Spatial and temporal limits of motion perception across variations in speed, eccentricity, and low vision

Joseph S. Lappin

Vanderbilt Vision Research Center
and Department of Psychology,
Vanderbilt University, Nashville, TN, USA

Duje Tadin

Center for Visual Science and Department of Brain
and Cognitive Sciences,
University of Rochester, Rochester, NY, USA

Jeffrey B. Nyquist

Vanderbilt Vision Research Center
and Department of Psychology,
Vanderbilt University, Nashville, TN, USA

Anne L. Corn

Vanderbilt Vision Research Center
and Department of Special Education,
Vanderbilt University, Nashville, TN, USA

We evaluated spatial displacement and temporal duration thresholds for discriminating the motion direction of gratings for a broad range of speeds (0.06°/s to 30°/s) in fovea and at ±30° eccentricity. In general, increased speed yielded lower duration thresholds but higher displacement thresholds. In most conditions, these effects of speed were comparable in fovea and periphery, yielding relatively similar thresholds not correlated with decreased peripheral acuity. The noteworthy exceptions were interactive effects at slow speeds: (1) Displacement thresholds for peripheral motion were affected by acuity limits for speeds below 0.5°/s. (2) Low-vision observers with congenital nystagmus had elevated thresholds for peripheral motion and slow foveal motion but resembled typically sighted observers for foveal motions at speeds above 1°/s. (3) Suppressive center–surround interactions were absent below 0.5°/s and their strength increased with speed. Overall, these results indicate qualitatively different sensitivities to slow and fast motions. Thresholds for very slow motion are limited by spatial resolution, while thresholds for fast motion are probably limited by temporal resolution.

Keywords: motion, speed, direction, peripheral vision, eccentricity, acuity, low vision, nystagmus, surround suppression

Introduction

Perceiving the direction of motion requires visual mechanisms jointly responsive to the spatial and temporal orders of changing stimulation. A basic design challenge arises from the wide range of speeds at which relevant image motions occur—over five orders of magnitude in human vision. The scale of motion mechanisms must somehow span a very wide spatiotemporal range.

Models of directionally selective motion mechanisms are typically bi-local—receiving inputs from pairs of non-directional neurons with receptive fields offset in space and time (Adelson & Bergen, 1985; Chichilnisky & Kalmar, 2003; DeAngelis & Anzai, 2004; De Valois & Cottaris, 1998; De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000; Nakayama, 1985; Reichardt, 1961; van Santen & Sperling, 1985; Watson & Ahumada, 1985). The detector's output 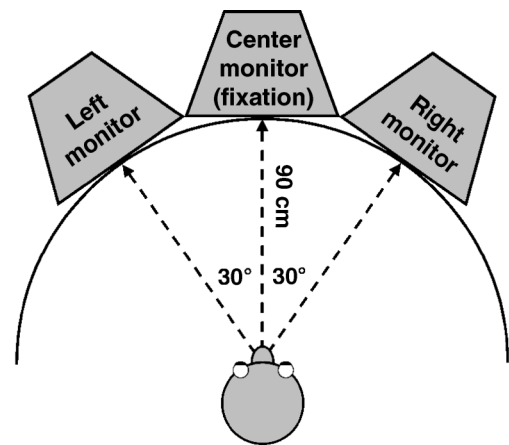is maximized when the image motion speed matches the spatial and temporal spreads of its paired receptive fields. Indeed, these motion models are usually designed to measure image speed.

Because the responses of motion mechanisms inevitably depend on image speed, we sought to determine how speed affects motion discrimination thresholds as measured by the smallest *spatial displacements* and *temporal durations* needed to discriminate between two opposite directions. For a given speed, displacement and duration thresholds are directly proportional, and the same data measures both. Variations in speed, however, affect these two measures differently: Increased speed implies increased displacement per unit time and decreased duration per unit space.

In addition to motion speed, we also investigated three visual parameters involving spatial resolution:

1. Motion discrimination thresholds were evaluated in fovea and at ±30° eccentricity.

2. Effects of speed were studied with two low-vision observers whose acuity was reduced by congenital nystagmus.
3. We manipulated stimulus size to determine whether speed affects suppressive spatial interactions in motion (cf., Tadin & Lappin, 2005a).

One aim of this study was to investigate limits of motion perception without relying on contrast and coherence thresholds. Psychophysical studies of motion sensitivity have often measured contrast thresholds (Anderson & Burr, 1987, 1991; Koenderink, Bouman, Bueno de Mesquita, & Slappendel, 1978a, 1978b, 1978c, 1978d; Watson, Barlow, & Robson, 1983; Watson & Turano, 1995). Contrast, however, turns out to have highly nonlinear effects on both psychophysical and physiological responses to motion. Spatial integration of motion signals gradually switches from spatial summation at low contrast to surround suppression at high contrast (Tadin & Lappin, 2005b; Tadin, Lappin, Gilroy, & Blake, 2003; Pack, Hunter, & Born, 2005), rendering large stimuli less discriminable as contrast increases. Thus, it is likely that spatial and temporal thresholds at high contrast will reveal properties of motion perception not found in contrast threshold experiments.

Indeed, motion speed and spatial resolution affected discrimination thresholds differently than in many previous studies. Motion speed exerted a consistent influence on thresholds in all conditions, and this influence was not affected by reduced spatial resolution in the visual periphery, except at very slow speeds. Slow and fast motions had qualitatively different effects, however, on the visual motion mechanisms affected by congenital nystagmus and on the strength of suppressive center–surround interactions.

General methods

To investigate motion perception in both central and peripheral fields, the display system consisted of three adjacent video monitors, one in the center and two at ±30° eccentricity (Figure 1). The monitors were CRT displays (21 in Sony E540, 1024 × 768 resolution, 120 Hz, with linearized 8-bit grayscale). Viewing was binocular at 90 cm, yielding 1.43 × 1.43 arcmin per pixel. The minimum ambient background luminances were 1.6, 1.6, and 1.7 cd/m^2, for the left, center, and right monitors, respectively; and the corresponding luminance maxima were 124.3, 126.2, and 129.6 cd/m^2. The small inequalities reflect difficulties in jointly calibrating the three monitors. Comparisons of results from two peripheral monitors showed that these luminance differences had no effects on the experimental results.

The experiments were controlled by MATLAB and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The stimulus patterns were Gabor-like patches in which a grating moved at a constant velocity inside a stationary

Figure 1. Schematic and photographic illustration of the three-monitor set-up.

spatial window. The stimulus spatial envelope was a 2D raised cosine. In most experiments, stimulus size (as measured by the radius of the circular spatial envelope) was 1.5°. The maximum contrast was 98.7%. Spatial frequency (SF) was varied in Experiment 1, but in others it was constant at 1 c/°. Initial gating phase was random. In most experiments, velocity (V) was a principal variable. For experiments where SF was fixed, velocity manipulations were proportional to temporal frequency (TF) changes: $V(°/s) = TF(c/s) ÷ SF(c/°)$.

Stimulus duration was adjusted by a QUEST staircase procedure (Watson & Pelli, 1983), estimating the stimulus duration required for 82% correct responses. In most experiments, the temporal envelope was a raised cosine, except for Experiment 4 where a square envelope with half-Gaussian tails was used. (We had begun using such temporal envelopes in other studies to maintain better constancy of the temporal onset and offset ramps over variations in stimulus duration. This small change in the temporal envelope turned out to have no discernable effect on the results, however.) These smoothly changing temporal envelopes offer a temporal equivalent of sub-pixel sampling, permitting very brief motion durations—because a smooth contrast change is approximated by the changes

over discrete 8.3-ms samples of the 120-Hz CRT monitor. Duration was always specified as the interval above the half-height of the temporal envelope.

Each trial was initiated by a fixating observer. This triggered a 400-ms fixation-only interval, followed by a brief stimulus presentation. Stimulus motion occurred in two alternative directions, usually left or right. The observer's task was to identify motion direction by pressing one of two keys. In Experiments 1–3, each experimental block contained 75 trials, with 25 trials and independent threshold estimates for each of the three field regions. The motion direction (e.g., left/right) and location (left, center, or right monitor) varied randomly between trials, and all other stimulus parameters were constant within each block. In Experiment 4, each block contained two interleaved 25-trial staircases. Each threshold was estimated by averaging the results of four to six QUEST staircases. For each condition, these experimental blocks were always preceded by two blocks of practice trials. The observers were well-practiced volunteers, fully informed about the experimental conditions.

