Effects of retinal eccentricity and acuity on global-motion processing

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Abstract The present study assessed direction discrimination with moving random-dot cinematograms at retinal eccentricities of 0, 8, 22, and 40 deg. In addition, Landolt-C acuity was assessed at these eccentricities to determine whether changes in motion discrimination performance covaried with acuity in the retinal periphery. The results of the experiment indicated that discrimination thresholds increased with retinal eccentricity and directional variance (noise), independent of acuity. Psychophysical modeling indicated that the results for eccentricity and noise could be explained by an increase in channel bandwidth and an increase in internal multiplicative noise.

Keywords Motion · Coherent motion · Eccentricity

The visual tasks important for normal function of a moving observer involve motion processing in the peripheral visual field. For example, studies have shown the importance of motion in the retinal periphery for vection (Brandt, Dichgans, & Koenig, 1973), balance (Lee & Lishman, 1975; Lestienne, Soechting, & Bertoz, 1977), spatial orientation (Held, Dichgans, & Bauer, 1975), and the perception of heading (Dyre & Andersen, 1997). Although studies have demonstrated the importance of motion processing in central vision for locomotion, balance, and heading (Andersen & Braunstein, 1985; Andersen & Dyre, 1989; Warren, Morris, & Kalish, 1988), stimulation of the peripheral visual field (i.e., regions between 25 and 40 deg of eccentricity) is clearly of critical importance for the perception and control

of locomotion (Brandt et al., 1973; see Andersen, 1986, for a review).

It is well documented in the literature that motion sensitivity declines as a function of retinal eccentricity (e.g., Baker & Braddick, 1985; Johnson & Scobey, 1980; Orban, Van Calenbergh, De Bruyn, & Maes, 1985; van de Grind, Koenderink, & van Doorn, 1987). This is consistent with neurophysiological studies indicating that the neurons in visual cortex that respond to more retinally eccentric locations have larger receptive fields (Van Essen, Newsome, & Maunsell, 1984). The increase in receptive-field size has an effect on the ability to detect and discriminate motion at retinally eccentric locations. For example, sensitivity to optic flow,¹ which involves the integration of local motion directions (Koenderink, 1986), declines as a function of eccentricity (Atchley & Andersen, 1998). This reduction may result from increased error in the integration process, due to internal noise when estimating local motion directions (Crowell & Banks, 1996; see also Atchley & Andersen, 1998). As a result, the visual system is less sensitive to optic flow in more peripheral regions of the visual field, and must process large-field coherent motion (also referred to as *global motion*) in order for the perception of observer motion to occur (Atchley & Andersen, 1998). For example, Dyre and Andersen (1997) found that determining the direction of self-motion or heading was based on asymmetric global-motion information across different regions of the retinal periphery. Recent research has shown the importance of this information for steering control (Duchon & Warren,

¹ *Optic flow* refers to motion patterns, such as expansion, contraction, curl, and deformation, that are based on differences in local motion direction (Koenderink, 1986). These patterns are distinct from global motion, which is based on local motion that is in a single direction. For a detailed discussion of these differences, see Atchley and Andersen (1998).

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2002). These results, considered together, suggest that global-motion processing in the peripheral field is of critical importance for tasks such as the perception of self-motion.

An important issue examined in previous research was determining the ability of observers to extract coherent motion in foveal vision when noise was present. To examine this issue, researchers have required observers to judge the motion direction of random-dot stimuli in which a coherent motion direction was altered by varying the direction of local motion. This task, referred to as a *global-motion task*, has been used to determine the tolerance of the visual system to a noisy motion signal. For example, Williams and Sekuler (1984) presented subjects with random-dot cinematograms (RDCs) in which a directional noise component, sampled from a uniform distribution, was added to the individual dot velocities. Observers were able to perceive global coherent motion when the range of local motion directions was as large as 220 deg. However, accuracy for detecting global motion declined with an increase in the range of the distribution.

