POSITIONAL UNCERTAINTY IN PERIPHERAL AND AMBLYOPIC VISION

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Abstract—Three experiments were performed to examine positional acuity and the role of spatial sampling in central, peripheral and amblyopic vision. In the first experiment, 3-line bisection acuity was compared to grating acuity. In normal foveal vision bisection acuity represents a hyperacuity. In anisometropic amblyopes, bisection acuity is reduced in rough proportion to their grating acuity. In strabismic amblyopes, and in the normal periphery, bisection acuity is reduced to a greater extent than grating acuity. This result implies that reduced contrast sensitivity of the spatial filters is not sufficient to account for the increased positional uncertainty found in peripheral vision and in strabismic amblyopia. In order to test the hypothesis that the high degree of positional uncertainty evident in these visual systems is a consequence of sparse spatial sampling, bisection thresholds and width discrimination thresholds were measured with stimuli comprised of discrete samples. The results showed that normal foveal vision and the vision of anisometropic amblyopes show little benefit from adding discrete samples to the stimulus. In contrast, the normal periphery, and the central field of strabismic amblyopes demonstrate marked positional uncertainty which can be efficiently reduced in proportion to the square root of the number of samples (up to about 10) comprising the stimulus in the direction orthogonal to the discrimination cue. In aggregate the results suggest that anisometropic and strabismic amblyopia are fundamentally different. The positional uncertainty in anisometropic amblyopia is consistent with the reduced sensitivity of the spatial filters. The data of the normal periphery and of the central field of strabismic amblyopes suggest that the cortical sampling grain imposes a fundamental limit upon their positional acuity.

INTRODUCTION

In normal foveal vision, relative position can be judged with exquisite accuracy (Westheimer, 1975, 1981). In an attempt to account for the accuracy of foveal positional discrimination, several recent models have been proposed (Watt and Morgan, 1985; Klein and Levi, 1985; Maddux, 1985; Carlson and Klopstein, 1985; Nielsen et al., 1985; Wilson, 1986a). A common feature of these models is that they are based upon the responses of spatial filters, and that the contrast response of these filters places a fundamental limit upon the accuracy of positional discrimination.

Compared to the normal fovea there is marked positional uncertainty in peripheral (Bourdon, 1902; Westheimer, 1982; Levi et al., 1985; Yap et al., in preparation) and amblyopic vision (Levi and Klein, 1982a, b; 1983; 1985; Bradley and Freeman, 1985; Rentschler and Hilz, 1985). In peripheral vision, positional acuity declines more rapidly with eccentricity than does grating acuity or contrast sensitivity (Westheimer, 1982; Levi et al., 1985). For example, at 2.5° in the periphery, grating acuity is reduced by about a factor of 2, whereas vernier acuity is reduced 4 or 5 fold. Strabismic amblyopes show a qualitatively and quantitatively similar decoupling of vernier and grating acuity (Levi and Klein, 1985).

Recently Bradley and Freeman (1985) have suggested that the poor vernier acuity of amblyopes can be simply accounted for on the basis of their reduced contrast sensitivity. Our results in anisometropic amblyopes are compatible with this notion; however, the results suggest that the positional uncertainty of strabismic amblyopes and of the normal periphery cannot be simply explained on the basis of reduced contrast sensitivity of their spatial filters.

Both the spatial filtering and the sampling properties of the visual system may place fundamental limits on position discrimination (Klein and Levi, 1985). In peripheral vision, the density of cones and ganglion cells diminishes rapidly.
(Rolls and Cowey, 1970; Østerberg, 1935). Rods intrude between cones, introducing disorder into the regular cone mosaic found in the fovea (Hirsch and Miller, 1985). Moreover, the inverse cortical magnification factor (i.e. the number of degrees of visual space/mm of cortex) rises precipitously with eccentricity (Daniel and Whitteridge, 1961; Dow et al., 1981; Tootell et al., 1982; Van Essen et al., 1984; Perry and Cowey, 1985). While these profound alterations in the anatomy and physiology of the visual pathways occur within the central 10°, the optics of the eye remain approximately constant (Jennings and Charman, 1981). Thus, sparse spatial sampling in the periphery may lead to increased positional uncertainty (Snyder, 1982). We have hypothesized (Levi and Klein, 1985) that the abnormal binocular interactions which occur in strabismic amblyopes may lead to similar neural consequences in primary visual cortex—i.e. a sparse sampling grain due to fewer and/or scrambled cortical connections.

The present paper addresses the question of spatial sampling. The first two experiments utilize a 3-line bisection paradigm to probe the spatial properties of foveal, peripheral and amblyopic vision. We use bisection for several reasons: (1) Bisection thresholds depend critically upon the separation between the lines, thus the function relating bisection threshold to separation can be compared in each visual system. (2) Bisection represents a simple one dimensional task, which unlike vernier acuity, is not complicated by orientation cues (Sullivan et al., 1972; Watt et al., 1983; Levi and Klein, 1983; Watt and Campbell, 1985). Moreover, the recent computational models of Klein and Levi (1985) and Wilson (1986) are able to predict bisection thresholds in normal foveal vision, over a wide range of line separations. (3) We have shown previously that bisection thresholds are abnormal in amblyopes (Levi and Klein, 1983) and that similar to vernier acuity, anisometropic amblyopes show optimal bisection thresholds reduced in proportion to their grating acuity while strabismic amblyopes show an additional loss in bisection acuity.

In the present paper, (1) the bisection results are extended to peripheral vision and to a new group of amblyopes, (2) bisection experiments are performed with stimuli comprised of discrete samples in order to investigate the sampling characteristics of foveal, peripheral and amblyopic vision, and (3) width discrimination experiments are performed with stimuli comprised of discrete samples in order to further explore sampling and to learn whether spatial information is sampled along the direction of the lines of the target (as originally suggested by Hering, 1899).