Experiment 1

Joint effects of speed and spatial and temporal frequencies

Here we sought to distinguish the effects of SF, TF, and V. These variables cannot be manipulated independently, as they involve two degrees of freedom. We hypothesized that increases in either V or TF should yield lower temporal thresholds, as their increases yield larger spatial displacements and local contrast changes within a fixed time interval. The effects of varying SF are less certain. Similar values of V composed of different combinations of SF and TF might yield similar thresholds, but the opposite might occur if spatial and temporal resolutions tend to trade with one another.

A second aim was to compare sensitivities of foveal and peripheral motion mechanisms to image motions varying in V as well as SF and TF. Previous studies of central and peripheral motion sensitivities, using different methods, have found that the periphery is tuned to lower SFs and higher speeds (Coletta, Williams, & Tiana, 1990; Galvin, Williams, & Coletta, 1996; Johnston & Wright, 1985; Kelly, 1984, 1985; Koenderink et al., 1978a, 1978b, 1978c, 1978d; McKee & Nakayama, 1984; van de Grind, Koenderink, & van Doorn, 1986, 1987; van de Grind, Koenderink, van Doorn, Milders, & Voerman, 1993; van de Grind, van Doorn, & Koenderink, 1983; Virsu, Rovamo, Laurinen, & Näsänen, 1982; Wright & Johnston, 1985). Our pilot studies, however, suggested that the present method yields more similar estimates of foveal and peripheral sensitivities to motion.

Thresholds were estimated for four values of V (0.25, 1, 4, and 8°/s) and three values of SF (0.5, 1, and 2 c/°),

yielding 12 randomly interleaved conditions. For each V, TFs were determined by the SFs, ranging from 0.125 Hz to 16 Hz. On each trial, a single moving patch appeared briefly on one of the three monitors, with the stimulus location chosen pseudo-randomly. Thresholds were estimated for four observers (two co-authors).

Results

The results are shown in Figure 2. Thresholds for the two peripheral fields were very similar, so only the average of these two thresholds is shown. Top and bottom panels show the same data, expressed as spatial displacement (Figure 2A) and temporal duration thresholds (Figure 2B). Note that for a given velocity, the displacement and duration thresholds are directly proportional: Relationships among the six data points for each speed are the same in both graphs. Variations in speed, however, can affect the spatial and temporal thresholds differently.

1. Indeed, displacement and duration thresholds were oppositely affected by changes in V. As expected, duration thresholds decreased as V increased, but
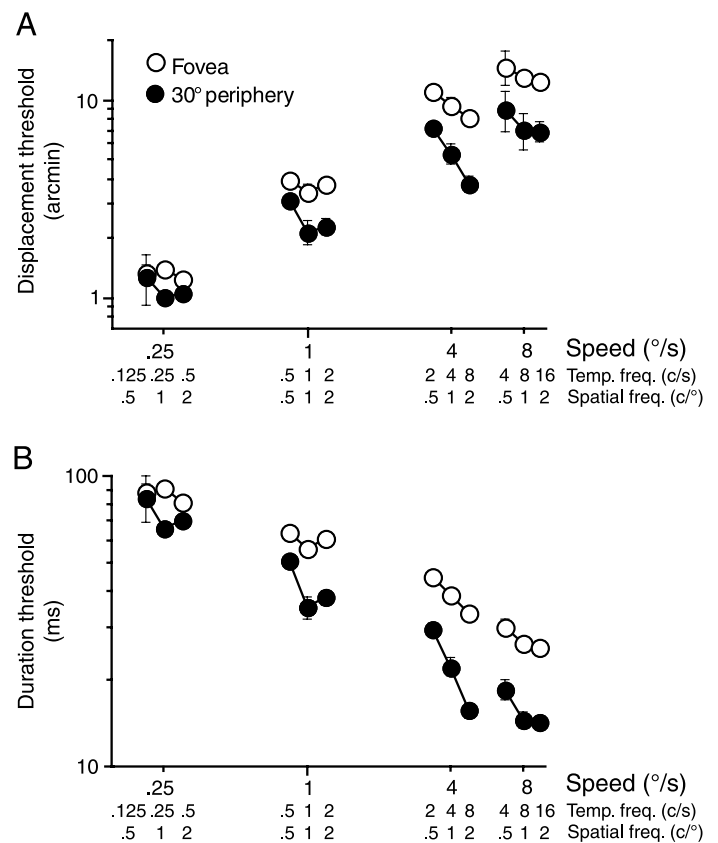

Figure 2. (A) Spatial displacement and (B) temporal duration thresholds for motion discrimination as a function of velocity, temporal frequency, and spatial frequency. Error bars are ±1 *SEM* between observers. Note that the two panels show the same data—expressed either as the spatial distance or the temporal duration of motion.

displacement thresholds increased with *V*. This finding is further explored in Experiment 2.

2. Across variations in *V*, TF, and SF, these particular motions were more visible in the periphery than the fovea. Central and peripheral thresholds were similar only for stimuli with the slowest *V* (0.25°/s) and lowest SF (0.125c/°), which also yielded the highest duration thresholds. For $V \geq 1$°/s, peripheral thresholds were usually about 60% of those for the fovea. Relative sensitivity of the fovea and periphery depends on other stimulus and task parameters, however—so the present comparison is not general. We will return to this issue.

3. As measured by displacement thresholds, resolution at 30° eccentricity was surprisingly good. The average peripheral threshold for *V* = 0.25°/s was just 1.11 arcmin. This quantitative estimate of threshold spatial displacement, however, depends on the definitions of stimulus duration and threshold. Here, stimulus duration was defined as the portion of the temporal envelope above the half-height, so visual information might have been obtained over greater temporal durations. Thresholds would have been lower, however, if the accuracy criterion were less than 82%. Nevertheless, under these conditions, spatial displacement thresholds were lower at 30° eccentricity than in the fovea.

4. Discrimination thresholds depended on all three variables, *V*, TF, and SF, but stimulus speed seems the primary influence. Thresholds were influenced by both TF and SF, but their effects depended on one another, and were reduced when *V* was equated. The relative influence of *V* and TF was analyzed by correlating the log displacement thresholds with log (*V*) and log(TF). In the fovea, the correlation between log displacement threshold and log(V) was $r^2 = 0.99$; and the correlation in the periphery was $r^2 = 0.95$. The corresponding correlations for log(TF) were $r^2 = 0.79$ and 0.68, for fovea and periphery, respectively. Thus, velocity had greater influence, even though the TF range was much larger than the *V* range (128-fold vs. 32-fold). This result is consistent with neurophysiological data showing that at least some MT neurons are tuned to stimulus speed rather than temporal frequency (Perrone & Thiele, 2001; Priebe, Cassanello, & Lisberger, 2003).

Experiment 2

A closer look at image speed and spatial resolution

Do fast and slow image motions have qualitatively different effects on visual motion mechanisms? If foveal and peripheral thresholds are more similar at slow than at fast speeds, then the effects of speed might differ in the fovea and periphery. Here, we used a wider range of speeds to examine such effects.

In Experiment 2, SF was 1.0 c/°, for both central and peripheral fields. Speed (*V*) ranged from 0.08 to 20°/s. Thresholds were estimated for three observers. All had participated in Experiment 1, and two were co-authors.

Results

As in Experiment 1, the displacement and duration thresholds were oppositely affected by speed (Figure 3). Faster motions were seen more quickly, but they required larger spatial displacements. These results cannot be described by a simple model in which effects of speed on displacement thresholds correspond to a fixed temporal duration, nor were duration thresholds determined by a fixed spatial displacement. Such models would predict psychophysical functions that parallel either iso-duration or iso-displacement lines in Figure 3. The data, however, suggest that spatial and temporal limits have different influence at different speeds.