Watamaniuk, Sekuler, and Williams (1989) examined the ability of observers to discriminate between two global-motion directions. Subjects were presented with RDCs in which the individual dot directions were sampled from a Gaussian distribution. A two-alternative forced choice procedure was used in which subjects were sequentially presented two global-motion displays and were asked to indicate which display contained upward motion. Angular discrimination thresholds were derived. The results indicated that discrimination thresholds increased with a decrease in local motion duration and with an increase in the standard deviation of the Gaussian distribution (Watamaniuk et al., 1989). Subjects showed considerable tolerance for noise and made discrimination judgments when the standard deviation was as high as 51 deg.

Watamaniuk and Sekuler (1992) used the same task to examine the temporal and spatial integration limits. Temporal limits were assessed by systematically varying the duration of the stimuli. Spatial limits were assessed by varying the area of the global-motion display. The results indicated that temporal integration occurred for durations of up to 465 ms, while spatial integration occurred for stimulus displays that measured up to 63 deg². These results indicate that the visual system integrates local motion signals over long durations and across large areas of the visual field.

The perception of two-dimensional global coherent motion in the retinal periphery has been largely unexamined. The detection of coherent motion in the retinal periphery was examined by varying the presence of noise (scintillating random dots; van de Grind, Koenderink, van Doorn, Milders, & Voerman, 1993). In addition, some studies have examined age-related changes in the detection of global motion in the retinal periphery (Atchley & Andersen,

1998). In their research, Mareschal, Bex, and Dakin (2008) examined discrimination of the direction of coherent-motion stimuli presented in the retinal periphery. Subjects were presented with global-motion displays and were asked to determine whether the overall direction of motion was clockwise or counterclockwise relative to vertical. The motion stimuli were presented at the fovea and at 4, 8, and 16 deg in the peripheral visual field. Using an equivalent noise model, they examined whether the changes in motion sensitivity as a function of retinal eccentricity were the results of an increase in internal noise or of reduced sampling efficiency. Their results indicated that the elevated thresholds as a function of eccentricity were due to an increase in internal local direction uncertainty, with no change in sampling efficiency. However, it is worth noting that this effect was not consistent across all subjects.

For the present study, we examined a number of important issues regarding global-motion perception and retinal eccentricity. The Mareschal et al. (2008) study had focused on motion sensitivity for stimuli presented at eccentricities as large as 16 deg. However, the perception of self-motion can involve much larger eccentricities, including motion patterns presented between 25 and 40 deg (Brandt et al., 1973). Thus, an important issue in the present study was to examine the discrimination of global motion for eccentricities greater than 16 deg.

The second issue concerned acuity and the discrimination of global motion, which can be considered to involve two different processing stages: One stage is the pooling of local velocity information to determine a motion direction, and the second involves discriminating one motion direction from a second motion direction. This second stage is likely to be related to changes in the spatial scale of visual mechanisms across the visual field, and therefore related to acuity. It is well documented in the literature that acuity and spatial resolution decline with increased eccentricity (Berkley, Kitterle, & Watkins, 1975; Virsu & Rovamo, 1979). With regard to motion processing, Tynan and Sekuler (1982) showed that reaction times to motion onset increased and the perceived speed decreased with eccentricity, possible due to changes in the spatial scale of motion detectors as a function of eccentricity. In addition, other studies have shown the importance of spatial scale in global-motion processing in central vision (Morgan, 1992; Morgan & Fahle, 1992; Smith, Snowden, & Milne, 1994). These studies, considered together, suggest that global-motion processing is dependent on spatial scale, which may vary as a function of eccentricity. To our knowledge, no studies have assessed the effects of acuity on global-motion processing in the retinal periphery. Evidence of relationships between acuity and eccentricity and between global-motion processing and eccentricity would be evidence of a single spatial scaling factor for these processes. Thus, our second issue

was to determine whether changes in global-motion perception—as a function of eccentricity—covaried with acuity performance.

The third issue was to assess the changes in motion processing that vary with retinal eccentricity using a psychophysical model. The Mareschal et al. (2008) study modeled the contributions of internal and external noise on motion coherence thresholds. Other studies examining motion coherence have modeled performance using the combined inputs of motion channels in which channel bandwidth, sampling, additive internal noise, and multiplicative internal noise are considered (Bennett, Sekuler, & Sekuler, 2007; Watamaniuk et al., 1989; Williams, Tween, & Sekuler, 1991). In the present study, we examined the roles of channel bandwidth, sampling efficiency, multiplicative internal noise, and additive internal noise on changes in global-motion perception at increasing retinal eccentricities using a motion mechanism model.

