



## Local motion processing limits fine direction discrimination in the periphery

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### ABSTRACT

Visual sensitivity is reduced in the periphery for many discrimination tasks. Previously it has been reported that motion coherence thresholds are higher for dot stimuli presented in the periphery, a finding that could arise either from (a) impaired motion integration or (b) from motion integrators inheriting more noisy local directional signals. We sought to disentangle these factors using an equivalent noise paradigm. We report a deterioration in discrimination thresholds in the periphery that does not result from reduced visibility and is fully accounted for by an increase in local directional uncertainty with no change in sampling efficiency. Changes in motion coherence thresholds with stimulus eccentricity, measured using similar stimuli, exhibit a high degree of inter-subject variability.

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### 1. Introduction

For static images, visual acuity decreases with eccentricity (Kelly, 1984; Rovamo, Virsu, & Nasanen, 1978) and even when stimuli are increased in size and/or contrast to compensate for reduced acuity (*M-scaling*), performance decreases with eccentricity for tasks of widely differing complexity, such as phase discrimination (Bennett & Banks, 1987; Bennett & Banks, 1991; Rentschler & Treutwein, 1985; Stephenson, Knapp, & Braddick, 1991), line-orientation sensitivity (Levi, Klein, & Aitsebaomo, 1984), discrimination of isolated (Strasburger, Harvey, & Rentschler, 1991) or crowded (Toet & Levi, 1992) alphanumeric characters, image classification (Juttner & Rentschler, 1996), reading (Chung, Mansfield, & Legge, 1998; Fine, Peli, & Pisano, 1993; Latham & Whitaker, 1996) and face identification (Melmoth, Kukkonen, Makela, & Rovamo, 2000). For appropriately *M*-scaled dynamic images, motion detection (McKee & Nakayama, 1984; Smith, Hess, & Baker 1994; Solomon & Sperling, 1995; van de Grind, van Doorn, & Koenderink, 1983; Whitaker, Makela, Rovamo, & Latham, 1992; Wright & Johnston, 1983), discrimination (McKee & Nakayama, 1984; Waugh & Hess, 1994; Wright & Johnston, 1983), and velocity discrimination (McKee & Nakayama, 1984) are approximately invariant across the retina. Furthermore, peripheral vision can be more sensitive to motion (Wright, 1987) and flicker (Kelly, 1971a; Kelly, 1971b) at high temporal frequencies, although apparent speed can appear reduced (Johnson & Wright, 1986).

Using a motion coherence paradigm (the minimum number of dots required to move coherently within a field of randomly moving dots in order to sustain a criterion threshold level), direction discrimination thresholds have been found to be higher in the periphery than in the fovea for normally sighted subjects (Raymond, 1994) and glaucoma patients (Joffe, Raymond, & Chrichton, 1997). When direction discrimination was assessed using drifting gratings, Levi et al. (1984) reported that thresholds deteriorated in the periphery in both normal and amblyopic eyes. It remains unclear, however, what limits observers' performance in these tasks. Wright (1987) reports that when drifting gratings were equalized by a scaling factor to take into account the change in spatial scale in the periphery, peak sensitivity to motion was constant across the visual field. van de Grind, Koenderink, and van Doorn (1987) examined signal:noise thresholds for motion detection in the fovea and periphery of scaled dot stimuli as a function of velocity and contrast. They found that the determining factor in the signal:noise ratios was the contrast of the dots, specifically, thresholds deteriorated more slowly in the fovea than in the periphery when the contrast was lowered. This is consistent with McKee and Nakayama (1984) who found that velocity discrimination of moving gratings was poorer in the periphery as a result of lower spatial resolution but was contrast invariant down to roughly 10% contrast. Although it appears that motion thresholds can be equated across the visual field in some tasks when the stimuli are appropriately scaled in either size or contrast, it has yet to be determined what actually limits performance in the periphery. In principle changes in performance could be accounted for entirely or partially by changes in the size or bandwidth of motion sensor receptive fields, changes in their spacing and numbers, or increases in their levels of internal noise.

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Here, we use an equivalent noise (EN) paradigm to examine changes in direction discrimination across the visual field and to disentangle the relative influence of the factors listed above. This methodology has previously been used successfully to examine the integration of oriented and drifting elements (e.g., Dakin, 2001; Dakin, Mareschal, & Bex, 2005a; Dakin, Mareschal, & Bex, 2005b; Heeley, Buchanan-Smith, Cromwell, & Wright, 1997; Lu & Doshier, 1999; Watamaniuk & Heinen, 1999), and relies on the assumption that a psychophysically measured threshold results from the sum of both internal and external sources of noise. Given that observers' thresholds are estimates of response variance, by expressing external noise imposed onto the stimulus in terms of variance, thresholds ( $\sigma_{obs}$ ) can be decomposed into internal noise ( $\sigma_{int}$  which represents the precision of a stimulus sample), sampling efficiency ( $n_{samp}$  which represents the number of samples being recruited for the task), and external noise ( $\sigma_{ext}$ ) using a variance summation model. These different components are illustrated schematically in Fig. 1 for the motion integration task used here. Fig. 1a illustrates how internal noise limits the precision with which the direction of each moving element is coded by the local motion detectors. Fig. 1b illustrates how the number of samples averaged by global motion integrators limits the precision with which the overall direction of the stimulus can be represented. In our experiment, the stimuli consist of a set of moving Gaussian dots each of whose direction was drawn from a wrapped normal distribution. Increasing the standard deviation of the direction distribution increases external directional noise (Fig. 1c). The EN fit to direction discrimination thresholds as a function of external noise is illustrated on the graph in Fig. 1c where the symbols represent direction thresholds, the solid line the EN fit, and the parameters in the caption represent the derived estimates of internal noise and sampling efficiency. The dashed line shows how sampling efficiency modulates thresholds at all levels of external noise