In both fovea and periphery, thresholds were spatially limited at slow speeds and temporally limited at high
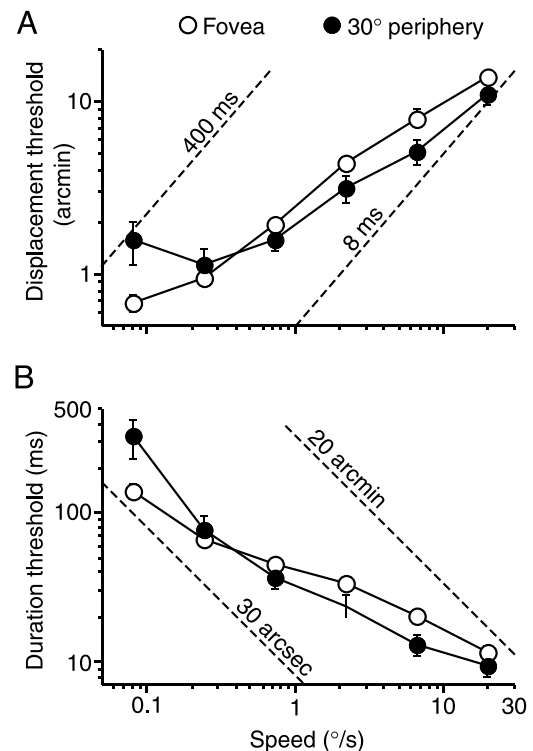

Figure 3. (A) Displacement and (B) duration thresholds for motion direction discriminations as a function of image speed. Parallel dashed lines connect points with constant temporal durations (A) and points with constant spatial displacements (B). Two such lines were selected in each panel to roughly bracket the data points. Error bars are ±1 *SEM*.

speeds. That is, displacement thresholds approach lower bounds as speeds become very slow, while duration thresholds approach lower bounds at fast speeds. These limits are most pronounced for slow speeds in the periphery where it appears that the lower spatial limit is just over 1 arcmin. This is particularly noteworthy, as low spatial thresholds for discriminating peripheral motion are a type of hyperacuity—below resolution limits associated with the peripheral cone density (Galvin et al., 1996).

Another characteristic of these results is that speed affected relative thresholds for foveal and peripheral motions. Thresholds were lower in the fovea at the slowest speeds but lower in the periphery at speeds above 0.5°/s. These results are likely related to the different spatial acuities in the fovea and periphery, as discussed above. However, this and other direct quantitative comparisons of foveal and peripheral thresholds are necessarily not general but stimulus specific. This idea is confirmed in the following experiment.

Experiment 2A: Surround suppression in fovea

For most speeds, the thresholds in Experiments 1 and 2 were lower in periphery than fovea. The generality of this result is questionable, however. Stimulus parameters such as SF, size, and contrast have different effects in fovea and periphery, suggesting that the relative thresholds probably depend on stimulus parameters.

One relevant factor is stimulus size. Tadin et al. (2003; Tadin & Lappin, 2005b) reported that duration thresholds at high contrast increased with increasing size, a result suggesting suppressive surround mechanisms. Importantly, the critical size for strong surround suppression increased with eccentricity. Thus, for a fixed size, surround suppression may be greater in the fovea. To examine this effect, we reduced the stimulus size from 1.5° (as in the preceding experiments) to 0.75° radius. Eighteen stimulus conditions included three speeds (2.2, 6.6, and 20°/s), three visual field locations (fovea and ±30°), and two sizes (1.5° and 0.75° radius). SF was 1 c/°. The observer (JN, one of the authors) had served in other experiments in this and other studies. Thresholds were estimated from at least 3 blocks of trials for each of the 18 conditions. For these speeds in the preceding experiment, thresholds were lower in periphery than fovea.

As suspected, surround suppression affected foveal but not peripheral thresholds. In the fovea, large stimuli had higher thresholds, averaging 1.45 times larger than those for the small stimuli. In the periphery, however, thresholds were similar for large and small sizes (0.96 ratio), consistent with our previous report (Tadin et al., 2003). Thus, as in the preceding experiment, thresholds for large stimuli were lower in the periphery than the fovea, but the small stimuli produced the opposite result: Ratios of peripheral to foveal thresholds averaged 0.80 for large stimuli and 1.19 for small stimuli.

The implication of this simple experiment is clear: The values of foveal and peripheral thresholds depend on the choice of stimulus parameters. Specifically, foveal sensitivities were underestimated in Experiments 1 and 2. Foveal and peripheral thresholds are more similar when the stimulus size is reduced to weaken foveal surround suppression.

Experiment 3

Effects of speed and eccentricity on motion discrimination by observers with nystagmus

Congenital nystagmus (CN) yields reductions in both acuity and motion sensitivity (Abadi, Whittle, & Worfolk, 1999; Acheson, Shallo-Hoffman, Bronstein, & Gresty, 1997; Nyquist, Lusk, Lappin, Corn, & Tadin, 2005). Thus, the linkage between reduced spatial acuity and motion perception in CN may differ from the small effect of acuity on peripheral motion discrimination. The effect of CN on motion perception is known to involve extra-retinal mechanisms, probably cortical (Abadi et al., 1999). The possible effects of speed and eccentricity on this reduced motion sensitivity, however, are not known.

We explored this issue by studying two low-vision observers with CN, using methods and conditions like those in Experiment 2. Observer TN (arbitrary initials), age 12, also has colaboma; and AK (arbitrary initials), age 10, has ocular albinism and accompanying photosensitivity. With refractive correction, TN's Snellen acuities had been measured as 20/450 left eye, 20/200 right, and 20/160 binocular; and corrected acuities for AK were previously measured as 20/200 in both eyes. Both observers exhibited duration thresholds for slow motions that were too long to preclude saccadic eye movements to the peripheral stimuli, so we were not able to test the slowest motions, especially in the periphery. The direction of motion for these observers was vertical rather than horizontal. In pilot experiments with typically sighted observers, we found no difference in sensitivities to horizontal and vertical motions, but for those with horizontal nystagmus, vertical motions are more visible. The following stimulus parameters were investigated: For low-vision observer TN, SF = 1 c/°; and V = 0.44, 0.72, 2.2, 6.6, and 20°/s. For the other low-vision observer AK, SF = 0.75 c/°; TF = 0.1, 1.6, and 18.75 Hz; and V = 0.13, 2.13, and 25°/s. Data for this observer were collected prior to data collection for the other observers, when we had expected lower SF stimuli to be more readily visible by low-vision observers. This 25% difference in SF is, however, unlikely to yield substantial changes in the results (see Figure 2).

Results

Effects of image speed on discrimination thresholds in the central and peripheral fields of these two observers are shown in Figure 4. Average thresholds for three typically sighted and well-practiced observers are shown for comparison, replotted from Figure 3. The effects of CN on motion discrimination were highly speed dependent; and these effects were also different in the central and peripheral fields. In the central field, a deficit for the low-vision observers occurred only at slow speeds but not above 2°/s. Remarkably, performance of the low-vision observers for speeds 2°/s and above was similar to that of the typically sighted observers, all of whom were much more practiced at this task.

The detrimental effects of CN were greater in the periphery, even at high speeds. Explanations for these interactive effects of speed, eccentricity, and CN on motion perception remain to be discovered. Other recent studies have also found reduced sensitivity to peripheral stimuli in some persons with low vision (Nyquist, 2007).

Experiment 4

Effects of speed on surround suppression

Surround suppression is a perceptual effect that resembles center–surround antagonism in directionally selective neurons in cortical area MT (Tadin et al., 2003). Psychophysically, surround suppression is evident as an increase in thresholds for discriminating high-contrast patterns as the stimulus size increases. If MT neurons are indeed a key neural correlate of these psychophysical observations, then the strength of surround suppression should depend on speed: Directionally selective MT neurons typically prefer velocities above 1°/s and lose their directional selectivity at velocities below 0.5°/s (Lagae, Raiguel, & Orban, 1993; Pack et al., 2005; Priebe, Lisberger, & Movshon, 2006). Here we investigated whether psychophysical surround suppression exhibits a similar dependency on stimulus speed.

Thresholds were measured for large (6.0°) and small (1.25°) motion patches in the central field. Previous experiments had found that these two sizes yield clearly different thresholds in the central field. Analogous results were found previously for peripheral stimuli, except that larger stimuli were required to elicit surround suppression (Tadin et al., 2003). Thus, we restricted our measurements here to foveal motions.

Seven values of V were tested, over a 500-fold range from 0.06°/s to 30°/s. Stimuli were presented on a 200-Hz CRT monitor (Totuku PROCALIX; ATI Radeon 9200 Mac Edition graphics card), with 800 × 600 resolution. Viewing was binocular at 83 cm, yielding 2 × 2 arcmin pixel size. Average gray-screen luminance was 37.4 cd/m^2.

