



# Vernier and contrast discrimination in central and peripheral vision

Dennis M. Levi<sup>a,\*</sup>, Paul V. McGraw<sup>b</sup>, Stanley A. Klein<sup>c</sup>

<sup>a</sup> College of Optometry, University of Houston, Houston, TX 77204-6052, USA

<sup>b</sup> Department of Optometry, University of Bradford, Bradford BD7 1DP, UK

<sup>c</sup> School of Optometry, University of California, Berkeley, CA 94720, USA

Received 18 February 1999; received in revised form 27 October 1999

## Abstract

The present paper asks whether Vernier offset discrimination is limited by the observer's sensitivity to local contrast change in both central and peripheral vision. To answer this question we compared Vernier discrimination and contrast discrimination thresholds (specified in the same units) for a pair of narrow ribbons of cosine gratings. Because the ribbons are narrow, *both* the offset information (for Vernier discrimination) and the contrast information (for contrast discrimination) are highly localized. We found that when the stimuli are narrow ribbons, the local contrast cue *is* the limiting factor in Vernier discrimination. However, our results also show that integration of information along the length of the gratings (the ribbon width) is: (i) different for Vernier and contrast discrimination, and (ii) for Vernier discrimination the integration of information along the length of the gratings differs qualitatively in central and peripheral vision. For narrow ribbons, the peripheral 'template' for ribbon Vernier acuity is not as well matched to the stimulus (in two-dimensional spatial frequency space) as the foveal 'template'. © 2000 Elsevier Science Ltd. All rights reserved.

*Keywords:* Vernier discrimination; Contrast discrimination; Spatial vision; Hyperacuity; Psychophysics; Peripheral vision

## 1. Introduction

In the preceding paper (Levi, Klein & Carney, 2000) we used ribbons of cosine grating with a Vernier offset between the ribbons, combined with oblique masking, to measure the orientation, spatial frequency and width tuning of the mechanisms underlying Vernier acuity. A simple 'template' model, in which the 'mechanism' is a windowed version of the stimulus, was able to account for many of the features of our data, including the bimodal shape of the orientation tuning function, the systematic effect of ribbon spatial frequency on the peaks of the spatial frequency and orientation tuning functions, and the systematic effect of ribbon width.

Our template model is based on the test-pedestal approach (Hu, Klein & Carney, 1993; Levi, Klein & Wang, 1994), in which the stimulus is decomposed into a test pattern (the cue) plus a pedestal. The template

mechanism measures the local contrast change associated with the Vernier offset (in the preceding paper we make the additional assumption that the mechanism that detects the Vernier offset is closely matched to the test pattern). The key assumption of the template model is that the change in local contrast introduced by the Vernier offset provides the cue for Vernier discrimination. The notion that local contrast information is the critical limiting factor in Vernier acuity is not new (see e.g. Hartridge, 1923; Findlay, 1973; Morgan & Aiba, 1985; Morgan, 1986). However, the test-pedestal approach allows the Vernier offset at threshold to be expressed as the equivalent contrast change, and thus provides a method for directly assessing whether the observer's sensitivity to contrast limits their sensitivity to Vernier offset.

In direct comparisons, under limited conditions, the Vernier discrimination threshold can be reasonably well predicted by the contrast discrimination threshold (Hu et al., 1993; Levi et al., 1994). However, it is instructive to look at where the test-pedestal model fails (i.e. where

\* Corresponding author. Fax: +1-713-743-1888.

E-mail address: dlevi@uh.edu (D.M. Levi)

the Vernier offset at threshold is not predicted by the contrast discrimination threshold), since this provides important information about factors other than contrast, which limit performance. One instance in which the test-pedestal model fails is when the stimulus grating is long, presumably because the information for Vernier discrimination is localized, while the entire stimulus is used for contrast discrimination. Thus, using long gratings, the test-pedestal model predictions were poor, especially at high spatial frequencies (i.e. the contrast at the Vernier offset discrimination threshold was more than a factor of ten higher than the contrast discrimination threshold [see, e.g. Hu et al., 1993, Figs. 6 and 8]). A similar failure occurs in peripheral vision, where the Vernier offset discrimination thresholds are elevated more than contrast discrimination (Hess & Field, 1993) or detection (Levi et al., 1994) thresholds. Hess and Field (1993) measured both alignment thresholds and contrast discrimination using well separated Gabor patches; however, under their conditions, the alignment task is almost contrast independent, and is probably limited by the observers' ability to localize the contrast envelope (a nonlinear process). Levi et al. (1994) did not measure contrast discrimination thresholds in the periphery of their observers, but noted that their abutting Vernier thresholds were elevated more in peripheral vision than their contrast detection thresholds. However, in the Levi et al. (1994) study, the foveal stimuli were long, and the length of the grating was further increased for peripheral viewing. As discussed above, increasing the grating length may have provided an advantage for contrast detection or discrimination relative to Vernier, and it is not clear whether increasing the grating length in peripheral vision may actually have placed the periphery at a disadvantage.

The purposes of the present paper, were threefold: first, to revisit the question of whether Vernier discrimination is limited by the observer's sensitivity to local contrast change, by directly comparing Vernier discrimination and contrast discrimination thresholds (specified in the same units) for narrow ribbons of cosine grating. Because the ribbons are narrow, *both* the offset information (for Vernier discrimination) and the contrast information (for contrast discrimination) are highly localized. Second, to explore the role of ribbon width (grating length) on foveal and peripheral Vernier and contrast discrimination. Specifically, we are interested in whether the integration of information along the length of the gratings differs qualitatively in central and peripheral vision. Third, to compare the two-dimensional spatial frequency tuning of the mechanisms underlying foveal and peripheral Vernier acuity, using masking.

## 2. Methods

### 2.1. Stimuli

The stimuli, a pair of vertical ribbons (3' wide horizontally unless otherwise specified) of horizontal cosine grating [ $\cos(2\pi fy)$ ] with a vertical Vernier offset between the ribbons, were identical to those described in the preceding paper (Levi, Klein & Carney, 2000 — Plate 1). The ribbons were separated by a 3' gap to optimize both the Vernier and contrast discrimination thresholds (Hu et al., 1993), and were presented for a duration of 1 s. As in the preceding paper, for foveal viewing, stimuli of 4 c/deg or greater were viewed from a distance of 4 m. For lower spatial frequencies the viewing distance was decreased in inverse proportion to spatial frequency. For peripheral viewing (5° temporal visual field), stimuli of 2 c/deg or greater were viewed from a distance of 1.33 m. Although this scaling procedure increased the height of the ribbons, unless otherwise specified, for all spatial frequencies and both eccentricities, the ribbons were always  $\approx 3'$  wide and were separated by 3'. Unless otherwise specified, the ribbon contrast was 40%.

### 2.2. Psychophysical methods

Vernier and contrast discrimination thresholds were measured (in separate runs) using a self-paced rating-scale method of constant stimuli (for a detailed description see Levi et al., 1994). On each trial, one of five randomly selected offsets (for Vernier discrimination) or contrasts (for contrast discrimination) was presented. The observer's task was to judge whether the position or contrast of the 'test' ribbon (on the right) was equal to, higher or lower than the reference ribbon (on the left) by giving one of five integer ratings from  $-2$  to  $+2$ . The step size was chosen, on the basis of pilot experiments, to be close to the observer's threshold. For Vernier, the shifts never exceeded one quarter of a cycle (90°). Feedback as to the magnitude and direction of the offset or contrast was given after each trial. Thresholds were obtained by calculating a maximum-likelihood function estimate of the  $d'$  values for each stimulus and interpolating to a  $d'$  equal to 1 using a linear transducer. In different runs we varied the spatial frequency, contrast and width of the ribbons. The thresholds reported are the means of at least four runs of 125 trials per run, weighted by the inverse variance, and represent the ability to discriminate the direction of offset. The error bars are  $\pm 1$  S.E., reflecting the larger of the within and between run variance (Klein & Levi, 1985). In the Vernier experiments, the position of the grating was randomly jittered from trial to trial, to preclude the use of any unwanted position cues.

Four observers with corrected-to-normal vision (two of the authors and two other highly experienced psychophysical observers who were naive as to the purpose of this study) participated in these experiments. Only three of the four performed the experiments in the periphery. Viewing was monocular.

### 2.3. Comparing Vernier and contrast discrimination thresholds

Vernier thresholds were compared to contrast discrimination thresholds by converting from thresholds in min arc to thresholds expressed as a Weber fraction  $\Delta c/c$ . The first step is to convert the spatial offset  $d$  (min) to a phase shift  $\phi$  (rad).

$$\phi = 2\pi fd/60 \quad (1)$$

where  $f$  is the spatial frequency in c/deg. The second step is to go from  $\phi$  to  $\Delta c/c$  (Levi, et al., 1994). For the Vernier detection task of distinguishing an aligned grating from a grating with an offset the relationship is:

$$\Delta c/c_{\text{detection}} = 2 \sin(\phi/2) \quad (2)$$

Eq. (2) would be appropriate for the masking experiments of Levi et al. (2000) where all the offsets were unidirectional. For an experiment in which the task was to discriminate an upward offset from an equal downward offset the connection between phase and Weber fraction is:

$$\Delta c/c_{\text{discrimination}} = \sin(\phi). \quad (3)$$

For the present discrimination experiments we use Eq. (3) rather than Eq. (2). The main point to make about

the two definitions of Weber fractions is that they are very close in magnitude except for the very highest phase shifts. The discrimination to detection ratio is:

$$(\Delta c/c_{\text{discrimination}})/(\Delta c/c_{\text{detection}}) = \cos(\phi/2). \quad (4)$$

This ratio is between 0.9 and 1.0 for phase shifts below  $50^\circ$  (true for all except the most extreme situations).

