VERNIER ACUITY, CROWDING AND AMBLYOPIA*

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(Received 4 September 1984; in revised form 14 November 1984)

Abstract—When a vernier target is flanked by a pair of optimally positioned flanks, offset discrimination is strongly degraded. Spatial interference with vernier acuity was studied in each eye of observers with unilateral amblyopia associated with strabismus, anisometropia or both, and were compared to the functions obtained in the normal periphery (Levi et al., 1985). The results showed that: (1) For both strabismic and anisometropic amblyopes, as in normal central and peripheral vision, the extent of spatial interference was proportional to the unflanked vernier threshold. (2) For anisometric amblyopes, grating and vernier acuity are affected similarly. (3) For strabismic amblyopes, like the normal periphery, vernier and grating acuity are decoupled, with vernier falling off faster than grating acuity. (4) The preferred eyes of strabismic but not anisometropic amblyopes have poorer vernier acuity than the normal controls. A conceptual framework for amblyopia based upon spatial filtering and spatial sampling is discussed.

INTRODUCTION

"Crowding" or spatial interference is a well documented characteristic of the acuity of amblyopic eyes (Stuart and Burian, 1962; Flom et al., 1963a; Hess and Jacobs, 1979). In a clinical setting, such effects are manifest as better acuity with single optotypes than with a line of optotypes. Flom et al. (1963) measured the spatial extent of interference with acuity by placing flanking bars at various distances from a near threshold Landolt C. They found that the linear extent of interference was far greater in amblyopic than in normal eyes, but that when scaled to the unflanked acuity, the extent of interference was similar in normal and amblyopic eyes. Similar observations were reported by Hess and Jacobs (1979). These authors noted that the abnormalities in acuity and contour interaction could not be accounted for on the basis of eccentric fixation.

Interference effects are ubiquitous in spatial vision. Such effects also occur for orientation discrimination (Westheimer et al., 1976), stereacuity (Butler and Westheimer, 1978) and vernier acuity (Westheimer and Hauske, 1975; Levi et al., 1985). These tasks are considered to be "hyperacuity" tasks, resulting in thresholds which, in normal central vision, are much smaller than the diameter of a single foveal cone, and are therefore considered to reflect cortical processing (Barlow, 1981; Westheimer, 1981).

In the preceding article we described the effects of spatial interference with vernier acuity in central and peripheral vision. Our results showed that although vernier acuity falls off rapidly in peripheral vision, the extent of spatial interference was proportional to the unflanked vernier threshold. Thus, in central and peripheral vision the maximum interference with vernier acuity occurs when flanks are placed about 30 times the unflanked threshold distance from the target. The performance of amblyopic eyes on spatial tasks has often been qualitatively compared to the normal periphery (Flynn, 1967; Levi et al., 1981; Katz et al., 1984). Thus, in the present paper we describe measurements of spatial interference with vernier acuity in each eye of observers with unilateral amblyopia associated with strabismus, anisometropia or both. Because practice effects are important in hyperacuity (McKee and Westheimer, 1978) our observers were given extensive practice. The results showed that: (1) For both strabismic and anisometropic amblyopes, as in normal central and peripheral vision, the extent of spatial interference is proportional to the unflanked vernier threshold. (2) For anisometric amblyopes, grating and vernier acuity are affected similarly, (3) For strabismic amblyopes, like the normal periphery, vernier and grating acuity are decoupled, with vernier falling off faster than grating acuity. (4) The preferred eyes of strabismic but not anisometropic amblyopes have poorer vernier acuity than the normal controls.

METHODS AND STIMULI

The methods and stimuli were identical to those described in Experiments I and III of the preceding paper (Levi et al., 1985). In brief, the stimulus consisted of a continuously presented horizontal, bright "reference" line. A "test" line was flashed for 250 msec in one of 5 positions either aligned with the
Table I