Discrimination thresholds were measured for three well-practiced observers, one of whom is a co-author. A fourth observer also completed the experiment, but his data were excluded due to evident floor effects in thresholds at the two highest speeds. Nevertheless, he showed the same pattern of results as the other three observers.
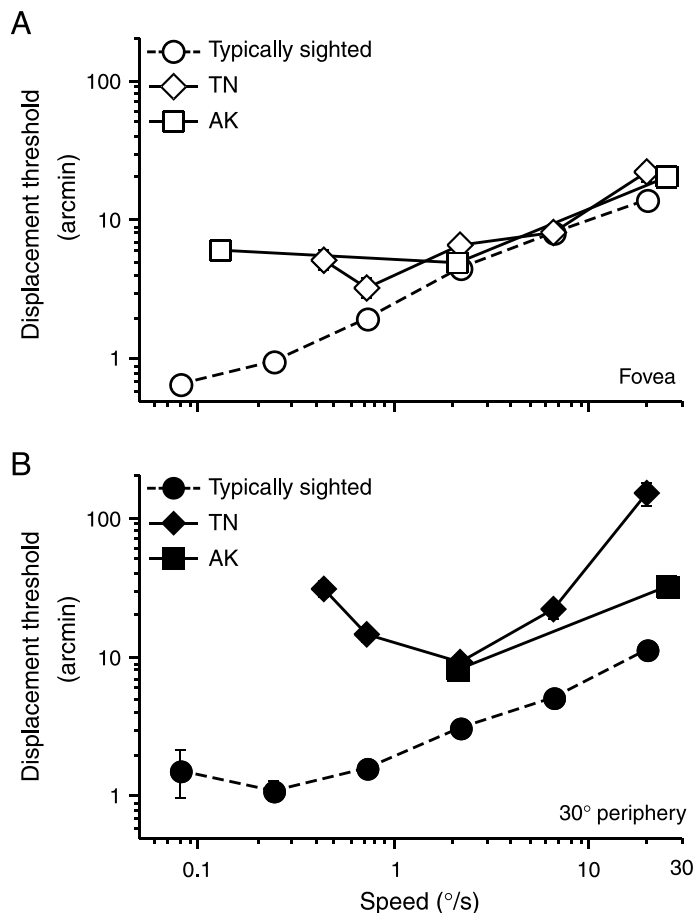

Figure 4. Spatial displacement thresholds for discriminating motion in the fovea (A) and at ±30° in the periphery (B). Data for two low-vision observers with congenital nystagmus are given by the solid lines; data for typically sighted observers are given by the dashed lines, replotted from Figure 3. Error bars are ±1 *SEM*, based on multiple trial blocks for the low-vision observers and on multiple observers for the typically sighted.

Results

As in the previous experiments, increasing stimulus speed yielded lower duration thresholds (Figure 5). The key result is that the thresholds for large moving stimuli were higher at all but the slowest speeds—a result indicating surround suppression. Importantly, the difference in thresholds for the large and small stimuli increased with speed, indicating that the strength of

surround suppression increases with speed (Figure 5B). These effects of size and speed, with an increasing effect of size at higher speeds, were found for all three observers. For all speeds ≥0.7°/s, each observer's thresholds were substantially greater for the large stimulus, with only negligible differences at the slowest speed (0.06°/s).

Finally, these results are consistent with Experiment 2 and show that duration thresholds do not follow constant spatial displacements over variations in speed. Faster speeds require larger spatial displacements. Furthermore, the lower spatial limit for direction discriminations appears to be about 30 arcsec—consistent with Experiment 2.

Experiment 4A: How speed affects spatial interactions at low contrast

Psychophysical surround suppression in motion depends on contrast, with suppression at high contrast but spatial summation at low contrast (Tadin & Lappin, 2005b; Tadin et al., 2003). The finding that high speed amplifies surround suppression at high contrast (Figure 5) suggests that high speed might also alter spatial interactions at low contrast, perhaps yielding suppression rather than summation of fast, low-contrast motions.
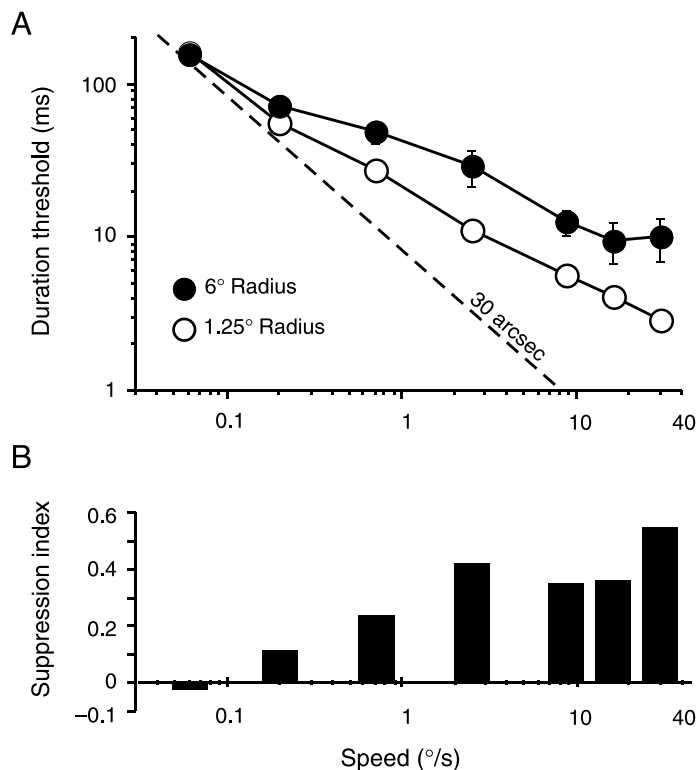

Figure 5. The effect of speed on surround suppression. (A) Duration thresholds for two stimulus sizes. Error bars are ±1 *SEM* between observers. (B) Estimated suppression index for each speed. Suppression index is defined as $\log_{10}$(threshold for the 6° stimulus) − $\log_{10}$(threshold for the 1.25° stimulus).

To address this question, we replicated Experiment 4 at low contrast, where previous studies found spatial summation rather than suppression. A complication, however, is that speed also affects contrast thresholds for discriminating motion (e.g., Virsu et al., 1982). If the same contrast were used for all speeds, then the resulting differences in visibility rather than speed per se might cause differences in spatial interactions. Thus, we first estimated observers' contrast thresholds for briefly presented (250 ms) small (1.25°) stimuli at the same range of speeds as in Experiment 4. Two observers from Experiment 4 participated in this experiment. These contrast thresholds varied as a U-shaped function of speed, with the lowest thresholds (0.39%) for an intermediate speed of 2.5°/s, and increasing about 10-fold for the slowest and fastest speeds. The obtained contrast thresholds were then doubled and used to find the duration thresholds for discriminating large (6°) and small (1.25°) stimuli at the same speeds as in Experiment 4.

This experiment yielded results opposite those in the preceding experiment. Instead of surround suppression, spatial summation occurred at all speeds: Thresholds for large stimuli were always lower than those for small stimuli. The average suppression index was −0.33 (*SD* = 0.14, range = −0.12 to −0.50), with negative numbers indicating summation. Moreover, thresholds for the large, low-contrast stimuli at speeds ≥0.70°/s were lower than those for the high-contrast stimuli of the same size in Experiment 4. Thus, as found previously (Tadin & Lappin, 2005b; Tadin et al., 2003), surround suppression increases with contrast; large stimuli have lower thresholds at low contrast.

Direct comparisons of thresholds for different speeds at low contrast are ambiguous because stimuli were not equally visible across speeds. Both observers reported that the slow- and high-speed stimuli were easier to see than those with the lowest contrasts and intermediate speeds. Nevertheless, at all speeds tested, low contrast yielded spatial summation.

Discussion

A general finding of this study was that speed has large effects on thresholds for motion perception. As speed increased, duration thresholds decreased and displacement thresholds increased. Both effects are intuitive: With greater speed, (a) a given displacement occurs in less time, and (b) larger displacement occurs within a given duration.

Figure 3 shows that these effects of speed are not described by a simple model with a constant threshold for either displacement or duration. Rather, the roles of spatial and temporal limits vary with speed. Discrimination thresholds for slow-speed motion were evidently limited

by acuities for small spatial shifts. The brief duration thresholds for high-speed motion, on the other hand, were probably constrained temporally by neural limits on encoding rapidly changing stimulation.

This changing role of spatial and temporal limits over variations in speed contrasts with Burr and Corsale's (2001) finding that reaction times to motion onset were directly proportional to the temporal period of grating motion. They examined a narrower range of speeds, however—0.25 to 10°/s—that excluded very slow and fast speeds where spatial and temporal processing limits are best revealed.