## 3. Results

### 3.1. The effect of ribbon spatial frequency

Both Vernier discrimination and contrast discrimination thresholds are strongly dependent on spatial frequency. When plotted in the conventional units (arc sec for Vernier and  $\Delta c/c$  for contrast discrimination), the Vernier and contrast thresholds appear to have different spatial frequency dependence (Fig. 1A and B). In both foveal and peripheral vision, Vernier thresholds (in arc sec) fall almost linearly as spatial frequency increases up to 8–10 c/deg, while contrast discrimination thresholds increase slightly over the same range. However, when plotted in the same units ( $\Delta c/c$  — see Section 2 above, and the Appendix of Levi et al., 1994 for details), both contrast and Vernier discrimination thresholds have the same dependence on spatial frequency (Fig. 2). Most importantly, the absolute values of the Vernier and contrast discrimination thresholds are quite similar — both in the fovea and at  $5^\circ$  in the periphery.

The present results show a very close concordance between the Vernier discrimination threshold and the

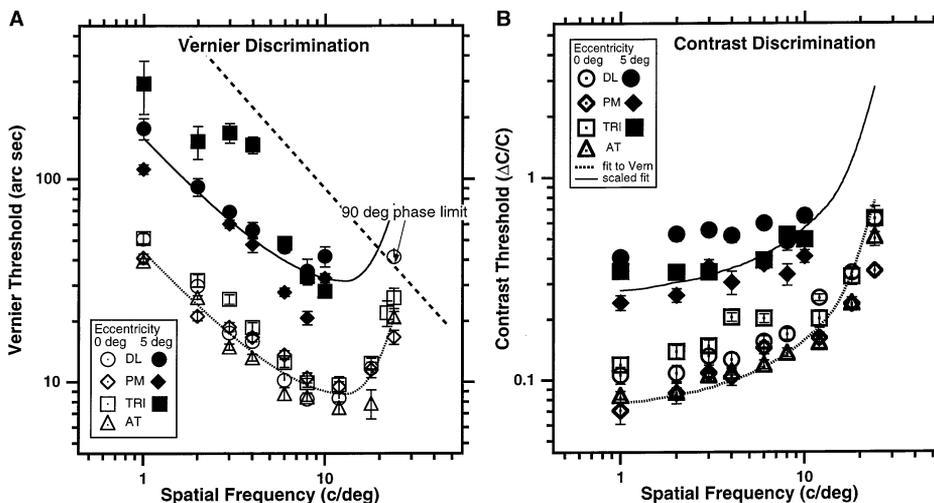


Fig. 1. (A) Vernier offset discrimination thresholds (in arc sec) versus ribbon spatial frequency in the fovea (open symbols), and at  $5^\circ$  in the temporal field (solid symbols). Data are for three observers. The dotted lines are Cauchy functions fit to the (group) foveal data (Eq. (1)). The solid line is the foveal data shifted upward by a scale factor ( $\approx 3.7$ ). The dashed  $45^\circ$  line is the  $90^\circ$  phase limit. (B) Contrast discrimination thresholds (specified as a Weber fraction,  $\Delta c/c$ ) versus ribbon spatial frequency in the fovea (open symbols), and at  $5^\circ$  in the temporal field (solid symbols). The dotted lines are Cauchy functions fit to the (group) foveal data (Eq. (1)). The solid line is the foveal data shifted upward by a scale factor ( $\approx 3.7$ ).

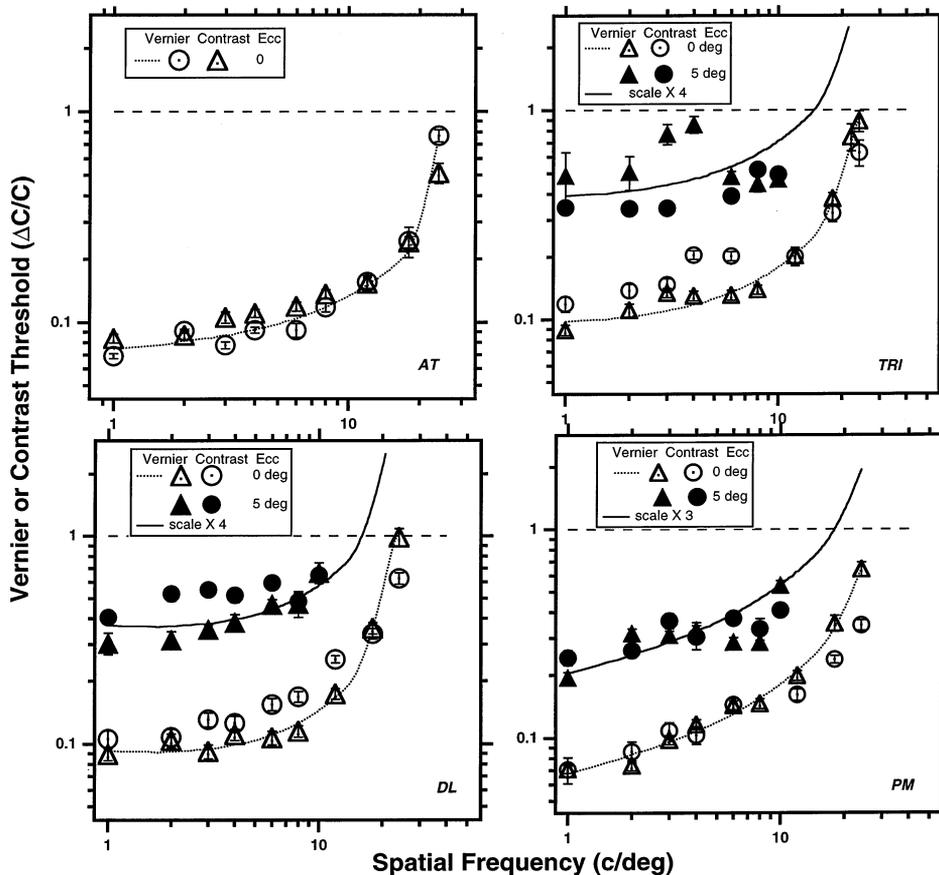


Fig. 2. The data of Fig. 1A (Vernier discrimination—triangles) and B (contrast discrimination — circles) are replotted here with both specified as a contrast Weber fraction ( $\Delta c/c$ ). Each panel shows a different observer at the fovea (open symbols) and at 5° in the temporal field (solid symbols). The dotted lines are Cauchy functions fit to the individual foveal data (Eq. (1)). The solid line is the foveal data shifted upward by a scale factor (noted in the figure). The dashed horizontal line is the 90° phase limit for Vernier.

contrast discrimination threshold (when specified in the same units) for narrow cosine ribbons. By limiting the length of the gratings (the ribbon width) both tasks are limited by the same information (the local contrast change). Surprisingly, the results are similar in foveal and peripheral (5° temporal field) vision — in contrast to the studies of Levi et al. (1994) which used long gratings that were size scaled for peripheral viewing, and Hess and Field (1993) who used well separated Gabor patches. Below we examine the difference between foveal and peripheral performance more closely, and then consider both the effects of ribbon contrast and ribbon width.

### 3.2. The effect of eccentricity

It is clear that peripheral thresholds in both tasks are worse (higher) than foveal thresholds (Figs. 1 and 2), but behave in a similar manner. The dotted lines in Figs. 1 and 2 are double Cauchy functions (Levi et al., 1994) fit to the foveal Vernier thresholds of Fig. 1 and converted to  $\Delta c/c$  in Fig. 2. The solid lines are the foveal fits shifted vertically (by eye) to provide a rea-

sonable fit to the peripheral data. The vertical shift is noted (as the scale factor) in the legend of Fig. 2. For the three observers, the scale factor is approximately 3.7, corresponding to an  $E_2$  value (Levi, Klein & Aitsebaomo, 1985) of approximately 1.9° (i.e. assuming thresholds increase linearly with eccentricity, the foveal threshold for both tasks doubles at about 1.9°). The results are surprising, because they differ quite dramatically from a previous study (Levi et al., 1994) using similar methods but stimuli that differed in their length (long gratings versus ribbons), gap (abutting versus 3'), contrast (80 versus 40%) and visual field (lower versus temporal). In that study, foveal and peripheral Vernier thresholds were quite similar at low spatial frequencies, but diverged at high spatial frequencies. Thus, at 8 c/deg, peripheral Vernier thresholds were about a factor of 20 worse (higher) than foveal Vernier thresholds. Below we examine the effects of contrast and ribbon width in order to try to understand which factors result in the paradoxical worsening of Vernier acuity with wider, more visible stimuli, and we will revisit the issue of scaling in Section 4.

### 3.3. The effect of ribbon width

In foveal vision, increasing the width of an 8 c/deg ribbon improves contrast discrimination and surprisingly, degrades Vernier discrimination (Fig. 3 small symbols). Increasing ribbon width increases the visibility of the stimuli, and provides additional information for the contrast judgment. Thus, for ribbons longer than about 6–8', Vernier thresholds are worse than contrast thresholds. This trend is much exaggerated in the periphery (large symbols in Fig. 3). Thus, while peripheral Vernier and contrast thresholds are reasonably close for narrow ribbons, they differ by approximately six- to sevenfold for the widest stimuli. This paradoxical effect of ribbon width was explored extensively for foveally viewed high spatial frequency gratings (10–20 c/deg) by Hu et al. (1993), and they suggested that rather than comparing Vernier and contrast discrimination under identical conditions, they should be compared under their optimal conditions. Their reasoning is that there are multiple ways to degrade performance, and factors, which may impair performance in one task, may have little effect on the other. Therefore, one must look to the optimal conditions to assess the visual system's capabilities. How the system can be degraded is important, but it seems that should be considered after first understanding the optimal case. In the periphery, for the 8 c/deg data of Fig. 3, that would mean comparing Vernier with a 12' ribbon, to contrast discrimination with a ribbon almost

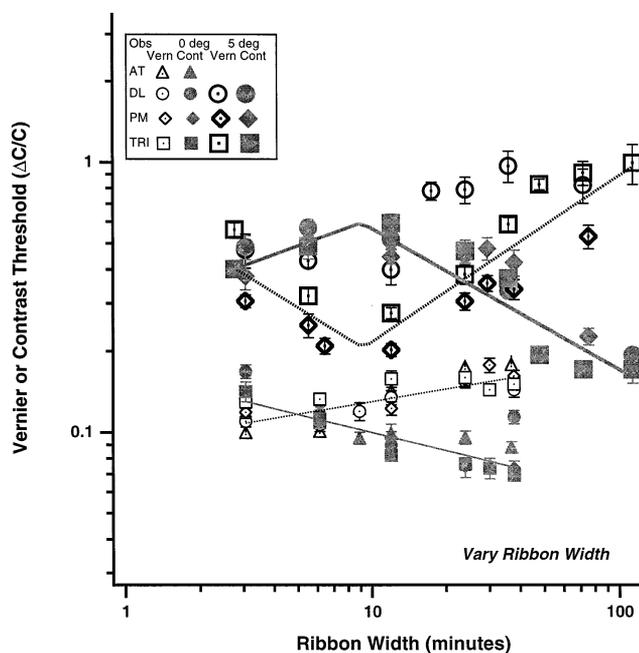


Fig. 3. The effect of ribbon width on Vernier (open symbols) and contrast (solid symbols) discrimination in foveal (small symbols) and peripheral (large symbols) vision. Ribbon spatial frequency is 8 c/deg. Thresholds for both tasks are specified as Weber fractions ( $\Delta c/c$ ).

ten times wider! Even making this extreme comparison, Vernier thresholds tend to be worse than the contrast discrimination thresholds in the periphery.