(i.e., a vertical shift in the function) and the dotted line shows how internal noise mostly modulates thresholds at low levels of external noise. In the present manuscript, we use the EN paradigm to determine whether the higher direction thresholds measured in the peripheral visual field result from elevated internal noise, from reduced sampling efficiency or a combination of both sources of error.

2. Methods

2.1. Stimuli

Stimuli were fields of 32 moving Gaussian elements ( $\sigma_{x,y} = 3$  arcmin), presented within a circular window of radius  $2^\circ$ . All elements were of "infinite-life-time" and were wrapped to the diametrically opposite point as they moved out of the window. Movies were 500 ms long and updated at 37.5 Hz. Elements had a velocity of approximately 5.6°/s and moved with directions drawn from a wrapped normal (WN) distribution, defined on the range  $\theta \in [0, 2]\pi$  by the probability density function:

$$f(\theta) = \frac{1}{\sigma\sqrt{2\pi}} \sum_{k=-\infty}^{\infty} \exp\left[-\frac{(\theta - \mu - 2\pi k)^2}{2\sigma^2}\right] \quad (1)$$

2.2. Procedure

Details of the experimental procedure and fitting techniques can be found in Dakin et al. (2005a). Briefly, subjects were presented with a field of 32 moving Gaussian elements and were required to make a judgment of their overall direction: either clockwise or counter-clockwise of vertical (upwards). The center of the stimuli was presented at the fovea, and at eccentricities of  $4^\circ$ ,  $8^\circ$ , and  $16^\circ$  in separate runs. The direction of the referent motion was indicated by crosshairs present on the screen at the same time as the stimulus. Subjects signaled their response by pressing one of two keys on a computer keypad. Feedback, in the form of an audible beep, was given for incorrect responses.

The direction of motion of each element was randomly drawn from WN distributions (Eq. (1)) with eight different standard deviations ( $\sigma$ ):  $0.5^\circ$ ,  $1.0^\circ$ ,  $2.0^\circ$ ,  $4.0^\circ$ ,  $8.0^\circ$ ,  $16.0^\circ$ ,  $23.0^\circ$ ,  $32.0^\circ$ ,  $45.0^\circ$ , or  $64.0^\circ$ . A method of constant stimuli was used to

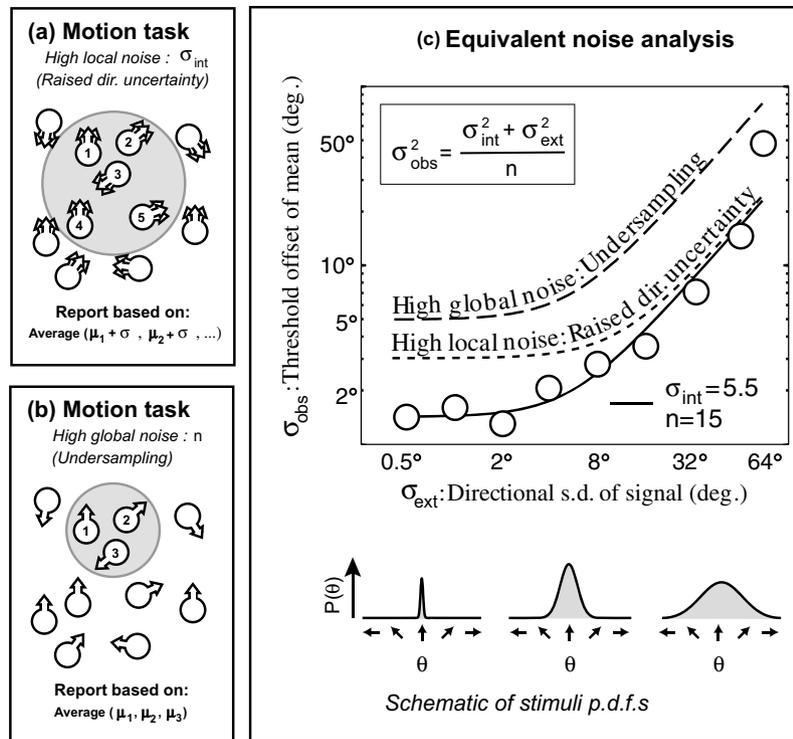


Fig. 1. (a) Direction discrimination of a set of moving elements is limited both by (a) local factors (the precision of each direction-estimate—illustrated here schematically by the range of multiple arrow-heads) and (b) global factors (the number of directions combined—illustrated by the area of the shaded region). (c) Thresholds are plotted as a function of the range of directions present in the stimulus ( $\sigma_{ext}$ ), observers' performance (open circles) is good when external directional noise ( $\sigma_{ext}$ ) is low and deteriorates as it increases. Equivalent noise exploits additivity of variance to model the data (boxed equation) in terms of external noise ( $\sigma_{ext}$ ), internal local noise ( $\sigma_{int}$ ) and global sampling limits on integration ( $n$ ). In the example shown, the observer pooled approximately 15 local direction-estimates, each with a precision of  $5.5^\circ$ .

estimate the psychometric function at each  $\sigma_{\text{ext}}$  level. Blocks of 272 trials probed 17 stimulus levels for each condition (i.e., 16 trials per stimulus level). At least two complete runs were undertaken for each subject in all conditions.