Motion discrimination in fovea and periphery

General statements about the relative motion sensitivities of the fovea and periphery are not necessarily meaningful because the relative thresholds depend on the stimulus parameters—e.g., size, SF, contrast, and speed—and the discrimination task. Nevertheless, the present study found greater similarities of foveal and peripheral motion sensitivities than indicated by many previous studies: For speeds above 0.5°/s, thresholds were not correlated with the anatomical and physiological factors that limit static spatial acuity in fovea and periphery.

Densities of photoreceptors, ganglion cells, and cortical neurons all decrease with increased eccentricity, and receptive field sizes increase (Curcio & Allen, 1990; Curcio, Sloan, Kalina, & Hendrickson, 1990; Drasdo, 1977; Kaplan, 2004; Martin & Grünert, 2004; Rodieck, 1998). Correspondingly, visual acuity also decreases in proportion to eccentricity (Anstis, 1974; Banks, Sekuler, & Anderson, 1991). Physiological responses of cells in macaque cortical areas V1 and V2 also exhibit correlations between speed sensitivity and eccentricity, where foveal receptive fields prefer slow speed and those in the periphery prefer faster speeds (Orban, Kennedy, & Bullier, 1986). Correlations of motion sensitivity with eccentricity and acuity seem functionally relevant to the ecological optics of locomotion, where expanding optic flow fields stimulate the retina with average speeds proportional to eccentricity (van de Grind, 1994; van de Grind, Koenderink, & Doorn, 1992; Warren, 2004).

Previous psychophysical studies using longer stimulus durations and often using contrast and coherence thresholds have generally found that motion sensitivity correlates with eccentricity and spatial acuity. Contrast thresholds for motion detection scale with eccentricity and spatial acuity (Kelly, 1984, 1985; Koenderink et al., 1978a, 1978b, 1978c, 1978d; Virsu et al., 1982). Koenderink et al. (1978b) found that the most visible image speed was proportional to eccentricity, increasing about 6- to 10-fold from fovea to 50°. Across photopic to quantum-limited scotopic luminances, contrast thresholds for a given TF were roughly constant over the visual field if stimulus size

and velocity were made proportional to static acuity at each eccentricity (Koenderink et al., 1978a, 1978b, 1978c, 1978d). Other psychophysical measures correlated with eccentricity and acuity include signal/noise thresholds in random-pixel arrays (Koenderink, van Doorn, & van de Grind, 1985; van de Grind et al., 1983, 1986, 1987, 1993), speed discrimination (McKee & Nakayama, 1984), differential motion detection (McKee & Nakayama, 1984), minimum velocity thresholds (Johnston & Wright, 1985), and perceived direction reversals (Coletta et al., 1990; Galvin et al., 1996).

Duration thresholds in the present study, however, contrast with all the preceding literature: Motion stimuli with the same SF and speed in both fovea and periphery yielded thresholds that were usually lower in the periphery than the fovea. If the spatial periods (SF^{-1}, °/c) and speeds of these stimuli had matched the relative acuities of the fovea and periphery, as in the study of Koenderink et al. (1978a, 1978b, 1978c, 1978d), then differences between foveal and peripheral thresholds would have been much greater. In fact, we tried this approach in pilot experiments, using sizes and speeds 4–5 times greater in periphery than fovea. The result was substantially *lower* thresholds in periphery. Thresholds were much more similar in the present experiments when speed and size were the same in fovea and periphery. (In the pilot experiments, we first obtained acuity thresholds for each observer by finding the smallest size—spatial envelope and SF^{-1}, with 4 visible cycles—permitting direction discriminations of 10-Hz motions. Spatial sizes of stimuli for the main experiment were then set at twice these acuity thresholds.)

Because duration thresholds for speeds above 0.5°/s were not limited by peripheral acuity, one might expect similar results for reaction times to motion onset. This is, essentially, what Tynan and Sekuler (1982) found. Reaction times (RTs) to motion of high-contrast dot patterns for speeds above 4°/s were invariant with eccentricity. RTs also decreased as motion speed increased. As in the present study, the effects of eccentricity depended on motion speed, with slow speeds (0.25°/s) yielding slower responses at greater eccentricities.

The present thresholds for the slowest motions were higher in the periphery than the fovea, but even these peripheral spatial thresholds were surprisingly low. Galvin et al. (1996) estimate the Nyquist frequency at 30° eccentricity as about 10 c/° (peak-trough resolution = 3 arcmin), based on cone densities (Curcio et al., 1990) and on perceived motion reversals across varied SFs. Here, peripheral thresholds for slow speed were below these limits, averaging 1.57 and 1.13 arcmin for speeds of 0.08 and 0.24°/s. These low thresholds can be partly explained by our definition of stimulus duration as the interval with contrast above half maximum. The smallest displacement thresholds in the fovea, however, were slightly *higher* than the roughly 0.5 arcmin resolution limits indicated by cone densities—averaging 0.68 and

0.96 arcmin for speeds of 0.08 and 0.24°/s. The present peripheral thresholds were also lower than the 2–3 arcmin threshold for differential motion found by McKee and Nakayama (1984) at 30° eccentricity.

Not surprisingly, the present spatial displacement thresholds—at the shortest durations for direction discrimination—are higher than those found with long-duration repeating oscillations in the fovea (e.g., Nakayama & Tyler, 1981; Wright & Johnston, 1985). The present effects of eccentricity and speed also differ from those for long-duration stimuli (e.g., Johnston & Wright, 1985; Seiffert & Cavanagh, 1998; Wright & Johnston, 1985).

Is the similarity of foveal and peripheral thresholds for moderate and fast motion relevant to visual function? Perhaps this uniformity facilitates visual coherence of global image motions in the moving eyes of active observers.

Motion speed affects observers with nystagmus

"Low vision" refers to non-correctable low acuity. The causes of low vision are many, but involuntary ocular nystagmus is a frequent secondary effect, and congenital nystagmus (CN) may cause low vision. CN usually involves a slow-phase drift of fixation followed by a quick-phase saccadic return (Abadi, 2002). The direction of eye movement usually is predominantly horizontal, as in the two observers we tested. Temporal frequencies of oscillation typically are in the range of 2–6 Hz, with amplitudes about 2–8° and peak slow-phase velocities often above 100°/s (Abadi & Dickinson, 1986; Abadi et al., 1999; Abadi & Worfolk, 1989; Clement et al., 2002; Jacobs & Dell'Osso, 2004; Shallo-Hoffman, Dell'Osso, & Dun, 2004). Reduced contrast sensitivity, orientation discrimination, and acuity of CN patients are believed to reflect cortical mechanisms, perhaps related to amblyopia (Abadi & King-Smith, 1979; Bedell, 2006; Chung & Bedell, 1995; Ukwade, Bedell, & White, 2002). Nystagmus also reduces motion sensitivity (Abadi et al., 1999; Acheson et al., 1997). CN usually does not cause oscillopsia (perceived instability of the visual world); but instability is perceived if images are artificially stabilized (Abadi et al., 1999), implying an extra-retinal negative feedback.

We had previously found high duration thresholds for motion discrimination in observers with CN (Nyquist et al., 2005). Later pilot studies, however, suggested that low-vision motion sensitivity might be better for faster motions than for the relatively slow speeds (1–2°/s) we used initially. When we examined this in Experiment 3, thresholds for two low-vision observers were elevated for slow foveal and for peripheral motions, but resembled typically sighted observers for foveal motions for speeds above 1°/s. Saccadic interruptions might hinder sensitivity to slow motions, as the longer presentations may be more vulnerable to saccadic interruption. This possibility, however, does not explain the high peripheral thresholds for these observers.

The interactive effects of CN, speed, and retinal locus warrant further investigation. The finding that low-vision observers have high thresholds for peripheral motion, even at high speeds, may be relevant to visual function. Perhaps the moving visual fields of these observers are perceptually less coherent than those of typically sighted observers. Perhaps these differences in motion threshold are pertinent to suggestions that children with low vision are often less attentive than typically sighted children to the peripheral visual fields (Nyquist, 2007).

Surround suppression depends on speed

Center–surround antagonism is a key property of motion-sensitive neurons in primates, characterized by decreased neural responses as the stimulus size increases (Allman, Miezin, & McGuiness, 1985; Born, Groh, Zhao, & Lukasewycz, 2000; Born & Tootell, 1992; Jones, Wang, & Sillito, 2002). This property of single neurons may underlie psychophysical observations that motion discriminations of high-contrast stimuli worsen with increased stimulus size (Tadin & Lappin, 2005b; Tadin et al., 2003). Similarities between psychophysical surround suppression and neurophysiological center–surround antagonism in MT neurons suggest a link between the two domains (Churan, Khawaja, Tsui, & Pack, 2008; Pack et al., 2005).