Experiment I: Bisection Thresholds

Methods and stimuli

The stimuli consisted of thin, bright, high-contrast lines generated on the CRT of a computer (Commodore 2001) with a green phosphor. The display was modified so that the stimuli could be very precisely positioned (see Klein and Levi, 1985 and Levi et al., 1985 for details). Room illumination was normal and viewing was always monocular. For the bisection experiment the outer horizontal "reference" lines were presented continuously. A horizontal "test" line was flashed for 150 msec in one of 5 positions equally spaced about the bisection point. The use of briefly flashed, horizontal lines serves to minimize the influence of unsteady fixation, common in amblyopes. In our previous bisection experiments (Levi and Klein, 1983), the stimuli consisted of multiple lines, all flashed simultaneously, and it may have been difficult for the amblyope to attend to the "test" line. This difficulty is eliminated by the present stimulus. For testing of normal (control) observers, and for the nonamblyopic eyes, the stimulus was viewed from a distance of 8.46 m. At this distance the lines were 30' long and 2' wide. For testing the periphery the stimulus size was "scaled" in proportion to recent estimates of the cortical magnification factor (Dow et al., 1981; Tootell et al., 1982; Van Essen et al., 1984). This scaling, found to be appropriate for vernier acuity (Levi et al., 1985) and for 3-dot bisection (Yap et al., in preparation), was accomplished by keeping the physical stimulus the same at all eccentricities and varying the viewing distance according to

$$d = d_p/(1 + E/0.77)$$

where $E$ is the eccentricity in degrees and $d_p$ is the distance used for foveal viewing. The scaling factor (0.77°) affects line length and line width. In the present experiments the precise scaling factor is not critical for the following reasons: the lines were long enough in the fovea that the bisection threshold had reached an asymptotic value where it was insensitive to line length. The foveal line width (2°) was far below the eye's resolution so only the effective luminance of the line would be affected by the scaling parameter. Since the lines...
were far above threshold the luminance plays a small role. A control bisection experiment with a 7-fold increase in width (directly related to luminance) did not alter thresholds. Similarly, in Experiment II, the line width had no effect on threshold.

For the amblyopic eyes, the stimulus dimensions were also “scaled” in proportion to their acuity in order to match the test conditions for amblyopes and the periphery. This was accomplished by testing the amblyopic eye at a closer viewing distance, in proportion to the Snellen acuity.

The observers’ task was to judge the position of the test line relative to the bisection point by giving numbers from −2 to +2. Feedback as to the direction and magnitude of offset was provided after each trial. This self-paced method of constant stimuli with multiple responses has been described elsewhere (Levi and Klein, 1983). Thresholds for discrimination of the position of the test lines were obtained by calculating a maximum likelihood estimate of the $d'$ values for each stimulus and interpolating to $d' = 0.675$, equivalent to the 75% correct level. This analysis is a multiple-criterion probit analysis.

Data were collected in blocks of 125 trials with the spacing of the reference lines, eccentricity, or eye (in the case of amblyopes) varying between blocks. The computer randomized the position of the test lines, tallied the responses and provided feedback following each trial. Grating acuity was also measured using the method of adjustment with a horizontal square-wave grating patch consisting of 5 cycles equal in length, color and luminance to the lines used for the bisection experiments.

Observers for all experiments

Eighteen observers participated in one or more of the experiments. Three normal observers served as controls. Two were authors (D.L. and Y.L.Y.), while the third (D.K.) was naive as to the purpose of the experiments. Fifteen amblyopes with anisometropia (4), strabismus (4) or both (7) also participated. All were given extensive practice prior to data collection. For the periphery experiments Y.L.Y., D.L., D.K. and J.M. (anisometropic amblyope) with corrected-to-normal vision in his preferred eye were tested monocularly. Each of the observers was highly trained in peripheral spatial discriminations, and was given extensive practice on these bisection tasks prior to data collection.

All observers had clear media, normal fundi and were appropriately optically corrected during the experiments. Visual characteristics of the observers are given in Table 1.

Results

Figure 1 shows how bisection thresholds vary as a function of separation. The shaded region
in Fig. 1(A) and 1(B) are the full range of thresholds of the 3 normal control observers with foveal viewing. The open and solid symbols in Fig. 1(A) are the data of J.M. and Y.L.Y. at 1.25°, 2.5°, 5°, and 10° in the lower visual field. The Snellen acuity of Y.L.Y (measured with the same crowded Davidson and Eskridge charts as used for the amblyopes) at each eccentricity is shown near the appropriate curve. The data in Fig. 1(B) are for the amblyopic eyes of 4 amblyopes with constant strabismus with Snellen acuities ranging from 20/40 to 20/680. There are several points of interest. For the normal observers viewing foveally (shaded region), for separations greater than 3°, thresholds are a more or less constant fraction (1/30) of the separation, i.e. Weber's law (Volkmann, 1858; Andrews and Miller, 1978; Klein and Levi, 1985). At small separations the thresholds represent a "hyperacuity". For the normal periphery [Fig. 1(A)], at large separations, bisection thresholds also fall along a straight line, although the fractional threshold (Δs/s) becomes somewhat worse with eccentricity. As eccentricity increases, the optimal separation becomes larger, and the optimal bisection threshold is elevated. The data of four representative strabismic amblyopes* shown in Fig. 1(B) are qualitatively similar to that of the periphery.

Figure 2 plots the optimal bisection acuity (in minutes) at each eccentricity against the grating acuity (solid circles and squares). Two lines are shown on the graph. The dashed line has a slope of 1. This would be expected if grating acuity and bisection acuity declined at the same rate in

