition did not differ from the MAE for the small adapting pattern. This result is in accord with the observer's perception of the "cut" pattern, which was typically perceived as a small moving object surrounded by moving segments. The MAE for the "occluded" condition was much smaller, approaching the MAE for the big adapting

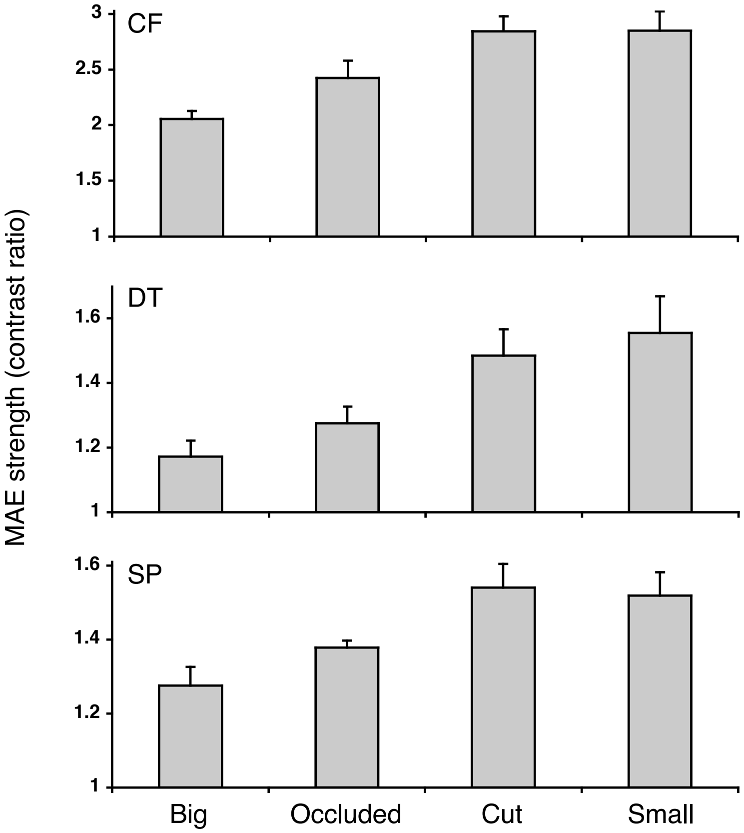

Figure 9. Effects of implied occlusion and stimulus size on the MAE strength for three subjects (Experiment 2). Error bars are SEM.

pattern. This result, again, corresponded with the observers' perception, as the occluded pattern was usually perceived as the large moving stimulus moving behind the occluder.

In summary, we find that the strength of surround suppression is not determined solely by the spatial extent of the stimulus pattern. Surround suppression, as measured by MAE, is also affected by whether the moving pattern is perceived as a large object or as disconnected small objects. Specifically, surround suppression occurs when we perceive a large moving object, but not when the "same" stimulus is perceived as multiple moving fragments.

In the present experiment, we used *implied* occlusion to manipulate how a moving grating is perceived. As occlusion generally entails a solid occluder between the observer and the occluded object, a more direct way to manipulate occlusion is to stereoscopically place an occluder in front of the moving object. Furthermore, the "cut" and "occluded" conditions differ as the "occluded" condition contains a random-dot texture. In the next experiment, we investigated surround suppression with stereo occlusion to better mimic real world occlusion and to minimize the differences between conditions.

Experiment 3

Methods

Stimuli were shown on a linearized monitor (1024 x 768 resolution, 60 Hz). Viewing was binocular through a stereoscope at 95 cm (yielding 1.35 x 1.35 arcmin per pixel). Ambient illumination was 0.01 cd/m^2. Background luminance was 30.0 cd/m^2. Stimuli were moving gratings. Spatial and temporal frequency were 1 cycle/° and 4°/s, respectively. Contrast was 99.9%. Three observers participated in the experiment. All procedures complied with institutionally reviewed guidelines for human subjects.

Four different adapting conditions were used, with two critical conditions illustrated in Figure 10. High contrast "fusers" shown in Figure 10 were present in all conditions. Again, note that the central region (i.e., the region where MAE was measured) was identical in four conditions:

- Small adapting pattern. A moving grating at zero disparity was presented in a disk with a diameter of 1.75°.
- Big adapting pattern. A moving grating at zero disparity was presented in a disk with a diameter of 8°.
- "Occluder behind" the big adapting pattern. Same as the big adapting pattern except that a background color (i.e., invisible) occluder was stereoscopically placed at the *uncrossed* disparity (5.4 arcmin) as shown in Figure 10. The width of the occluder sections was 2°. The central grating patch was identical to the small adapting pattern (diameter = 1.75°).
- "Occluder in front" of the big adapting pattern. This condition was identical to the "Occluder behind" condition except that a background color occluder was stereoscopically placed at the *crossed* disparity (5.4 arcmin).

"Occluder behind" and "Occluder in front" conditions were compared because the spatial extent of motion was identical in two conditions, but the perceived motion differed. In the "occluder behind" condition, observers generally perceived a small central grating that appeared

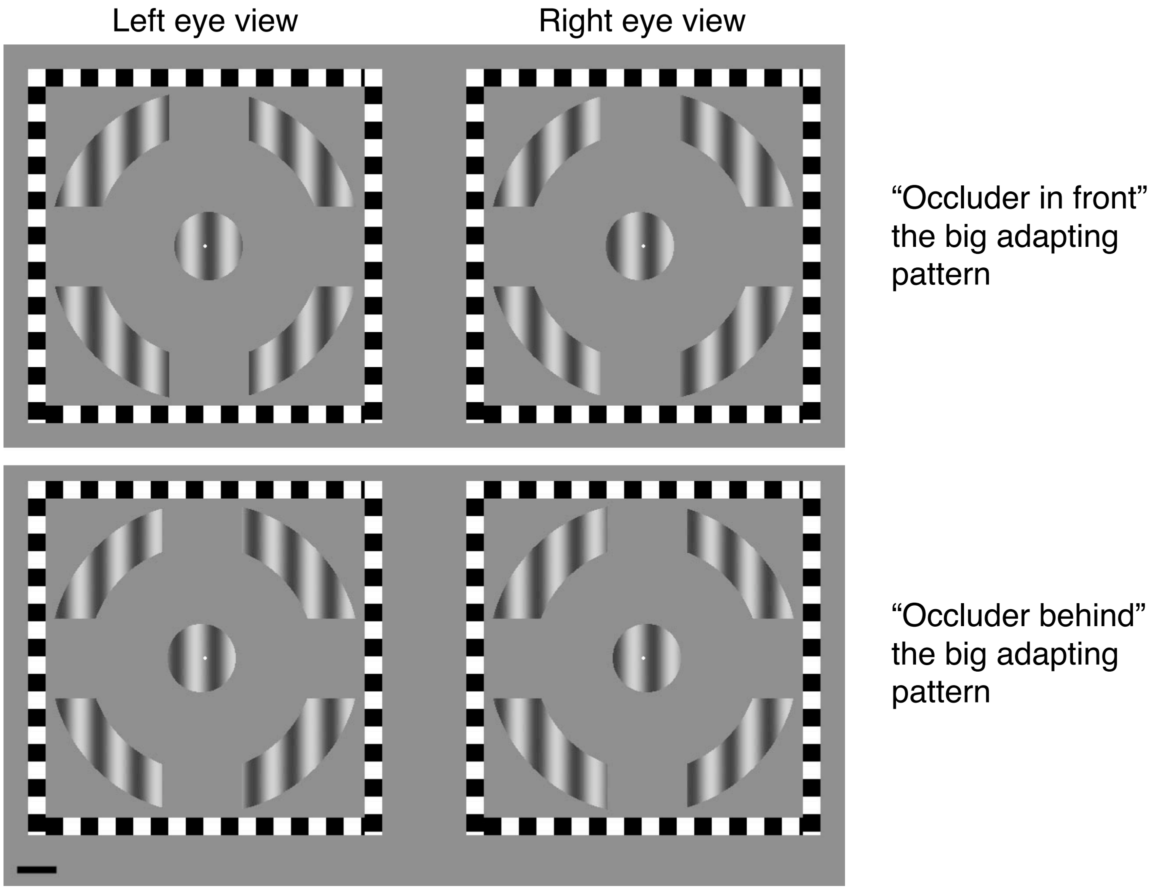

Figure 10. Single-frame snapshots of the stimuli in two critical Experiment 3 conditions. Scale bar in the bottom left corner is 1°. Grating pattern outlines were always stationary. In separate experimental runs, the grating pattern drifted either leftward or rightward. These illustrations are made for free-fusing.

as separate from the surrounding grating patches. In the “occluder in front” condition, however, observers generally perceived a large moving grating behind a rigid occluder.

MAE was measured using the procedure described in Experiment 1. The test stimulus was slightly smaller than the small adapting pattern (diameter = 2°) to minimize the effect of fixational eye movements (Murakami & Shimojo, 1995).

Results and Discussion

The small adapting pattern yielded a larger MAE than the large adapting pattern (Figure 11), replicating the results of Experiments 1 and 2. Analogous to the results of Experiment 2, the MAE strength differed between “occluder in front” and “occluder behind” conditions. The MAE

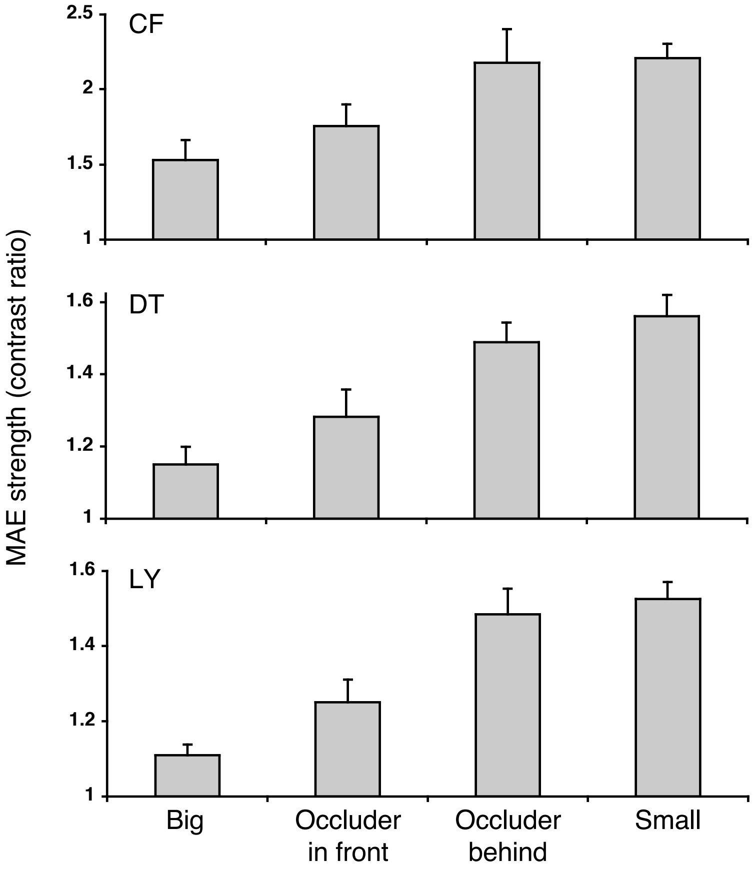

Figure 11. Effects of 3D occlusion and stimulus size on the MAE strength for three subjects (Experiment 3). Error bars are SEM.

for the "occluder behind" condition was similar to the MAE induced by the small adapting pattern. In contrast, the MAE for the "occluder in front" condition was significantly smaller. This result was in accord with observers' perception of the "occluder in front" stimulus, which was typically perceived as a large moving stimulus.

Taken together with the results of Experiment 2, the Experiment 3 results show that surround suppression of motion signals is affected by cues other than motion. The strength of surround suppression is seemingly determined not only by the stimulus size, but by also whether the stimulus is perceived as a large moving surface.

In the next experiment, we investigated whether surround suppression can be modulated by changing surround disparity while keeping the center stimulus at the fixation plane.