Raw data were combined across runs and fit using a bootstrapping method (Foster & Bischof, 1997) employing a wrapped cumulative Gaussian, which allowed for the periodicity in psychometric functions derived from direction discrimination tasks. Data plotted in figures show the bootstrapped fits of all data pooled across all runs for that condition/subject; error bars are the 95% confidence intervals on the fits.

### 2.3. EN model fitting procedure

We started by using a Nelder-Mead/simplex minimization method (the *fminsearch* function in Matlab), to perform a weighted fit of the 2-parameter EN model (Fig. 1; weights were the inverse of the confidence intervals derived above) to our threshold estimates as a function of directional variability. This yields the best fitting parameters ( $\sigma_{\text{int}}$  and  $n_{\text{samp}}$ ) for a given data set. At the two highest levels of directional standard deviation, the best fitting EN prediction undershoots subjects' thresholds because it does not take into account directional wrapping. For this reason, the two parameters obtained from the fit were used to run a Monte Carlo simulation (which did take into account wrapping) using the particular combination. Results from this Monte Carlo simulation are overlaid on observers' thresholds in the figures.

We calculated confidence intervals on these parameters using the bootstrapped estimates of threshold derived using the procedure described above. Specifically, bootstrapping the psychometric functions gives us a very large number of estimates of threshold at each level of directional variability (these are what are used to derive confidence intervals above). We can use these distributions to construct a synthetic set of thresholds by simply taking a random sample from each distribution, at each level of directional variability, and then fitting the EN model to this synthetic data set. These data can be fit using the same procedure as applied to the original data to give the best fitting parameters ( $\sigma_{\text{int}}$  and  $n_{\text{samp}}$ ) for a given synthetic data set. These parameters are recorded and the whole procedure (synthesise-refit-record) repeated 1000 times to yield distributions of the two parameters of the fit for a given starting data set. The 25th and 975th element of a sorted list of these parameters is our estimate of the 95% confidence intervals on a given EN parameter.

### 2.4. Apparatus

Stimuli were generated with an Apple Macintosh G4 computer running Matlab (MathWorks Ltd). The programs controlling the experiment incorporated elements of the PsychToolbox (Brainard, 1997). Stimuli were presented on a La Cie 22" Electron Blue monitor fitted with a video attenuator. The attenuated signal was amplified and copied (using a line-splitter) to the three guns of the monitor to generate a monochrome image. The display was calibrated using code from the VideoToolbox (Pelli, 1997) and a Minolta LS 110 photometer, and then linearized using look-up tables in software (to give pseudo 12-bit contrast accuracy). The monitor operated at a resolution of 1024 × 768 pixels (24 pixels per cm) with a vertical blanking rate of 75 Hz. Stimuli were viewed monocularly by the dominant eye at a distance of 67 cm, and had a mean background luminance of 50 cd/m<sup>2</sup>.

### 2.5. Observers

The three authors (wearing optical correction as necessary) served as observers in the main experiment. All are experienced at psychophysical tasks involving motion perception.