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**Table 1**

<table>
<thead>
<tr>
<th>Observer</th>
<th>Age/Sex</th>
<th>Eye</th>
<th>Rx.</th>
<th>Acuity</th>
<th>Fixation</th>
<th>Strabismus</th>
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<tbody>
<tr>
<td>Normal controls</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.K.</td>
<td>25/M</td>
<td>O.S.</td>
<td>-5.50/-1.0 \times 157</td>
<td>20/16</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>Y.L.Y.</td>
<td>25/F</td>
<td>O.D.</td>
<td>pl</td>
<td>20/15</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>D.L.</td>
<td>38/M</td>
<td>O.S.</td>
<td>-1.0</td>
<td>20/13</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td><strong>Constant strabismus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K.L.</td>
<td>25/M</td>
<td>O.D.</td>
<td>+0.25/-0.50 \times 145</td>
<td>20/40</td>
<td>0.5° Nasal E.F.</td>
<td>Constant R. E.T., 6°</td>
</tr>
<tr>
<td>R.L.</td>
<td>33/M</td>
<td>O.D.</td>
<td>-0.75</td>
<td>20/12</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>T.O.</td>
<td>24/F</td>
<td>O.D.</td>
<td>-0.25/-0.50 \times 60</td>
<td>20/12</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>W.S.</td>
<td>26/M</td>
<td>O.D.</td>
<td>-0.25 \times 95</td>
<td>20/12</td>
<td>Central</td>
<td>None</td>
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<tr>
<td><strong>Anisometropia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K.P.</td>
<td>25/M</td>
<td>O.D.</td>
<td>+2.25</td>
<td>20/77</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>R.J.</td>
<td>47/M</td>
<td>O.D.</td>
<td>-0.50/-0.25 \times 180</td>
<td>20/18</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>L.C.</td>
<td>19/F</td>
<td>O.D.</td>
<td>+2.25</td>
<td>20/30</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>J.M.</td>
<td>23/M</td>
<td>O.D.</td>
<td>-2.75/-0.50 \times 180</td>
<td>20/15</td>
<td>Central</td>
<td>Occasional L. XT</td>
</tr>
<tr>
<td><strong>Constant strabismus and anisometropia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>J.V.</td>
<td>28/M</td>
<td>O.D.</td>
<td>+0.75/-0.25 \times 70</td>
<td>20/20</td>
<td>Central</td>
<td>Constant L. E.T., 8°</td>
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<tr>
<td>D.M.</td>
<td>30/M</td>
<td>O.D.</td>
<td>+4.50/-0.50 \times 23</td>
<td>20/80</td>
<td>1° Nasal</td>
<td>Constant L. E.T., 3°</td>
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<tr>
<td>T.D.</td>
<td>18/F</td>
<td>O.D.</td>
<td>+8.75</td>
<td>20/20</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>S.S.</td>
<td>26/M</td>
<td>O.D.</td>
<td>+3.25</td>
<td>20/12</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>R.W.</td>
<td>20/F</td>
<td>O.D.</td>
<td>+1.25/-0.50 \times 60</td>
<td>20/12</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>J.B.</td>
<td>26/F</td>
<td>O.D.</td>
<td>+2.00/-1.00 \times 180</td>
<td>20/23</td>
<td>Central</td>
<td>None</td>
</tr>
<tr>
<td>R.M.</td>
<td>24/F</td>
<td>O.D.</td>
<td>-18.25/-4.25 \times 003</td>
<td>20/60</td>
<td>Unsteady 1-2° E.F.</td>
<td>Constant R. X.T., 10°</td>
</tr>
</tbody>
</table>

*We use the term "strabismic amblyopes" for all amblyopes with constant unilateral strabismus, since amblyopes with both strabismus and anisometropia behave similarly to strabismics (see also Hess and Pointer, 1985).
The data of the amblyopic eyes of the anisometropic amblyopes (As) fall close to the line with unity slope, implying that grating acuity and bisection acuity are affected similarly. However, the data of the amblyopes with constant strabismus (B's and S's) fall close to the solid line fit to the data of the normal periphery. The results are similar to those shown for vernier vs grating acuity (Levi and Klein, 1985) and show that while position acuity (vernier and bisection) and grating acuity of anisometropic amblyopes are similarly affected, these acuities do not decline at the same rate in the periphery and in strabismic amblyopes. In these two visual systems the data are qualitatively and quantitatively similar in showing optimal position acuity more degraded than grating acuity (Levi and Klein, 1982a, b, 1983, 1985). As a control, several of the amblyopes were also tested with a bisection stimulus was was seven times brighter, with no appreciable change in their results.

A matter of "scale"? For a variety of detection and resolution tasks, central and peripheral vision are similar when the stimulus dimensions are appropriately scaled (Koenderink et al., 1978; Rovamo et al., 1978; Limb and Rubenstein 1977; Swanson and Wilson, 1985). For example, with appropriate scaling peak contrast sensitivity is similar in central and peripheral vision and a single scale factor suffices to superimpose the entire curves (and the underlying filters). Data of this sort has been reported by a number of investigators and the scale factor needed to superimpose curves obtained at the fovea and at 7.5° is estimated to be approximately 2–4 (see Swanson and Wilson, 1985 for a recent review).

For plots of bisection thresholds vs separation (e.g. Fig. 1), the scaling needed to superimpose the functions in central and peripheral vision is represented by a lateral shift along the 45° meridian, since both the abscissa and ordinate have dimensions of angular size. To equate position thresholds in the fovea and at 7.5°, the scale factor is approximately 10–12, which is 3–5 times larger than that needed for the contrast sensitivity function (Yap et al., in preparation).

Figure 3 shows the contrast sensitivity function for each eye of strabismic and anisometropic amblyope J.V. Contrast thresholds were obtained with horizontal sinewave gratings using a 2-alternative forced-choice procedure (see Katz et al., 1984 for details). For testing the
Fig. 3. Contrast sensitivity functions for horizontal sine-wave gratings for each eye of strabismic and anisometropic amblyope J.V. The field size was 6° for the preferred eye (open circles) and 12° for the amblyopic eye (solid circles). Thresholds (79% correct) were obtained using a two-interval forced-choice procedure. Note that the peak sensitivities of the two eyes are equal, and the curves can be superimposed by shifting the curves along the horizontal axis by a single scale factor (1.5).

amblyopic eye (solid circles), the field size was doubled in order to “scale” the stimulus in approximate proportion to the cutoff spatial frequency. The data of the amblyopic eye are shifted to the left, similar to the shift in the scaled contrast sensitivity function found in peripheral vision (Rovamo et al., 1978). Firstly, the peak sensitivities of the two eyes are equal, and secondly, a single scale factor of 1.5 suffices to superimpose the two curves. The scale factor is similar to the 1.6 fold loss in grating acuity (cutoff spatial frequency) obtained with square wave gratings in Experiment I for this observer, suggesting that our grating resolution measure provides a reasonable estimate of the scale factor for the entire contrast sensitivity function.