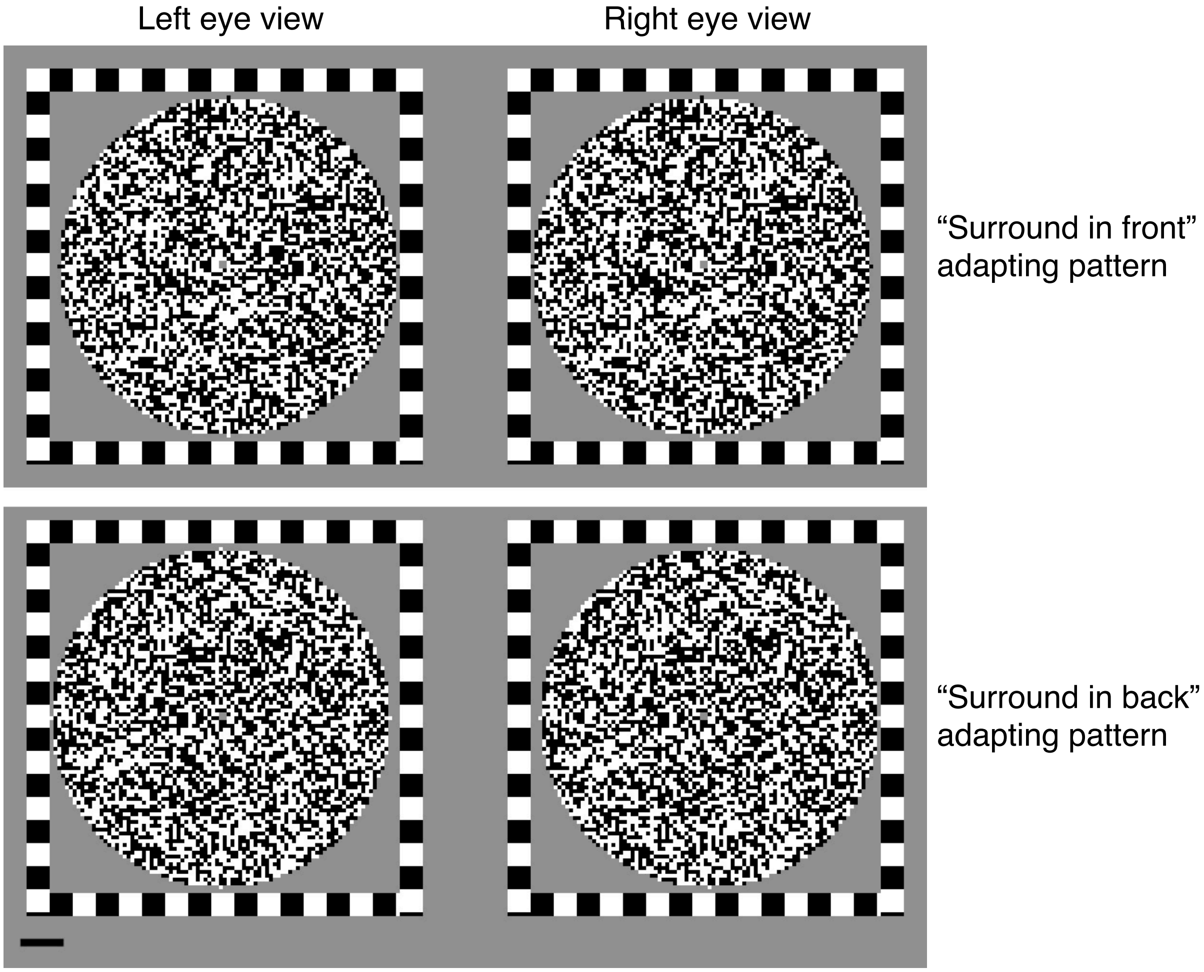

Figure 12. Single frame snapshots of the stimuli in two critical Experiment 4 conditions. Scale bar in the bottom left corner is 1°. In separate experimental runs, the random-texture pattern drifted either leftward or rightward. These illustrations are made for free-fusing.

Experiment 4

Methods

Stimuli were shown on a linearized monitor (1024 x 768 resolution, 60 Hz). Viewing was binocular through a stereoscope at 95 cm (yielding 1.35 x 1.35 arcmin per pixel). Ambient illumination was 0.01 cd/m^2. Background luminance was 30.0 cd/m^2. Stimuli were moving random-dot textures. We used moving random-dot textures because such stimuli created a better impression of depth than sinewave gratings. Size of each dot was 5.4 x 5.4 arcmin. Speed was

3.17°/s. Contrast was 99.9%. Three observers participated in the experiment. All procedures complied with institutionally reviewed guidelines for human subjects.

Four different adapting conditions were used. Two critical conditions are illustrated in Figure 12. High contrast "fusers" were present in all conditions. As in the previous experiments, the central region was identical in all four conditions.

- Small adapting pattern. A moving random-dot texture at zero disparity was presented in a disk with a diameter of 2.5°.
- Big adapting pattern. A moving random-dot texture at disparity was presented in a disk with a diameter of 8°.
- "Surround in front" adapting pattern. This stimulus consisted of the center and 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 is that the surround was presented with crossed disparity of 5.4 arcmin, thus appearing closer to the observer.
- "Surround in back" adapting pattern. This condition was identical to the "Surround in front" condition except that the surround was presented with uncrossed disparity (5.4 arcmin), thus appearing further away from the observer.

The experimental procedure was adjusted to work with a random-dot texture stimulus. The test stimulus was a partially correlated random-dot texture moving in the opposite direction from the adapting pattern. The diameter of the test stimulus was 2° (slightly smaller then small adapting pattern). A partially correlated test stimulus was used to null the MAE from the adapting pattern. That is, motion correlation of the test stimulus was adjusted until the test stimulus appeared to have no apparent motion direction. The motion correlation required for MAE nulling was taken as a measure of MAE strength (higher correlation indicates stronger MAE).

The initial adaptation was for 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. After viewing the test stimulus, observers indicated the perceived direction. The motion correlation of the test stimulus was adjusted under the control of two interleaved 'one-up—one-down' staircases. 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 and Discussion

We found that adapting to a smaller moving pattern resulted in stronger MAE than adapting to a larger moving pattern (Figure 13). This result generalizes the findings obtained with drifting gratings (Experiments 1, 2 and 3) to moving random-dot textures. Moreover, when the surround was presented stereoscopically at a different depth plane (either in front or behind the center), an intermediate MAE strength was measured. This finding suggests that surround suppression diminishes when center and surround regions are stimulated by motions at different disparities.

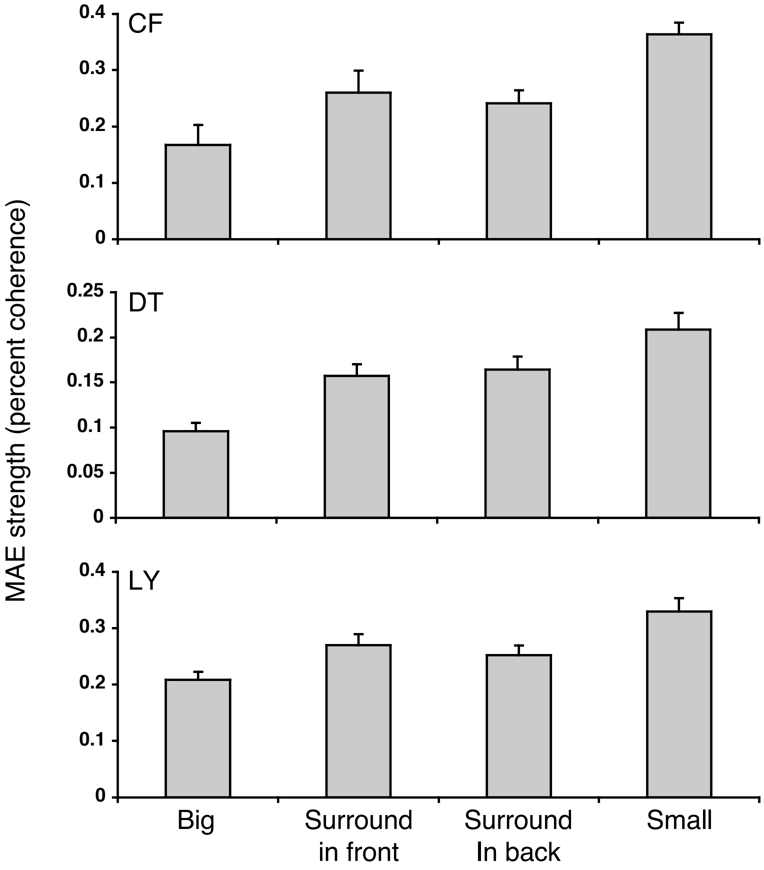

Figure 13. Effects of surround disparity and stimulus size on the MAE strength for three subjects (Experiment 4). Error bars are SEM.

The present result can be added to numerous findings about the interactions between motion perception and stereopsis (e.g., Nawrot & Blake, 1991; Tittle & Braunstein, 1993; Van Ee & Anderson, 2001). This coupling of motion and stereopsis is also reflected in 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 et al, 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 and Newsome, 1999; Maunsell & Van Essen, 1983). Given the disparity selectivity of MT neurons, within MT there exist computational resources for 'inhibiting' surround suppression if center and surround motions are at different depths. This hypothesis is supported by recent neurophysiological results (Bradley & Andersen, 1998).

Bradley and Andersen (1998) investigated the interaction between surround suppression and disparity sensitivity in MT. They found that the disparity tuning of center and surround regions tend to be different. That is, 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 depths. Surround suppression increased as either surround motion or its depth became more similar to motion in the center, indicating that the effects of disparity and motion are additive. Thus, when a neuron is unsuppressed it is ambiguous whether that is due to the surround motion being different from the center motion or because the surround motion is at a different depth.

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). This interpretation is consistent with the present results (Figure 13).

The typical physical arrangement of an object and its background usually results in objects usually being closer to the observer than their background. This environmental regularity is reflected in absolute disparity tuning of the center and surround regions of MT neurons; the center region tends to prefer near (crossed) disparities (Bradley & Andersen, 1998). A perceptual analogue of this neurophysiological asymmetry is not found in our results. A reason for this discrepancy is not immediately obvious.

General Discussion

We demonstrated surround suppression using MAE. We then used MAE as an experimental tool to study how more complicated stimulus arrangements affect center-surround interactions in motion and showed that surround suppression of motion signals is affected by cues other than motion. Evidently, suppression occurs when the visual context suggests a large moving surface. If the context suggests multiple moving surfaces, suppression is greatly reduced, even when local motion signals stay unchanged.

The findings described in this chapter (Experiments 2, 3, & 4) would be greatly enhanced if they would reverse at low contrast. This would strengthen the link between the present findings and surround suppression, as surround suppression is known to diminish with decreasing contrast (Figure 7; Tadin et al., 2003; Pack & Born, personal communication). Replication of Experiments 3 and 4 at low contrast is precluded by the observation that stereopsis breaks down at low contrasts (Cormack, Stevenson, & Schor, 1991). Replication of Experiment 2 at low contrast was similarly unsuccessful because lowering the contrast changed the perceptual appearance of the critical conditions. The interior grating edges in the "cut" condition did not appear sharp as in Figure 8. Most importantly, the cut sections were not visible because they "filled in" with the surrounding grating pattern. This increased spatial pooling at low contrast is consistent with the ideas put forth in this dissertation, but unfortunately, it fundamentally changes the appearance of the crucial stimulus.

The observation that center-surround MT neurons are suppressed when both center and surround regions are stimulated by the same direction of motion has been used to support the link between surround suppression and figure-ground segregation (Allman et al., 1985b). The assumption behind this argument is that suppression occurs because the center and surround are responding to the same visual feature (e.g., a large background motion). For this mechanism to be efficient, it should not be inhibited if different visual features stimulate the surround and center regions even when they are moving in the same direction. Indeed, this seems to be suggested by both the present findings and the neurophysiological results (Bradley & Andersen, 1998). The results presented in this chapter show that motion perception almost appears to behave ‘intelligently’ by employing suppressive interactions only in situations when the spatial pattern of motion appears to comprise a large moving surface.

In summary, the properties of surround suppression described in this chapter highlight a possible functional role of surround suppression in figure-ground segregation. This important functional link is explored more directly in Chapter VII.

CHAPTER VI

INVESTIGATION OF THE TEMPORAL PROPERTIES OF CENTER-SURROUND INTERACTIONS IN MOTION USING A REVERSE CORRELATION METHOD

Introduction

Surround interactions presumably involve neural circuits different from the circuits underlying the response tuning of the receptive field center. Initial explorations by Allman et al. (1985b) demonstrated that the surround suppression latency is 40 ms longer than the latency of the center response, suggesting that additional processing steps are required for the suppressive surround influence.

What pattern of neural connectivity might give rise to MT surround suppression? Tanaka et al. (1986) pointed out that at least three possible wiring schemes might underlie center-surround antagonism in MT. One possibility is that synaptic connections made by V1 inputs to MT neurons construct center-surround receptive fields. Indeed, some aspects of MT receptive field structure can be explained in terms of the inputs from V1 (e.g., Livingstone et al., 2001). Such a wiring scheme, however, conflicts with the low incidence of center-surround receptive-fields in layer IV of MT (Raiguel et al., 1995; Born, 2000) — the layer receiving the input from V1. An observation that the surround response is delayed (Allman et al., 1985b) is also at odds with the V1 feedforward hypothesis.

Another possibility is that feedback connections from higher visual areas, such as MST, construct the inhibitory surrounds in MT. This possibility is appealing as large receptive fields in MST seem to correspond to the large inhibitory surrounds in MT. It is also analogous to the results suggesting the role of MT feedback in surround suppression of V1 neurons (Hupé et al., 1998). Such a wiring scheme is also consistent with the reported delay of surround inhibition (Allman et al., 1985) that may allow for the transfer of signals to MST and back to MT. Furthermore, the response latencies of MT neurons with surrounds are longer than those of non-surround neurons (Raiguel et al., 1999), thus allowing even more time for a feedback signal to arrive “on time”. The main problem with the MST feedback hypothesis is that it has trouble accounting for the spatially complex heterogeneous surrounds in MT, which account for 80% of MT surround neurons (Xiao et al., 1997a, 1998). Such surrounds often have isolated inhibitory sub-regions that are much smaller than MST receptive fields.

The remaining possibility is that surround inhibition is mediated via intrinsic MT connections (Born & Tootell, 1992; Raiguel et al., 1995, 1999). Born & Tootell (1992) pointed out that wide-field neurons are likely candidates for the source of surround inhibition in MT. Similar to MST receptive fields, wide-field neurons integrate motion signals over a large area, but unlike MST neurons, they are potentially only one synapse away from center-surround neurons. Non-surround MT neurons (e.g., most layer IV neurons) may also provide surround inhibition. Such neurons could play a role in constructing spatially heterogeneous surrounds (Xiao et al., 1997a) because of their smaller receptive fields. In summary, the exact circuitry behind surround suppression in MT is still unknown, although construction of MT surrounds via intrinsic MT connections seems to be a plausible explanation.