Here we asked whether the effects of speed on surround suppression correlated with the speed tuning of MT neurons. Previous psychophysical studies were restricted to speeds ranging from 2°/s (Tadin et al., 2003) to 20°/s (Tadin, Lappin, & Blake, 2006) and did not compare surround suppression across speeds. This is relevant because neurophysiological studies of MT neurons have found that directional selectivity in area MT disappears at speeds below approximately 0.5°/s (Lagae et al., 1993; Pack et al., 2005; Priebe et al., 2006). If MT neurons are responsible for psychophysical surround suppression, then surround suppression might not occur at very slow speeds below 0.5°/s. The present study confirmed this prediction and found that thresholds for large (6°) and small (1.25°) stimuli diverged as speed increased. The present experiment does not identify area MT as the locus of psychophysical surround suppression, but the results are consistent with this hypothesis.

What are the functional implications of the interaction between speed and surround suppression? Perhaps faster patterns are visually more spatially differentiated. We are now investigating such potential functional effects.

We also found here that at low contrast, surround suppression does not occur at any speed. Evidently, low-contrast motion signals are spatially integrated, regardless of speed. Spatial summation probably operates to improve detection and discrimination of low-contrast motion, sacrificing information about its spatial location.

General comments

Key findings in this study result directly from our use of duration and displacement thresholds. The assumption is that when the duration of sensory input is less than required for neural processing, perception will fail. The duration thresholds probably reflect both neural and stimulus limitations (Borghuis, 2003). Duration thresholds have been used in previous work on surround suppression (e.g., Betts, Taylor, Sekuler, & Bennett, 2005; Tadin & Lappin, 2005b; Tadin et al., 2003), on other aspects of motion perception (Mateeff, Dimitrov, & Hohnsbein, 1995; Tayama, 2000), color perception (Pokorny, Bowen, Williams, & Smith, 1979), and symmetry perception (Tyler, 2001). In the present study, the same method also measured spatial displacement thresholds. Small spatial displacements evidently limit motion discriminations at very slow speeds.

Visual responses to brief motions may differ from those at longer durations. Churan et al. (2008) recently found that brief stimulus durations selectively elicit directional responses from MT neurons with surround suppression, while MT neurons that prefer wide-field motions do not exhibit directional selectivity for brief stimuli of *any size*. Thus, MT neurons are directionally selective for brief stimuli only when either the size or contrast is small enough to evade the inhibitory surround response. One concern about brief motion stimuli is that their wider temporal frequency spectrum might result in motion energy spilling over into the opponent regions of Fourier space. This might explain difficulties in discriminating motion of brief, *large,* high-contrast stimuli (Derrington & Goddard, 1989), but it cannot explain the accurate discriminations and monotonic contrast effects for *small* stimuli nor the similar interactive effects of size and contrast obtained with long-duration stimuli (Paffen, Tadin, te Pas, Blake, & Verstraten, 2006; Tadin et al., 2003).

The data in Figure 3A indicate that thresholds for very slow motion, below 0.5°/s, reflect mainly spatial limits, probably associated with spatial acuities in the fovea and periphery. For speeds above 0.5°/s, spatial acuities seem to have little influence for typically sighted observers.

As speed increases, motion information seems increasingly limited by temporal rather than spatial resolution. For speeds above 20°/s, Figure 3B suggests that thresholds may be limited by the rate at which neurons can transmit information about brief, rapidly oscillating stimulation. Indeed, the duration thresholds in Experiments 1 and 2

resemble the time constants of retinal ganglion cells in response to image motion (Borghuis, 2003; Chichilnisky & Kalmar, 2003; Frechette et al., 2005). If the present behavioral thresholds actually approach the temporal resolution of retinal ganglion cells, then motion-sensitive mechanisms in the cortex must make very efficient use of retinal information. This suggestion is consistent with findings that (a) ganglion cell spike trains and behavioral detection can have similar sensitivities (Barlow, Levick, & Yoon, 1971; Borghuis, Ratliff, Smith, Sterling, & Balasubramanian, 2008; Dhingra, Kao, Sterling, & Smith, 2003) and (b) information can be efficiently transmitted by individual spikes in LGN neurons (Reinagel & Reid, 2002).

Effects of speed on the present direction discriminations differ from the effects on speed discriminations (McKee, Silverman, & Nakayama, 1986; Norman et al., 2008; Orban, de Wolf, & Maes, 1984; Tynan & Sekuler, 1982). Nevertheless, speed and direction discriminations are not directly comparable because they involve different variations among different stimuli. Speed discriminations probably require longer durations and greater spatial displacements than those described here and may exhibit different dependence on eccentricity. Indeed, Tynan and Sekuler (1982) found that reaction times and speed perception were influenced differently by both speed and eccentricity.

Most visual motion models are designed to encode speed (Adelson & Bergen, 1985; Chichilnisky & Kalmar, 2003; De Valois & Cottaris, 1998; De Valois et al., 2000; Frechette et al., 2005; Nakayama, 1985; Perrone, 2005; Reichardt, 1961; Simoncelli & Heeger, 2001; Stocker & Simoncelli, 2006; van Santen & Sperling, 1985; Watson & Ahumada, 1985; Weiss, Simoncelli, & Adelson, 2002). A generic model of a first-stage motion detector combines spike trains from two receptive fields, with one spike train temporally delayed relative to the other, parameterized by the spatial and temporal separations. Unlike speed discrimination, direction discrimination does not require information about spatial separation or spatial frequency, nor temporal separation or frequency. Ordinal properties of the spatiotemporal phase relations are sufficient, without reliance on multiple mechanisms tuned to different speeds, different spatial frequencies, etc.

Image motion is typically conceived as a temporal sequence of spatial positions occupied by a given stimulus, retinally encoded by the spatial and temporal positions of the stimulus-evoked spike trains (e.g., Chichilnisky & Kalmar, 2003; Frechette et al., 2005). This conception fits a moving bar but is less applicable to the present stimuli. Here, stimulation changed simultaneously throughout its spatial and temporal extents; and spike trains varied simultaneously over the ensemble of retinal ganglion cells. Motion information necessarily involved spatial and temporal phase relations in the optical stimulation, probably supported by coherent phase relations over the retinal ensemble—a suggestion reinforced by

other psychophysical evidence (Lappin, Donnelly, & Kojima, 2001; Lappin, Tadin, & Whittier, 2002).

Overall, this study found that speed has a major controlling effect on visual responses to moving patterns. Visual information about motion direction evidently requires little image data—brief durations of fast motion and small displacements of slow motion. The minimum-motion thresholds for direction discriminations in fovea and periphery revealed a clear dissociation of visual information about moving and stationary patterns: Visual information about modest to high-speed motion evidently is unaffected by the anatomical resolution of the retinal mosaic and cortex, quite unlike visual acuity for stationary or slowly moving patterns.

Acknowledgments

References

Abadi, R. V. (2002). Mechanisms underlying nystagmus. *Journal of the Royal Society of Medicine, 95,* 231–234. [PubMed] [Article]

Abadi, R. V., & Dickinson, C. M. (1986). Waveform characteristics in congenital nystagmus. *Documenta Ophthalmologica, 64,* 153–167. [PubMed]

Abadi, R. V., & King-Smith, P. E. (1979). Congenital nystagmus modifies orientational detection. *Vision Research, 19,* 1409–1411. [PubMed]

Abadi, R. V., Whittle, J. P., & Worfolk, R. (1999). Oscillopsia and tolerance to retinal image movement in congenital nystagmus. *Investigative Ophthalmology & Visual Science, 40,* 339–345. [PubMed] [Article]

Abadi, R. V., & Worfolk, R. (1989). Retinal slip velocities in congenital nystagmus. *Vision Research, 29,* 195–205. [PubMed]

Acheson, J. F., Shallo-Hoffman, J. A., Bronstein, A. M., & Gresty, M. A. (1997). Vertical and horizontal motion perception in congenital nystagmus. *Investigative Ophthalmology & Visual Science, 38,* S 1143.