<table>
<thead>
<tr>
<th>Observer</th>
<th>Age/Sex</th>
<th>Eye</th>
<th>Rx</th>
<th>Acuity*</th>
<th>Fixation†</th>
<th>Binocularity</th>
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<tr>
<td>T.S.</td>
<td>29/M</td>
<td>OD</td>
<td>Plano</td>
<td>20/15</td>
<td>Central</td>
<td>Normal</td>
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<td>20/15</td>
<td>Central</td>
<td>Normal</td>
</tr>
<tr>
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<td>20/20</td>
<td>Central</td>
<td>Normal</td>
</tr>
<tr>
<td>D.L.</td>
<td>36/M</td>
<td>OD</td>
<td>-1.0D</td>
<td>20/15</td>
<td>Central</td>
<td>Normal</td>
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**Constant strabismus**

| J.S.     | 22/F    | OD   | +1.0              | 20/16   | Central   | 1/2 nasal    |
|          |         | OS   | +1.0/-0.75 x 180  | 20/160  | Central   | 2 nasal      |

| R.G.     | 29/M    | OD   | -4.50/-1.25 x 90  | 20/15   | Central   | 1 temporal   |
|          |         | OS   | -4.00/-1.00 x 90  | 20/46   | Central   | 2 temporal   |
| J.B.     | 24/F    | OD   | +4.50/-0.75 x 100 | 20/22   | Central   | 1 temporal   |
|          |         | OS   | +4.75/-1.00 x 85  | 20/30   | Central   | 2 nasal      |

**Anisometropia**

| M.C.     | 30/F    | OD   | +1.0/-0.75 x 101  | 20/40   | Unsteady central | Occasional right exotropia, 8° |
|          |         | OS   | -1.75/-0.50 x 170 | 20/15   | Central         | Occasional left exotropia at near, 10° |
| J.M.     | 21/M    | OD   | -2.30/-0.25 x 160 | 20/15   | Central         | Unsteady central         |
|          |         | OS   | +2.25/-0.25 x 90  | 20/60   | Unsteady central | Unsteady central         |

**Strabismus and anisometropia**

| R.M.     | 22/F    | OD   | -18.25/-4.25 x 005| 20/680  | Unsteady 1-2   | Constant right exotropia, 10° |
|          |         | OS   | -2.25/-0.72 x 002 | 20/15   | Central         | Occasional left exotropia, 8° |
| J.Y.     | 27/M    | OD   | +0.75/-0.25 x 70  | 20/20   | Central         | Occasional left exotropia, 8° |
|          |         | OS   | +4.30/-0.30 x 23  | 20/80   | Unsteady 1 nasal | Occasional left exotropia, 8° |
| D.M.     | 29/M    | OD   | +0.00/-0.25 x 22  | 20/20   | Central         | Normal                     |
|          |         | OS   | +8.25             | 20/64   | Unsteady 1 nasal | Unsteady 1 nasal |

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*Acuity determined from a psychometric function using charts designed by Davidson and Eskridge.†Fixation determined with visuoscopy.¶Occasional exotropia noted on cover testing or when extremely fatigued.
reference line, or 1 or 2 distance modules above or below it. The distance modules were chosen to place the stimuli appropriately on the psychometric function. A schematic of the vernier stimulus with flanks is shown in the inset of Fig. 2. The observer's task was to judge whether the test line was high or low, and rate their confidence. The threshold was taken as the offset providing a $d' = 0.675$ (equal to the 75% correct discrimination level). All testing was monocular, with the untested eye patched with a black occluder. For the amblyopic eyes the stimulus size was "scaled" in proportion to their acuity (see preceding paper Experiment III). Each observer's grating acuity was also measured for square-wave gratings using a 3 alternative forced choice procedure (Levi et al., 1984).

Observers

Twelve adults between the ages of 27 and 43 participated in the experiment. Four observers with normal vision in each eye and normal binocular vision served as controls. Three were highly practiced psychophysical observers. The fourth had limited prior experience and was naive as to the purpose of the experiment. All had clear media and normal fundi, and wore appropriate refractive correction if needed.

Eight observers had unilateral amblyopia associated with strabismus, anisometropia or both. Relevant clinical characteristics are given in Table 1. All but one (D.M.) had a great deal of prior experience in forced-choice hyperacuity experiments. One observer (J.S.) had extensive psychophysical experience in several other laboratories. In the present experiment only her preferred eye was tested.

All of the observers were provided extensive practice with this specific task prior to data collection, and each block of 125 trials was preceded by 10-20 practice trials.