One approach for learning about neural circuits, such as center-surround antagonism, is to investigate their temporal properties (Lamme, Super & Spekreijse, 1998; Lamme & Roelfsema, 2000). The basic idea is that the timing of a specific neural response aspect can give us clues about whether the circuit involved is feedforward, horizontal or feedback. The earliest part of the response in the visual cortex is usually taken to reflect feedforward response, while the activity modulations that occur later in the response are often considered as evidence of feedback (e.g., Lamme, 1995).

What can we learn about the center-surround interactions in motion from their temporal properties? The 40 ms delay of suppression reported by Allman and colleagues (1985b) should be taken as a only rough estimate of the delay of suppression because 40 ms was also the bin size they used to average spikes. Until recently, temporal aspects of surround suppression have been relatively ignored. A recent study by Borghuis et al. (2003), using a temporal reverse correlation method, replicated the result of Allman et al. (1985b) and showed that the inhibitory component of the surround response lags after the excitatory center response. The suppression lag measured by Borghuis et al. (2003) is about 10 ms. This relatively short surround suppression delay is consistent with the hypothesis that MT surrounds are constructed via intrinsic MT circuits.

To investigate temporal properties of center-surround interactions, we developed a psychophysical temporal reverse method inspired by the reverse correlation study of Borghuis et al. (2003). Reverse correlation methods generally use white noise stimuli (e.g., Livingstone et al., 2001). The motion energy of such stimuli is relatively weak, requiring longer experiments. To maximize “usable” motion energy, Borghuis and colleagues (2003) used fully correlated random-dot patches that frequently changed direction as their stimulus. This modification resulted in a time-efficient design where a large number of parameters can be explored.

A psychophysical analogue of the reverse correlation method is the classification images technique. This method was introduced in vision research by Ahumada (1996) and has longer tradition in audition (Ahumada & Lovell, 1971). Most of the experiments using classification images investigated spatial aspects of vision, with only a few experiments exploring temporal questions (Neri & Heeger, 2002). A classification image experiment typically involves an observer performing a detection or discrimination task on a stimulus presented in random noise. Emulating the reasoning of Borghuis et al. (2003), we developed a temporal reverse correlation method that relied on fully correlated motion stimuli that frequently changed directions. We use the term reverse correlation to describe the method used in this chapter because our stimulus design and the analysis are more similar to the neurophysiological reverse correlation method than the psychophysical classification images technique.

We investigated whether the discriminability of center motion is influenced by the specific surround motion direction at a specific time relative to the occurrence of the center motion. Next, we explored whether the timing of surround influence changes with changes in surround contrast. This experimental question was motivated by observations that neuronal latencies increase with decreasing contrast (Lennie, 1981; Maunsell & Gibson, 1992; Maunsell et al., 1999).

Methods

Stimuli

Stimulus patterns were created in MatLab with the Psychophysics Toolbox (Brainard, 1997) and Video Toolbox (Pelli, 1997) and shown on a linearized monitor (800 x 600 resolution, 200 Hz). To obtain 200 Hz refresh rate, which was critical for the present experiment, we used a high-speed Totoku PROCALIX monitor driven by a VillageTronic MP 960 graphics card. Viewing was binocular at 83 cm (yielding 2 x 2 arcmin per pixel). Ambient illumination was 4.8 cd/m^2. Background luminance was 42.3 cd/m^2. Stimuli were moving random-dot textures. The size of each dot was 6 x 6 arcmin, black or white, with equal probability. Three observers

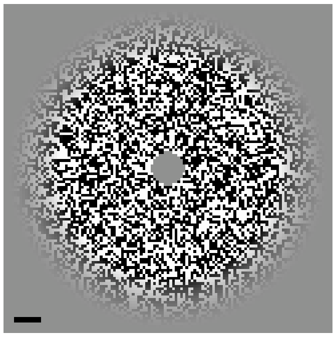

Figure 14. Single-frame snapshot of the surround pattern. The random-dot texture moved either up or down, with the direction randomly chosen every 5 ms. Such motion sequences were typically perceived as *very fast* up-down jitter. The central hole, the location where the center motion appeared, was stationary. Scale bar is 1°.

participated in the experiment. All procedures complied with institutionally reviewed guidelines for human subjects.

A moving random-dot surround (Figure 14) was 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 diameter of the uniform disk section was 8.2° and the width of the fading border was 2.05°, resulting in the 12.3° stimulus diameter. In the center of the moving random-dot texture was a small hole (diameter = 1.3°) where the center random-dot pattern was briefly presented on each trial. The contrast of the center was 92%. In four different conditions, the surround contrasts were 92%, 27%, 6.5%, and 1.7%.

The temporal sequence of events is illustrated in Figure 15. The surround pattern was presented for 500 ms, during which the random-dot texture moved randomly in the vertical

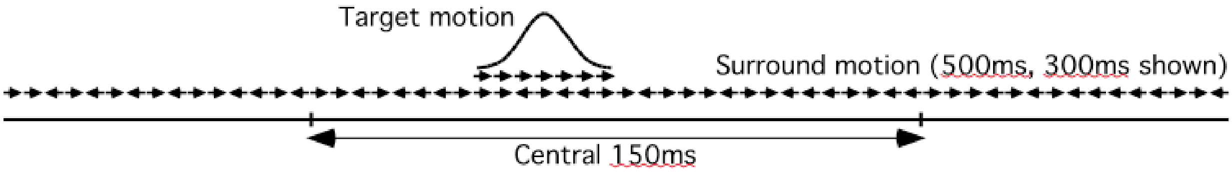

Figure 15. An example of the temporal sequence of surround and center motion events. For illustration purposes motions were depicted as horizontal. The motions in the experiment were vertical. The Gaussian envelope over the center (i.e., target) motion depicts contrast modulation of the center motion in time.

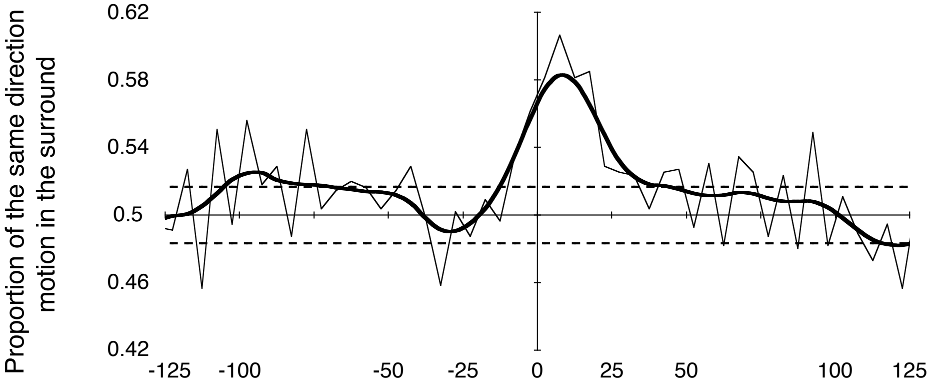

Figure 16. Illustration of the raw data sample and the Gaussian smoothing of the raw data. The data sample is for the incorrect trials of observer DT in a condition with high contrast (92%) surround. Dashed horizontal lines are ±2 standard deviations derived from the simulation illustrated in Figure 17.

direction at 20°/s (i.e., randomly jittered up-down). A new direction (up or down) was randomly selected every 5 ms (every frame on a 200 Hz monitor). At a randomly chosen time during the central 150 ms, the center stimulus was briefly presented and moved either up or down at 20°/s. The center contrast was ramped on and off with a temporal Gaussian envelope (duration is defined as the 2σ of the temporal Gaussian). The observers' task was to identify the direction of the center pattern. Performance was kept near 70% correct by two interleaved adaptive staircases adjusting the center pattern duration. Duration thresholds in this experiment were very low (as low as 5 ms) because of the fast center speed. For example, a 6.86 ms threshold (which was observer DT's average threshold in four conditions) would be shown in 5 video frames with contrasts that are 1.4%, 34.6%, 100%, 34.6%, and 1.4% of the peak contrast.

Analysis

To quantify the temporal aspects of center-surround interactions, we separately analyzed temporal sequences of surround motion that occurred during correct and incorrect trials. For both correct and incorrect trials, the specific goal was to look for patterns in the temporal sequence of surround motions that were different than expected by a random process.

To perform such an analysis, surround motions were coded relative to the center motion on trial by trial basis. If the 5 ms motion step in the surround was the same as the center motion, it was coded as 1. If it was opposite to the center motion, it was coded as 0. For every trial, this resulted in the temporal sequence of 0's and 1's with the origin (i.e. 0 ms point) aligned with the peak of the center motion. Correct and incorrect trial sequences were averaged separately and smoothed with a moving Gaussian window. The standard deviation (σ) of the smoothing Gaussian was 7.5 ms; this σ removed most of the noise but did not affect the overall shape of the result. Figure 16 shows an example of an actual raw data and the result of smoothing. All the analyses were done on smoothed raw data.

A basic assumption behind this method is that if surround motion has no influence on the discriminability of the center motion, then after many trials the result at each 5ms time interval would approach 0.5 (i.e. equal proportion of the same and opposite directions in the surround). If, for example, the occurrence of the same direction motion at a specific 5ms interval increases the likelihood of making a mistake, then the result for the incorrect trials at that time interval would be greater than 0.5. Note that the incorrect trials are more informative than the correct trials; in a 2AFC design, a correct response is often a correct guess. Hence, to increase the number of incorrect trials, a relatively low performance level (70% correct) was maintained.

The method yields meaningful results only after a large number of trials; i.e., when the random noise starts to 'average out'. All subjects ran 2,500 trials per condition, with the first 500 trials discarded as practice. Observers typically ran 1000 trials per session. Given the 70% threshold in the experiment, there were about 600 incorrect trials and 1400 correct trials for each condition. The total number of trials in this experiment was 30,000 (the data presented in Figure 21 required an additional 20,000 trials).

To quantify the variability expected by the random process alone, we ran a Monte Carlo simulation of the experiment assuming that surround has *no* influence on the discriminability of center motion. The details were as follows: 2000 random sequences of surround motion were generated, and center motion was randomly chosen for each surround sequence. Surround motion sequences were coded with 1's and 0's as described above. 70% of those sequences were labeled as correct trials and the remaining 30% of the sequences were incorrect trials. Correct and incorrect trial sequences were averaged separately and were smoothed with a moving Gaussian window (σ = 7.5 ms), as shown in Figure 16. This simulation was repeated 100 times, yielding 100 incorrect trial curves (shown in Figure 17) and 100 correct trial curves. We estimated two standard deviation boundaries from these two sets of curves.

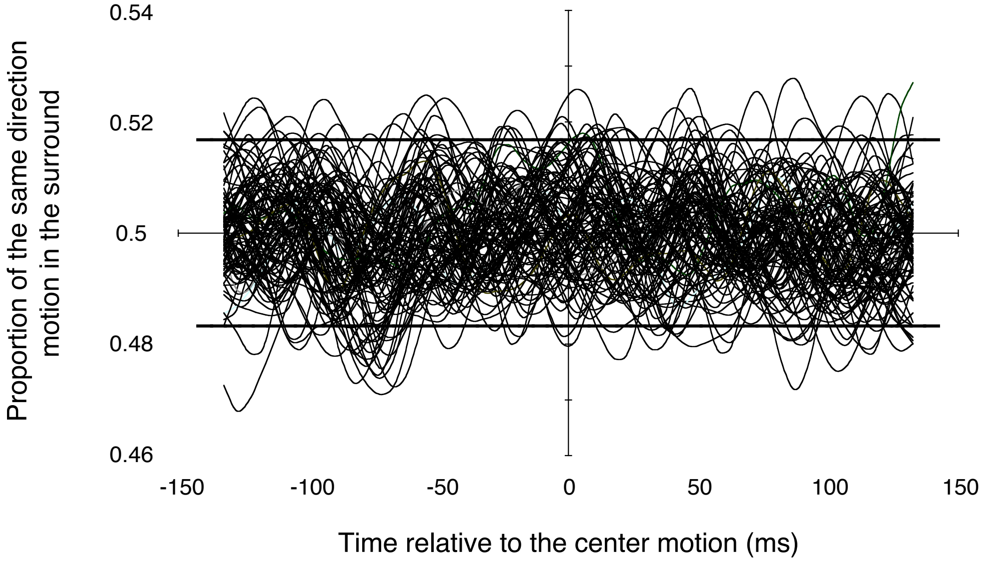

Figure 17. The result for the incorrect trials of 100 2000-trial Monte Carlo simulations of the temporal reverse correlation experiment assuming no surround influence on the center. Bold horizontal lines depict ±2 standard deviations of the simulation result.

This method is designed to yield a temporal profile of the surround influence on the center motion. This temporal profile is characterized by five parameters:

(1) direction of influence (peak greater or less than 0.5),

(2) strength of influence (deviation of the peak influence from 0.5),

(3) peak time (the time of the peak influence relative to the center motion),

(4) start time (the earliest time at which significant influence is observed), and

(5) duration of influence (time between the start time and the stop time).

Of particular interest is to determine whether any of these parameters change with changes in surround contrast.