## 3. Results

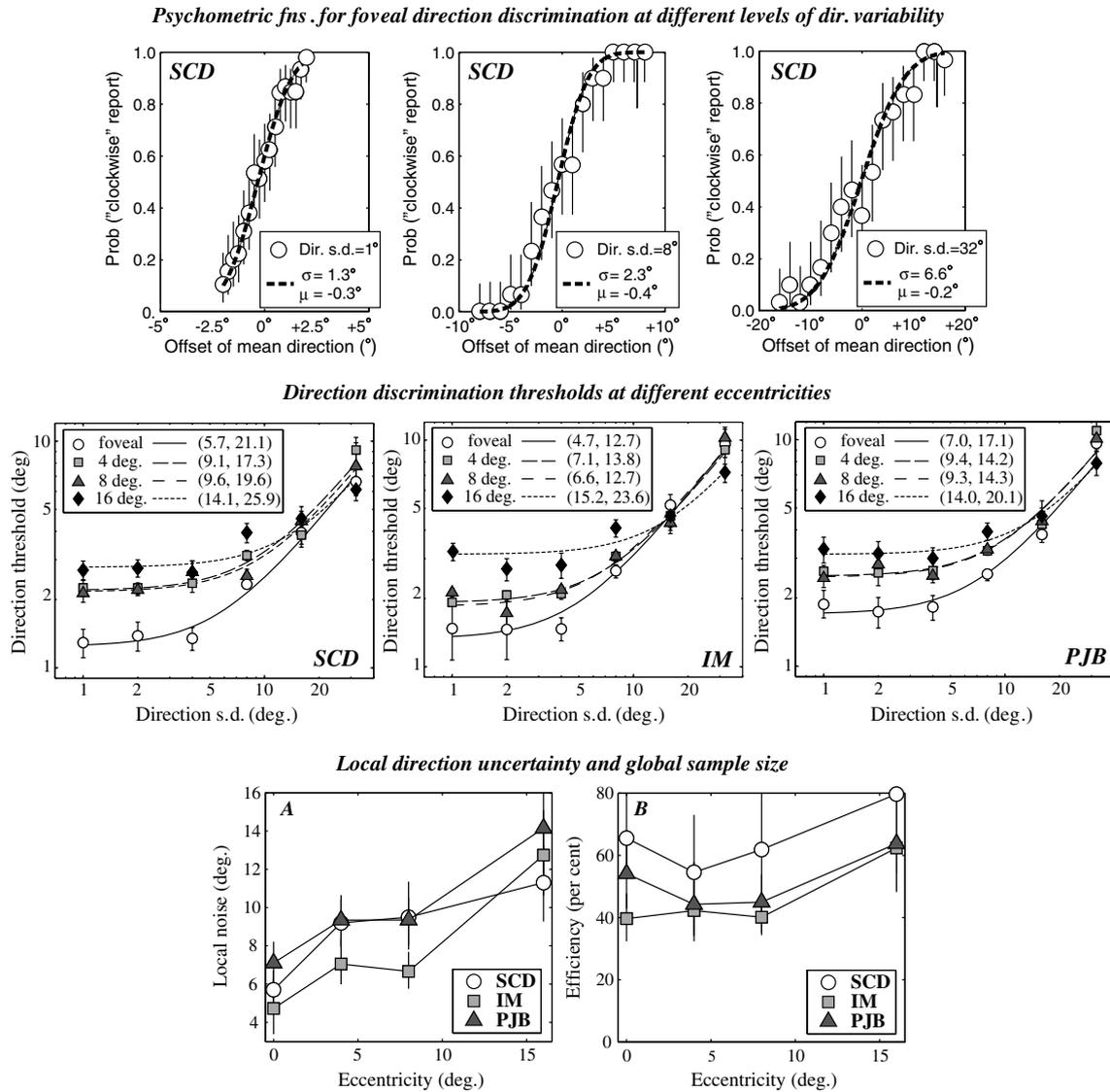
Fig. 2, top row plots three sample psychometric functions for one observer at three levels of directional variability from which estimates of direction thresholds were obtained. Fig. 2, middle row plots the directional offset required for three observers to discriminate the direction of motion of a field of moving dots as a function of the directional noise added to the stimulus. At low levels of directional noise (up to direction s.d. of roughly 10°), thresholds are lowest in the fovea and increase with increasing eccentricity. However, at higher levels of directional noise the curves in the four different eccentricities converge. This pattern of results is indicative of an increase in local noise, but with little or no change in sampling efficiency (e.g., see Fig. 1c, fine dashed lines). This is confirmed by the estimated values of internal noise and sampling efficiency in the boxed legends: as eccentricity increases the values of internal noise increase (roughly threefold) whereas sampling efficiency remains relatively constant, with only one observer (IM) displaying a moderate increase in efficiency at the furthest eccentricity.

In order to highlight the changes in internal noise and sampling efficiency, these parameters are plotted separately as a function of eccentricity in the bottom two rows of Fig. 2. It is apparent that local noise (Fig. 2a) increases with eccentricity for all observers whereas there is no systematic change in sampling efficiency as plotted as the percentage of total dots in the display (Fig. 2b) across the different viewing conditions.

An obvious concern in interpreting these data is to determine how much influence stimulus contrast, or more specifically the visibility of the stimuli as they are presented further into the periphery, may have on measured thresholds. We first measured contrast detection thresholds at the four eccentricities used in Experiment 1 (0°, 4°, 8°, and 16°) for a stimulus with no external direction noise ( $\sigma_{\text{ext}} = 0^\circ$ ). The results, shown in Fig. 3A confirm that contrast detection thresholds for a moving stimulus increase with eccentricity. Next we examined the role of this loss in stimulus visibility on estimates of internal noise and sampling efficiency. We repeated the direction discrimination task in the fovea at different levels of stimulus contrast. Fig. 3A shows that there was a fourfold loss in contrast sensitivity between 0° and 16°, so we examined a 6.25-fold contrast range that more than covered this change in contrast sensitivity. Fig. 3A also shows that thresholds at 16° were approximately 10% contrast, so our motion stimuli in Experiment 1 were approximately 5 times detection threshold. We therefore examined foveal motion sensitivity from approximately 2.5 times (8% contrast) to 17 times (50% contrast) detection threshold to cover this range of stimulus visibilities (assessed as multiples of contrast threshold).

Fig. 3b and c plots direction thresholds and corresponding EN fits for the two observers in the fovea at three contrast levels. The corresponding levels of internal noise and sampling efficiency are in the boxed legends. Neither observer showed any systematic change in sampling efficiency as a function of contrast and observer SCD showed no systematic change in internal noise. Observer IM showed a small increase in internal noise (to 6.5°) at low contrasts that was much less than the increase with eccentricity (to 15.2°). In terms of visibility, the lowest contrast level tested (8%, roughly 2.5 times detection threshold) was lower than that of the stimuli at 16° eccentricity (at 50% contrast, they were at 5 times their detection thresholds). This suggests that the raised level of internal noise in the periphery does not result from reduced visibility of the stimuli.