We examined the effects of retinal eccentricity on global-motion perception and acuity. Subjects viewed two sequentially presented global-motion patterns and were asked to indicate whether the global-motion direction of the second stimulus was clockwise or counterclockwise of the direction in the first display. Fixation was monitored using an eye-tracker. To examine whether changes in global-motion discrimination thresholds covaried with acuity, we assessed Landolt-C acuity (the size of the minimum detectable gap) at each retinal location and analyzed the motion discrimination results using the acuity measures as a covariate.

Method

Subjects

The subjects were seven undergraduate students from the University of California, Riverside. All observers were paid for their participation, were naive regarding the purpose of the experiment, and had normal or corrected-to-normal visual acuity.

Design

Two independent variables were manipulated: retinal eccentricity (0, 8, 22, and 40 deg) and the standard deviation of noise sampled from a Gaussian distribution (0, 4.5, 18, and 36). In addition, Landolt-C acuity measures were taken at each retinal eccentricity.

Apparatus

All of the stimuli were presented using a dual-processor (3.0-GHz) Dell Dimension XPS system with an ATI 9800 Pro graphics card. The displays were two identical high-contrast

NEC monitors (resolution of $1,024 \times 768$ and operating at 85 Hz). A chinrest was used to maintain a constant viewing distance of 80 cm to the center of both monitors. The spatial separation between the centers of the two monitors was 40 deg of visual angle. The experiment was performed monocularly using an eye patch to occlude each subject's left eye. An Eyelink II eyetracking system was used to ensure that subjects maintained fixation on an onscreen target. The experimental setup was located in a dark room, and responses were input with a standard keyboard.

Stimuli and procedure

The experimental stimuli were computer-generated random-dot cinematograms. In all conditions, 256 dots were randomly plotted on a 10×10 deg square with a circular visible viewing area 9 deg in diameter. The luminances of the dots and background were 60 and 0.05 cd/m², respectively. The dot density was 2.56 dots/deg², and approximately 163 dots were visible in the circular viewing area on any single frame. The speed of dot motion was 10%/s. If a dot moved out of the display area, it was recycled to a random position on the opposite edge and received a new motion direction from the distribution.

The angular path of each individual dot was randomly assigned from an array of 256 pairs of x - y incremental values. The x - y pairs were generated according to a Gaussian distribution. The standard deviation (SD) of the distribution determined the amount of noise (deviation in motion direction relative to the mean direction) in the stimulus. Higher standard deviations produced distributions with greater ranges of directions, and thus resulted in increased noise in the motion stimuli. We tested four SD levels: 0, 4.5, 18, and 36. The dots moved in a “random walk,” according to which each individual dot received a new random direction on every sixth frame. This is similar to the short-duration random-walk dot motion used in previous studies on global coherent motion (Watamaniuk & Sekuler, 1992). In addition, the spatial displacements were of sufficient extent to allow observers to perceive motion at each eccentricity examined.

The dot stimuli were placed at one of four offsets from a fixation point to vary retinal eccentricity. The retinal eccentricities tested were 0, 8, 22, and 40 deg. To ensure that the eccentricities tested were not confounded by eye movements the observers' fixations were monitored on each trial. If their fixations drifted more than 1 deg from the fixation point, the trial was repeated.

Observers were presented with two sequentially presented displays of random dots, sampled from distributions that had matching SD s but that differed in mean direction. The stimuli were presented for 12 frames (141 ms) and were separated by an interstimulus interval of 500 ms. The subjects' task was to indicate whether the angular direction of

the second display was clockwise or counterclockwise of the motion in the first display. The global-motion direction of the standard stimulus was either clockwise (45 deg) or counterclockwise (315 deg) and was jittered by ± 10 deg. The direction of the comparison stimulus varied from that of the standard stimulus by up to ± 30 deg. The clockwise and counterclockwise standards were used in separate blocks.