Results

The incorrect trial results of the temporal reverse correlation experiment are shown in Figure 18. The obtained temporal profiles significantly differ from what is expected by chance alone (Figure 17), indicating that the surround motion had an effect on the discriminability of the center motion. Temporal profiles lay above 0.5 for all observers and all surround contrasts, indicating that *same* direction of motion in the surround increased the probability of making a

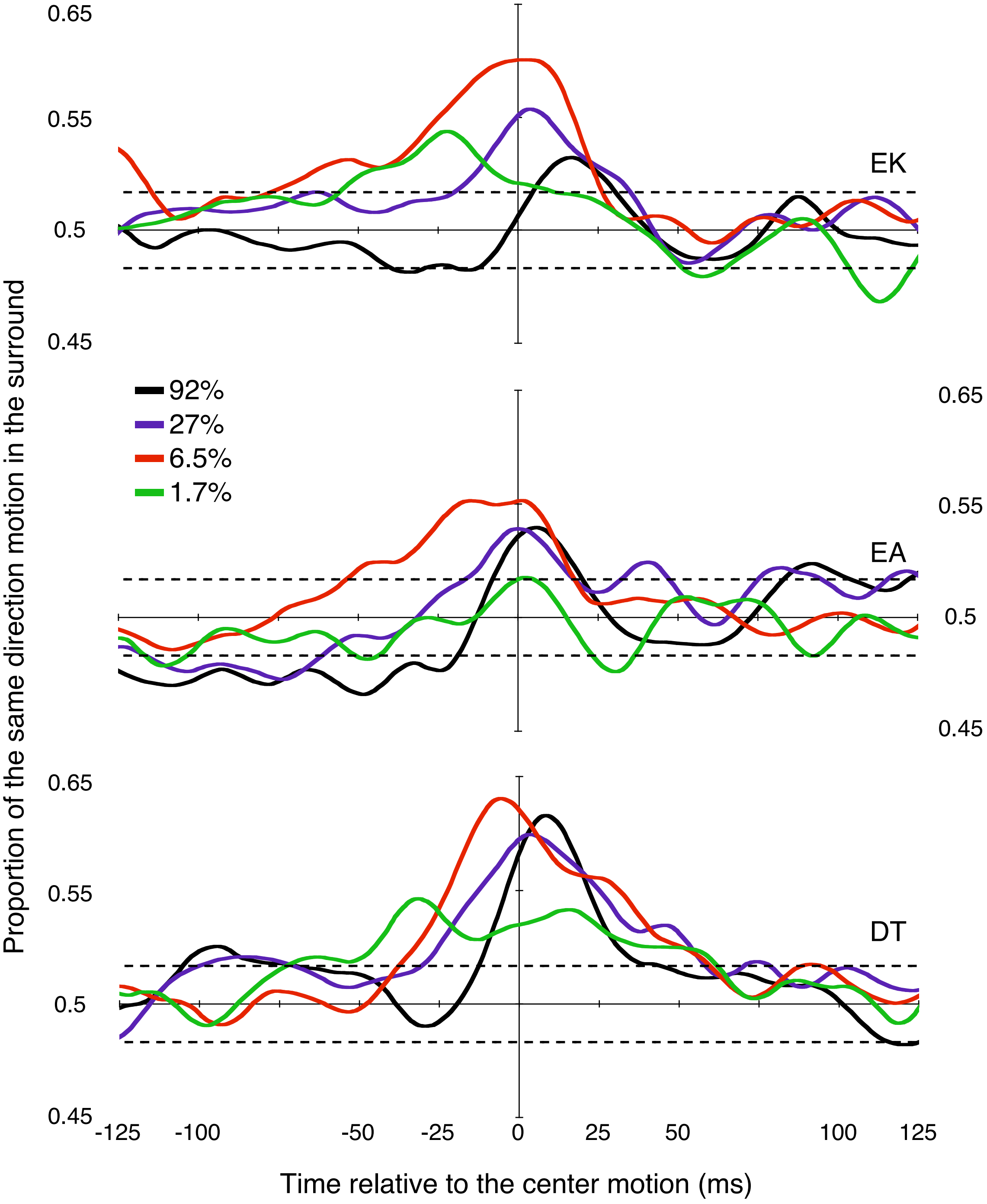

Figure 18. Temporal reverse correlation functions depicting incorrect trial results for three observers. Each curve represents data for a given surround contrast. Data were smoothed as illustrated in Figure 16. Dashed horizontal lines are ±2 standard deviations derived from the simulation illustrated in Figure 17.

mistake. Note that these results also indicate decreased probability for making a mistake when the surround moved in the opposite direction. Thus, Figure 17 results can be interpreted as same-direction suppression, opposite-direction facilitation or the combination of the two effects. Same-direction suppression seems more likely because other findings in this proposal are consistent with such a hypothesis and because a recent binocular rivalry study demonstrated the lack of opposite-direction facilitation in motion perception (Paffen, Tadin, te Pas, van der Smagt, Lappin, & Verstraten, in press).

To get a better estimate of the temporal characteristics of the surround influence, the individual results were averaged (Figure 19). Quantitative estimates of these temporal characteristics are presented in Table 1. Peak time, start time (both marked with arrows in Figure 19) and the duration of influence show a systematic dependence on surround contrast: the temporal profile of surround influence was longer, started earlier and peaked earlier as the surround contrast was decreased. These results may be a result of longer and more variable neural response latencies at low contrast (Maunsell et al., 1999; Lennie, 1981; Maunsell & Gibson, 1992).

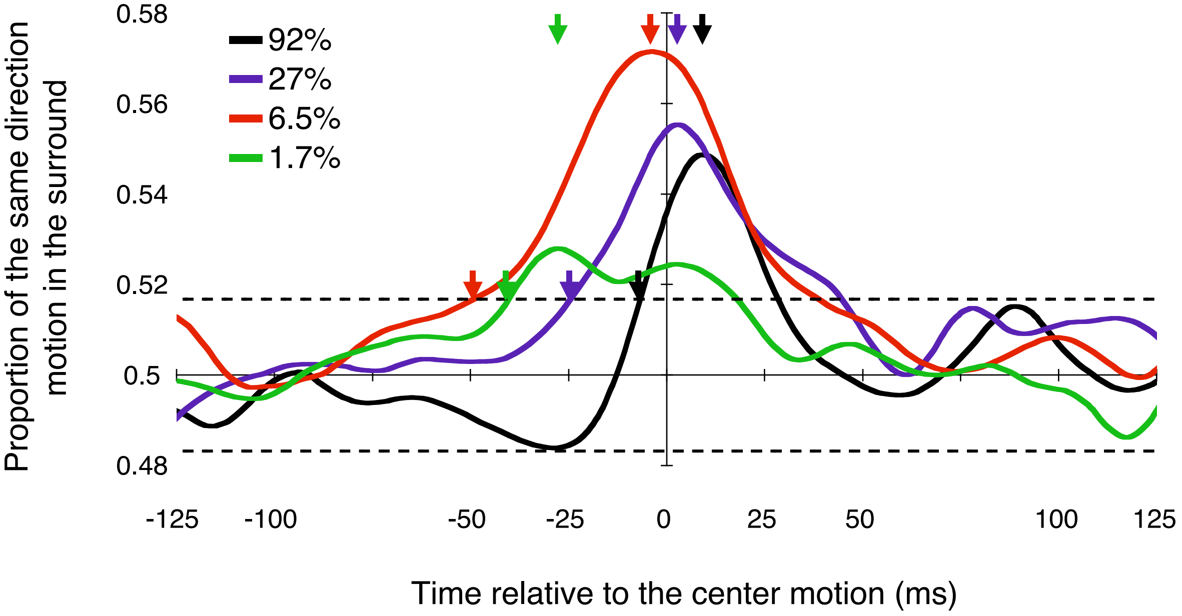

Figure 19. Temporal reverse correlation functions depicting incorrect trial results averaged over three observers. For each surround contrast, colored arrows indicate the peak surround influence (top arrows) and the times at which surround influence first reaches significance (arrows along the dashed line). Other figure details are as described in Figure 18.

Table 1. Quantitative description of the temporal profiles in Figure 19. Measures presented in the table are defined in the Methods. *Strength of influence* is also expressed in terms of standard deviations away from 0.5 (in parenthesis). *Peak time* and *start time* are also shown as relative to 92% surround contrast estimates (in parenthesis). To obtain a more precise estimate of *peak time*, it was calculated as a weighted average of data within ±10 ms of temporal point where the surround influence was strongest.

	Surround contrast			
	92%	27%	6.5%	1.7%
Direction of influence	same dir. suppression	same dir. suppression	same dir. suppression	same dir. suppression
Strength of influence	0.548 (5.8 σ)	0.555 (6.6 σ)	0.571 (8.5 σ)	0.528 (3.3 σ)
Peak time	8.1 ms (0 ms)	2.6 ms (5.5 ms)	-2.6 ms (10.8 ms)	-27.3 ms (35.5 ms)
Start time	-2.5 ms (0 ms)	-22.5 ms (20 ms)	-47.5 ms (45 ms)	-37.5 ms (35 ms)
Duration of influence	35 ms	70 ms	90 ms	60 ms

There was also a noticeable difference in the strength of influence for different surround contrasts. This difference is partially due to the interaction between the Gaussian smoothing of the data and the variable duration of influence for different conditions. That is, smoothing of a narrow function (e.g., 92% contrast condition) reduces its height (see Figure 16) more than smoothing of a broad function. Pre-smoothing peaks of 92%, 27% and 6.5% contrast conditions were 0.563, 0.565 and 0.585, respectively. Possible explanations for the differences among temporal profile functions for different contrasts are considered in the Discussion.

The reverse correlation experiment was designed to maximize the usability of incorrect trials, but we also found significant effects in correct trials. The average temporal profile for correct trials is shown in Figure 20. The temporal profiles are now below 0.5, indicating that observers were less likely to correctly identify motion direction when there was same direction motion in the surround. This is simply a re-formulation of the result for incorrect trials. The details of the temporal profiles for different contrast (e.g., peak time, start time and the duration of the influence) are similar to those estimated from the incorrect trials.

We attempted to repeat the above described reverse correlation experiment with low-contrast center motion, but the results did not differ from chance. A potential problem was that

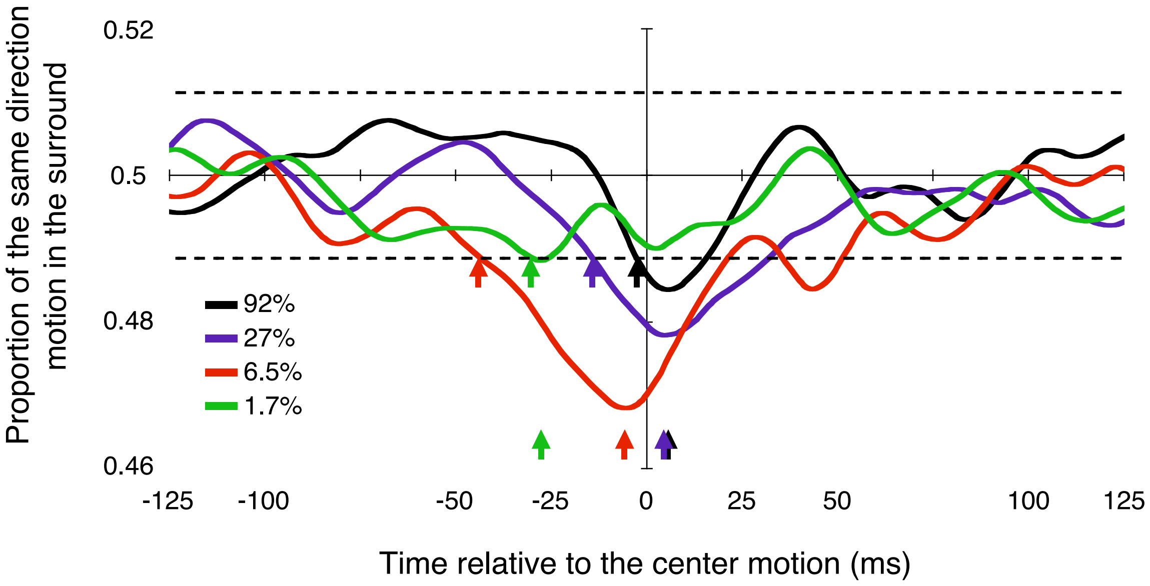

Figure 20. Temporal reverse correlation functions depicting correct trial results averaged over three observers. For each surround contrast, colored arrows indicate the peak surround influence (top arrows) and the times at which surround influence first reaches significance (arrows along the dashed line). Dashed horizontal lines are ±2 standard deviations derived from the Monte Carlo simulation described in the Methods. Other figure details are as described in Figure 18.

the duration threshold for the low-contrast center motion was typically an order of magnitude higher than with high-contrast center motion. This is critical because the success of the reverse correlation experiment depends on having a very brief target motion. With a prolonged center motion, a large number of surround motions will have "an opportunity" to influence discriminability of center motion, essentially averaging each others opposite influences. To get around this problem we made the following changes to the reverse correlation method:

- Duration thresholds for the low-contrast center were lowered by replacing the Gaussian temporal envelope with a trapezoid-like temporal envelope. This new profile was created by truncating the top half of the Gaussian profile and adding 0.5 (i.e., 50% contrast) to the truncated profile. For example, a 17.4 ms threshold (average threshold for the data shown in Figure 20) would be shown in eleven 5-ms frames with contrasts that are 52%, 57%, 73%, 100%, 100%, 100%, 100%, 100%, 73%, 57%, and 52% of the peak center contrast. This was still a relatively long stimulus presentation, but it was much shorter than the threshold stimulus duration when the standard Gaussian envelope was used.