We have explored the effect of ribbon width on Vernier acuity over a range of ribbon spatial frequencies. In the fovea, at low spatial frequencies, increasing ribbon width from  $\sim 3$  to 120' has little influence on Vernier thresholds (large symbols and Fig. 4A), but as noted above, at high spatial frequencies increasing ribbon width paradoxically degrades Vernier acuity (small symbols in Fig. 4A). The effect of increasing ribbon width at low spatial frequencies appears to be qualitatively different in the periphery (large symbols Fig. 4B). At low frequencies, increasing ribbon width first improves Vernier acuity and then, beyond a critical width (which varies with spatial frequency), thresholds increase. Interestingly, for long ribbons ( $\approx 60'$ ) thresholds for a broad range of spatial frequencies converge to a value of around 90–100 arc sec (1.5–1.6'). The critical ribbon width in peripheral vision is around one spatial period. This can be seen more clearly in Fig. 4D, where the data of Fig. 4B have been replotted with the abscissa specified in grating periods (i.e. for each ribbon spatial frequency, ribbon width is divided by the grating period). Fig. 4 illustrates that any *simple* peripheral scaling is likely to be problematic. Making the stimuli too narrow *or* too wide will adversely affect the periphery (Fig. 4B and D). Thus, there does not seem to be any simple 'local scale' factor (Watson, 1987; Whitaker, Rovamo, MacVeigh & Makela, 1992) that will make the width functions similar in foveal and peripheral vision, particularly at low spatial frequencies, since the curves differ qualitatively.

### 3.4. The effect of ribbon contrast

The close correspondence between Vernier and contrast discrimination thresholds for narrow (3') ribbons holds over the entire contrast range in the fovea (we measured Vernier discrimination from near threshold to 80% contrast, and contrast discrimination from near threshold to 60% contrast). This close correspondence can be seen in Fig. 5A (small symbols — which shows how performance for both tasks varies with contrast-specified relative to the contrast detection threshold [in contrast threshold units, i.e., CTU] for 8 c/deg ribbons). However, the correspondence is less clear with peripheral viewing. One problem is that the range of suprathreshold contrasts for these tiny ribbons is very limited in the periphery — only up to about three to four times the contrast detection threshold. Widening the ribbons to 24', lowers the detection threshold, making it possible to make measurements over a larger range of suprathreshold contrast levels (greater than 60 CTU in the fovea and up to  $\approx 20$  CTU at  $5^\circ$  — Fig. 5B). With these wider ribbons, in foveal viewing, it is

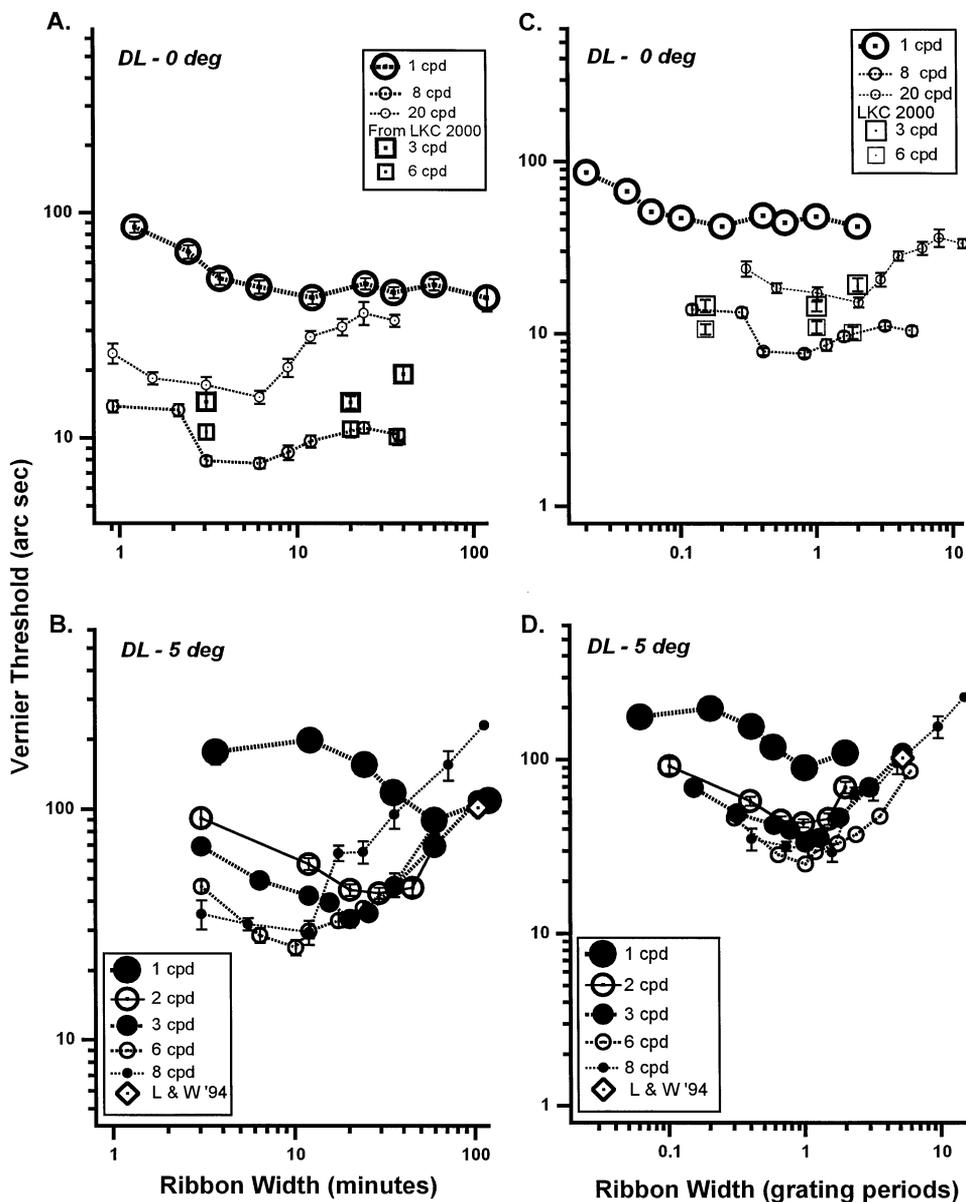


Fig. 4. The effect of ribbon width on Vernier acuity over a range of ribbon spatial frequencies. Data are shown for different ribbon spatial frequencies (coded by symbol size). (A) Fovea. The squares are from data of Levi et al. (2000), using identical stimuli, but for detection of a unidirectional Vernier offset. (B) Periphery (5°). The open diamond shows line Vernier data of observer DL for a long line (105 arc min) from Levi and Waugh, 1994. (C) The data of Fig. 4A have been replotted with the abscissa specified in grating periods (i.e. for each ribbon spatial frequency, it is the ribbon width divided by the ribbon period). (D) The data of Fig. 4B have been replotted with the abscissa specified in grating periods. The open diamond plots DL's line Vernier data at a width corresponding to the number of periods of a 3 c/deg grating (based on the spatial frequency tuning of line Vernier acuity at 5° shown in Fig. 2B of Levi & Waugh, 1994).

clear that contrast and Vernier thresholds co-vary; however the close correspondence in absolute values is lost — Vernier thresholds (specified as  $\Delta c/c$ ) are uniformly higher than the corresponding contrast thresholds. Presumably the full width of the ribbon is not useful for the Vernier judgment. In peripheral vision, the equivalence between Vernier and contrast thresholds is lost with wide ribbons. Contrast thresholds (large solid symbols in Fig. 5B) improve markedly with contrast, while Vernier thresholds do not (large open symbols in Fig. 5B). For these wide

ribbons, Vernier thresholds remain close to the 90° phase limit (corresponding to  $\Delta c/c = 1$ ) over the entire contrast range. The slopes of the best power function fit to the Vernier and contrast discrimination versus contrast data of Fig. 5 are summarized in Table 1. This 'disconnect' between Vernier and contrast discrimination thresholds in the periphery is similar to that reported by Hess and Field (1993) and also to the 'disconnect' between Vernier and contrast *detection* thresholds in the periphery (Levi et al., 1994).

### 3.5. Masking experiments. Spatial frequency tuning for narrow and wide ribbons

As shown in the preceding manuscript, when the ribbon width is less than one spatial period, there was an upward shift in the spatial frequency of the mechanism selected for Vernier discrimination. For the 8 c/deg ribbons used in these ‘width’ experiments one spatial period is 7.5'; thus, increasing the ribbon width (at least up to 7.5') may have resulted in selection of a

lower spatial frequency mechanism for Vernier discrimination. To test this notion, we used oblique masking (as in the preceding paper) to estimate the spatial frequency tuning for narrow (3') and wide (24') 8 c/deg ribbons. The methods and stimuli were identical to those used in the preceding paper. The test ribbon (contrast 40%) and the mask (contrast 20%) were both 8 c/deg, and were presented simultaneously for 1 s. The mask angle was 20°. The spatial frequency tuning functions (Fig. 6 and Table 2), show that for foveal (but not peripheral) Vernier, increasing the ribbon width resulted in a shift in the spatial frequency tuning toward lower spatial frequencies. The  $\approx 40\%$  shift in the peak of the spatial frequency tuning with ribbon width (plotted as the peak spatial period in Fig. 6C) is roughly comparable to the  $\approx 30\%$  increase in thresholds. It is interesting to note that there is no shift in spatial frequency tuning with ribbon width in the periphery. For wide ribbons, the spatial frequency tuning is identical in foveal and peripheral vision; however for narrow ribbons (3') the spatial frequency tuning function is shifted toward higher spatial frequencies in the fovea.