On each trial, the observer was presented with a fixation point and a 9-deg-diameter circle that indicated the location and region of the motion stimuli. Once the subject had fixated on the fixation point, he or she pressed the space bar to initiate the trial. Following the barpress, the circle disappeared and was replaced with the motion stimuli. If during the trial the subject initiated an eye movement greater than 1 deg, the trial was terminated, a red “X” was presented in the center of the screen to inform the subject that an eye movement had occurred, and the trial was repeated. If the subject’s fixation was maintained during the trial, then at the end he or she was prompted for a response. Auditory feedback (a high tone for a correct response and a low tone for an incorrect response) was provided on each trial.

The dependent variable was the minimum detectable angular separation, in degrees, between the two motion stimuli. We used Lieberman and Pentland’s (1982) parameter estimation by sequential testing (Best PEST) procedure to determine a threshold (75% point using a two-interval forced choice procedure). The angular direction of the comparison stimulus was adjustable in 1-deg direction increments. The threshold algorithm was terminated when five steps surrounding an estimated threshold contained 85% of the weight of the entire array of possible angular magnitudes.

In addition to the motion discrimination thresholds, Landolt-C acuity thresholds were determined at each of the four retinal eccentricities. On each trial, the subject was presented with a fixation point and a circle (6-deg diameter) indicating the location of the Landolt-C. The luminances of the Landolt-C target and background were the same as the luminances of the dots and background. Once subjects had fixated the fixation point, they initiated the trial by pressing the space bar, at which time the surrounding circle would disappear and the “C” stimulus was presented for 141 ms. On each trial, the gap in the “C” was positioned at one of four cardinal directions; left, right, up, or down. The subject indicated the orientation of the “C” using the arrow keys on the keyboard. Eye movements were monitored using the same procedure that was used in the motion discrimination task. Thresholds were derived using a four-alternative forced choice version of the Best PEST (four-alternative forced choice Best PEST estimates of the 62.5% threshold). This method resulted in acuity thresholds ranging from 0.02 (limited by the display resolution) to 0.74 deg of visual angle.

The experiment was run over 2 days. Subjects were first trained for the motion discrimination task. Following training, they were required to pass a practice test before proceeding to the experiment, to ensure that the subjects understood the task. The practice test consisted of 12 trials, presented in central vision, in which the difference in motion direction between the standard and comparison stimuli was 30 deg. No local motion noise ($SD = 0$ -deg noise level) was present in the practice test. Subjects were required to be correct on 10 out of 12 trials before proceeding to the experiment, and Landolt-C acuity thresholds were derived following the practice test. Subjects were then presented eight blocks of trials, with different eccentricity conditions presented across blocks and in a random order. Within each block, subjects were presented a single run of the adaptive staircase for each noise condition, presented in a random order. Thus, two thresholds were derived at each eccentricity (two replications of the four eccentricity conditions, for a total of eight blocks), with the average of the two thresholds used in the analysis. Subjects were allowed rest breaks between blocks and were dark-adapted for several minutes before data collection.

Results

Thresholds for each subject in each condition were analyzed using a 4 (eccentricity) $\times$ 4 (noise) analysis of variance (ANOVA). The results are shown in Fig. 1. The main effect of eccentricity was significant, $F(3, 18) = 8.03$, $p < .05$. The mean angular thresholds for the 0-, 8-, 22-, and 40-deg eccentricities were 8.07, 9.39, 10.93, and 13.66 deg, respectively. Post hoc tests (Tukey HSD) indicated significant differences ($p < .05$) between the 0- and 40-deg and the 8- and 40-deg retinal eccentricity conditions. The main effect of noise was also significant, $F(3, 18) = 31.9$, $p < .05$. The mean angular thresholds for the 0, 4.5, 18, and 36 SD conditions were 7.8, 7.2, 11.2, and 15.75, respectively. Post hoc comparisons indicated significant differences ($p < .05$) between all pairwise comparisons, with the exception of the 0 and 4.5 SD conditions.