- To reduce the number of different surround directions that may have an influence on the discriminability of the center motion during each trial, a new direction of surround motion was randomly chosen every 10 ms or, in a separate condition, every 15 ms. This reduced the number of motion direction changes in a given time period.
- Center contrast was chosen to be relatively low, but still high enough to yield moderately low thresholds. Based on the results of pilot explorations, a 5.25% center contrast was used in the 10 ms surround motion condition and a 6% contrast was used in the 15 ms surround condition.

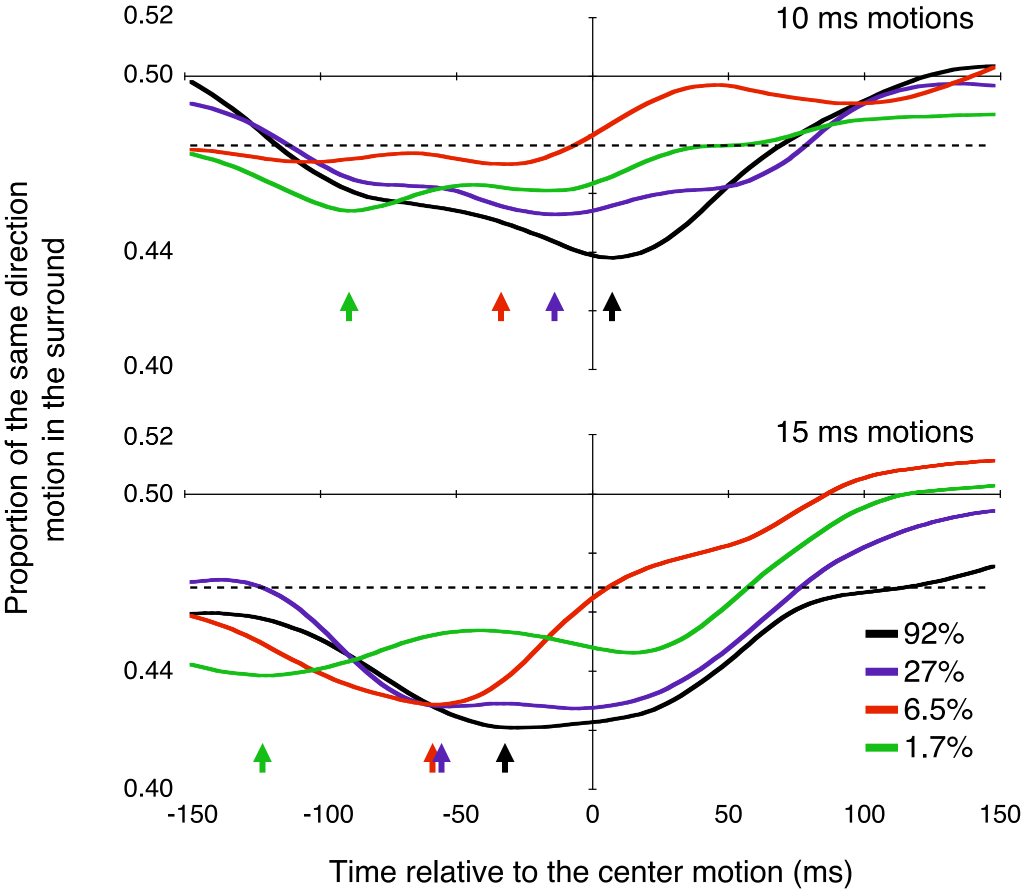

Figure 21. Temporal reverse correlation functions depicting incorrect trial results for observer EA in the low-contrast center condition. The top and bottom panels show data for the displays in which the surround was constrained to move in a given direction for 10 and 15 ms, respectively. For each surround contrast, colored arrows indicate the peak surround influence. The raw data was smoothed with a moving Gaussian ($\sigma = 22.5$ ms). Separate Monte Carlo simulations were performed to estimate two standard deviation boundaries. The details of the simulations were as described in the Methods except that surround motion parameters were adjusted to match the changes we made.

The results for one subject who completed the low-contrast center experiment are shown in Figure 21. The reverse correlation temporal profiles are much broader than in the high-contrast center experiment. This broadening is most likely due to the longer center motion presentation and changes we made to the surround motion.

The most important aspect of the low-contrast center result is that the temporal profiles are the inverted version of the high-contrast center profiles (contrast Figure 21 with Figure 19). This indicates that *same* direction surround motion decreased the probability of making a mistake, suggesting same-direction facilitation. To confirm that this result is not somehow a consequence of a change in surround motion parameters, a pilot exploration was conducted using 10ms and 15ms surround motions with a high-contrast center. The results yielded broad temporal profiles resembling those in Figure 21, but, in contrast with Figure 21 results, all profiles hovered above 0.5.

The broad temporal influence functions for low-contrast center motion preclude accurate estimation of their temporal characteristics. Nevertheless, the peaks (i.e., dips) of the functions appear to have the same dependence on surround contrast as the high-contrast center: progressively earlier peak times with decreasing contrast (Figure 21).

Discussion

The temporal reverse correlation method allowed us to estimate the temporal properties of center-surround interactions with relatively high precision, especially for very brief high-contrast center motion. These results were obtained from surround motions that were perceived simply as a very fast up-down jitter. Observers noted that it was impossible to consciously perceive what surround motion sequence occurred just before and during center motion presentation. This makes it all that more remarkable that the analysis of the raw data revealed strong and reliable patterns of surround influence on the discriminability of the center motion.

We describe interactions between center and surround motions and their dependency on relative direction, contrast and timing. Same-direction surround motion reduced the discriminability of high-contrast center motion and improved the discriminability of low-contrast center motion, regardless of surround contrast. The timing of the observed center-surround interactions depended on surround contrast; as the contrast of the surround decreased, surround motion needed to occur earlier relative to the center motion to have an effect on observers' performance.

The longer neural latency associated with weaker visual stimuli (Maunsell et al., 1999) may explain differences in the start and peak time of the temporal profile for different contrast surrounds (Figure 19). A "slow" low-contrast surround signal must be initiated well before the center signal to arrive on time to interact with the center signal. A "fast" high-contrast surround should be initiated only slightly before the center signal for the interaction to occur. An interesting aspect of our result is that the peak times of the 27% and 92% contrast surrounds are actually ahead of the *physical* occurrence of the center motion — an observation that on the face value conflicts with the physiologically observed delay of suppression (Allman et al., 1985b; Borghuis et al., 2003). This observation, however, is compatible with the speculation that the visual latency of the center motion is relatively slow. The peak contrast of the center motion was 92%, but most of the center motion was at much lower contrast because its contrast was ramped on and off with a Gaussian envelope — likely prolonging the center motion latency. Note that because the center motion latency is unknown, the present method cannot measure the latency difference between the center and surround signals. Only the relative latency difference for different contrast surrounds can be estimated.

Increased variability in the latency of low-contrast stimuli (Maunsell et al., 1999) may explain the broader temporal influence functions for low contrast surrounds. Specifically, the increased range of surround latencies at low contrast extends the range of time points when surround motion can occur and still interact with the center motion. On the other hand, less variable latency of high-contrast stimuli restricts the range of relative temporal offsets for which the center and surround will interact.

We also show that the contrast of the center determines whether the spatial interactions in motion are suppressive or facilitatory (Figure 19 vs. Figure 21). This is an important observation that extends the initial psychophysical description of surround suppression (Tadin et al., 2003). Tadin et al. (2003) did not vary the contrasts of the center and surround separately, precluding any conclusions about whether the center or the surround contrast determines the sign of their interaction. The present finding is consistent with modeling work suggesting that the activity level of the classical receptive field (i.e., center) determines the nature of center-surround interactions. Specifically, surround suppression is hypothesized to occur at high levels of center activity, while surround facilitation should be more pronounced at low levels of center activity (Stemmler, Usher & Niebur, 1995; Somers at al., 1998).

An important motivator for using the reverse correlation in neurophysiology is its time-efficiency — reverse correlation can be computed for every spike. In contrast, the psychophysical reverse correlation described here is extremely time-inefficient. Instead of using frequent spikes as the basis of the computation, we rely on infrequent observers' responses. Nevertheless, the potential benefits of this technique are well worth the extra effort. The psychophysical temporal reverse correlation may be adapted to investigate other visual mechanisms where different components of the response may have different temporal profiles such as iso-orientation suppression (Bair, Cavanaugh & Movshon, 2003), figure-ground discrimination (Lamme, 1995) and illusory contour processing (Ramsden, Hung & Roe, 2001).

CHAPTER VII

ROLE OF CENTER-SURROUND SUPPRESSION IN MOTION-BASED FIGURE-GROUND DISCRIMINATION

Introduction

As detailed in the previous chapters, center-surround surround suppression plays a prominent role in the visual processing of motion. This observation is supported by both neurophysiological (e.g., Born et al., 2000) and psychophysical (e.g., Tadin et al., 2003) evidence. Psychophysically, 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 the face value, surround suppression appears to hinder rather than enhance vision.

One way to rationalize this seemingly maladaptive visual mechanism is a hypothesis that surround suppression has an important functional role. The reduced visibility of large moving patterns, then, can be considered a "side effect" of surround suppression. As shown in the previous chapters, studying side effects of surround suppression may give us insights in how center-surround mechanisms operate, but it can only offer suggestions about their functional roles. This chapter describes two experiments designed to test a possible functional link between surround suppression and motion-based figure-ground segregation.

Vision is remarkably good at detecting relative motion and segregating moving surfaces (e.g., Regan, 1989; Braddick, 1993; Nawrot et al., 1996; Lappin, Donnelly & Kojima, 2001), but it is an open question whether these visual abilities fully or even partially derive from center-surround mechanisms. One experimental strategy for linking a perceptual mechanism such as surround suppression with its possible function is to investigate whether the changes in stimulus parameters that affect the mechanism also affect its putative function. An obvious choice in this case is stimulus contrast, as surround suppression shows strong and counterintuitive dependence on contrast. The hypothesis is that as surround suppression gets stronger with increasing contrast, figure-ground discriminations will improve in a similar manner. This hypothesis, which predicts a *negative* correlation between motion-discriminations of a large stimulus and figure-ground discrimination, was investigated in the first experiment.

By testing a large number of observers in various surround suppression tasks, we have noticed that participants vary in the strength of surround suppression. Such individual variability is usually considered a nuisance in psychophysical experiments and measures are often taken to minimize between-subject variability (e.g., by testing only well-practiced observers). Individual variability, however, can be exploited to study functional links between various visual functions (Wilmer, in press). In Experiment 2, we looked for the correlation between observers' ability to perceive motion-defined forms and their surround suppression strength.

Experiment 1

Methods

In all experiments, stimulus patterns were created in MatLab with the Psychophysics Toolbox (Brainard, 1997) and Video Toolbox (Pelli, 1997) and were shown on a linearized monitor (1024 x 768 resolution, 120 Hz). Viewing was binocular at 83 cm (yielding 1.5 x 1.5 arcmin per pixel). Ambient illumination was 4.8 cd/m^2. Background luminance was 60.5 cd/m^2.

The stimuli were moving random-dot patterns consisting of light and dark pixels (each 3 x 3 arcmin) presented in a raised cosine envelope (Figure 22). From frame to frame of the animation, half of the pixels shifted in one direction (6.2°/s) while the remaining pixels were randomly regenerated (50% correlation). These conditions produced vivid motion perception at suprathreshold exposure durations. The size was fixed and relatively large (stimulus diameter = 10.57°). To allow presentation of brief motion stimuli, stimulus contrast was ramped on and off with a temporal Gaussian envelope (duration is defined as the 2σ of the temporal Gaussian). Duration thresholds (82%) were estimated by interleaved Quest staircases. For each condition, four observers ran four pairs of interleaved staircases, with the first pair discarded as practice. Feedback was provided. All procedures complied with institutionally reviewed guidelines for human subjects.

The motion discrimination task and the figure-ground discrimination task were conducted at 6 contrast levels (9% - 92%). This yielded 12 conditions, whose order was randomized. In the motion discrimination task, observers identified motion direction of a random-dot pattern that moved either upward or downward (Figure 22). In the figure-ground discrimination task, observers discriminated between two motion-defined shapes (Figure 22, 45° rightward tilted ellipse vs. 45° leftward tilted ellipse). The pixels within the elliptic region moved either upward or downward (direction randomly chosen on each trial), while the pixels outside the elliptic

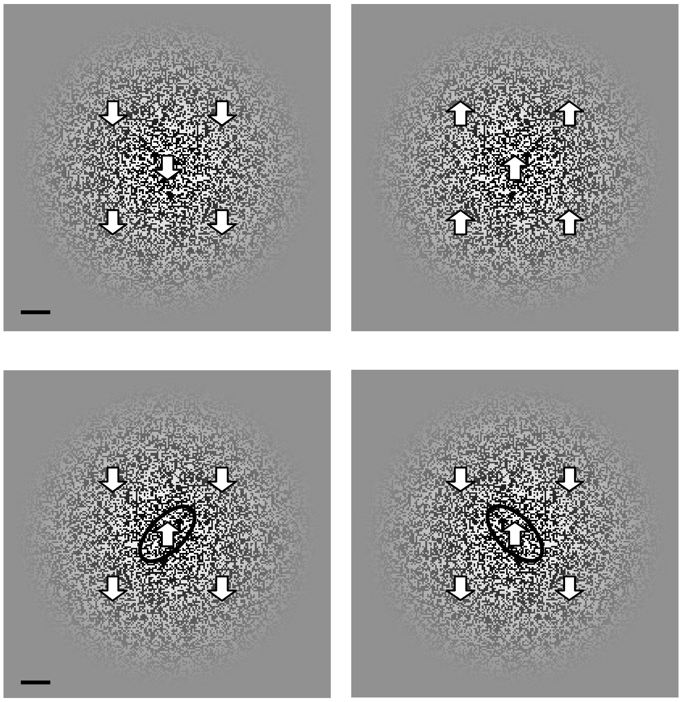

Figure 22. Single-frame snapshots of stimuli in the motion-discrimination (top panels) and figure-ground tasks (bottom panels). White arrows depict direction of motion. Oval outlines in the bottom panels indicate the subsections of the stimulus within which random-dot pattern moved in the opposite direction from the rest of the stimulus. The outline and arrows were not present in the actual stimulus. Scale bar is 1°.

region moved in the opposite direction. Long and short axes of the ellipse were 2.28° and 1.14°, respectively. Note that the single frames from the motion and figure-ground discriminations tasks are indistinguishable (i.e., both are featureless random-dot patterns as shown in Figure 22).