Most previous studies of direction discrimination in the periphery used fields of dots and measured motion coherence thresholds (the minimum number of coherently moving signal dots within a field of randomly moving noise dots that supports a criterion direction discrimination level). We have discussed elsewhere (Dakin et al., 2005a) the limitations of the motion coherence task and its inability to disambiguate between the different sources of error that can limit performance. In a final experiment, we examine how observers perform on a motion coherence task in the periphery in order to compare motion coherence thresholds with EN analysis. In a first experiment, motion coherence thresholds (83% correct "up" versus "down" direction) were measured for stimuli consisting of 32 dots presented in a circular aperture of 2° radius for the three authors. We found that thresholds were constant across the four eccentricities tested (0°, 4°, 8°, and 16°). We subsequently re-measured motion coherence thresholds for 6 observers using 256 dots in order to reduce the motion signal carried by a single dot (with 32 dots, each carries a signal of 3%) and to approximate earlier MC tasks. Motion coherence thresholds with 256 dots are plotted in Fig. 4 for the three authors and three naive observers. Surprisingly, we do not find a consistent trend in the data across observers. The three authors do not show much change with eccentricity (consistent with the MC thresholds obtained with 32 dots), one observer's thresholds (HF) increase with eccentricity, and two observers (SBG and ALR) show a reduction of motion



**Fig. 2.** Direction discrimination thresholds obtained from sample psychometric functions (top row) are plotted as a function of the range of directions present within the stimulus (direction s.d.) for three observers at four eccentricities; fovea (open circles), 4° (squares), 8° (triangles), and 16° (diamonds) (middle row). The curves are EN fits to the data. Numbers in parenthesis in the boxed legends are the estimated internal noise and number of samples, respectively. The bottom row plots for each observer, the estimates of (A) internal noise and (B) sampling efficiency from the EN fits to the data in the top row. Error bars show 95% confidence intervals.

coherence thresholds with eccentricity. It is possible that observers employ different strategies to perform this task or that motion coherence results might be affected by more complex parameters. For example, the impression of motion transparency is quite strong in the fovea but reduced in the periphery. It may be that for the two observers who performed unexpectedly badly in the fovea, motion transparency interfered with their ability to judge the direction of motion, whereas the other observers may have been able to more reliably discount or ignore the percept. This is in accordance with the finding that observers are able to blend motion patterns in the periphery, but not in the fovea (De Bruyn, 1997). However, given the inconsistency of results with this technique as well as its limitations for teasing apart different sources of noise, we would suggest that equivalent noise is a more appropriate measure of motion discrimination performance.

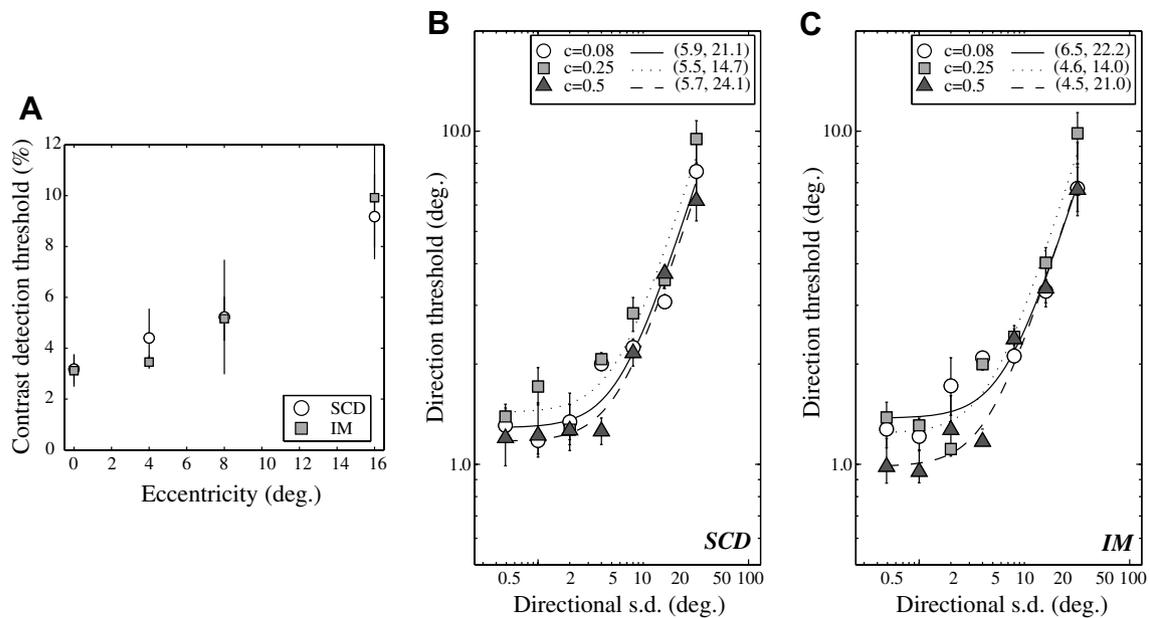
**4. Discussion**

We used an equivalent noise paradigm to examine motion sensitivity changes in the peripheral visual field. Observers made fine