Figure 4(A) shows bisection thresholds as a function of separation for the preferred (N’s) and amblyopic (A’s) eyes of an anisometropic (J.M.). The shaded region is the range of
thresholds of three normal observers. The dashed line shows the effect of applying the scale factor obtained from J.M.'s grating acuities. For anisometropic amblyope J.M., the scale factor shifts the entire curve of the amblyopic eye so that at all but the smallest separations they fall within the range of normal thresholds. This is similar to results of bisection using multiple lines on anisometropic amblyopes (Levi and Klein, 1983). In contrast, the data of Fig. 4(B) for J.V.'s (strabismic and anisometropic) amblyopic eye do not superimpose upon the normal thresholds. The optimal threshold, even after scaling, is elevated by a factor of about 4 and occurs at a wider (scaled) separation. Moreover, the Weber's law portion of the curve shows a somewhat flatter slope than normal. Figure 4(C) shows the bisection results of the normal periphery at 2.5°. Like the results of the strabismic amblyope, the scaling factor estimated by grating acuity fails to superimpose the peripheral and central functions. At 2.5° there is approximately an extra factor of three loss in bisection thresholds after scaling for resolution.

The foregoing discussion suggests that the loss of positional information of anisometropic amblyopes is approximately proportional to the resolution loss. If, as suggested in the introduction, the contrast responses of spatial filters places a fundamental limit upon positional acuity in normal vision, then the most parsimonious explanation for the high positional uncertainty of anisometropic amblyopic eyes is that they have reduced contrast sensitivity at high spatial frequencies (Levi and Harwerth, 1977; Hess et al., 1980; Bradley and Freeman, 1981). In strabismic amblyopes and in the normal periphery, there appears to be an extra loss of positional information. In the following experiments we test the hypothesis that the high degree of positional uncertainty evident in these visual systems is a consequence of sparse spatial sampling.

**Experiment II: Bisection with discrete stimuli**

**Methods and stimuli**

Highly practiced observers judged whether a briefly flashed (100 msec) test line bisected two continuously viewed horizontal reference lines. The lines were comprised of discrete samples (dots), each approximately 1 min of arc (well matched to the point spread function of the eye) separated by intersample spaces of variable extent. The intensity of each sample was 5–6 times the observer’s detection threshold. We varied both the number of samples comprising each line and the interspace size. The vertical separation of the lines was chosen to be optimal for each observer, condition, eye and eccentricity based upon preliminary testing using a stimulus consisting of 5 samples. The separation is given for each observer in Table 2. The same signal detection methodology as used in Experiment 1 was used to obtain thresholds for making this spatial discrimination. Viewing was monocular. Each threshold is based upon 250–600 trials.

**Results**

Figure 5 shows the foveal data of normal observer D.L. In the left panel (A) bisection threshold (ΔS/S) is plotted as a function of the total pattern length (i.e. length of samples plus interspaces) in minutes of arc. Each plotted number indicates the number of 1 minute samples. In the right panel (B) the thresholds are plotted as a function of the number of samples, with each number indicating the size of the interspace in minutes. There are several points to note with respect to these figures. Firstly, our results suggest that the critical factor in determining the threshold was not the total pattern length (i.e. length of samples plus interspaces)
Table 2

<table>
<thead>
<tr>
<th>Condition</th>
<th>Observer</th>
<th>Vertical separation (min)</th>
<th>Threshold for 1 sample (arc sec) ( (Y_0) )</th>
<th>Asymptotic No. of samples ( (X_a) )</th>
<th>Slope (( S/))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal fovea</td>
<td>D.L.</td>
<td>3</td>
<td>16.4 ± 0.80</td>
<td>7.8 ± 1.7</td>
<td>-0.29 ± 0.04*</td>
</tr>
<tr>
<td></td>
<td>D.K.</td>
<td>3</td>
<td>17.4 ± 0.65</td>
<td>5.4 ± 1.3</td>
<td>-0.30 ± 0.04*</td>
</tr>
<tr>
<td>Anisometropic amblyopia</td>
<td>L.C.</td>
<td>5</td>
<td>64.0 ± 5.5</td>
<td>10.8 ± 5.8</td>
<td>-0.35 ± 0.06*</td>
</tr>
<tr>
<td></td>
<td>R.J.</td>
<td>7.5</td>
<td>62.2 ± 7.6</td>
<td>6.2 ± 3.8</td>
<td>-0.30 ± 0.07*</td>
</tr>
<tr>
<td>Periphery (2.5°)</td>
<td>D.L.</td>
<td>12.4</td>
<td>191.6 ± 11.3</td>
<td>11.1 ± 2.0</td>
<td>-0.48 ± 0.04</td>
</tr>
<tr>
<td></td>
<td>D.K.</td>
<td>12</td>
<td>233.5 ± 10.6</td>
<td>9.5 ± 0.9</td>
<td>-0.43 ± 0.04</td>
</tr>
<tr>
<td>Strabismic amblyopia</td>
<td>J.V.</td>
<td>13</td>
<td>219.8 ± 25</td>
<td>5.3 ± 0.9</td>
<td>-0.66 ± 0.11</td>
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<tr>
<td></td>
<td>T.D.</td>
<td>5</td>
<td>97.7 ± 10.5</td>
<td>7.0 ± 1.4</td>
<td>-0.52 ± 0.08</td>
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<td></td>
<td>R.L.</td>
<td>6.7</td>
<td>110.8 ± 8.1</td>
<td>10.0 ± 2.6</td>
<td>-0.58 ± 0.09</td>
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<tr>
<td></td>
<td>T.O.</td>
<td>12</td>
<td>104.7 ± 8.3</td>
<td>11.6 ± 2.6</td>
<td>-0.43 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>K.L.</td>
<td>5</td>
<td>114.8 ± 17.5</td>
<td>16.2 ± 7.8</td>
<td>-0.50 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>W.S.</td>
<td>10</td>
<td>117.5 ± 9.1</td>
<td>7.2 ± 1.7</td>
<td>-0.42 ± 0.07</td>
</tr>
</tbody>
</table>

Values were obtained by nonlinear regression of the form \( \log Y = \log Y_o + SI^* \log X \) for \( X < X_a \) and \( Y = \log Y_o + SI^* \log X_a \) for \( X > X_a \) where \( Y \) is the threshold in arc sec, \( X \) is the number of samples and \( Y^0, SI \), and \( X_a \) are the 3 free parameters. The SAS statistical package was used.