Results

Results from the motion discrimination task (Figure 23, filled circles) showed decreasing performance with increasing contrast. This replicated the previous result with the large moving stimuli (Tadin et al., 2003) and may be taken to indicate that surround suppression increases with increasing contrast. On the other hand, performance in the figure-ground discrimination task improved with contrast (Figure 23, empty circles).

A notable aspect of the results is that whenever there was an increase in motion discrimination thresholds there was often a proportional decrease in figure-ground discrimination thresholds. This pattern of results was observed in all subjects in spite of differences in overall performance and in the average data (note large differences in y-axis ranges). The only noteworthy exception is low-contrast data in the motion discrimination task for subject EK. The lack of further improvement with decreasing contrast for EK is perhaps suggestive of a floor effect for that subject. The relationship between surround suppression and figure-ground discrimination was quantified by correlation coefficients between the two tasks. Remarkably, average data and the data for 3 out of 4 subjects yielded correlations greater than –0.98 ($p \ll 0.001$). Correlation for observer EK was –0.85 ($p < 0.05$).

Furthermore, for all observers the two functions crossed at some intermediate contrast, with motion discrimination being more difficult than figure-ground discrimination at high contrasts. At 92% contrast, perceiving the motion of a large pattern was on average over 6 times harder than perceiving the shape of a motion-defined figure within the same sized pattern.

Discussion

We found a strong negative correlation between figure-ground discrimination and motion discrimination in an experiment where both tasks were performed at different contrast levels. We take this result to indicate a positive correlation between figure-ground discrimination and surround suppression. One possible interpretation of this result is that it suggests a functional link between surround suppression and motion-based figure-ground discriminations.

Separate studies using different stimuli and methods have shown that figure-ground discrimination is harder at low contrast (Regan, 1989; Takeuchi, Yokosawa & De Valois, 2004) and that surround suppression is more pronounced at high contrast (Tadin et al., 2003), thus foreshadowing the negative correlation found in the current experiment. The present experiment, however, compared these two tasks by keeping most stimulus parameters constant (size, speed, spatial envelope, dependent variable, motion correlation, and motion type — i.e., moving random-dot pattern). The only difference between the two stimulus patterns was the addition of a motion-defined figure in one task by simply reversing the direction of motion within a small elliptic region.

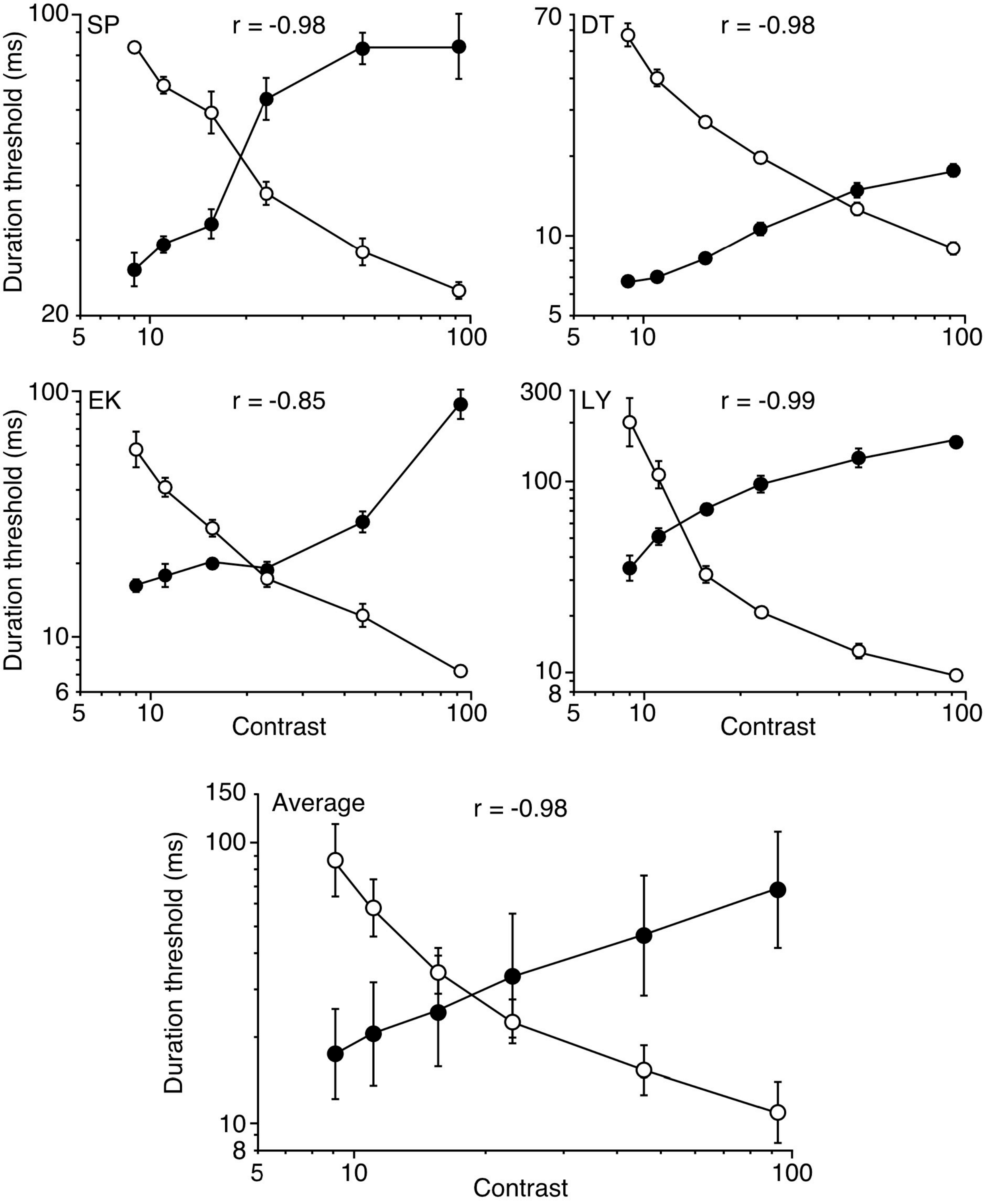

Figure 23. Results of Experiment 1. The data for four observers are shown in the top panels. The average data are shown in the bottom panel. Filled symbols show data from the motion-discrimination task. Empty symbols show data from the figure-ground discrimination task. Error bars are SEM.

While the stimuli used for the two tasks in this experiment are very similar, the computational requirements for motion discrimination and figure-ground segregation are conflicting (Braddick, 1993). Perceiving motion direction of a coherently moving object requires motion signals to be summed over space and integrated into a single estimate of direction. In contrast, perceiving a motion-defined shape requires spatial differences in motion signals to be "highlighted." Thus, the conflict is whether different local motion estimates are integrated or differentiated. How does vision deal with these two diametrically opposing processing demands?

One pragmatic solution for vision is to emphasize either integration or differentiation depending on the stimulus conditions. The strength and quality of motion signals varies substantially depending on the stimulus properties. When motion signals are weak (e.g., at low contrast), they are more susceptible to noise. Such low-visibility motion might even require extended spatial integration just to be perceived at all. Thus, it makes functional sense to emphasize spatial integration in low-visibility conditions. On the other hand, when motion signals are strong, spatial variations in motion direction and speed detected by local motion mechanisms are less likely to be corrupted by noise and more likely to reflect 'actual' motion differences. Employing mechanisms such as surround suppression to highlight differences within spatially distributed motion signals seems appropriate. This adaptive balance between integration and differentiation is consistent with our results.

One interesting aspect of the results is that subjects varied in how much direction discrimination thresholds worsened with contrast and how much figure-ground discriminations improved with contrast. Notably, observers whose suppression became more pronounced with increasing contrast tended to show greater improvement in the figure-ground discrimination task (contrast observers SP and LY). This trend motivated us to explore individual variability in surround suppression and figure-ground discrimination. The basic hypothesis is that if two visual functions/tasks are related, either by sharing a common underlying mechanisms or if one function is "the mechanism" for the other, then performance in the two tasks may co-vary between individuals.

For example, schizophrenic patients who have deficits in a simple speed discrimination task tend to have more problems with smooth pursuit eye movements (Chen, Nakayama, Levy, Matthysse & Holzman, 1999). Before this result can be interpreted as a link between these two visual functions, several alternative explanations must be considered. Most importantly, a possibility that this link may be an indicator of a general visual-motor impairment must be ruled out by either having an appropriate normalizing control task or by recruiting participants with comparable levels of impairment.

Keeping in mind the need for appropriate control, in the second experiment, we investigated whether observers with stronger surround suppression tend to be better at perceiving motion-defined shapes.

Experiment 2

Methods

The stimuli were moving random-dot patterns consisting of light and dark pixels (each 3 x 3 arcmin). From frame to frame of the animation, all of the pixels shifted in one direction either at 3.1°/s or 6.2°/s (100% correlation). Stimulus contrast was ramped on and off with a temporal Gaussian envelope (duration is defined as the 2σ of the temporal Gaussian). Peak contrast was maximum available (92%). Duration thresholds (82%) were estimated by interleaved Quest staircases. For each condition, 21 observers ran four pairs of interleaved staircases, with the first pair discarded as practice. Feedback was provided. All procedures complied with institutionally reviewed guidelines for human subjects.

Separate sessions were conducted for each speed (3.1°/s and 6.2°/s), with the order of conditions randomized within each session. Four different tasks (Figure 24) were conducted at two speeds:

1. Small-pattern motion discrimination ("Small"): Direction discrimination (left vs. right) of a small moving stimulus presented in a raised cosine envelope (diameter = 2.4°)
2. Big-pattern motion discrimination ("Big"): Direction discrimination (left vs. right) of a large moving stimulus presented in a raised cosine envelope (diameter = 11.6°)
3. Figure motion discrimination ("Figure motion"): Direction discrimination (left vs. right) of motion presented in an elliptic spatial envelope. Long and short axes of the motion-defined shape were 2.28° and 1.14°, respectively. Ellipse tilt (45° leftward tilt vs. 45° rightward tilt) was randomly chosen on the first trial of each experimental run and kept constant for the remaining trials.

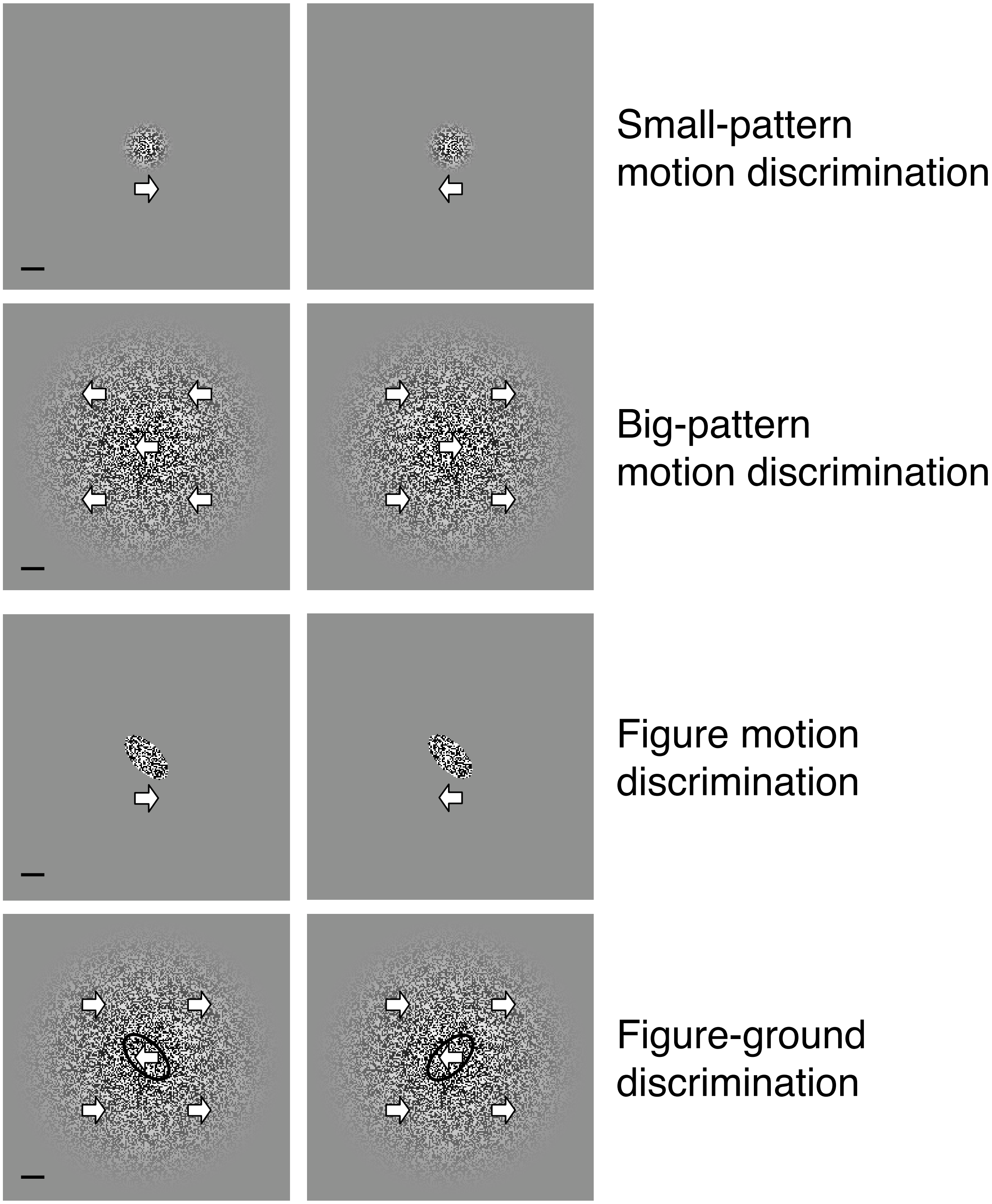

Figure 24. Single-frame snapshots of the four tasks in the Experiment 2. White arrows depict direction of motion. Oval outlines in the bottom panels indicate the subsections of the stimulus within which random-dot pattern moved in the opposite direction from the rest of the stimulus. The outline and arrows were not present in the actual stimulus. Scale bar is 1°.