### 3.6. The peripheral ‘template’

In the preceding manuscript we argued for a ‘template’ model, in which the visual system attempts to find an efficient template match to the ‘cue’. Due to the two-dimensional nature of the task (and stimuli), a single spatial frequency or orientation ‘slice’ does not adequately capture the masking. In order to examine the peripheral ‘template’, we have replicated the ‘hot spot’ masking experiment (Plate 4 in the preceding paper) at 5° for ribbon spatial frequencies of 1 and 3 c/deg using narrow ribbons. We have focussed on these low spatial frequencies because these ribbons show marked departures from scaling, but are sufficiently visible to make measurements with masks. The results are interesting, and are shown in Plate 1 in the same format as the foveal data (Plate 4) of the preceding paper. Like the fovea, the strongest threshold elevations, as expected, occur at a *vertical* spatial frequency corresponding to the ribbon spatial frequency. However, they occur at a *horizontal* spatial frequency about a factor of two lower than in the fovea. Interestingly, the threshold elevations are much smaller in the periphery (maximally only about a factor of 2.5), so that masked thresholds are actually lower (in absolute terms) in the periphery than in the fovea under conditions that correspond to the foveal hot spot. For example, near the foveal hotspot masked thresholds are about 414 arc sec for a 1 c/deg ribbon ( $f_y \approx 1$  c/deg;  $f_x \approx 4$  c/deg) and 91 arc sec for a 3 c/deg ribbon ( $f_y \approx 3$  c/deg;  $f_x \approx 5-6$  c/deg). For the corresponding conditions in the periphery, masked thresholds are  $\approx 136$  and 55 arc sec for 1 and 3 c/deg, respectively. This can

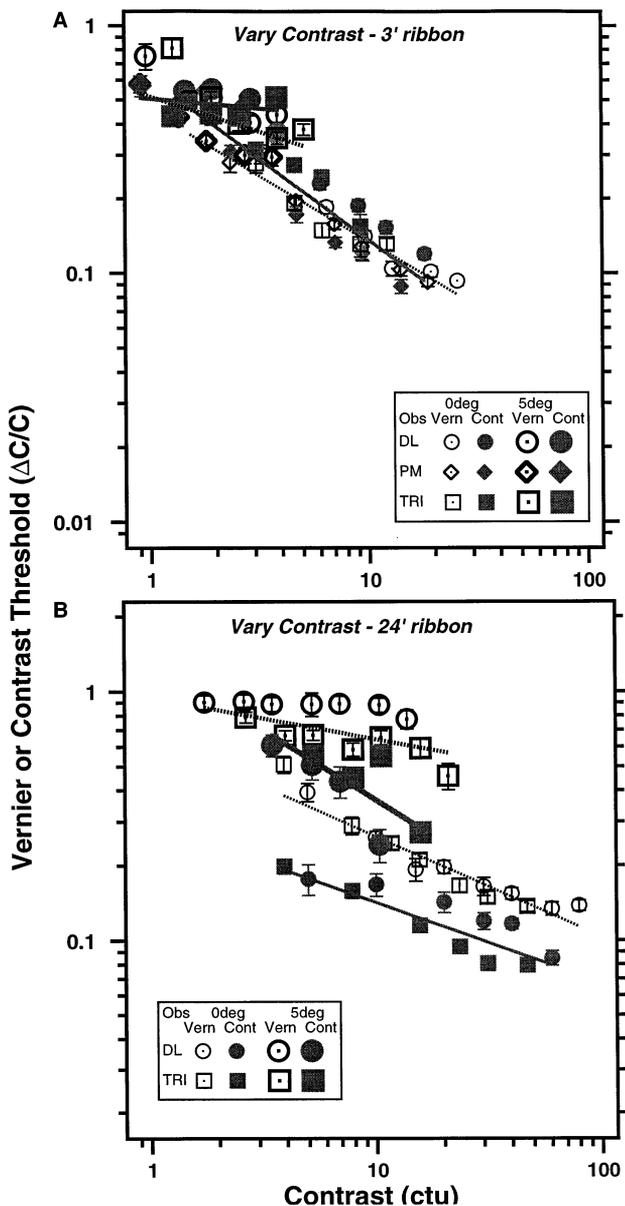


Fig. 5. The effect of ribbon contrast (specified relative to the contrast detection threshold [CTU]), on Vernier (open symbols) and contrast (solid symbols) discrimination in foveal (small symbols) and peripheral (large symbols) vision. Thresholds for both tasks are specified as Weber fractions ( $\Delta c/c$ ). The lines are power functions fit to all the Vernier discrimination (dotted lines) and contrast discrimination (solid lines) data. (A) 3' ribbons; (B) 24' ribbons.

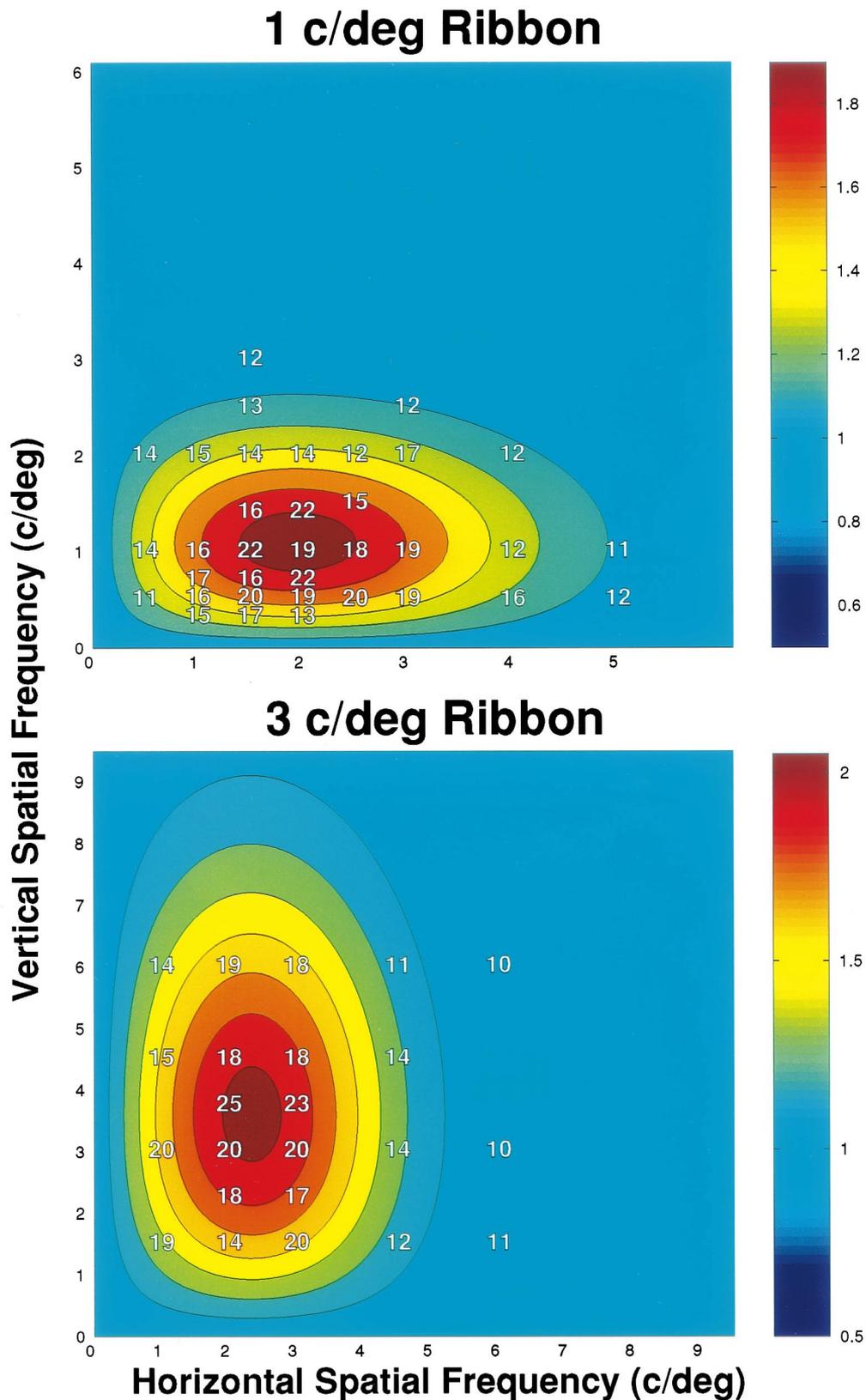


Plate 1. Iso-threshold elevation functions in 2-D Fourier space. The abscissa and ordinate represent the mask horizontal and vertical frequency components respectively, and the numbers show the threshold elevation ( $\times 10$ ) produced by each mask. The color-coded iso-threshold elevation contours were obtained by fitting Gaussians to the raw data. The 'hot-spots' represent the masks (in 2-D Fourier space) that are most effective in raising threshold. Top, 1 c/deg ribbon; bottom, 3 c/deg ribbon.

