

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/m². Background luminance was 60.5 cd/m².

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 ($0.67^\circ - 5^\circ$) and contrasts (2.9% - 92%), yielding 30 different conditions. Spatial frequency and speed were fixed at 1 cycle/ $^\circ$ 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 ($1^\circ - 4^\circ$).

Broadband (random-dot) motion experiment

The stimuli consisted of light and dark pixels (each 3×3 arcmin) presented in a spatial Gaussian envelope. From frame to frame of the animation, half of the pixels shifted in one direction ($6.2^\circ/\text{s}$) 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 ($1.2^\circ - 7.8^\circ$) at different eccentricities ($0^\circ - 54^\circ$), yielding 24 conditions (contrast was fixed at 92%). Spatial frequency was $0.5 \text{ cycles}/^\circ$ and the speed was $4^\circ/\text{s}$. 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 ($0.67^\circ - 5^\circ$) with spatial frequency fixed at $0.5 \text{ cycle}/^\circ$, 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/ $^\circ$.

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 ($8^\circ/\text{s}$) 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.

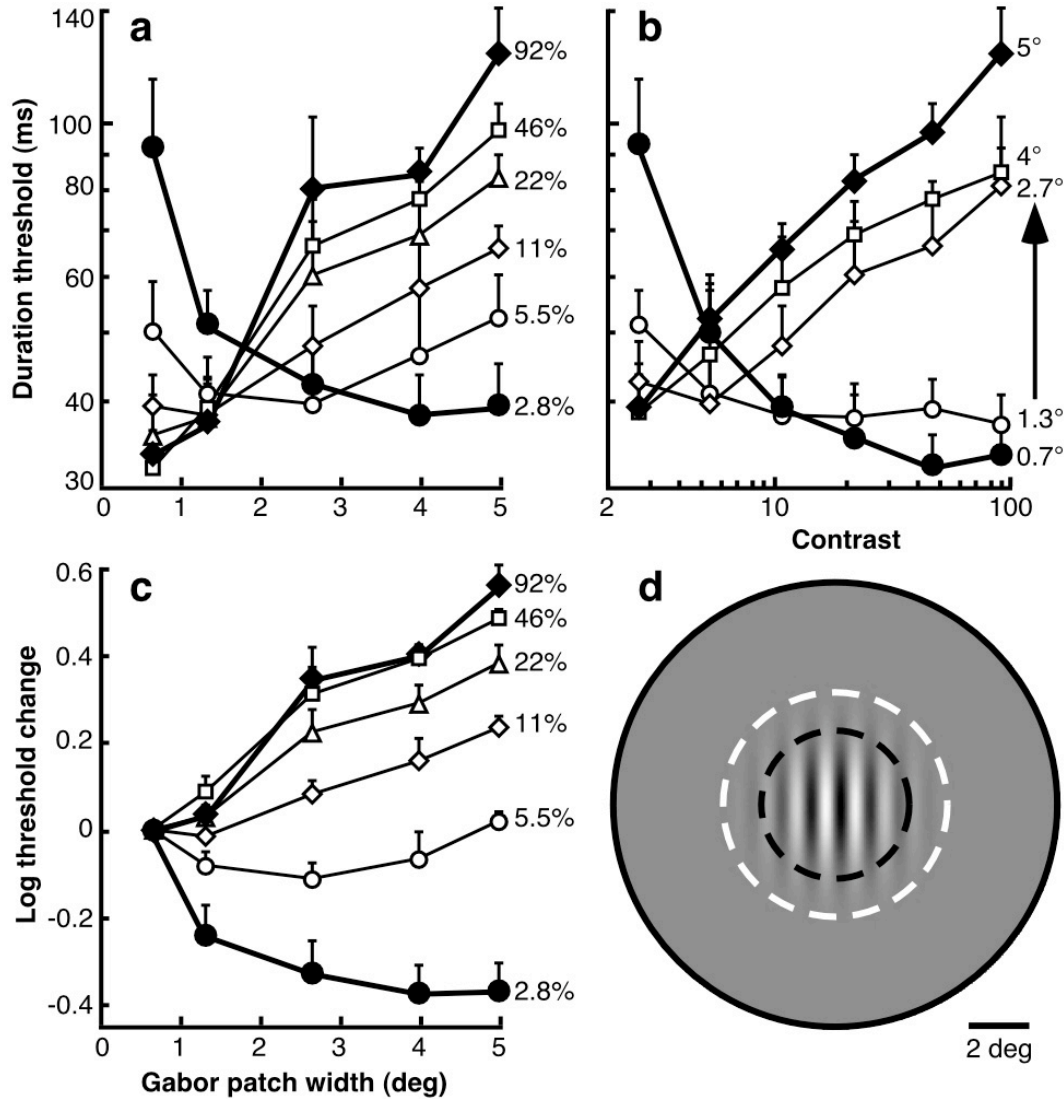


Figure 2. Effects of size and contrast on motion perception. Individual data points are averages for five observers. Error bars are SEM. (a), Duration thresholds as a function of stimulus size at different contrasts. (b), Duration thresholds as a function of contrast for a range of stimulus sizes. (c), 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 (0.7°) 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 2.7° 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 ($r = 3\sigma = 4^\circ$) is indicated by the light dashed circle.