Error bars equal 1 standard error.

*Not consistent with a slope of -0.5 at the 0.000001 level, whereas all the other data are consistent with a slope -0.5 at the 0.05 confidence level.

but simply the number of 1 min of arc samples. This can be seen by noting that the dispersion of the data in Fig. 5(A) is greater than in Fig. 5(B). In Fig. 5(A) for example, thresholds obtained with 5 samples (shown by the 5's) have similar values despite variations in total pattern length from 10 to 50 min. Similarly, thresholds for 2 samples (2's) are essentially the same for total pattern lengths from 3 to 10 min. When thresholds are plotted as a function of the number of discrete samples [Fig. 5(B)] on the other hand, they show a systematic decrease up to about 5 samples and then level off. At any given number of samples large variations in the size of the interspaces [shown by the number in Fig. 5(B)] have little influence on the thresholds. In order to provide a more quantitative basis for the assertion that the number of samples is the more important parameter, all of the data for all subjects and conditions were fitted using nonlinear regression with a broken line fit of the form shown by the dashes in Fig. 5(B). Two models were evaluated, (I) that threshold is a nonlinear function (broken line) of the number of samples and (II) that threshold is a nonlinear function of total pattern length. The total \( \chi^2 \) (across observers, eyes and eccentricity) for models I and II were 172 and 226 respectively (127 degrees of freedom). These values are significantly different (at the 0.025 level; \( F \)-test) with model I giving the better fit to the data, thus we conclude that the number of samples is the critical factor. The \( \chi^2 \) value of 172 is quite good considering the presence of between run variability.

Figure 6 summarizes the results for foveal, peripheral and amblyopic vision. In Fig. 6(A), the foveal data of D.L. are plotted along with data of a second normal observer. Note that the ordinate is given in arc seconds. For the normal fovea, as the number of samples increased from 1 to 5, thresholds improved only slightly. Additional samples beyond 5 had no further effect upon thresholds and with even a single sample...
Fig. 6. Bisecting thresholds (arc sec) are plotted as a function of the number of samples. (A) For two normal observers viewing foveally. The numbers in each graph represent the size of the interspaces in minutes. Each graph has been fitted with a broken line using non-linear regression. Thresholds decrease as the number of samples increases to approximately 5. For foveal vision, the slope is approximately -0.3. The addition of samples beyond 5 has no further influence on foveal bisecting thresholds. (B) At 2.5° in the lower visual field. Thresholds decrease as the number of samples increases to approximately 10. A slope of -0.5 (i.e., thresholds proportional to the square root of the number of samples) provides a reasonable fit for the data of the periphery. The addition of samples beyond 10 has no further influence on peripheral bisecting thresholds. (C) For the amblyopic eyes of two observers with strabismic amblyopia. The data are remarkably similar to that of the normal periphery in showing a slope equal to approximately -0.5. (D) For 2 anisometropic amblyopes. Although thresholds are elevated, the slopes of the lines are similar to those of the normal fovea (-0.3).
thresholds are smaller than the intercone spacing (about 30 arc sec in the fovea). Figure 6(B) shows data of the same observers at 2.5° in the lower visual field. The data differ both quantitatively and qualitatively from those of the fovea. Firstly, the threshold for a single sample is more than a factor of 10 higher than that of the fovea. The threshold for a single sample (in the absence of spatial and temporal averaging) may provide an estimate of the intrinsic positional uncertainty of the visual system. For the periphery, positional uncertainty is high due to the wider spacing and increased irregularity of the cone mosaic (Hirsch and Miller, 1985), and the precipitous decrease in the cortical magnification factor (Dow et al., 1981; Tootell et al., 1982; Van Essen et al., 1984). What is of special interest here is that the threshold for a single sample is considerably larger than the intercone spacing at 2.5° (approximately 70 arc sec), suggesting that it is the cortical sampling grain rather than the cone mosaic which limits position discrimination in the periphery. Secondly, in the periphery, adding samples has a strong effect upon bisection thresholds. For an "ideal detector" that is limited by the spatial sampling grain, the positional uncertainty would be reduced in proportion to the square root of the number of independent samples. In the log-log axes of Fig. 6 this would mean a slope of −0.5. A lower slope (like that of the fovea) would indicate that sparseness of sampling was not the factor limiting spatial discrimination. Table 2 provides the parameters for the broken line fits to the data in Fig. 6. Shown are the thresholds for a single sample, the asymptotic number of samples and the slopes and their associated standard errors. The data of the periphery are compatible with the slope of −0.5, showing that thresholds decrease in proportion to the square root of n (where n is the number of discrete samples) up to n ≈ 10. Beyond this, adding more samples has no additional effect on thresholds. The effect of adding samples is not simply explained by luminance summation, since making a single sample 7 times brighter did not improve the bisection threshold (see also Experiment III).

Figure 6(C) shows data of the amblyopic eyes of 2 observers with strabismic amblyopia. The spatial vision of strabismic amblyopes has previously been compared to that of the normal periphery (Experiment I) and the data shown in Fig. 6(C) for bisection bear a remarkable similarity to the results of the normal periphery. For the strabismic amblyopes, like the normal periphery, position uncertainty is high with only one sample, and thresholds improve in proportion to the square root of the number of discrete samples. For both of these visual systems, increasing the number of discrete samples from 2 to 8 (a factor of 4) resulted in a 2 fold reduction in threshold, whereas for the normal fovea thresholds improved by only 20–30%. In normal peripheral vision, the high degree of spatial uncertainty with few samples can be readily understood on the basis of the anatomy and physiology of the retina and cortex. In strabismic amblyopia, we hypothesize that abnormal binocular interactions result in similar neural consequences—i.e. a sparse spatial sampling grain due either to insufficient cortical neurons to provide accurate position signals or to a scrambling of the neural signals. A sparse sampling grain and/or scrambling of neural signals would introduce positional noise which is uncorrelated between stimulus samples in peripheral and strabismic amblyopic vision.