Table 1  
Power function fits<sup>a</sup>

| Ribbon width | Observer | Fovea Vernier    | Fovea contrast   | 5° Vernier       | 5° Contrast      |
|--------------|----------|------------------|------------------|------------------|------------------|
| 3'           | DL       | $-0.65 \pm 0.08$ | $-0.51 \pm 0.08$ | $-0.36 \pm 0.08$ | $-0.55 \pm 0.04$ |
|              | PM       | $-0.55 \pm 0.04$ | $-0.73 \pm 0.26$ | $-0.40 \pm 0.09$ | $-0.12 \pm 0.20$ |
|              | TRI      | $-0.61 \pm 0.05$ | $-0.56 \pm 0.14$ | $-0.31 \pm 0.08$ | $-0.10 \pm 0.19$ |
| 24'          | DL       | $-0.35 \pm 0.03$ | $-0.31 \pm 0.04$ | $-0.04 \pm 0.04$ | $-0.79 \pm 0.14$ |
|              | TRI      | $-0.50 \pm 0.03$ | $-0.40 \pm 0.25$ | $-0.18 \pm 0.04$ | $-0.63 \pm 0.07$ |

<sup>a</sup> Exponents of the best-fitting power functions to the Vernier or Contrast discrimination threshold versus contrast data of Fig. 5 (8 c/deg ribbons).

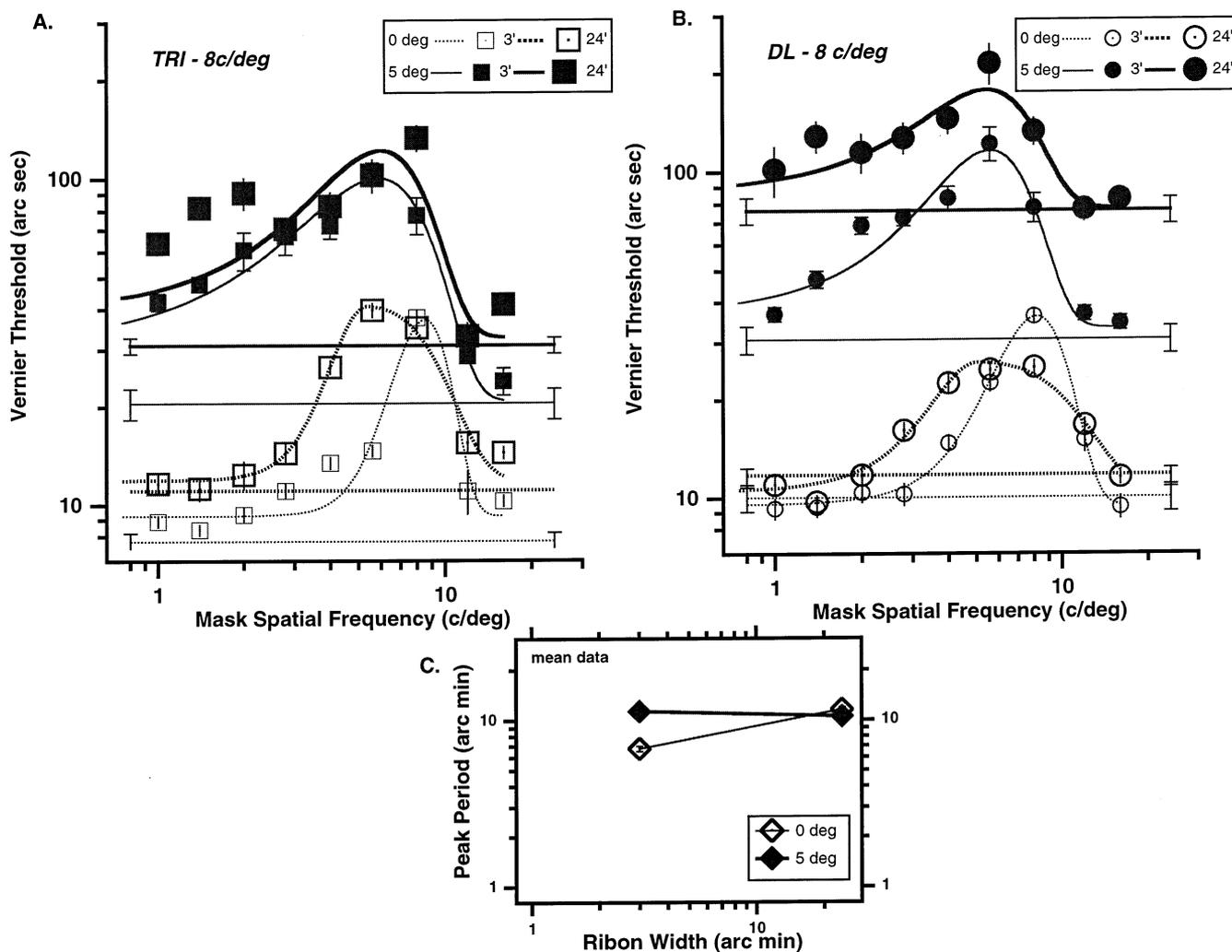


Fig. 6. Spatial frequency tuning functions (obtained using oblique masking). Vernier discrimination thresholds (specified in arc sec) are plotted against the spatial frequency of an oblique mask. Data are shown in both central (open symbols) and peripheral (solid symbols) vision for 3' ribbons (small symbols) and for 24' ribbons (large symbols). The lines are single or double Gaussian fits to the data. (A) Observer DL; (B) observer TRI; (C) plots the spatial period at which peak masking occurred (in minutes — i.e. 60/peak spatial frequency) against the ribbon width.

be seen more clearly in Fig. 7 which shows the absolute Vernier thresholds (in arc sec) of the fovea and periphery for masks with a vertical spatial frequency of 1 c/deg (top) or 3.0 c/deg (bottom) with different horizontal spatial frequencies (corresponding to horizontal cut through the hotspots shown in Plate 1 of the

present paper, and Plate 4 in the preceding paper). We believe that the extremely high foveal thresholds in the hotspot, are in some respects similar to the masking of Lincoln's face by quantization (Harmon & Julesz, 1973), and the masking of faces in Chuck Close's paintings by 'blocking' (Pelli, 1999). In these faces, the

Table 2  
Spatial frequency tuning parameters for 8 c/deg ribbon

| Observer | Eccentricity (°) | Ribbon width (') | Unmasked threshold (arc sec) | Peak spatial frequency (c/deg) <sup>a</sup> |
|----------|------------------|------------------|------------------------------|---|
| DL       | 0                | 3                | 10 ± 0.96                    | 8.15 ± 0.06                                 |
|          | 0                | 24               | 11.8 ± 0.55                  | 5.05 ± 0.41                                 |
|          | 5                | 3                | 30.8 ± 2.98                  | 5.62 ± 0.42                                 |
|          | 5                | 24               | 76.3 ± 6.96                  | 5.46 ± 0.31                                 |
| TRI      | 0                | 3                | 7.74 ± 0.48                  | 8.52 ± 0.64                                 |
|          | 0                | 24               | 11.1 ± 0.57                  | 5.34 ± 0.27                                 |
|          | 5                | 3                | 20.6 ± 2.26                  | 5.87 ± 0.13                                 |
|          | 5                | 24               | 31 ± 1.74                    | 6.00 ± 0.97                                 |

<sup>a</sup> Peak spatial frequency is determined by fitting either one or two Gaussians (whichever provides the better fit — Levi & Waugh, 1994) to the data.

high spatial frequency masks render the faces invisible, and the observer evidently cannot access the low spatial frequency content of the face. Similarly in the fovea, the high horizontal spatial frequencies in the mask render the low spatial frequency information (which is present in a filter model — see preceding paper) inaccessible. It remains a mystery as to why under certain circumstances the high frequency masker is effective while in other circumstance (Stromeyer & Julesz, 1972) there is negligible masking. In peripheral vision, we suggest that the high horizontal spatial frequencies in the mask are only weakly represented in the visual nervous system (they are much less visible) so that the observer can still use lower frequency filters to perform the task.

Because the periphery does not show ‘hot spots’ like the fovea (i.e. narrow regions of very strong masking with threshold elevations of 8- to 12-fold) a single Gaussian provides a good fit to the data (whereas the fovea required a double Gaussian fit). Fig. 8 (top panel) provides a direct comparison of the peaks of the vertical and horizontal spatial frequency tuning (derived from the Gaussian fits to the ‘hot-spots’) in foveal (f) and peripheral (p) vision. It is interesting to compare the fovea and periphery. For both 1 and 3 c/deg ribbons, there is a large (downward) shift in the peak of the horizontal spatial frequency tuning of the periphery (relative to the fovea) for both ribbon frequencies. For comparison, the dot-dashed line shows the horizontal spatial frequency peak of the simple template-model. It is clear that the foveal ‘template’ is a reasonably close match to the model, while the peripheral template is shifted toward lower spatial frequencies. The large shift in horizontal frequency, but not in vertical frequency, suggests that for these stimuli, scaling is not simple. Indeed, as noted in the Appendix of Levi et al. (2000), the strong threshold elevation in the foveal ‘hot spot’ provides strong evidence against a filter model and in favor of a template model, in which the optimal mechanism is closely matched to the stimulus. The absence of a hot spot in the periphery suggests that peripheral

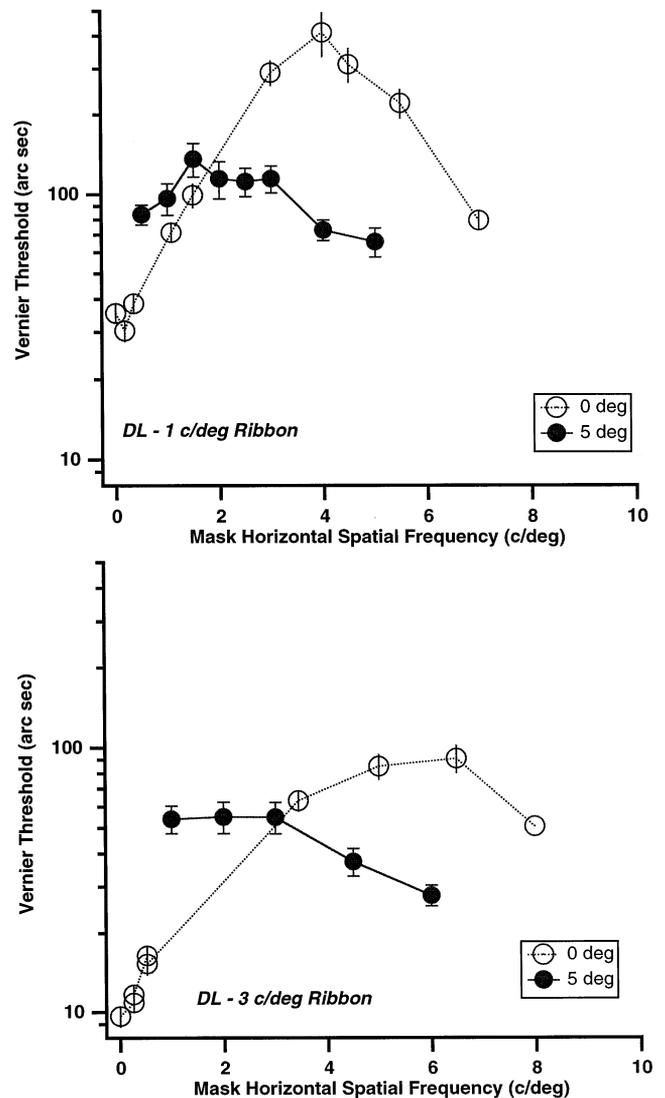


Fig. 7. The absolute Vernier thresholds (in arc sec) of the fovea and periphery for masks with a vertical spatial frequency of 1 c/deg (top) or 3.0 c/deg (bottom) with different horizontal spatial frequencies (corresponding to horizontal cut through the hotspots shown in Plate 1 of the present paper, and Plate 4 in the preceding paper).