The interaction between retinal eccentricity and noise was significant, $F(9, 54) = 2.1$, $p < .05$. To examine this interaction in detail, we conducted an analysis of the simple main effects of eccentricity at each noise level (Keppel & Wickens, 2004). The simple effect of eccentricity was significant ($p < .05$) in the 0 [$F(3, 18) = 6.1$], 4.5 [$F(3, 18) = 5.1$], and 18 [$F(3, 18) = 7.7$] SD noise conditions. The simple effect for the 36 SD noise condition was not significant [$F(3, 18) = 1.1$]. Thus, the significant Eccentricity $\times$ Noise interaction was due to an effect of eccentricity for all noise levels, with the exception of the 36 SD noise condition.

Fig. 1 (Left) Effects of noise and retinal eccentricity on global-motion discrimination. Error bars indicate ± 1 standard error. (Right) Model predictions of performance as a function of noise and retinal eccentricity

The effect of eccentricity on acuity was significant, $F(3, 18) = 47.0, p < .05$. The mean acuities for the 0-, 8-, 22-, and 40-deg eccentricities were 0.027, 0.172, 0.377, and 0.545 deg, respectively. Post hoc comparisons (Tukey HSD test) indicated significant differences ($p < .05$) between all pairwise comparisons. An analysis of covariance (ANCOVA) was used to determine whether the effect of eccentricity on global-motion discrimination was independent of acuity by using the Landolt-C acuity scores at each eccentricity as a covariate. If the main effect of eccentricity for motion discrimination was independent of changes in acuity, then we should find a significant effect of eccentricity after factoring out the variability due to acuity changes. However, if the main effect of eccentricity for motion discrimination was associated with changes in acuity as a function of eccentricity, then the ANCOVA results should not be significant. These results indicated that the main effect of eccentricity was significant, $F(3, 15) = 3.73, p < .05$. The eta-squared of the main effect of eccentricity from the initial ANOVA was .54, whereas the eta-squared of the main effect of eccentricity from the ANCOVA was .41. These results indicate that although acuity varied as a function of eccentricity, it only accounted for 13% of the variability in the motion detection data, and when acuity was controlled for, the effects of eccentricity on motion detection accounted for 41% of the variability in the data. Thus, motion discrimination varied as a function of eccentricity, independent of acuity.

Model fit of the experimental data

The results were fit to a motion mechanism model to determine what factors might account for the effects of retinal

eccentricity on global-motion performance. The version of the model examined in the present study was adapted from models previously presented by Bennett et al. (2007), Watamaniuk, Sekuler, and McKee (2011), Watamaniuk et al. (1989), and Williams et al. (1991). An important characteristic of this model is that it uses one or more mechanisms tuned to a particular aspect of a visual stimulus, such as spatial frequency or the direction of local motion. The response of each individual mechanism is determined by the similarity of the stimulus to the center of its tuning function, which is based on a Gaussian distribution restricted to a range of acceptable inputs (the mechanism bandwidth). Williams et al., using a motion metamer experiment in foveal vision, found that the optimal number of mechanisms was 12, with a half-amplitude half-bandwidth of 30 deg. Each of these mechanisms was tuned to a direction evenly spaced across the 360-deg range of the motion directions. Each mechanism (also referred to as a *channel*) analyzes local motion signals within the respective bandwidth of the channel. The activation of a channel increases exponentially as a function of the correspondence between the pooled motion direction and the optimal motion direction of the channel. Summation of the activation level of all channels can be used to estimate the direction of global motion (Bennett et al., 2007; Watamaniuk et al., 2011).

The response of a channel to a local motion signal is defined as follows:

$$t_{\theta}(d) = \frac{e^{-(d-\theta)^2/2b^2}}{b\sqrt{2\pi}} \quad (1)$$

where d is the local-motion vector, θ is the tuning direction of the channel, and b is the bandwidth of the channel (also, its standard deviation). The total activation of a channel to a

global-motion cinematogram is determined by

$$r_{\theta} = \left[\sum_{n=1}^{\#Vectors} t_{\theta}(d_n) \right] \bullet \gamma + \eta \quad (2)$$

The activations for each vector (d_n) are summated and then multiplied by a Gaussian random variable γ (mean = 1, $SD = \rho$) and added to a Gaussian random variable η (mean = 1, $SD = \sigma$). The activations for each channel (r_{θ}) were half-wave rectified and raised to a power, q , and combined by vector addition. The estimated direction produced by the model is defined as the phase of the resultant vectors. The resulting directions of two motion vector arrays were compared. If the motion direction of the second array was greater than the first, it was recorded as a correct judgment.