RESULTS

Practice effects

Figure 1 shows the effects of practice on vernier acuity (without flanks) for observer D.M. (strabismic and anisometropic amblyope) who had no prior psychophysical experience. The N's are the data with his preferred eye viewing. Circles are the amblyopic eye. The symbols at the extreme right show the final asymptotic value achieved after more than 2000 practice trials with each eye with the unflanked vernier target. These data were obtained over several sessions and were interspersed with practice trials with flanks at various positions. The main effect of this practice was to lower thresholds of the amblyopic eye by about a factor of 40%, and to reduce the standard errors of the data. Interesting similar practice effects occur in the normal periphery (Westheimer, 1982a). For comparison purposes, we have also plotted the effects of practice upon thresholds in the normal periphery (5° in the lower visual field of the preferred eye of observer J.M.) as shown by the p's.

Preferred eyes of amblyopes

Figure 2 shows the influence of flanks upon the vernier thresholds of the preferred eyes of eight amblyopic observers. The leftmost points are thresholds with no flanks. The open symbols are preferred eyes of anisometropic amblyopes, solid symbols strabismic amblyopes, and half-solid symbols for observers with both anisometropia and constant strabismus. The shaded region is the total range of thresholds of the 4 normal control observers. The results of the preferred eyes, like those of the controls show strong spatial interference, with thresholds raised three to four-fold by appropriately positioned flanks. It is of interest to note that the preferred eyes of the two anisometropic amblyopes have unflanked thresholds

Fig. 1. Effects of practice for the nonamblyopic (n's) and amblyopic eye (circles) of observer D.M. The P's show comparable results for 5° in the periphery for the preferred eye of observer J.M. The error bars show ±1 SE (where not shown, the error bar did not exceed the size of the symbol).
of amblyopes. Open symbols are anisometropic normal control observers. The inset is a schematic of the solid symbols observers with both strabismus and anisometropia. The symbols nearest the ordinate are unflanked thresholds. The shaded area is the range of thresholds for 6 normal control observers. The inset is a schematic of the vernier stimulus and the flanks.

Fig. 2. Vernier threshold vs flank separation for the preferred eyes of 8 amblyopes. Open symbols are anisometropic amblyopes, solid symbols, strabismic amblyopes, and half-solid symbols observers with both strabismus and anisometropia. The symbols nearest the ordinate are unflanked thresholds. The shaded area is the range of thresholds for 4 normal control observers. The inset is a schematic of the vernier stimulus and the flanks.

Similar to those of the normal observers. For the 6 observers with strabismus, on the other hand, the unflanked thresholds are almost a factor of two higher than the normals (8.4'-12.5') and show spatial interference over a wider range of flank distances. These data, cannot be explained on the basis of practice, since our observers were all highly experienced. Control experiments with long viewing durations, vertically oriented targets and 2.8 mm pinholes make it unlikely that the results can be explained by poor fixational eye movements or accommodation, since thresholds were not improved by any of these manipulation.

Amblyopic eyes

In comparison to the normals, and the preferred eyes, amblyopic eyes show unflanked vernier thresholds which are elevated, and spatial interference extends over greater distances. Figure 3 shows the data of 6 amblyopic eyes with unflanked vernier thresholds ranging from about 15' (J.B.) to 250' (R.M.). For each amblyopic eye, there are strong flankling effects; note however, that extent of spatial interference appears to be related to the unflanked vernier threshold. For example, J.B. with an unflanked threshold of 15' shows the strongest interference at about 6' while R.M., with an unflanked threshold of almost 250' shows the strongest interference when the flanks are about 70' from the target. Note that the two sets of data shown for R.M. are for two different flank configurations. The circles are the standard short flanks used for all of the observers. The triangles show longer flanks like those used by Westheimer and Hauske (1975) i.e. 50', of the length of the test line and extending across the offset. It is interesting that these extended flanks give approximately the same shape curve, but with slightly higher threshold values.

The relationship between the unflanked threshold and the distance at which the spatial interference was strongest is shown in Fig. 4. Shown in this figure are the results of the control eyes (dots), preferred eyes (p's) and amblyopic eyes (A's, S's and B's) for anisometropes, strabismics and observers with both. Also shown here are data of the normal periphery (open squares and circles from preceding article) and the periphery of the amblyopic eye of an anisometropic amblyope (solid squares). The solid line has a slope of 1. On these log-log coordinates, this linear relationship would be expected if the distance of the flanks which gave the strongest masking scaled to the unflanked vernier threshold. The actual slope of the best fit line was 1.11 ± 0.18 (r = 0.96), compatible with a linear scaling. Thus, the results suggest that for the normal fovea, the periphery and for both eyes of amblyopes, the strongest spatial interference occurs with contours about 30 times the unflanked threshold distance from the target. This relationship seems to hold both for strabismic and anisometropic amblyopes.