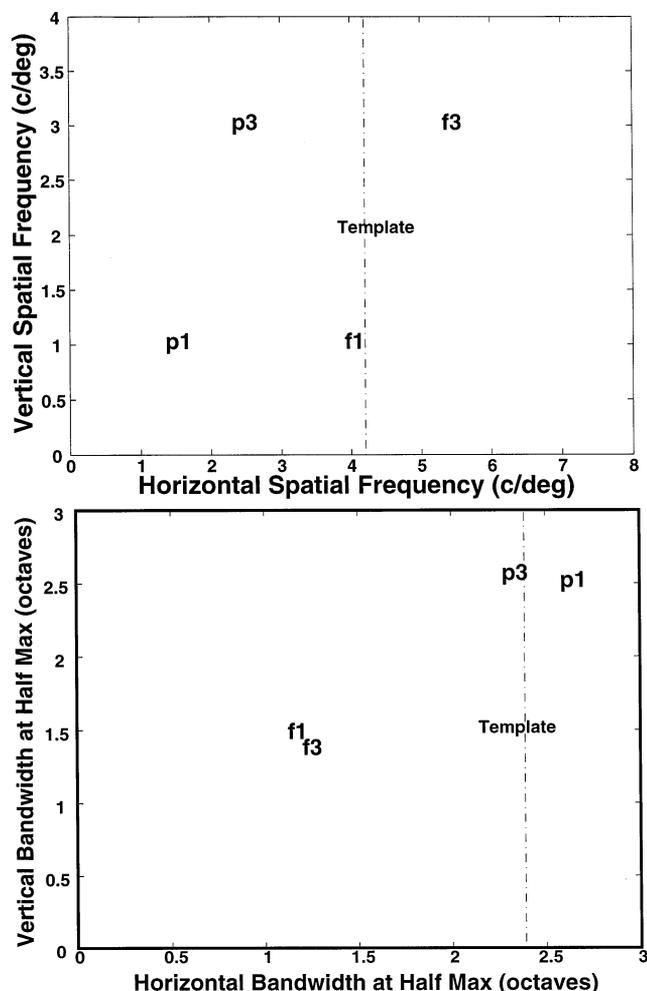


Fig. 8. (Top panel) Compares the peaks of the vertical and horizontal spatial frequency tuning (derived from the Gaussian fits to the 'hot-spots') in foveal (f) and peripheral (p) vision. The peripheral spectrum is derived from the Gaussian fit shown in Plate 1; the foveal spectrum is from Levi et al. (2000) Plate 4. For both 1 and 3 c/deg ribbons, there is the large (downward) shift in the peak of the horizontal spatial frequency tuning of the periphery relative to the fovea for both ribbon frequencies. The horizontal spatial frequency peak of the simple template-model is shown by the dot-dashed line. (Lower panel) Compares the bandwidths of the horizontal and vertical spatial frequency tuning functions (derived from the Gaussian fits to the 'hot-spots') in foveal (f) and peripheral (p) vision. The bandwidths are specified at half maximum, in octaves. The peripheral bandwidths are considerably broader than the foveal bandwidths in both the horizontal and vertical dimensions. The template model has a horizontal bandwidth (dot-dashed line) much closer to that of the periphery than to the fovea.

vision may be limited in the templates that it can construct.

The lower panel of Fig. 8 compares the bandwidths of the horizontal and vertical spatial frequency tuning functions (derived from the Gaussian fits to the 'hot-spots') in foveal (f) and peripheral (p) vision. The bandwidths are specified at half maximum, in octaves, and it is clear that the peripheral bandwidths are con-

siderably broader than the foveal bandwidths in both the horizontal and vertical dimensions. The larger apparent bandwidth of the periphery may be due to using a single rather than a double Gaussian to fit the data.

#### 4. Discussion

##### 4.1. Does local contrast discrimination limit Vernier discrimination?

Using narrow ribbons of cosine grating we compared Vernier discrimination and contrast discrimination, with performance specified in the same units — as a contrast Weber fraction ( $\Delta c/c$ ). In foveal vision, over a wide range of spatial frequencies and contrasts, we found that the local contrast change at the Vernier threshold was almost identical to the contrast discrimination threshold. The close similarity of the Vernier and contrast thresholds can be seen more directly by plotting the Vernier discrimination thresholds (for all observers and spatial frequencies) against the corresponding contrast discrimination thresholds (in the same units). The data obtained with narrow (3') ribbons and foveal viewing are shown in Fig. 9A (open symbols) and B (small open circles). In this plot, the foveal (open circles) data cluster close to the 1:1 line (the dotted line), and the best fitting power functions does not differ significantly from a slope of unity (Table 3 top row). We therefore conclude that foveal Vernier thresholds for these stimuli are limited by the observers' sensitivity to the local contrast information produced by the offset. Our foveal results confirm and extend the results of Hu et al. (1993) and Levi et al. (1994), and provide convincing evidence for the role of local contrast information in Vernier discrimination. Although this notion (that local contrast information is the critical limiting factor in Vernier acuity) is not new (Hartridge, 1923; Findlay, 1973; Morgan & Aiba, 1985), making the connection quantitatively requires a number of assumptions. However, our test-pedestal approach allows the Vernier offset at threshold to be expressed as the equivalent contrast change, and can thus be directly compared with the observer's contrast discrimination threshold.

When the stimuli are narrow ribbons, the local contrast cue is the limiting factor in foveal Vernier discrimination. However, the correspondence between Vernier and contrast discrimination is less clear with peripheral viewing (solid symbols in Fig. 9, and see also Table 3). In Fig. 9A (vary spatial frequency data from Fig. 2) both the foveal (open circles) and peripheral (solid circles) data cluster close to the 1:1 line (the dotted line). The best fitting power functions to the data do not differ significantly from a slope of unity (Table 3 top two rows). On the other hand, for peripheral vision

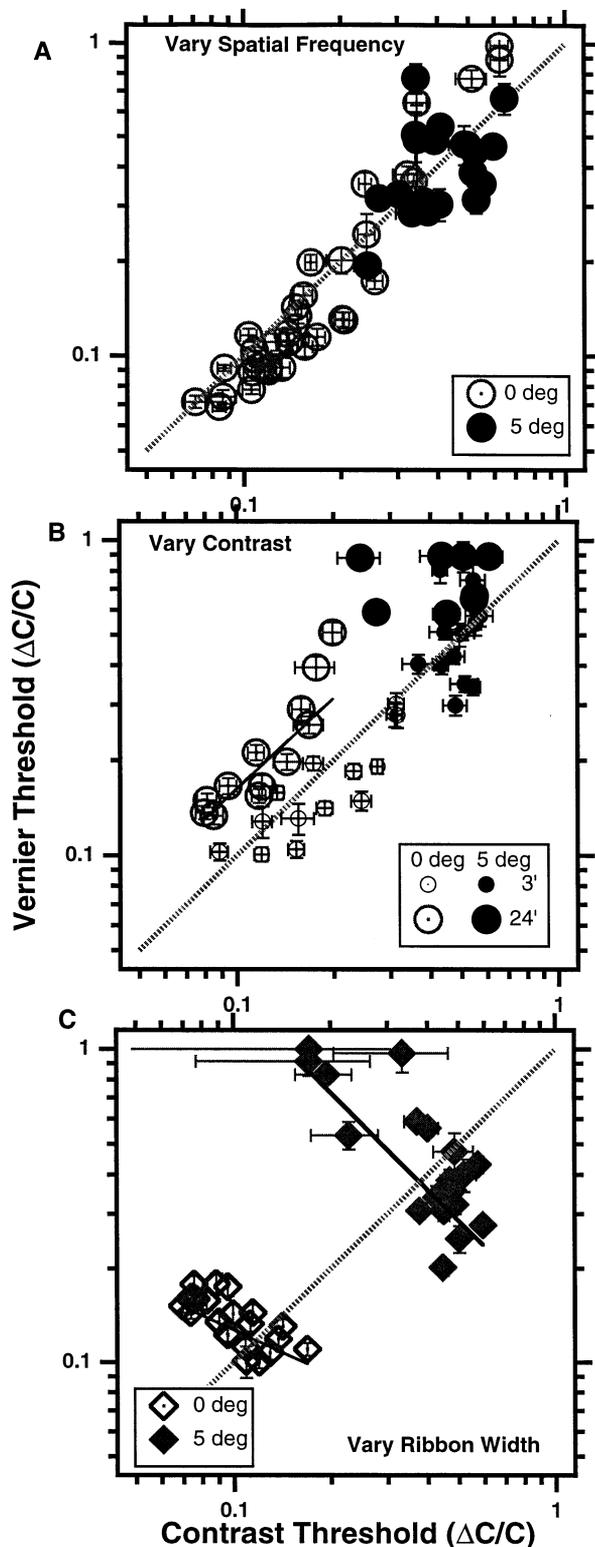


Fig. 9. Vernier discrimination threshold versus contrast discrimination threshold in the fovea (open symbols) and periphery (solid symbols). Each datum represents a Vernier discrimination threshold plotted against the contrast discrimination threshold (specified in the same units —  $\Delta c/c$ ) and measured under identical stimulus conditions. The dotted line in each panel is the 1:1 line. (A) Varying ribbon spatial frequency (from Figs. 1 and 2). (B) Varying ribbon contrast for 3' wide ribbons (small symbols — from Fig. 5A) and 24' wide ribbons (large symbols from Fig. 5B). (C) Varying ribbon width (from Fig. 3).

the slope of the best fitting power function relating Vernier and contrast discrimination when varying the contrast (Fig. 9B [data from Fig. 6]; fourth row of Table 3) is essentially zero.