To simulate the experimental data, two randomly generated Gaussian arrays of motion vectors were generated. Both vector arrays were assigned a SD matching one of the four tested in the experiment (0, 4.5, 18, or 36). The second vector array was assigned a mean direction greater than the first, in 1-deg increments ranging from 1 to 30. Both motion vector arrays contained the same number of elements matching the characteristics of the stimuli multiplied by a scaling factor (163 visible dots * 2 motion vectors * scaling factor). Human discrimination thresholds were acquired using the Best PEST (Lieberman & Pentland, 1982), which estimates 75% correct. For each SD level, the percent correct of all 30 levels of average motion direction difference were calculated. The separation level nearest to but less than 77.5% correct was used as the simulated threshold.

The values of the model's parameters were chosen on the basis of previous research and by preliminary simulations. The summation exponent, q , amplifies larger channel activations, thus increasing the overall effect on model performance. We set the value of q at 2, which is an appropriate value for the stimulus duration we used (Bennett et al., 2007; Watamaniuk et al., 1989). Preliminary Monte Carlo simulations were run to determine the best-fitting values for the scaling factor and for the number of channels. Watamaniuk (1993) found evidence that only a portion of the motion vectors are incorporated from an RDC. The results of the preliminary simulations indicated that the optimal scaling factor was 0.225. This closely matched the value of .23 found by Watamaniuk (1993). Williams et al. (1991) found that the optimal number of mechanisms was 12, with each mechanism equally spaced and having a half-amplitude half-bandwidth of 30 deg. Our preliminary simulations indicated that the best fit to the subjects' data was with 12 mechanisms, but that channel bandwidth could vary with retinal eccentricity. In addition, our preliminary simulations indicated that additive internal noise, as well as multiplicative internal noise, could vary with increasing retinal eccentricity.

The goal of the model simulations was to determine the optimal parameters of the model that predicted human discrimination accuracy at different retinal eccentricities. To simulate performance changes across the visual field, we manipulated channel bandwidth, additive internal noise, and internal multiplicative noise. Channel bandwidth (b) was tested at the following values—30, 33, 36, 40, 45, 52, 60, and 72. Additive internal noise (σ) was tested at 12 levels, ranging from 0.025 to 0.3 in increments of 0.025. Multiplicative internal noise (ρ) was tested at 20 levels, ranging from 0.025 to 0.5 in increments of 0.025. To simulate the retinal eccentricity conditions, thresholds for the four external noise levels (SD s of the vector arrays) were obtained at every combination of bandwidth (b), additive internal noise (σ), and multiplicative internal noise (ρ). For each SD level, 5,000 trials were run at all 30 separation levels between average directions of the motion vector arrays. The simulation produced 1,920 sets of threshold values.

To examine different model outcomes, we assessed model performance by limiting at least one of the three parameters in the simulation to a single value across different retinal eccentricities. This produced six possible combinations of free and constant parameters. Within each of these parameter conditions, we determined the values resulting in the lowest root-mean squared error (RMSE) for the experimental data, using the following constraint: Each parameter value must be greater than or equal to the values at lower (more central) retinal eccentricities. The best fit to the experimental data was found by holding additive internal noise at 0.125 while letting bandwidth and multiplicative noise vary with retinal eccentricity. The results of the best-fitting model are shown in Fig. 1. The correlation between subject performance and the model simulation was .96 and had an RMSE of 1.47. The RMSEs for the individual conditions, as well as the values of channel bandwidth and multiplicative internal noise, are presented in Table 1. For comparison, the next best-fitting model had a total RMSE of 1.6. This model held bandwidth at 40 deg and held additive noise at 0.125 across retinal eccentricities, while multiplicative noise varied between 0.1 at eccentricity 0 and 0.475 at eccentricity 40. Overall, the results of the simulation indicate that the effects of retinal eccentricity and noise on human performance