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A, Optics and Image Science, 2,* 284–299. [PubMed]

Allman, J., Miezin, F., & McGuiness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception, 14,* 105–126. [PubMed]

Anderson, S. J., & Burr, D. C. (1987). Receptive field size of human motion detection units. *Vision Research, 27,* 621–635. [PubMed]

Anderson, S. J., & Burr, D. C. (1991). Spatial summation properties of directionally sensitive mechanisms in human vision. *Journal of the Optical Society of America A, Optics and Image Science, 8,* 1330–1339. [PubMed]

Anstis, S. M. (1974). Letter: A chart demonstrating variations in acuity with retinal position. *Vision Research, 14,* 589–592. [PubMed]

Banks, M. S., Sekuler, A. B., & Anderson, S. J. (1991). Peripheral spatial vision: Limits imposed by optics, photoreceptors, and receptor pooling. *Journal of the Optical Society of America A, Optics and Image Science, 8,* 1775–1787. [PubMed]

Barlow, H. B., Levick, W. R., & Yoon, M. (1971). Responses to single quanta of light in retinal ganglion cells of the cat. *Vision Research, 11,* 87–101. [PubMed]

Bedell, H. E. (2006). Visual and perceptual consequences of congenital nystagmus. *Seminars in Ophthalmology, 21,* 91–95. [PubMed]

Betts, L. R., Taylor, C. P., Sekuler, A. B., & Bennett, P. J. (2005). Aging reduces center–surround antagonism in visual motion processing. *Neuron, 45,* 361–366. [PubMed] [Article]

Borghuis, B. G. (2003). *Spike timing precision in the visual front-end.* Doctoral thesis, Universiteit Utrecht, Utrecht, The Netherlands.

Borghuis, B. G., Ratliff, C. P., Smith, R. G., Sterling, P., & Balasubramanian, V. (2008). Design of a neuronal array. *Journal of Neuroscience, 28,* 3178–3189. [PubMed] [Article]

Born, R. T., Groh, J. M., Zhao, R., & Lukasewycz, S. J. (2000). Segregation of object and background motion in visual area MT: Effects of microstimulation on eye movements. *Neuron, 26,* 725–734. [PubMed] [Article]

Born, R. T., & Tootell, R. B. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature, 357,* 497–499. [PubMed]

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436. [PubMed]

Burr, D. C., & Corsale, B. (2001). Dependency of reaction times to motion onset on luminance and chromatic contrast. *Vision Research, 41,* 1039–1048. [PubMed]

Chichilnisky, E. J., & Kalmar, R. S. (2003). Temporal resolution of ensemble visual motion signals in primate retina. *Journal of Neuroscience, 23,* 6681–6689. [PubMed] [Article]

Chung, S. T., & Bedell, H. E. (1995). Effect of retinal image motion on visual acuity and contour interaction in congenital nystagmus. *Vision Research, 35,* 3071–3082. [PubMed]

Churan, J., Khawaja, F. A., Tsui, J. M., & Pack, C. C. (2008). Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT. *Current Biology, 18,* R1051–R1052. [PubMed] [Article]

Clement, R. A., Whittle, J. P., Muldoon, M. R., Abadi, R. V., Broomhead, D. S., & Akman, O. (2002). Characterization of congenital nystagmus waveforms in terms of periodic orbits. *Vision Research, 42,* 2123–2130. [PubMed]

Coletta, N. J., Williams, D. R., & Tiana, C. L. (1990). Consequences of spatial sampling for human motion perception. *Vision Research, 30,* 1631–1648. [PubMed]

Curcio, C. A., Sloan, K. R., Kalina, R. E., & Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology, 292,* 497–523. [PubMed]

Curcio, C. A., & Allen, K. A. (1990). Topography of ganglion cells in human retina. *Journal of Comparative Neurology, 300,* 5–25. [PubMed]

DeAngelis, G. C., & Anzai, A. (2004). A modern view of the classical receptive field: Linear and nonlinear spatiotemporal processing by V1 neurons. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 704–719). Cambridge, MA: MIT Press.

Derrington, A. M., & Goddard, P. A. (1989). Failure of motion discrimination at high contrasts: Evidence for saturation. *Vision Research, 29,* 1767–1776. [PubMed]

De Valois, R. L., & Cottaris, N. P. (1998). Inputs to directionally selective simple cells in macaque striate cortex. *Proceedings of the National Academy of Sciences of the United States of America, 95,* 14488–14493. [PubMed] [Article]

De Valois, R. L., Cottaris, N. P., Mahon, L. E., Elfar, S. D., & Wilson, J. A. (2000). Spatial and temporal receptive fields and directional selectivity. *Vision Research, 40,* 3685–3702. [PubMed]

Dhingra, N. K., Kao, Y. H., Sterling, P., & Smith, R. G. (2003). Contrast threshold of a brisk-transient ganglion cell in vitro. *Journal of Neurophysiology, 89,* 2360–2369. [PubMed] [Article]

Drasdo, N. (1977). The neural representation of visual space. *Nature, 266,* 554–556. [PubMed]

Frechette, E. S., Sher, A., Grivich, M. I., Petrusca, D., Litke, A. M., & Chichilnisky, E. J. (2005). Fidelity of the ensemble code for visual motion in primate retina. *Journal of Neurophysiology, 94,* 119–135. [PubMed] [Article]

Galvin, S. J., Williams, D. R., & Coletta, N. J. (1996). The spatial grain of human peripheral vision. *Vision Research, 36,* 2283–2295. [PubMed]

Jacobs, J. B., & Dell'Osso, L. F. (2004). Congenital nystagmus: Hypotheses for its genesis and complex waveforms within a behavioral ocular motor system model. *Journal of Vision, 4*(7):7, 604–625, http://journalofvision.org/4/7/7/, doi:10.1167/4.7.7. [PubMed] [Article]

Johnston, A., & Wright, M. J. (1985). Lower thresholds of motion for gratings as a function of eccentricity and contrast. *Vision Research, 25,* 179–185. [PubMed]

Jones, H. E., Wang, W., & Sillito, A. M. (2002). Spatial organization and magnitude of orientation contrast interactions in primate V1. *Journal of Neurophysiology, 88,* 2796–2808. [PubMed] [Article]

Kaplan, E. (2004). The M, P, and K pathways of the primate visual system. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 481–506). Cambridge, MA: MIT Press.

Kelly, D. H. (1984). Retinal inhomogeneity. I. Spatiotemporal contrast sensitivity. *Journal of the Optical Society of America A, Optics and Image Science, 1,* 107–113. [PubMed]

Kelly, D. H. (1985). Visual processing of moving stimuli. *Journal of the Optical Society of America A, Optics and Image Science, 2,* 216–225. [PubMed]

Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E., & Slappendel, S. (1978a). Perimetry of contrast detection thresholds of moving spatial sine wave patterns. I. The near peripheral visual field (eccentricity 0 degrees–8 degrees). *Journal of the Optical Society of America, 68,* 845–849. [PubMed]

Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E., & Slappendel, S. (1978b). Perimetry of contrast detection thresholds of moving spatial sine wave patterns. II. The far peripheral visual field (eccentricity 0 degrees–50 degrees). *Journal of the Optical Society of America, 68,* 850–854. [PubMed]

Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E., & Slappendel, S. (1978c). Perimetry of contrast detection thresholds of moving spatial sine wave patterns. III. The target extent as a sensitivity controlling parameter. *Journal of the Optical Society of America, 68,* 854–860. [PubMed]

Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E., & Slappendel, S. (1978d). Perimetry of contrast detection thresholds of moving spatial sine wave patterns. IV. The influence of the mean retinal illuminance. *Journal of the Optical Society of America, 68,* 860–865. [PubMed]

Koenderink, J. J., van Doorn, A. J., & van de Grind, W. A. (1985). Spatial and temporal parameters of motion detection in the peripheral visual field. *Journal of the Optical Society of America A, Optics and Image Science, 2,* 252–259. [PubMed]

Lagae, L., Raiguel, S., & Orban, G. A. (1993). Speed and direction selectivity of macaque middle temporal neurons. *Journal of Neurophysiology, 69,* 19–39. [PubMed]

Lappin, J. S., Donnelly, M. P., & Kojima, H. (2001). Coherence of early motion signals. *Vision Research, 41,* 1631–1644. [PubMed]

Lappin, J. S., Tadin, D., & Whittier, E. J. (2002). Visual coherence of moving and stationary image changes. *Vision Research, 42,* 1523–1534. [PubMed]

Martin, P. R., & Grünert, U. (2004). Ganglion cells in mammalian retinae. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 410–421). Cambridge, MA: MIT Press.