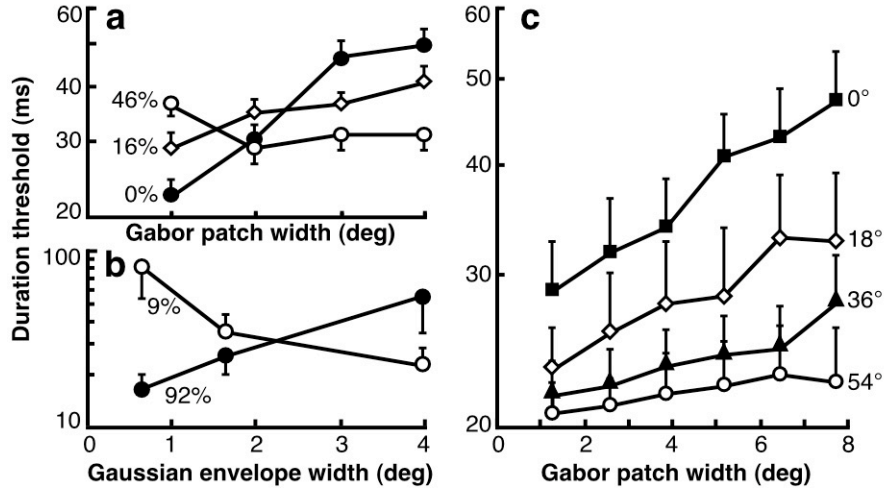


Figure 3. Results from added noise, random-dot and eccentricity experiments. (a), Duration thresholds as a function of stimulus size at different noise contrasts. (b), Duration thresholds as a function of random-dot stimulus size at different contrasts. (c), Duration thresholds as a function of stimulus 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 $6.2^\circ/\text{s}$ (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

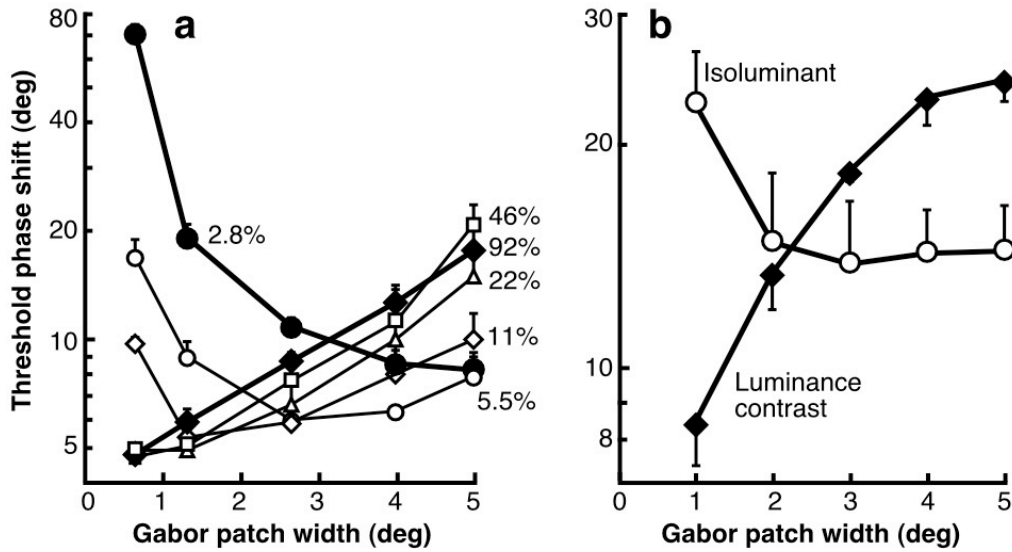


Figure 4. Results from phase shift and isoluminant motion experiments. (a), Phase shift thresholds as a function of stimulus size at different contrasts. (b), Phase shift thresholds as a function of stimulus size for luminance contrast and isoluminant stimuli. Error bars are SEM.

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.