Table 1 Best-fitting parameter estimates (channel bandwidth, multiplicative internal noise, and root-mean square error) per eccentricity condition for our data

Eccentricity	b	ρ	RMSE
0 deg	36	0.225	1.55
8 deg	36	0.35	1.14
22 deg	36	0.375	1.61
40 deg	40	0.475	1.53

can be accounted for by an increase in channel bandwidth and an increase in internal multiplicative noise as a function of retinal eccentricity.

Discussion

The results of the present study indicate several important findings regarding global-motion processing and retinal eccentricity. First, they indicate that performance varied as a function of retinal eccentricity for stimuli presented at eccentricities greater than or equal to 22 deg. The results for smaller eccentricities are consistent with those of Mareschal et al. (2008), which showed no consistent effect of eccentricity on global-motion discrimination for eccentricities up to 16 deg. However, the results of the present study indicate that at greater eccentricities the perception of coherent motion declines.

It is well known that acuity changes as a function of retinal eccentricity. This change in acuity might account for the decreased performance in discriminating motion directions in the periphery, because discriminating motion directions is dependent on the observer to distinguish the two directions (a resolution issue). To assess this issue, we used Landolt-C acuity measures as a covariate to assess the role of acuity in motion discrimination. The results indicated that global-motion processing varied as a function of eccentricity, independent of visual acuity. These results, consistent with the results of previous research on optic flow and retinal eccentricity (Atchley & Andersen, 1998), suggest that declines in performance as a function of eccentricity are not due to the same processes that result in decreased acuity as a function of eccentricity.

The modeling results indicated that performance could be accounted for by an increase in channel bandwidth and an increase in multiplicative noise with eccentricity. These results are consistent with previous neurophysiological studies of motion processing. For example, Orban, Kennedy, and Bullier (1986) found decreased direction selectivity (i.e., increased bandwidth) of motion-sensitive neurons in V1 and V2 as a function of eccentricity. The change in multiplicative internal noise with eccentricity, however, is a novel result. This finding might be accounted for by differences in the processing of photoreceptors. Barlow (1962) showed that observers have lowered efficiency in judging brightness in low-luminance as compared to high-luminance conditions. Lillywhite (1981) suggested that this loss of efficiency is due to multiplicative internal noise rather than to declines in receptor function. If the effects obtained in the Barlow study were the result of the activation of rods under low luminance conditions, this suggests that the present finding of increased multiplicative noise for peripheral regions of the visual field may be due to the

function of the rods. The density of cones decreases sharply at eccentricities greater than 2 deg (with minimal density levels for eccentricities equal to or greater than 10 deg), whereas the density of rods increases in the retinal periphery, with a peak density at 18–20 deg (Curcio, Sloan, Kalina, & Hendrickson, 1990; Hood & Finkelstein, 1986). In addition, recent research by Raphael and MacLeod (2011) examined the relative contributions of the cones and rods at different luminance adaptation levels and different eccentricities. Their results suggest that for eccentricities of 16 deg, visual performance is almost entirely dependent on rods at mesopic levels of adaptation. In the present study, we examined motion sensitivity beyond 16 deg and at luminance levels consistent with the mesopic luminance levels examined by Raphael and MacLeod. Thus, our finding that multiplicative internal noise increased with retinal eccentricity may be explained by increased dependence on rod function in the retinal periphery. An important issue for future research will be to examine in detail the role of rod function on motion sensitivity in the retinal periphery.

In summary, the results of the present study show declines in motion sensitivity as a function of eccentricity that can be accounted for by changes in motion channel bandwidth and multiplicative noise. These changes in sensitivity provide a strong rationale for why the visual system would use two different analyses for visual tasks such as locomotion and spatial orientation. In central vision, where motion sensitivity is optimal, the visual system uses optic flow information that is based on estimates of local changes in motion direction. At more retinal-eccentric regions, the visual system uses coherent motion and spatially integrates local velocity information to determine how an observer is moving through space.

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