A slope of −0.5 is not a necessary consequence of high intrinsic positional uncertainty. The data of the two anisometropic amblyopes also showed high thresholds with a single sample [Fig. 6(D)]. However, their thresholds,
like those of the normal fovea, declined with a slope of approximately $-0.3$ (see Table 2). Figure 7 shows another difference between the data of strabismic and anisometropic amblyopes. For each observer, the bisection threshold for 1 sample ($Y_0$ from Table 2) are plotted against the observers' Snellen acuity (both thresholds are expressed in arc sec). Snellen acuity at a $d'$ of 0.675 was measured with Davidson-Eskridge charts which maintain a constant (high) degree of contour interaction as shown in the inset of Fig. 7. For the normal fovea (F's) and for anisometropic amblyopes (A's), bisection thresholds ($Y_0$) are 2-3 times lower than Snellen acuity, while for strabismic amblyopes (S's) the two values are quite similar. The bisection threshold is not merely proportional to Snellen acuity, it is equal to Snellen acuity. We have previously suggested a close link between the bisection and Snellen acuities of strabismic amblyopes (Levi and Klein, 1982a, b, 1983). The present result show a similar correspondence for the normal periphery. The present results also suggest that spatial sampling in anisometropic amblyopia is qualitatively similar to that of the normal fovea, and provide further evidence that strabismic and anisometropic amblyopia are fundamentally different.

One of the most surprising findings of Experiment II was that two visual systems with degraded spatial vision (the periphery and strabismic amblyopia) combine spatial information from discrete samples more efficiently than does the normal fovea, i.e. both of the degraded visual systems benefit more from adding discrete samples than does the fovea—performing like "ideal detectors." Our hypothesis is that these two visual systems have high spatial uncertainty as a consequence of sparse spatial sampling and thus benefit from the addition of spatial samples. In order to further test this hypothesis and to learn more about the nature of the mechanisms involved in spatial sampling a width discrimination experiment was performed.

**Experiment III: Width discrimination with discrete samples**

**Methods and stimuli**

The stimuli used in this experiment are shown schematically in Fig. 8. The observer's task was to judge the horizontal separation between the centers of two small boxes (shown by SEP in Fig. 8: the base separation of the two boxes is given in each graph). In an experimental run the boxes were briefly presented (100 msec) with one of five separations. The observer's task was to judge whether the horizontal distance between the two boxes was wider or narrower than the implicit reference (i.e. the mean of the five separations) by giving numbers from $-2$ to $+2$. Feedback as to the direction and magnitude of the offset was given following each trial. Each experimental run of 125 trials was preceded by 15–20 practice trials. This method is similar to that used by Westheimer and McKee (1977) for 2-line separation discrimination. Thresholds (defined at a $d'$ of 0.675) are the mean of at least four runs per stimulus with the order of stimuli relevant for comparison counterbalanced.

Each box was actually comprised of 4 tiny dots (illustrated schematically in Fig. 8). In order to vary the number of samples we manipulated the distances between the 4 dots comprising each of the two boxes. When they were close together (10") and thus unresolved, they represent a single sample. When the dots were separated so that they could be resolved (1.2' for foveal vision and 2.4' or 3.6' for peripheral and amblyopic vision) they provided 4 discrete samples. By this device the total luminance of each box stimulus was balanced and was approximately twenty times the observers' detection threshold for the unresolved dots.

**Results**

The histograms in Fig. 8 show the discrimination threshold for unresolved (1 sample), and resolved dots (4 samples). For the normal fovea [Fig. 8(A)] and for two anisometropic amblyopes [Fig. 8(B)], thresholds for the two conditions were identical. For strabismic amblyopic eyes [Fig. 8(C)], and for the normal periphery [Fig. 8(D)] thresholds were strongly reduced for the resolved dots.

These results confirm the observation of Experiments II that the spatial sampling characteristics of peripheral and strabismic amblyopic visual systems differ from those of the normal fovea and of anisometropic amblyopes. In peripheral and strabismic amblyopic vision the thresholds were reduced by approximately the square root of 2, suggesting the possibility that only two of the samples were effective. By separating the dots either horizontally only or vertically only [stimuli 2H and 2V in the inset of Fig. 8(D)] Levi and Klein (1986) showed that
only the 2 samples in the direction orthogonal to the discrimination cue contributed effectively to reduce the threshold. We have now replicated this surprising result on a third observer (Y.L.Y.) and her results are included in Fig. 8(A) and (D). This result is consistent with Hering's hypothesis regarding the averaging of discrete samples and suggests that this process is performed by oriented mechanisms.

What constitutes a discrete sample?
In order to determine the size of a discrete sample, we measured horizontal width discrimination thresholds for box stimuli consisting of just 2 tiny dots and systematically varied the vertical separation between the samples. We also measured 2-dot resolution thresholds for the same stimuli. The results are shown in Fig. 9. For the fovea, separating the samples verti-
Fig. 9. Horizontal width discrimination thresholds as a function of the vertical separation between the two samples constituting the stimulus. Note that foveally varying the intersample distance does not result in any improvement in thresholds (open circles and circles with dots). At 2.5° in the lower visual field, increasing the intersample distance so that the samples can be resolved, results in an improvement approximately equal to the square root of two (solid circles). For comparison data with 4 samples (2 horizontal and 2 vertical are shown by the squares). 2-dot resolution was measured with the same 2-dot stimuli using the method of constant stimuli with confidence ratings. The 2-dot resolution thresholds are shown by the arrows (open-foveal; solid at 2.5°).

cally either had no affect (s = 12.8' base separation—circles with dots) or made thresholds slightly worse (s = 3'—open circles.) At 2.5° in the lower visual field on the other hand (solid circles), increasing the separation between the samples so that they could be resolved (shown by the solid arrow) resulted in thresholds being reduced by approximately the square root of 2. For comparison, the squares show the thresholds obtained with the 4-dot stimulus used in Fig. 8.

**DISCUSSION**

The present results show that while one-dimensional position discrimination is remarkably good in foveal vision, there is marked positional uncertainty in peripheral and amblyopic vision.

A number of processes may influence spatial accuracy in psychophysical tasks:

1. Contrast sensitivity and suprathreshold contrast response function of the putative spatial filters (receptive fields)
2. Receptive field size and spacing (sampling density)
3. Combination of spatial samples
4. Orderliness of the spatial metric.