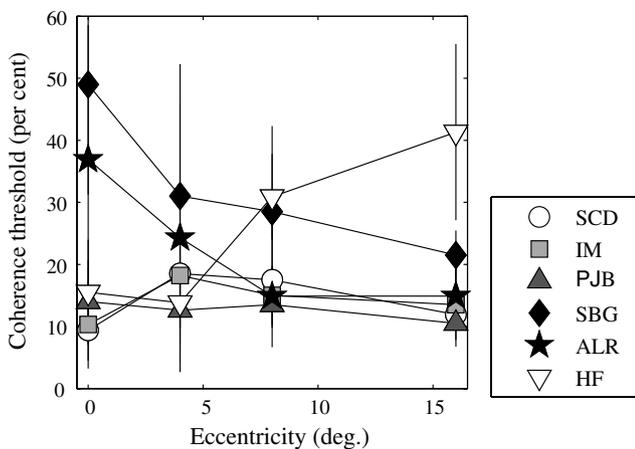
judgments of the direction of motion of a field of moving dots containing different levels of direction variability. We report that direction discrimination thresholds increased with eccentricity and that this increase was almost exclusively the result of an elevation in their internal/local noise. Control experiments showed that the raised internal noise was not related to a reduction of the visibility of the stimuli in the peripheral visual field. We compare our thresholds to those obtained using a standard motion coherence task and report that motion coherence thresholds do not show a consistent relationship with eccentricity. This highlights one of a number of its limitations for the investigation of motion integration.

**4.1. Increase in internal noise in the periphery**

It has been reported that when stimuli are scaled for visibility (either by varying their contrast or size), performance in the periphery can approximate that in the retina for certain tasks. This has often been taken as an indication that the underlying factor limiting visual performance in the periphery is the spatial scale



**Fig. 3.** Contrast effects on direction discrimination. (A) Contrast detection thresholds for two observers as a function of eccentricity. Direction discrimination thresholds for three different levels of stimulus contrast (shown in the caption) as a function of directional noise in the fovea for SCD (B) and IM (C). Curves are EN fits and the estimated internal noise and sampling efficiency are shown in the boxed legends.



**Fig. 4.** Motion coherence thresholds as a function of retinal eccentricity for six subjects. Thresholds represent the percentage of 256 dots required to move coherently for observers to correctly identify (83% correct) the direction of motion.

of the receptors involved (Thomas, 1987; Wright, 1987; Wright & Johnston, 1983). Our results show that in the peripheral visual field, observers' thresholds are limited by the level of internal noise; in our task, observers' uncertainty about the direction of individual elements of the stimulus. We think it likely that this increase in local directional uncertainty reflects properties of local motion detectors—i.e., in early visual areas—with receptive fields located in the peripheral visual field. Consistent with this view Urban, Kennedy, and Bullier (1986) have reported that direction selectivity decreases with eccentricity in V1.

It might seem curious that the substantial rise in local directional uncertainty does not lead to a consistent elevation in motion coherence thresholds (MCT) in subjects who performed both tasks. The most likely explanation for this is simply that observers do not need to have a fine representation of the directions of signal elements of MCT displays, but only to correctly recognize when they are signal elements. Beyond this it is hard

to be certain since there is no clear optimal strategy for solving MCT tasks that could in principle be limited by either local or global noise. Our data would be consistent with MCTs being limited (for most subjects at least) by global integration in the periphery.

Another feature of our EN results is that sampling efficiency for global motion integration is relatively constant across the visual field. Global sampling efficiency is likely set by the receptive fields of motion integrators, i.e., motion selective neurons located in later stages of motion processing in the visual cortex. The well-known rate of increase of receptive field size with eccentricity observed in V1 (e.g., Smith et al., 1994) decreases as one moves through the motion pathway to MT (Mikami, Newsome, & Wurtz, 1986) until by MST there is no dependency of RF size on eccentricity at all (Raiguel et al., 1997) If neurons in these areas are responsible for pooling local motion signals across space then these findings would be closely consistent with our finding that sampling efficiency is relatively unaffected by stimulus eccentricity.

Our findings on motion coherence thresholds may relate to recent work reporting that the perception of global biological motion in dot displays is relatively unimpaired under peripheral presentation (Thompson, Hansen, Hess, & Troje, 2007). However, these authors also report that the addition of noise dots is damaging to biological motion perception in the periphery, a deficit that they interpret as evidence peripheral motion perception is poor at performing signal segregation. With respect to this conclusion our data are equivocal. Some subjects do show elevated motion coherence thresholds in the periphery—which would presumably be consistent with impaired signal segregation—but most do not. Furthermore, our EN data cannot speak to this issue (since all dots are signal dots).