4. Figure-ground discrimination (“Figure-ground”): Observers discriminated between two motion-defined shapes (45° leftward tilted ellipse vs. 45° rightward tilted ellipse). The stimulus pattern was presented in a raised cosine envelope (diameter = 11.6°). The pixels within the elliptic region moved either leftward or rightward (direction randomly chosen on each trial), while the pixels outside the elliptic region moved in the opposite direction. Spatial parameters of the motion-defined shape were identical to the ellipse in the “figure motion” task.

An important issue in the analysis and interpretation of the data from these four tasks is that observers vary in their general ability to perceive motion. For example, while a high threshold in the big-pattern motion task is often suggestive of strong surround suppression, high thresholds may also indicate overall decreased motion sensitivity. To address this issue we computed two normalizing measures from the raw data.

Small-pattern and big-pattern motion tasks were used to get an estimate of a “suppression index” for each observer:

suppression index = log(big-pattern thresh.) – log(small-pattern thresh.)

Figure-ground discrimination and figure motion tasks were used to calculate “figure-ground efficiency” for each observer:

figure-ground efficiency = log(figure motion thresh.) – log(figure-ground discr. thresh.)

Results

Average duration thresholds in four tasks for two speeds are shown in Table 2. In all direction discrimination tasks, performance improved with the increasing speed — a result consistent with previous results (Lappin, Borghuis, Tadin, Lankheet, & van de Grind, 2002). Figure-ground discrimination thresholds were the lowest overall and were unaffected by two-fold change in speed. Good performance in the figure-ground task was expected as the experiment was conducted at high contrast (see Experiment 1). Note that because of the increase in the motion discrimination thresholds with decreasing speed, figure-ground efficiency was higher at low speeds (also illustrated in Figure 25).

Table 2. Average duration thresholds from four tasks, suppression index and figure-ground efficiency at 3.1°/s and 6.2°/s. Standard deviations are given in the parentheses.

	Small	Big	Figure motion	Figure-ground	Suppression index	Figure-ground efficiency
3.1°/s	20.2 ms (6.7 ms)	31.9 ms (12.5 ms)	18.1 ms (5.9 ms)	11.8 ms (3.1 ms)	0.188 (0.066)	0.176 (0.133)
6.2°/s	14.7 ms (4.6 ms)	25.1ms (8.5 ms)	14.0 ms (4.1 ms)	11.5 ms (3.1 ms)	0.220 (0.115)	0.078 (0.113)

To estimate how much performance depended on the overall ability to perceive motion, we computed correlations among all four tasks (Table 3). As expected, all correlations were positive, which simply indicates that observers who performed well on one motion perception task tended to perform well on other motion tasks. An important exception is a lack of correlation between "Big" and "Figure-ground" tasks. One explanation of this result is that in addition to general motion sensitivity, which tends to correlate these tasks, there is another factor that has an opposite effect on "Big" and "Figure-ground" tasks. This potential explanation is revisited below.

Table 3. Between-subject correlations among four experimental tasks at 3.1°/s and 6.2°/s (* = $p < 0.5$, ** = $p < 0.01$; *** = $p < 0.001$.

3.1°/s	Small	Big	Figure motion	Figure-ground
Small	1	.75***	.92***	.58**
Big		1	.75***	.07
Figure motion			1	.49*
Figure-ground				1

6.2°/s	Small	Big	Figure motion	Figure-ground
Small	1	.93***	.91***	.34
Big		1	.83***	.11
Figure motion			1	.46*
Figure-ground				1

The critical result illustrating the relationship between the *suppression index* and *figure-ground efficiency* is shown in Figure 25. There was a significant positive correlation between the strength of suppression and the observer's *figure-ground efficiency*. Moreover, observers with

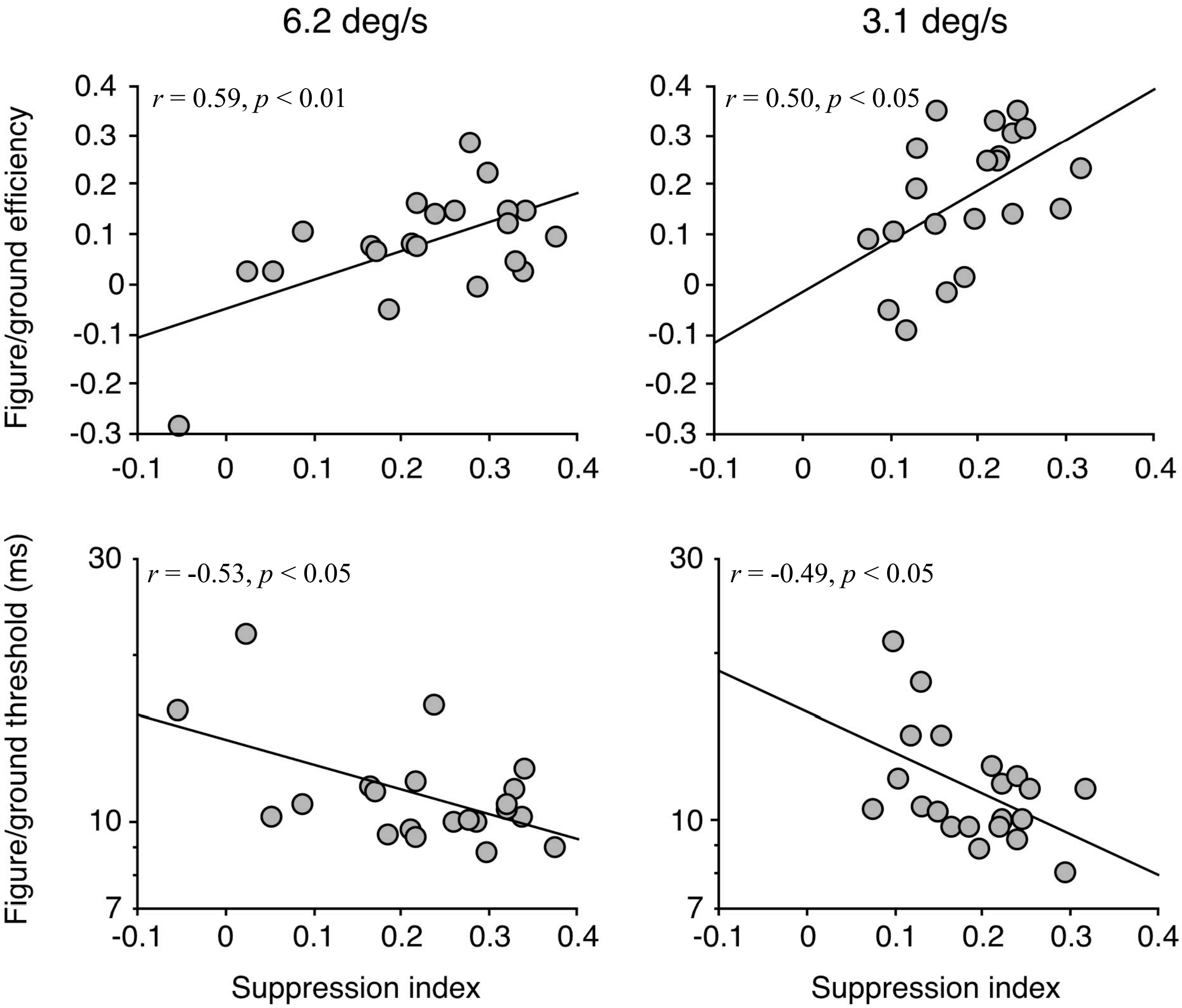

Figure 25. Results of Experiment 2. Top panels show the relationship between the Suppression index and Figure-ground efficiency for 21 observers. Bottom panels show the relationship between the Suppression index and figure-ground thresholds for 21 observers.

strong surround suppression tended to have lower figure-ground discrimination thresholds. This result along with the observation that suppression is associated with increasing "Big" task thresholds (at 6.2°/s, $r = 0.69$, $p < 0.01$; at 3.1°/s, $r = 0.53$, $p < 0.05$) may account for the lack of correlation between "Big" and "Figure-ground" tasks (Table 3).

Discussion

We found that individual observers who show strong surround suppression tended to perform better in a motion-based figure-ground discrimination task. This finding was made possible because of individual variability in both surround suppression and the ability to perceive motion-defined forms. An obvious way to extend these results is to study populations with either very strong or very weak surround suppression. We have previously found that schizophrenic patients with strong negative symptoms show very weak surround suppression (Tadin et al., in preparation). Plans are underway to test if such patients show poor performance in a figure-ground discrimination task.

A recent conference report (Betts, Taylor, Bennett & Sekuler, in press) found that elderly observers show reduced surround suppression. In fact, elderly observers are better than young observers at perceiving the motion of large high-contrast patterns. This finding suggests reduced suppression in elderly and is consistent with observations that intracortical inhibition is reduced in senescent monkeys (Schmolesky, Wang, Pu & Leventhal, 2000; Leventhal, Wang, Pu, Zhou, & Ma, 2003). In monkeys, old age is associated with the broader direction tuning and increased spontaneous activity (Schmolesky et al., 2000), possibly a consequence of decreased ability to produce inhibitory neurotransmitter GABA (Leventhal et al., 2003). It is tempting to speculate that the reduction in GABA is responsible for the *improved* ability of elderly observers to perceive large-high contrast moving patterns.

Coincidently, a 63-year-old observer had the lowest *figure-ground efficiency* and the lowest and fourth lowest *suppression index* in two tasks. This was not due to a deficit at perceiving motion, as his thresholds in the motion discrimination tasks were consistently in the top 20%.

General Discussion

We report two correlation experiments that suggest a link between surround suppression and motion-based figure-ground discrimination. Within subjects, we found that increasing surround suppression with increasing contrast was highly correlated with improving figure-discrimination thresholds. Between subjects, we found that observers demonstrating strong surround suppression tend to be better at perceiving a motion-defined figure.

As both of the described experiments report correlations, we stop short of asserting that our results establish a functional link between surround suppression and figure-ground discrimination. Such a link, however, provides a parsimonious explanation for both within- and between-subject results reported in this chapter.

CHAPTER VIII

CONCLUDING REMARKS

Partially adapted from Tadin, D., & Lappin, J. S. (in press). Linking psychophysics and physiology of center-surround interactions in visual motion processing. In L. R. Harris & M. Jenkin (Eds). *On seeing spatial form*. Oxford University Press

Linking psychophysics and neurophysiology of center-surround interactions in motion

General principles

A fundamental but challenging problem in all areas of science is to link macroscopic and microscopic analyses of a system. Understanding how a complex system operates in a changing environment requires knowledge about both the dynamics of environmental conditions and the dynamics of the system's components. Causal relationships operate simultaneously on multiple levels and also between levels. Thus, macroscopic and microscopic processes are interdependent.

In vision research, perception is usually considered to constitute the macroscopic level of analysis. On the level of perception, the transmission of information is between the visual environment and one's perception of the environment (typically indicated by behavioral output). The neural mechanisms of vision (i.e., spatiotemporal patterns of spike trains) constitute the microscopic level of analysis. The transmission of information on the microscopic level must equal (or exceed) the transmission of information on the level of perception (Lappin & Craft, 2000). This follows from (1) the assumption that perception is derived wholly and exclusively from neural activity and from (2) the general principle related to the second law of thermodynamics: Information about the input stimulation of the retina can only be lost but not created by the visual processes that lead to behavioral responses. Therefore, behavioral discriminations (i.e., perception) cannot be more precise or reliable than differences between the retinal stimuli or neurophysiological responses to these stimuli. These two levels of analysis for visual motion processing are illustrated in Figure 26.