First we consider the implications of each of these factors, and then ask to what extent they may apply to the psychophysical performance observed in central, peripheral and amblyopic vision. A detailed account of the many factors involved in the bisection task is discussed by Klein and Levi (1985).

Several recent models of spatial vision have attempted to account for the high precision of foveal positional acuity on the basis of the contrast response function of spatial filters (Watt and Morgan, 1985; Klein and Levi, 1985; Madden, 1985; Carlson and Klopfenstein, 1985; Nielsen et al., 1985; Wilson, 1986a). A general theme of each of these models is that there are multiple bandpass filters (receptive fields). Multiple filter sizes are needed to account for bisection thresholds with a wide range of interline separations (e.g. Klein and Levi, 1985; Wilson, 1986a) and to provide for high resolution (Watt and Morgan, 1985). Reduced contrast response or increased receptive field size would result in a commensurate reduction of grating acuity and positional acuity.

Barlow (1979) and Crick et al. (1981) suggested that the high precision of positional judgements requires explicit interpolation with a sampling density on the order of 5-6 sec of arc. However, none of the recent filter-based models require fine grained spatial sampling of this order. Sparse sampling of the filters (i.e. increasing the distance between neighboring receptive fields of the same size) could result in reduced grating acuity and a more marked loss in position discrimination, since localized cues could be missed (Klein and Levi, 1985; Wilson, 1986b). Another consequence of sparse spatial sampling is that positional noise would be uncorrelated between sampling elements in the visual system. Thus, each sample of the stimulus would be independently localized—resulting in the square root relationship between positional acuity and the number of discrete stimulus samples. Discrete samples would be combined efficiently in a sparsely sampled visual system.

When sparse sampling does not occur (because of the point spread function of the eye, and/or overlap of receptive fields), combining stimulus samples will have less effect upon positional acuity.

Visual space is mapped in an orderly topographic fashion at various levels of the normal visual system. Disorder (or scrambling) of the spatial metric results in diffusion of the stimulus, so that it would be equivalent to sparse sampling in its effect upon localized positional...
information, but should have less impact upon contrast sensitivity and grating acuity. One possible source of disorder could be sparse spatial sampling.

Central vs peripheral vision

Position acuity declines more rapidly than grating acuity or contrast sensitivity in peripheral vision. It is unlikely that this additional loss of positional acuity can be accounted for by differences in the suprathreshold contrast response functions of foveal and peripheral vision (Swanson and Wilson, 1985; Wilson, 1986b). Thus, we have hypothesized that both the filtering (optical and neural) and the sampling characteristics of the visual system place fundamental limitations upon the accuracy of position discrimination. The results of Experiments II and III show that one dimensional spatial information from discrete samples can be combined along the length of targets as originally proposed by Hering. In normal foveal vision, this process has a relatively small impact upon the accuracy of spatial discrimination. However, in the normal periphery, the addition of spatial samples in the direction orthogonal to the discrimination cue reduces thresholds in proportion to the square root of the number of samples as would be expected in an ideal detector with uncorrelated noise at an early stage of visual processing. In normal peripheral vision, the high degree of spatial uncertainty with few samples can be understood on the basis of the anatomy and physiology of the retina and cortex which results in a sparse neural sampling grain (Rolls and Cowey, 1970; Dow et al., 1981; Tootell et al., 1982; Van Essen et al., 1985).

While each cone does not provide an independent sample of the stimulus, each cortical connection could have its own independent positional jitter. Thus, foveal positional uncertainty will be reduced because the fovea already has multiple samples for averaging, even for a single-dot stimulus. Response saturation (a ceiling effect) would lead to the lowered effectiveness (slope = 0.3) of added samples in normal foveal vision. Thus, doubling the number of cortical samples in the fovea will have less effect than doubling the number of cortical samples in the periphery.

In foveal vision, the image of a single tiny dot is spread by the optical blur function of the eye over roughly 4–8 cones and, in addition, highly magnified in the cortex. Thus, in foveal vision even a single dot will be sampled by many cones and by many overlapping cortical receptive fields so sparse sampling is never present (Snyder, 1982). In the periphery, cone density falls off rapidly. By 2.5 deg cone density is reduced by a factor of 2 (Österberg, 1935), with little change in the eye's optics. Thus only 1–2 cones would be stimulated by a dot (i.e. there are about 1/4 the number of cones within the area of the eye's point spread function at 2.5 deg). However, it is our contention that it is sparse cortical sampling that limits position discrimination. We offer three lines of evidence to support this contention. First, thresholds with a single sample are larger than the intercone spacing at 2.5 deg. Second, adding samples reduces positional uncertainty in peripheral vision only when they are added in the direction orthogonal to the discrimination cue. This orientation specific behavior is not likely a property of the retina, but is consistent with the properties of cortical mechanisms. Third, the results of the strabismic amblyopes is qualitatively similar to that of the periphery, and it is almost certain that the anomalies of strabismic amblyopes are cortical (see next section).

Anisometropic versus strabismic amblyopia

The present results show that anisometropic and strabismic amblyopes differ in two respects. Firstly, anisometropic amblyopes show losses in position acuity which are commensurate with their reduced grating resolution while strabismic amblyopes show an extra loss in position acuity (Experiment I). This replicates and extends our previous results for vernier and bisection acuity (Levi and Klein, 1982a, b, 1983, 1985). Secondly anisometropic and strabismic amblyopes differ in their spatial sampling characteristics (Experiments II and III). Anisometropic amblyopes sample spatial information in a manner like that of the normal fovea. The simplest explanation for the results of the anisometropic amblyopes is that their loss of grating acuity and positional acuity share a common basis. One hypothesis is that the loss of position acuity results from the reduced contrast sensitivity of high spatial frequency mechanisms (Levi and Klein, 1985; Bradley and Freeman, 1985). The effect of binocular competition induced by the monocular defocus which occurs in anisometropia (Copps, 1944; Jampolsky et al., 1955) would be expected to reduce the contrast sensitivity of small receptive fields (Eggers and Blakemore, 1978) but not affect the sensitivity or spatial sampling of large receptive fields. This explanation is consistent
with several observations regarding anisometropic amblyopes. Firstly, the reduced spatial localization of anisometropes but not of strabismic amblyopes can be mimicked by optical defocus (Flom et al., 1985) and by two-dimensional Gaussian blur (Toet et al., personal communication). Secondly, the reduced contrast sensitivity found centrally in anisometropic amblyopes differs from that of strabismics in that it persists in peripheral vision (Hess and Pointer, 1985), and under scotopic conditions (Hess et al., 1980). Interestingly, Hess and Pointer (1985) found that reduced contrast sensitivity was limited to the binocular segment of the visual field of anisometropic amblyopes, suggesting that binocular competition more or less proportional to the monocular defocus plays an important role in anisometropic amblyopia.