#### 4.2. Width tuning is different for Vernier and contrast discrimination

Our results show that integration of information along the length of the gratings (the ribbon width) is different for Vernier and contrast discrimination. Thus, widening the ribbons improves contrast discrimination, but paradoxically degrades Vernier discrimination (Figs. 3 and 9C). With wider ribbons, in foveal viewing, it is clear that contrast and Vernier thresholds co-vary (see Figs 5B and 9B, large open circles). The slope of the best fitting power function is close to 1 (Table 3 row 5); however the close correspondence in absolute values is lost — Vernier thresholds (specified as  $\Delta c/c$ ) are uniformly higher than the corresponding contrast thresholds. Presumably the full width of the ribbon is not useful for the Vernier judgment. In peripheral vision, with wide ribbons the equivalence between Vernier and contrast thresholds is lost (contrast thresholds improve markedly with contrast, while Vernier thresholds do not (Fig. 5B)). The lack of correspondence can also be seen in Fig. 9B (large solid symbols) and in Table 3 (row 6) where the slope of the best fitting power function is effectively zero.

Why do Vernier thresholds worsen as the gratings are elongated? Different parts of the stimulus may be important for Vernier versus contrast discrimination (see e.g. Whitaker, 1993). For example, it could be argued that only the part of the grating near the offset is relevant in the Vernier task. However, that would predict that Vernier thresholds are independent of ribbon width — i.e. that increasing the ribbon width would neither improve nor degrade performance. However, increasing the ribbon width degrades Vernier thresholds. This is most marked in the fovea at very high spatial frequencies (see Fig. 6, and Hu et al., 1993), and in peripheral vision (Fig. 4). We believe that, in part, the degradation in foveal vision may be due to a shift in the spatial scale of analysis toward lower spatial frequencies with increasing ribbon width. Evidence for such a shift is provided in the preceding paper (Levi et al., 2000) and in Fig. 6 of the present paper. Based on oblique masking, we showed that in foveal vision the spatial frequency tuning of Vernier acuity shifted towards lower spatial frequencies as the ribbon width was increased. Lower spatial frequency filters would have increased contrast sensitivity but reduced sensitivity to a Vernier offset, so an increase in Vernier thresholds would be expected (Levi & Waugh, 1994; Levi, Waugh & Beard, 1994). We found that the roughly 40% shift in spatial frequency tuning with 8

Table 3  
Vernier discrimination versus contrast discrimination specified in the same units ( $\Delta c/c$ ).

| Condition              | Ribbon width ( $\lambda'$ ) | Eccentricity ( $^\circ$ ) | Slope $\pm$ S.E.M. <sup>a</sup> | Figure(s)                    |
|------------------------|-----------------------------|---------------------------|---------------------------------|------------------------------|
| Vary spatial frequency | 3.1                         | 0                         | $0.98 \pm 0.09$                 | 2, 9A (open symbols)         |
| Vary spatial frequency | 3.1                         | 5                         | $0.71 \pm 0.18$                 | 2, 9A (solid symbols)        |
| Vary contrast          | 3.1                         | 0                         | $0.78 \pm 0.15$                 | 5A, 9B (small open symbols)  |
| Vary contrast          | 3.1                         | 5                         | $-0.11 \pm 0.17$                | 5A, 9B (small solid symbols) |
| Vary contrast          | 24                          | 0                         | $0.96 \pm 0.07$                 | 5B, 9B (large open symbols)  |
| Vary contrast          | 24                          | 5                         | $-0.02 \pm 0.24$                | 5B, 9B (large solid symbols) |
| Vary ribbon width      | –                           | 0                         | $-0.48 \pm 0.05$                | 3, 9C (open symbols)         |
| Vary ribbon width      | –                           | 5                         | $-1.03 \pm 0.20$                | 3, 9C (solid symbols)        |

<sup>a</sup> Power function fits to the data of Fig. 9.

c/deg ribbons was accompanied by an approximately 30% degradation in foveal Vernier thresholds (Fig. 6). However, this is unlikely to be the full explanation, since there is a substantial effect of ribbon width in peripheral vision, with no accompanying shift in spatial scale.

#### 4.3. Width tuning in Peripheral vision

The effects of ribbon width are more complicated in peripheral vision. In the periphery, we found that making the ribbons either narrower (shorter) or wider (longer) than about one grating period can degrade Vernier acuity (Fig. 4D). We will consider both of these effects. First, consider the improvement in peripheral Vernier acuity when the gratings are elongated to a width of about one period. A grating one period long might be expected to optimally stimulate a cortical filter which is optimally sensitive to the ribbon spatial frequency. Thus improvement in Vernier threshold with ribbon width should not be surprising. However, it does not occur in foveal vision. In the preceding manuscript we showed that for narrow low spatial frequency (foveally viewed) ribbons, the peak of the spatial frequency tuning curve was shifted toward higher spatial frequencies. Moreover, increases in ribbon width produced a systematic shift to lower spatial frequencies. Thus, in the fovea, the observer is able to engage an optimally sensitive template for Vernier, by trading-off filter size and sensitivity. In other words, the optimum template for a narrow, low spatial frequency ribbon, has a vertical spatial frequency closely matched to the ribbon frequency, but a higher horizontal spatial frequency. In the periphery the observer may not be able to engage higher spatial frequency filters (because of their low contrast sensitivity). Therefore, the improved performance as ribbon width increases to about one period may simply reflect that for narrow ribbons presented in the periphery the observer cannot engage an optimal template (with a high horizontal spatial frequency in 2-D Fourier space). It is less clear why peripheral thresholds are severely degraded when the

ribbon width exceeds one period. Our masking experiment (Fig. 4D) indicates no shift in the spatial scale of analysis when the ribbons are made wider in peripheral vision. Perhaps, despite a great deal of practice in making peripheral Vernier discriminations, observers are unable to attend to the salient parts of the stimulus (similar to the fovea at 20 c/deg). A simple hypothesis that can explain our results is that the peripheral integration area for Vernier acuity is too large for the localized cue when the stimuli are wide ribbons, so the template for peripheral Vernier acuity is not well matched to the stimulus when the ribbons are wide. Note that this anomalous effect is related to the presence of multiple cycles in the stimulus. The anomaly doesn't occur for single line stimuli. Thus perhaps with long ribbons the adjacent cycles may produce improper stimulation of the (tilted) optimal mechanisms.

#### 4.4. Eccentricity scaling of Vernier acuity re-visited

Our results may help to clarify the rather large discrepancies in the literature regarding the fall-off of Vernier acuity with eccentricity (see Beard, Levi & Klein, 1997 for a detailed discussion), even when restricted to abutting or nearly abutting Vernier. For example, consider DL's data (Fig. 3 — 8 c/deg). When the ribbon width is around 12', foveal and peripheral (5° eccentricity) Vernier thresholds differ by about a factor of 3 ( $E_2 \approx 2.5^\circ$ ); when the length is about 39', thresholds differ by a factor of about 7 ( $E_2 \approx 0.8^\circ$ ). An even bigger difference is evident at 8 c/deg in the data of Levi et al. (1994). Two factors clearly effect the fall-off in Vernier acuity: one is the target length-for gratings, making the targets too long (wide) or too short (narrow) degrades peripheral Vernier acuity more than foveal Vernier. The other factor is contrast (or visibility)-increasing contrast improves foveal Vernier more than peripheral Vernier (Fig. 5).

One approach to measurements in peripheral vision is to use a spatial scaling procedure in which measurements are made for stimuli of different sizes (varying length and width together) at each of several eccentric-

ities and then finding the size scaling factor that brings the data from different eccentricities into close correspondence (Watson, 1987; Whitaker et al., 1992). For line Vernier thresholds, this procedure makes the scaling depend strongly upon the short line lengths because of its coupling to visibility (because the line length and width co-varied, it makes the scaling depend strongly on stimuli with low visibility). Thus, it is not too surprising that Whitaker et al. (1992) found a scaling factor ( $E_2$ ) of around  $2^\circ$  for abutting line Vernier acuity (similar to our findings with short, low visibility ribbons). Note that this scaling procedure (similar to Watson's 1987 local scale method) would fail hopelessly on our data, because the curves relating pattern size to performance differ *qualitatively* in foveal and peripheral vision. However, stimulus visibility needs to be taken into account to prevent the foveal stimuli from becoming nearly invisible.