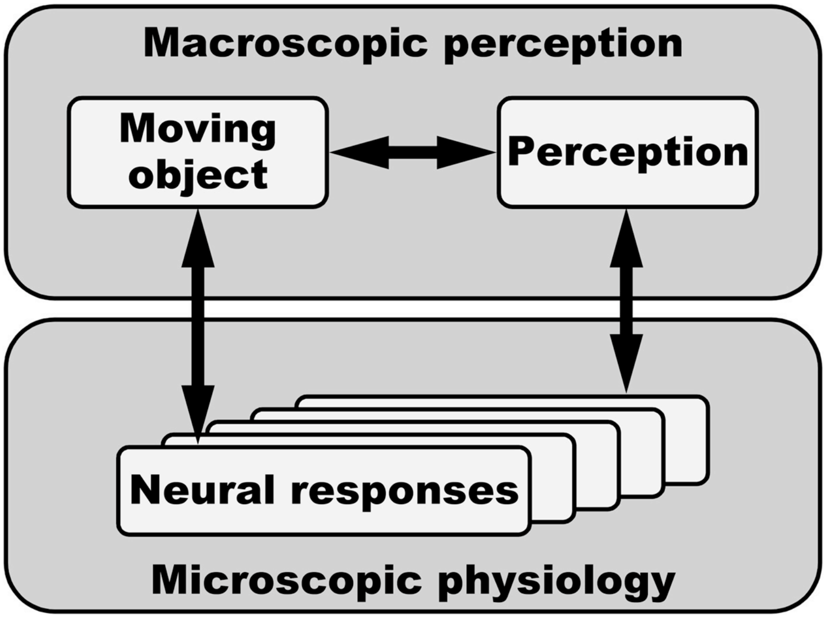

Figure 26. Illustration of the macroscopic and microscopic levels of analysis in visual motion processing.

The multi-level nature of information transmission from the visual environment to perception enables inferences about neurophysiological processes from psychophysical experiments and inferences about perceptual functions from neurophysiological observations. A well-known paper by Teller (1984) outlines the logic of a variety of 'linking propositions' for relating perceptual states with neurophysiological states. As Teller points out, such linking propositions are at least implicit if not explicit in interpreting a large body of research in visual psychophysics and neurophysiology.

The best-known linking proposition for inferring neurophysiological processes from perception was articulated by Brindley (1970, p. 133):

> …whenever two stimuli cause physically indistinguishable signals to be sent from the sense organs to the brain, the sensations produced by those stimuli, as reported by the subject in words, symbols or actions, must also be indistinguishable.

An important implication of this proposition (referred by Teller as *identity*) is its contrapositive: If an observer can behaviorally discriminate between two stimuli, then these stimuli must elicit different neurophysiological signals at the retina and at all subsequent neural stages leading to the behavioral response. That is, behavioral discrimination implies neurophysiological differences. These two propositions belong to the identity family outlined by Teller (1984) and are generally considered as strong logical statements.

These propositions might seem almost trivially obvious, but they have nontrivial applications (Brindley, 1970; Teller, 1984; Lappin & Craft, 2000). The classic experiments by Hecht, Schlaer & Pirenne (1942) and Bouman (1950) offer good illustrations, where behavioral experiments were used to demonstrate that a single photon is sufficient to excite a single photoreceptor. Moreover, most of the response variability for a given stimulus condition was attributable to physical variability of the stimulus rather than to the variability in neural signals.

These and other detection and discrimination experiments can be used to make inferences about neural mechanisms by relying on the identity proposition. In most psychophysical experiments, however, the overall *pattern* of results is what is important and not the exact value of the detection or discrimination threshold (e.g., the characteristic shape of the contrast sensitivity function). To link such results with the specific neural substrate, investigators typically look for the analogous patterns of results in the neurophysiological data. Such linking propositions, called analogies in Teller's systematization scheme, lack the logical rigor of the identity proposition but account for a majority of the linking propositions reported in the literature and in the present dissertation.

A major difficulty in the generation and testing of linking propositions is that one cannot be certain whether signals recorded in neurons in a given visual area are sufficient or even necessary for perceptual responses to the given stimulus. An apparent absence of difference in specific neural responses to two different stimuli typically does not imply that these stimuli are visually indiscriminable by an observer using responses of the whole visual system. Here the idea of a bridge locus becomes crucial (Teller, 1984). Bridge locus is defined as the set of neurons whose activity is necessary for the occurrence of a particular perceptual state. Linking propositions only make sense if they hold for the neurons constituting the bridge locus. Identifying the bridge locus can be difficult because visual areas and populations of neurons often overlap in their visual selectivity. For example, a large number of cortical areas are selective for motion (Sunaert, Van Hecke, Marchal & Orban, 1999), and may constitute bridge loci for different aspects of motion perception. Furthermore, visual cortex is far from being fully explored, thus one must consider a possibility that the bridge locus for a particular perceptual state is uncharacterized.

Our chances of succeeding in formulating and testing linking propositions largely depend on how well the relevant neural mechanisms have been characterized. A relatively detailed understanding of the neural circuitry underlying saccade planning and execution enables rigorous testing of linking propositions related to saccadic eye movements (Schall, 2004). On the other exterme, we have only a rough understanding of the neural mechanisms underlying intelligence (e.g., Gray, Chabris & Braver, 2003), which severely limits formulation and testing of linking propositions related to intelligence. Fortunately, our understanding of neural mechanisms underlying motion perception is far better than our understanding of the neural basis of intelligence. Visual motion perception is arguably the best understood sensory sub-modality (Albright & Stoner, 1995). This rich knowledge base detailing neural mechanisms of motion constitutes the backdrop for discussing the findings described in this dissertation.

Application of general principles to center-surround interactions in motion

The main conclusion of this dissertation is that psychophysically observed surround suppression may be the perceptual correlate of center-surround antagonism in the cortical area MT. The evidence for this conclusion comes from a series of experiments designed to obtain data that can be interpreted in relation to the neural mechanisms of motion perception. Thus, it is useful to analyze the reasoning behind the linking propositions that are explicit or implicit in the conclusions of those experiments.

All of the linking propositions in this dissertation are versions of the analogy proposition from Teller's (1984) systematization scheme. For example, increasing motion discrimination thresholds with increasing size at high contrast are *analogous* to the reduced activity of MT center-surround neurons with increasing stimulus size. However, it would be unfounded to conclude from this analogy alone that psychophysically observed surround suppression is the perceptual correlate of center-surround antagonism in MT. What is needed is a way to strengthen this analogy-based proposition.

There are two ways analogy-based inferences about neural mechanisms from psychophysical data can be strengthened. The first is by way of converging evidence — simply stated, many analogies are better than one. In motion perception research, fortunately, we have a relatively good understanding of the underlying neural mechanisms. This knowledge base can be exploited to plan different psychophysical experiments, each potentially designed to look at a different aspect of a specific neural mechanism. The results of such experiments, if consistent with each other, can generate enough converging evidence to justify linking those results to a specific neural mechanism.

We have observed surround suppression at high contrast in experiments utilizing a variety of psychophysical methods (e.g., duration thresholds, phase-shift thresholds, the MAE and the temporal reverse correlation). Collectively, the results of these experiments strongly suggest the existence of surround suppression in human motion perception. To link this psychophysical finding with a neural substrate, we designed a series of manipulations to explore how this result behaves under different stimulus conditions. All of these manipulations (summarized in Chapter III) yielded results analogous to the properties of center-surround MT neurons. This convergence of results strengthens the analogy proposition that links psychophysically observed surround suppression with center-surround antagonism in MT.

A second way of strengthening analogy-based inferential links is by testing neurophysiological predictions generated by psychophysical results. A psychophysicist generally has more flexibility in designing and conducting different experiments than a neurophysiologist studying the same problem. A psychophysical study design typically allows for a greater number of conditions and parameters to be explored. The results of such studies, especially if surprising in any way, can be used as predictors for a subsequent neurophysiological study. If such predictions are confirmed by neural data, the link between a given psychophysical result and a specific neural mechanism is strengthened.

Several testable predictions can be generated from the large number of psychophysical results reported in this dissertation. One of the central findings of the present dissertation is that surround suppression is only observed at high contrast. At low contrast, direction discriminations improve with increasing size. Based this result, we hypothesized that the balance between surround suppression and spatial summation in MT will exhibit similar contrast dependency. Unfortunately, virtually all published studies of surround suppression in MT were restricted to high-contrast moving stimuli. Following the completion of our initial psychophysical study, C. C. Pack and R. T. Born found that MT center-surround antagonism observed at high contrast substantially weakens or even disappears at low contrast (personal communication, August 2003). This finding shows that contrast-dependent pooling of spatially distributed signals is a prominent feature of neural computation in MT and corroborates the prediction generated from our psychophysical data.

The present results also predict that the sign of MT center-surround interactions is determined by the contrast of the motion stimulating the center region (from Chapter VI). Specifically, surround suppression should diminish with decreasing center contrast regardless of surround contrast. Another prediction is that that surround inhibition disappears at isoluminance (Chapter III). If these and other predictions from this dissertation are corroborated by neurophysiological data, then the analogy-based inferences suggesting a link between psychophysical surround suppression and MT center-surround antagonism will be strengthened.

Another issue that needs to be considered is the bridge locus for the linking propositions discussed above. Many of the experiments in this dissertation point to a link between psychophysically observed surround suppression and general properties of area MT (e.g., isoluminant motion, eccentric presentation and MAE experiments). However, not all MT neurons exhibit surround suppression. In addition to neurons that are inhibited by large moving objects (a.k.a. 'local motion' neurons), MT contains neurons that show no surround suppression and exhibit strong responses to large moving fields (so called 'wide field' neurons). These two types of neurons are segregated anatomically (Born & Tootell, 1992; Raiguel et al., 1995), and microstimulation has different behavioral effects depending on which type of neurons is stimulated (Born et al., 2000). Thus, current evidence indicates that these two types of neurons may have distinct functional roles, such that local motion neurons are more likely to be directly involved in perceiving object motion (Born et al., 2000). Most importantly, the analogy-based linking propositions from the results in the present dissertation do not hold for wide-field neurons. Only a sub-set of MT neurons — those with antagonistic center-surround receptive fields — makes up the bridge locus for the psychophysically observed surround suppression.

In summary, the inferences between perception and neurophysiology presented in this dissertation are analogy-based linking propositions. This type of a linking proposition is weak in the logical sense (Teller, 1984), but can be strengthened by converging evidence from different experiments and by subsequent tests of the neurophysiological predictions derived from the results of such experiments.

Future directions

A novel psychophysical finding often suggests a long list of possible follow-up experiments. One strategy is to simply redo the original experiment with new stimulus parameters. For example, one may wonder if surround suppression occurs with second-order motion. Such experiments will likely yield interesting and interpretable results, but they probably will not greatly affect the current understanding of surround suppression.

Any experiment whose outcome may potentially strengthen or weaken the link between surround suppression and MT center-surround antagonism is worth pursuing. Experiments that explore predictions generated from the results of this dissertation fall in this category. Some examples are given in the previous section.

Furthermore, it is important to learn more about the neurophysiology of center-surround interactions in motion. Without a clear understating of neurophysiology, it is difficult to formulate, strengthen or rejects various linking propositions. Tools available to author for investigation center-surround neurophysiology are fMRI and TMS with Randolph Blake and optical imaging with Vivien Casagrande. TMS, repetitive sub-threshold TMS in particular, may yield the most dramatic results. The specific hypothesis is that sub-threshold TMS over MT may improve discriminability of large high-contrast moving stimuli and reduce discriminability of small and low-contrast moving stimuli. The speculation is that TMS will affect overall motion processing in MT, including the mechanisms responsible for surround suppression.

Another promising line of research is to investigate center-surround interactions in special populations. We have already showed that that schizophrenic patients with strong negative symptoms show very weak surround suppression (Tadin et al., in preparation). Recently Betts et al. (in press) found similar results in elderly observers. Both of these populations are very good at discriminating large-high contrast motions, sometimes performing even better than control subjects. It will be interesting to investigate whether this reduction in surround suppression is associated with decreased ability to perceive motion-defined forms, as suggested in Chapter VII. On the other hand, it is worth exploring whether observers who are known to have problems at perceiving motion-defined objects, such as mentally retarded persons (Fox & Oross, 1992), also exhibit reduced surround suppression. Such observations would strengthen a functional link between surround suppression and motion-based figure ground discrimination.

Figure-ground discrimination, however, need not to be the only visual function associated with center-surround antagonism in motion. MT neurons with non-uniform surrounds are endowed with computational tools to represent surface shape from spatial patterns of motion (Xiao et al., 1995, 1997a, 1998; Buracas & Albright, 1996). A direct link between center-surround MT neurons and the perception of local shape characteristics is still lacking. Moving 3D shapes modulate the overall activity of area MT and the responses of its neurons (Bradley, Chang & Andersen, 1995), suggesting that MT neurons may indeed represent some properties of 3D shape. The important question is whether MT neurons represent only crude aspects of moving shapes (e.g., the existence of different moving surfaces at different depths) or their key shape characteristics (e.g., surface curvature).

The potential contribution of MT center-surround neurons to shape perception derives from their ability to implicitly estimate higher-order derivatives of smoothly changing velocity fields (Xiao et al., 1995, 1997a; Buracas & Albright, 1996). If this hypothesis is substantiated by psychophysical and neurophysiological evidence, then we may be able to conclude that center-surround neurons in MT are involved in representing 3D shape from retinal velocity fields. Psychophysical evidence linking center-surround interactions and the perception of motion-defined shapes is almost non-existent. One exception is the observation that the perception of SFM is affected by spatially proximal 2D motion patterns (Sereno & Sereno, 1999). Such 2D patterns are perhaps stimulating the surrounds of MT neurons responding to a SFM object and the resultant change in the surround influence is triggering the perceived change in SFM.

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