The "scaling" of the position acuity of anisometropic amblyopes to their grating acuity could occur either because the amblyopic eye uses larger mechanisms for making positional discriminations than does the normal eye, or because it uses the same size mechanisms, which have lower sensitivity (poorer signal-to-noise ratio). An alternative hypothesis is that there is a metrical "scrambling" of visual space in the visual system of anisometropic amblyopes which results in their reduced positional acuity (Hess and Watt, 1986). The recent experiments of Hess and Watt confirm that anisometropic amblyopes show marked positional uncertainty. They suggest that this is not a consequence of increased intrinsic blur, as might be expected if the amblyopic eye used larger mechanisms for positional tasks. Their results based on one-dimensional blur do not however rule out a deficit in the contrast sensitivity of the mechanisms involved in position discrimination. In their experiments, the lines of the target were set at the same suprathreshold luminance level in each eye; however it is likely that a thin line is detected by mechanisms near the peak of the contrast sensitivity function, while the position cue might be detected by smaller mechanisms (e.g. Watt and Morgan, 1985; Wilson, 1986a). Moreover, while scrambling of the spatial metric would be expected to result in marked losses in positional acuity, there is no reason to expect that it should have the same effect upon contrast sensitivity or grating acuity.

Is the loss of contrast sensitivity sufficient to account for all of the extant data of anisometropic amblyopes? Probably not; however, it provides a reasonable first approximation. It fails to provide a full account in two ways. Firstly, for bisection (with overlap) of small separations, flanks produce elevated thresholds in anisometropic amblyopes [Levi and Klein, 1983; also note that in Fig. 4(A) of the present paper that the upturn of the data of the amblyopic eye is sharper than the normal data at small separations]. Secondly, anisometropic amblyopes show relative phase discrimination is reduced to a greater extent than might be predicted from their contrast sensitivity (Pass and Levi, 1982; Lawden et al., 1982). These extra losses may have their basis in the reduced ability to discriminate local contrast changes (Badcock, 1984) or a scrambling of the labelling of on and off mechanisms of the amblyopic eye (Paul et al., 1986). The main effect, however, is that over a wide range of conditions, the loss of contrast sensitivity of the spatial filters of the amblyopic eye is commensurate with the loss of precision in positional tasks.

In strabismic amblyopia, the positional acuity is worse than would be predicted from their reduced grating resolution or contrast sensitivity (Experiment I) or suprathreshold contrast response function (Hess et al., 1983) and cannot be simply mimicked by optical blurring (Flom et al., 1985). Moreover the spatial sampling characteristics of strabismic amblyopes closely resemble that of the normal periphery except that the losses of strabismic amblyopes are most pronounced centrally (Katz et al., 1984; Hess and Pointer, 1985). Thus, we have hypothesized that the central visual field of strabismic amblyopes is sparsely sampled. Although strabismic amblyopes frequently demonstrate eccentric fixation, their spatial vision resembles that of the normal periphery even when repetitive targets are used to ensure that the stimulus is imaged upon the fovea (Levi and Klein, 1982a, b, 1985). Moreover, in the present study two strabismic amblyopes (T.O. and T.D.) showed central fixation. Thus, we hypothesize that in strabismic amblyopia, abnormal binocular interactions result in a sparse sampling grain centrally due to insufficient cortical neurons to provide accurate position signals and/or a scrambling of the neural signals. The consequence of this is increased positional noise which, like the normal periphery is uncorrelated between stimulus samples.

What is the nature of the sparse sampling in strabismic amblyopia? One possibility is that there is simply a widespread loss of cortical
neurones and/or a scrambling of functional connections from the central field of the amblyopic eyes. A second possibility comes from the recent work of Blasdel and Salama (1986). They have discovered that cortical modules (slightly less than 1 mm) contain continuous variations in orientation and ocular dominance along single but separate axes. In strabismic amblyopia, it is likely that the ocular dominance columns of the deviated eye shrink. Thus locally, in any given module, some orientations will simply not be represented in the amblyopic eye (Blasdel, personal communication). This form of undersampling, has several implications. Resolution and contrast sensitivity could be only slightly affected; however localized position and/or orientation judgements will be markedly affected. Moreover, since there may be gaps in the cortical representation of long lines which cross many modules there will be uncorrelated noise between discrete stimulus samples, and adding samples would improve localization of the lines.

In normal foveal vision, a threshold level Snellen letter (5 min of arc for a 20/20 letter) is approximately the size of one module. An absence of local information at all orientations within a module would be expected to exert a more profound effect upon Snellen acuity (where several orientations must be combined) than grating acuity, as occurs in strabismic amblyopia.

CONCLUSION

The present results pose difficulties for filter based models of spatial localization. Several models of spatial localization incorporate both spatial filtering and spatial sampling (e.g. Klein and Levi, 1985; Watt and Morgan, 1985; Wilson, 1986a). Precisely how spatial information is sampled by the visual cortex is currently not known (see Geisler and Hamilton, 1986). One implication of our results is that in peripheral vision the sensitivity of spatial filters may change more slowly with eccentricity than their sampling rate. Similarly in strabismic amblyopia, a loss of neurones or scrambling of their signals may have a more profound affect on the spatial sampling grain than on the sensitivity of the spatial filters. In normal foveal vision (and in anisometropic ambylopes) the filtering and sampling properties of the visual system are well balanced; however, in peripheral vision and in the central field of strabismic ambylopes our results suggest that it is the cortical sampling grain that imposes the fundamental limit upon performance.

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