4.2. Equivalent noise versus motion coherence thresholds

We find that motion discrimination thresholds result from a decrease in observers' accuracy to judge the direction of motion of individual dots. When compared to thresholds obtained using a standard motion coherence task, we find striking differences. Mainly, thresholds do not consistently increase as a function of

eccentricity, suggesting that different observers' may be performing the task using different strategies. We previously argued that a fundamental shortcoming of motion coherence is that it fails to distinguish between different types of noise underlying performance. Furthermore, only one of our subjects showed a loss in motion sensitivity with eccentricity when measured with a motion coherence task. Three of our subjects showed no change and two showed an improvement. We therefore argue that in addition to its lack of diagnostic power, the coarse direction discrimination (e.g., left versus right or up versus down) required render motion coherence insensitive to subtle changes in visual sensitivity. Part of the differences between subjects in performing the motion coherence task may arise from individual differences in the strategies adopted. For example, some subjects may discount certain non-target directions in the stimulus if they are able to do so and realize that they carry only noise. Other subjects may switch to different spatial scales to perform the task as their contrast sensitivity changes across the field. And finally, given that MC would be more vulnerable to crowding (a form of obligatory pooling) since some of the dots are signal, but most are noise, differences in thresholds may represent different observers' sensitivity to crowding. Our fine direction discrimination task and equivalent noise analysis attempts to bypasses some of these problems. In our stimuli, all elements and all spatial scales are 'signal' and so best performance is possible if all the elements in the stimulus are integrated.

#### 4.3. Clinical uses of equivalent noise

Amblyopia is a developmental disorder that reduces visual acuity in the affected eye. Recently, equivalent noise paradigms have been used successfully to examine the deficits underlying amblyopic subjects using orientation (Mansouri, Allen, Hess, Dakin, & Ehrh, 2004) motion (Hess, Mansouri, Dakin, & Allen, 2006), and letter identification (Pelli, Levi, & Chung, 2004) tasks. We suggest that a cross comparison between an observer's normal eye tested on a peripheral motion discrimination task and their amblyopic eye, might reveal similarities underlying their impaired performance (compared to normal foveal vision). Similarly, we have recently used equivalent noise techniques to analyze the motion sensitivity impairment in patients with Glaucoma (Falkenberg & Bex, 2007) a disease that is known to affect motion sensitivity, at least in its early stages (see Anderson (2006), for review). More recently we have used EN to examine whether reduced motion sensitivity in albino patients is attributable to nystagmus. We believe that the strength of the equivalent noise technique lies in its ability to rapidly distinguish the influence of different potential noise sources that ultimately limit subjects' behaviour. We argue that equivalent noise offers many advantages over alternative methods for assessing visual function and that it could be usefully employed to investigate a wide range of visual disorders as well age related visual deficits.