Mateeff, S., Dimitrov, G., & Hohnsbein, J. (1995). Temporal thresholds and reaction time to changes in velocity of visual motion. *Vision Research, 35,* 355–363. [PubMed]

McKee, S. P., & Nakayama, K. (1984). The detection of motion in the peripheral visual field. *Vision Research, 24,* 25–32. [PubMed]

McKee, S. P., Silverman, G. H., & Nakayama, K. (1986). Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Research, 26,* 609–619. [PubMed]

Nakayama, K. (1985). Biological image motion processing: A review. *Vision Research, 25,* 625–660. [PubMed]

Nakayama, K., & Tyler, C. W. (1981). Psychophysical isolation of movement sensitivity by removal of familiar position cues. *Vision Research, 21,* 427–433. [PubMed]

Norman, J. F., Pattison, K. F., Norman, H. F., Craft, A. E., Wiesemann, E. Y., & Taylor, M. J. (2008). The role of explicit and implicit standards in visual speed discrimination. *Perception, 37,* 889–901. [PubMed]

Nyquist, J. B. (2007). Perceptual training yields rapid improvements in visually impaired youth. Unpublished doctoral dissertation, Nashville, TN: Vanderbilt University.

Nyquist, J. B., Lusk, K. E., Lappin, J. S., Corn, A. L., & Tadin, D. (2005). Low vision differences between static and moving patterns in central and peripheral fields [Abstract]. *Journal of Vision, 5*(8):300, 300a, http://journalofvision.org/5/8/300/, doi:10.1167/5.8.300.

Orban, G. A., de Wolf, J., & Maes, H. (1984). Factors influencing velocity coding in the human visual system. *Vision Research, 24,* 33–39. [PubMed]

Orban, G. A., Kennedy, H., & Bullier, J. (1986). Velocity sensitivity and direction selectivity of neurons in areas V1 and V2 of the monkey: Influence of eccentricity. *Journal of Neurophysiology, 56,* 462–480. [PubMed]

Pack, C. C., Hunter, J. N., & Born, R. T. (2005). Contrast dependence of suppressive influences in cortical area MT of alert macaque. *Journal of Neurophysiology, 93,* 1809–1815. [PubMed] [Article]

Paffen, C. L., Tadin, D., te Pas, S. F., Blake, R., & Verstraten, F. A. (2006). Adaptive center–surround interactions in human vision revealed during binocular rivalry. *Vision Research, 46,* 599–604. [PubMed]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442. [PubMed]

Perrone, J. A. (2005). Economy of scale: A motion sensor with variable speed tuning. *Journal of Vision, 5*(1):3, 28–33, http://journalofvision.org/5/1/3/, doi:10.1167/5.1.3. [PubMed] [Article]

Perrone, J. A., & Thiele, A. (2001). Speed skills: Measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience, 4,* 526–532. [PubMed]

Pokorny, J., Bowen, R. W., Williams, D. T., & Smith, V. C. (1979). Duration thresholds for chromatic stimuli. *Journal of the Optical Society of America, 69,* 103–106. [PubMed]

Priebe, N. J., Cassanello, C. R., & Lisberger, S. G. (2003). The neural representation of speed in macaque are MT/V5. *Journal of Neuroscience, 23,* 5650–5661. [PubMed] [Article]

Priebe, N. J., Lisberger, S. G., & Movshon, J. A. (2006). Tuning for spatiotemporal frequency and speed in directionally selective neurons of macaque striate cortex. *Journal of Neuroscience, 26,* 2941–2950. [PubMed] [Article]

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information in the central nervous system. In W. Rosenblith (Ed.), *Sensory communication* (pp. 303–317). Cambridge, MA: MIT Press.

Reinagel, P., & Reid, C. R. (2002). Precise firing events are conserved across neurons. *Journal of Neuroscience, 22,* 6837–6841. [PubMed] [Article]

Rodieck, R. W. (1998). *The first steps in seeing.* Sunderland, MA: Sinauer.

Seiffert, A. E., & Cavanagh, P. (1998). Position displacement, not velocity, is the cue to motion detection of second-order stimuli. *Vision Research, 38,* 3569–3582. [PubMed]

Shallo-Hoffman, J., Dell'Osso, L. F., & Dun, S. (2004). Time-varying slow-phase component interaction in congenital nystagmus. *Vision Research, 44,* 209–220. [PubMed]

Simoncelli, E. P., & Heeger, D. J. (2001). Representing retinal image speed in visual cortex. *Nature Neuroscience, 4,* 461–462. [PubMed]

Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience, 9,* 578–585. [PubMed]

Tadin, D., & Lappin, J. S. (2005a). Linking psychophysics and physiology of center–surround interactions in visual motion processing. In M. R. M. Jenkin & L. R. Harris (Eds.), *Seeing spatial form* (pp. 279–314). New York: Oxford University Press.

Tadin, D., & Lappin, J. S. (2005b). Optimal size of perceiving motion decreases with contrast. *Vision Research, 45,* 2059–2064. [PubMed]

Tadin, D., Lappin, J. S., & Blake, R. (2006). Fine temporal properties of center–surround interactions in motion revealed by reverse correlation. *Journal of Neuroscience, 26,* 2614–2622. [PubMed] [Article]

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. [PubMed]

Tayama, T. (2000). The minimum temporal thresholds for motion detection of grating patterns. *Perception, 29,* 761–769. [PubMed]

Tyler, C. W. (2001). The symmetry magnification function varies with detection task. *Journal of Vision, 1*(2):7, 137–144, http://journalofvision.org/1/2/7/, doi:10.1167/1.2.7. [PubMed] [Article]

Tynan, P. D., & Sekuler, R. (1982). Motion processing in peripheral vision: Reaction time and perceived velocity. *Vision Research, 22,* 61–68. [PubMed]

Ukwade, M. T., Bedell, H. E., & White, J. M. (2002). Orientation discrimination and variability of torsional eye position in congenital nystagmus. *Vision Research, 42,* 2395–2407. [PubMed]

van de Grind, W. A. (1994). Limits and mechanisms of vision. In A. J. Kooijman et al. (Eds.), *Low vision* (pp. 28–37). Amsterdam, The Netherlands: IOS Press.

van de Grind, W. A., Koenderink, J. J., & van Doorn, A. J. (1986). The distribution of human motion detector properties in the monocular visual field. *Vision Research, 26,* 797–810. [PubMed]

van de Grind, W. A., Koenderink, J. J., & van Doorn, A. J. (1987). Influence of contrast on foveal and peripheral detection of coherent motion in moving random-dot patterns. *Journal of the Optical Society of America A, Optics and Image Science, 4,* 1643–1652. [PubMed]

van de Grind, W. A., Koenderink, J. J., & van Doorn, A. J. (1992). Viewing-distance invariance of movement detection. *Experimental Brain Research, 91,* 135–150. [PubMed]

van de Grind, W. A., Koenderink, J. J., van Doorn, A. J., Milders, M. V., & Voerman, H. (1993). Inhomogeneity and anisotropies for motion detection in the monocular visual field of human observers. *Vision Research, 33,* 1089–1107. [PubMed]

van de Grind, W. A., van Doorn, A. J., & Koenderink, J. J. (1983). Detection of movement in peripherally viewed random-dot patterns. *Journal of the Optical Society of America, 73,* 1674–1683. [PubMed]

van Santen, J. P., & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A, Optics and Image Science, 2,* 300–321. [PubMed]

Virsu, V., Rovamo, J., Laurinen, P., & Näsänen, R. (1982). Temporal contrast sensitivity and cortical magnification. *Vision Research, 22,* 1211–1217. [PubMed]

Warren, W. A. (2004). Optic flow. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 1247–1259). Cambridge, MA: MIT Press.

Watson, A. B., & Ahumada, A. J., Jr. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A, Optics and Image Science, 2,* 322–341. [PubMed]

Watson, A. B., Barlow, H. B., & Robson, J. G. (1983). What does the eye see best? *Nature, 302,* 419–422. [PubMed]

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33,* 113–120. [PubMed]

Watson, A. B., & Turano, K. (1995). The optimal motion stimulus. *Vision Research, 35,* 325–336. [PubMed]

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5,* 598–604. [PubMed]

Wright, M. J., & Johnston, A. (1985). The relationship of displacement thresholds for oscillating gratings to cortical magnification, spatiotemporal frequency and contrast. *Vision Research, 25,* 187–193. [PubMed]