On the other hand, using long lines 'scaled' to make the peripheral targets longer than the foveal targets several studies have reported  $E_2$  values of  $\approx 0.8$ – $1.0^\circ$  (e.g. Levi et al., 1985; Levi & Waugh, 1994). However, this method may penalize the periphery by making the stimuli too large. In their study, Levi and Waugh (1994) used masking to estimate the spatial scale of the mechanisms optimally sensitive to the line

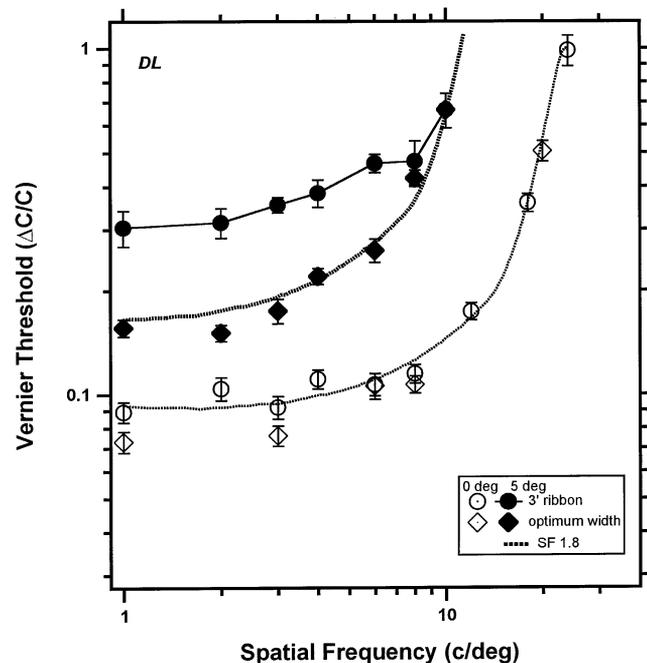


Fig. 10. Vernier discrimination threshold (specified as  $\Delta c/c$ ) versus ribbon spatial frequency for observer DL. The diamonds are 'optimal' width ribbons (from Fig. 4 plus other spatial frequencies not shown in Fig. 4). Circles are DL's 3 in. ribbon data. Open and solid symbols denote foveal and peripheral viewing respectively. The large dotted line is the fit to the foveal 3 in. ribbon data (small dotted line) shifted up and left by a factor of 1.8.

Vernier offset. In the periphery (at  $5^\circ$ ), their target lines were  $105'$  long, and the peak of the spatial frequency tuning function occurred at about  $3.0$  c/deg. If we assume that the observer used a mechanism optimally sensitive to  $3.0$  c/deg, it is interesting to compare the results of that study with those of DL (who was an observer in both experiments) with a  $3$  c/deg ribbon in Fig. 4B and D. For the comparable ribbon width ( $105'$ ) at  $3.0$  c/deg, DL's Vernier threshold was  $109.5 \pm 7$  arc sec, almost identical to his  $102 \pm 7$  arc sec ( $1.7 \pm 0.12$  arc min — see Levi & Waugh 1994, Fig. 2B) line Vernier threshold (shown by the open diamond in Fig. 4B and D). Levi and Waugh argued that the shift in spatial scale of analysis was not sufficient to account for the 'extra' degradation of peripheral Vernier thresholds. However, based on our analysis, the extra loss (about a factor of three at  $5^\circ$ ) may have been due to over-scaling. DL's threshold for an optimal width  $3$  c/deg ribbon is about  $33$  arc sec (approximately three times better than his thresholds with over-scaled lines). The optimal thresholds (obtained from Fig. 4, plus a few additional ribbon spatial frequencies) are shown in Fig. 10 (plotted as  $\Delta c/c$  — diamonds). It is clear that the optimal peripheral thresholds are considerably lower (better) than the  $3'$  ribbon thresholds over a wide range of spatial frequencies, and are also considerably better than the over-scaled grating data of Levi et al. (1994) for all spatial frequencies above  $2$  c/deg. Interestingly, these optimized peripheral data are simply a scaled version of the foveal ribbon data. The thick dotted line is the foveal fit (a Cauchy function), which has been shifted *both* horizontally (to the left) and vertically (upward) by a factor of  $1.8$ . At low spatial frequencies, where Vernier thresholds are approximately a constant Weber fraction (or phase shift), the roughly two-fold loss in the periphery may simply reflect the poorer contrast discrimination Weber fraction (see Figs. 2 and 3, and also Legge & Kersten, 1978; Bradley & Ohzawa, 1986). Vernier discrimination thresholds worsen at spatial frequencies above about  $10$  c/deg in the fovea and are about a factor of two lower at  $5^\circ$ . This scale shift may reflect in large measure the lower contrast sensitivity of the periphery. Thus, the roughly twofold scale factor (equivalent to an  $E_2$  of about  $5^\circ$ ) may, in part, be due to visibility (since the ribbons had the same physical contrast in fovea and periphery). While raising the stimulus contrast is not very effective in improving peripheral Vernier (Fig. 5), lowering the foveal contrast (to equalize visibility) would clearly degrade foveal performance, bringing it more closely into line with the periphery. In many previous studies (including our own), the periphery has been found to be very much poorer at Vernier acuity than predicted by the observer's contrast detection or discrimination. As

we have shown here, in part, the poor peripheral performance was due to using long stimuli (wide ribbons), which may have masked the cue. It is also of interest to note that at the ‘optimum’ ribbon width for Vernier in the periphery, contrast discrimination is also degraded in the periphery. This can be seen in Fig. 3 (for 8 c/deg ribbons). For example, in Fig. 3, at the ‘optimal’ (for Vernier) ribbon width of 12', DL's peripheral Vernier and contrast discrimination thresholds are elevated by about a factor of four to five. Increasing the ribbon width to around 100' improves the contrast jnd to about 0.15, but degrades the Vernier jnd to nearly 1.

What is clear from our studies is that scaling does not always work, particularly when the task involves a two-dimensional stimulus with different scaling properties in the two dimensions. Westheimer (1982) originally pointed this out by showing that the optimal Vernier threshold and optimal separation (in a two-dot alignment task) varied differently with eccentricity. Our results with ribbons show that the vertical and horizontal spatial frequencies contained in the mask scale differently. The peak vertical spatial frequency shows almost no variation with eccentricity (it is determined by the ribbon frequency) while the peak horizontal spatial frequency shifts downward by about a factor of two to three at 5° in the periphery (Fig. 8).

## 5. Summary

In summary, the purpose of the present study was to revisit the question of whether Vernier discrimination is limited by the observer's sensitivity to local contrast change, by directly comparing Vernier discrimination and contrast discrimination thresholds (specified in the same units). We found that when the stimuli are narrow ribbons, the local contrast cue is the limiting factor in Vernier discrimination. Our results also show that: (i) integration of information along the length of the gratings (the ribbon width) is different for Vernier and contrast discrimination. (ii) For Vernier discrimination the integration of information along the length of the gratings differs qualitatively in central and peripheral vision, because for narrow ribbons, the observer is not able to engage the optimal template in peripheral vision. It should be noted that central and peripheral vision do not differ qualitatively as a general rule. Indeed, Vernier acuity vs. stimulus size (Whitaker et al., 1992) and spatial frequency (Levi et al., 1985) has been shown to differ only quantitatively (i.e. by a simple scale factor). However, Vernier acuity versus gap size (Westheimer, 1982) does not obey simple scaling, because the effects of gap size and threshold vary at different rates in peripheral vision. The failure of scaling in Westheimer's experiment may have a similar

basis to the failure of scaling in the present experiments, i.e. because of the two-dimensional nature of the stimuli and task.

## Acknowledgements

Supported by grants RO1EY01728 and RO1EY04776 from the National Eye Institute. Paul V. McGraw was supported by a Vision Research Training Fellowship from the Wellcome Trust.

## References

- Beard, B. L., Levi, D. M., & Klein, S. A. (1997). Vernier acuity with non-simultaneous targets: the cortical magnification factor estimated by psychophysics. *Vision Research*, *37*, 325–346.
- Bradley, A., & Ohzawa, I. (1986). A comparison of contrast detection and discrimination. *Vision Research*, *26*, 991–997.
- Findlay, J. M. (1973). Feature detectors and Vernier acuity. *Nature*, *241*, 135–137.
- Harmon, L. D., & Julesz, B. (1973). Masking in visual recognition: effects of two dimensional filtered noise. *Science*, *180*, 1194–1197.
- Hartridge, H. (1923). Visual discrimination and the resolving power of the eye. *Journal of Physiology*, *57*, 52–67.
- Hess, R. F., & Field, D. (1993). Is the increased spatial uncertainty in the normal periphery due to spatial undersampling or uncalibrated disarray? *Vision Research*, *33*, 2663–2670.
- Hu, Q., Klein, S. A., & Carney, T. (1993). Can sinusoidal Vernier acuity be predicted by contrast discrimination? *Vision Research*, *33*, 1241–1258.
- Klein, S. A., & Levi, D. M. (1985). Hyperacuity thresholds of 1 second: theoretical predictions and empirical validation. *Journal of the Optical Society of America A*, *2*, 1170–1190.
- Legge, G. E., & Kersten, D. (1978). Contrast discrimination in peripheral vision. *Journal of the Optical Society of America A*, *4*, 1594–1598.
- Levi, D. M., Klein, S. A., & Aitsebaomo, A. P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research*, *25*, 963–977.
- Levi, D. M., Klein, S. A., & Wang, H. (1994). Discrimination of position and contrast in amblyopic and peripheral vision. *Vision Research*, *34*, 3293–3313.
- Levi, D. M., Klein, S. A., & Carney, T. (2000). Unmasking the mechanism for Vernier acuity: evidence for a template model for Vernier acuity. *Vision Research*, *40*, 951–972.
- Levi, D. M., Waugh, S. J., & Beard, B. L. (1994). Spatial scale shifts in amblyopia. *Vision Research*, *34*, 3315–3333.
- Levi, D. M., & Waugh, S. J. (1994). Spatial scale shifts in peripheral Vernier acuity. *Vision Research*, *34*, 2215–2238.
- Morgan, M. J., & Aiba, T. S. (1985). Vernier acuity predicted from changes in the light distribution of the retinal image. *Spatial Vision*, *1*, 151–161.
- Morgan, M. J. (1986). The detection of spatial discontinuities: Interactions between contrast and spatial contiguity. *Spatial Vision*, *1*, 291–303.
- Pelli, D. G. (1999). Close encounters—An artist shows that size effects shape. *Science*, *285*, 844–846.
- Stromeyer, C. F., & Julesz, B. (1972). Spatial-frequency masking in vision: Critical bands and spread of masking. *Journal of the Optical Society of America*, *62*, 1221–1232.

- Watson, A. B. (1987). Estimation of local spatial scale. *Journal of the Optical Society of America A*, 4, 1579–1582.
- Whitaker, D. (1993). What part of a Vernier stimulus determines performance? *Vision Research*, 33, 27–32.
- Whitaker, D., Rovamo, J., MacVeigh, D., & Makela, P. (1992). Spatial scaling of Vernier acuity tasks. *Vision Research*, 32, 1481–1491.
- Westheimer, G. (1982). The spatial grain of the perifoveal visual field. *Vision Research*, 22, 157–162.