#### References

- Anderson, R. S. (2006). The psychophysics of glaucoma: Improving the structure/function relationship. *Progress in Retinal and Eye Research*, 25, 79–97.
- Bennett, P. J., & Banks, M. S. (1987). Sensitivity loss in odd-symmetric mechanisms and phase anomalies in peripheral vision. *Nature*, 326, 873–876.
- Bennett, P. J., & Banks, M. S. (1991). The effects of contrast, spatial scale, and orientation on foveal and peripheral phase discrimination. *Vision Research*, 31, 1759–1786.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Chung, S. T., Mansfield, J. S., & Legge, G. E. (1998). Psychophysics of reading. XVIII. The effect of print size on reading speed in normal peripheral vision. *Vision Research*, 38, 2949–2962.
- Dakin, S. C. (2001). Information limit on the spatial integration of local orientation signals. *Journal of the Optical Society of America*, 18, 1016–1026.
- Dakin, S. C., Mareschal, I., & Bex, P. J. (2005a). Local and global limitations on direction integration assessed using equivalent noise. *Vision Research*, 24, 3027–3049.
- Dakin, S. C., Mareschal, I., & Bex, P. J. (2005b). An oblique effect for local motion: Psychophysics and natural movie statistics. *Journal of Vision*, 5, 878–887.
- De Bruyn, B. (1997). Blending transparent motion patterns in peripheral vision. *Vision Research*, 37, 645–648.
- Falkenberg, H. K., & Bex, P. J. (2007). Sources of motion sensitivity loss in glaucoma. *Investigative Ophthalmology & Visual Science*, 48, 2913–2921.
- Fine, E. M., Peli, E., & Pisano, K. (1993). Contrast enhancement does not appreciably increase the reading rate of scrolled text. *Investigative Ophthalmology & Visual Science*, 34, 789.
- Foster, D. H., & Bischof, W. F. (1997). Bootstrap estimates of the statistical accuracy of thresholds obtained from psychometric functions. *Spatial Vision*, 11, 135–139.
- Heeley, D. W., Buchanan-Smith, H. M., Cromwell, J. A., & Wright, J. S. (1997). The oblique effect in orientation acuity. *Vision Research*, 37, 235–242.
- Hess, R. F., Mansouri, B., Dakin, S. C., & Allen, H. A. (2006). Integration of local motion is normal in amblyopia. *Journal of the Optical Society of America*, 23, 986–992.
- Joffe, K. M., Raymond, J. E., & Chrichton, A. (1997). Motion coherence perimetry in glaucoma and suspected glaucoma. *Vision Research*, 37, 955–964.
- Johnson, A., & Wright, M. J. (1986). Matching velocity in central and peripheral vision. *Vision Research*, 26, 235–242.
- Juttner, M., & Rentschler, I. (1996). Reduced perceptual dimensionality in extrafoveal vision. *Vision Research*, 36, 1007–1022.
- Kelly, D. H. (1971a). Theory of flicker and transient responses. I. Uniform fields. *Journal of the Optical Society of America*, 61, 537–546.
- Kelly, D. H. (1971b). Theory of flicker and transient responses. II. Counterphase gratings. *Journal of the Optical Society of America*, 61, 632–640.
- Kelly, D. H. (1984). Retinal inhomogeneity. I. Spatiotemporal contrast sensitivity. *Journal of the Optical Society of America*, 1, 107–113.
- Latham, K., & Whitaker, D. (1996). A comparison of word recognition and reading performance in foveal and peripheral vision. *Vision Research*, 36, 2665–2674.
- Levi, D. M., Klein, S. A., & Aitsebaomo, P. (1984). Detection and discrimination of the direction of motion in central and peripheral vision of normal and amblyopic observers. *Vision Research*, 24, 789–800.
- Lu, Z. L., & Doshier, B. A. (1999). Characterizing human perceptual inefficiencies with equivalent internal noise. *Journal of the Optical Society of America*, 16, 764–778.
- Mansouri, B., Allen, H. A., Hess, R. F., Dakin, S. C., & Ehrh, O. (2004). Integration of orientation information in amblyopia. *Vision Research*, 44, 2955–2969.
- McKee, S. P., & Nakayama, K. (1984). The detection of motion in the peripheral visual field. *Vision Research*, 24, 25–32.
- Melmoth, D. R., Kukkonen, H. T., Makela, P. K., & Rovamo, J. M. (2000). The effect of contrast and size scaling on face perception in foveal and extrafoveal vision. *Investigative Ophthalmology & Visual Science*, 41, 2811–2819.
- Mikami, A., Newsome, W. T., & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *Journal of Neurophysiology*, 55, 1308–1327.
- 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.
- Pelli, D. G., Levi, D. M., & Chung, S. T. (2004). Using visual noise to characterize amblyopic letter identification. *Journal of Vision*, 4, 904–920.
- Raiguel, S., Van Hulle, M. M., Xiao, D.-K., Marcar, V. L., Lagae, L., & Orban, G. A. (1997). Size and shape of receptive fields in the medial superior temporal area (MST) of the macaque. *Neuroreport*, 8, 2803–2808.
- Raymond, J. E. (1994). Directional anisotropy of motion sensitivity across the visual field. *Vision Research*, 34, 1029–1037.
- Rentschler, I., & Treutwein, B. (1985). Loss of spatial phase relationships in extrafoveal vision. *Nature*, 313, 308–310.
- Rovamo, J., Virsu, V., & Nasanen, R. (1978). Cortical magnification factor predicts the photopic contrast sensitivity of peripheral vision. *Nature*, 271, 54–56.
- Smith, A. T., Hess, R. F., & Baker, C. L. Jr., (1994). Direction identification thresholds for second-order motion in peripherally viewed random-dot patterns. *Journal of the Optical Society of America*, 11, 506–514.
- Solomon, J. A., & Sperling, G. (1995). First and second-order motion and texture resolution in central and peripheral vision. *Vision Research*, 35, 59–64.
- Stephenson, C. M. E., Knapp, A. J., & Braddick, O. J. (1991). Discrimination of spatial phase shows a qualitative difference between foveal and peripheral processing. *Vision Research*, 31, 1315–1326.
- Strasburger, H., Harvey, L. O., & Rentschler, I. (1991). Contrast thresholds for identification of numeric characters in direct and eccentric view. *Perception & Psychophysics*, 49, 495–508.
- Thomas, J. P. (1987). Effect of eccentricity on the relationship between detection and identification. *Journal of the Optical Society of America*, 4, 1599–1605.
- Thompson, B., Hansen, B. C., Hess, R. F., & Troje, N. F. (2007). Peripheral vision: Good for biological motion, bad for signal noise segregation? *Journal of Vision*, 7, 1–7.
- Toet, A., & Levi, D. M. (1992). The 2-dimensional shape of spatial interaction zones in the parafovea. *Vision Research*, 32, 1349–1357.
- 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*, 4, 1643–1652.

- van de Grind, W. A., van Doorn, A. J., & Koenderink, J. J. (1983). Detection of coherent movement in peripherally viewed random-dot patterns. *Journal of the Optical Society of America*, 73, 1674–1683.
- Watamaniuk, S. N., & Heinen, S. J. (1999). Human smooth pursuit direction discrimination. *Vision Research*, 39, 59–70.
- Waugh, S. J., & Hess, R. F. (1994). Suprathreshold temporal-frequency discrimination in the fovea and the periphery. *Journal of the Optical Society of America*, 11, 1199–1212.
- Whitaker, D., Makela, P., Rovamo, J., & Latham, K. (1992). The influence of eccentricity on position and movement acuities as revealed by spatial scaling. *Vision Research*, 32, 1913–1930.
- Wright, M. J. (1987). Spatiotemporal properties of grating motion detection in the center and the periphery of the visual field. *Journal of the Optical Society of America*, 4, 1627–1633.
- Wright, M. J., & Johnston, A. (1983). Spatiotemporal contrast sensitivity and visual field locus. *Vision Research*, 23, 983–989.