For the normal control eyes, the function relating threshold to flank distance is tuned. As the flanks are moved from the peak of the function to larger distances, the threshold returns to its baseline value when the flanks are 2.5-3.5 times the peak distance. Similar results were found in the periphery and in the amblyopic eyes of both anisometropic and strabismic amblyopes.

This result is, at first glance quite surprising. In our previous studies of vernier acuity, using repetitive vernier gratings, we found that normal eyes and anisometropic amblyopes showed crowding at spatial frequencies within a factor of two of their grating acuity limit (Levi and Klein, 1982a,b). Strabismic amblyopes on the other hand, showed "crowding" at spatial frequencies well below their cutoff.

Grating acuity and vernier acuity

Figure 5 plots the unflanked vernier acuity of each observer against their grating acuity on log-log coordinates. Open circles are the normal control observers. The black A's, S's and B's are the amblyopic eyes of amblyopes with anisometropia, strabismus and both respectively. Two lines are shown on the graph. The dashed line has a slope of 1. Data would be expected to conform to this line if grating acuity and vernier acuity were affected in the same way. The solid line has the form $V = 0.7G - 0.3$ (where $V$ = vernier acuity and $G$ = grating acuity) and is the line fit to the data of the normal periphery (preceding paper, Fig. 9). This line shows that in the normal periphery vernier acuity declines more rapidly than grating acuity with eccentricity. Thus, loveay, ver-
Vernier acuity, crowding and amblyopia

Fig. 3. Vernier threshold vs flank separation for 6 amblyopic eyes. The shaded area shows the unflanked threshold ±1 SE. For R.M. the triangles show thresholds obtained with longer flanks (i.e. equivalent to those used by Westheimer and Hauske, 1975).

Fig. 4. The unflanked vernier threshold is plotted against the distance at which the flanks elevate thresholds maximally. The dots are for normal control eyes, P's for preferred eyes of amblyopes, S's, A's and B's for amblyopic eyes of strabismus, anisometropes and those with both. [The data of J.V. (Fig. 3) show two peaks, shown by the connected B's]. Open circles and squares are data for the normal periphery; solid squares for the periphery of the amblyopic eye of J.M. (see Fig. 6). The line has a slope of 1.

Vernier acuity is approximately 6", and is about 8 times better than grating acuity, whereas at 10', vernier acuity is less than a factor of two better than grating acuity. The data of the amblyopic eyes of strabismic amblyopes (S's and B's) are in remarkable agreement with the solid line. Since strabismic amblyopes frequently demonstrate eccentric fixation, two amblyopes with strabismus (J.V. and R.G.) and one with anisometropia (J.M.) were also tested with repetitive vernier gratings (preceding paper, Experiment 4 and Fig. 11). These extended vernier gratings ensured that the stimulus was imaged on the fovea as well as the eccentric locus (Levi and Klein, 1982a,b). The interline separation was large to avoid "crowding". The data are shown in Fig. 5 by the white S, white B and white A, connected to the black letters for the same observers. Data obtained under similar conditions for a third strabismic amblyope (white S), and for 5 other anisometropic amblyopes (white A's) are also shown. These data with uncrowded gratings, conform closely to the data obtained with classical (single) vernier stimuli and suggest that the results cannot be attributed simply to eccentric fixation.

These data are in agreement with the results of our previous studies (Levi and Klein, 1982a,b; 1983) in showing that vernier and grating acuity are affected similarly in anisometropic amblyopes and that...
Fig. 5. Unflanked vernier acuity vs grating acuity for normal control observers (open circles), preferred eyes of anisometropic amblyopes (P’s in squares) and amblyopic eyes of strabismic amblyopes (S’s in squares) and amblyopic eyes of strabismics (S’s). Anisometropes (A’s) and both (B’s).

Data are also shown for vernier acuity using repetitive vernier gratings (white letters). The dashed line has a slope of 1. On these log-log coordinates the line indicates vernier and grating acuity being linearly related. The solid line is for the normal periphery. In the preceding paper (Levi et al., 1985) we demonstrated that in normal vision the vernier acuity of the central visual field (from Levi et al., 1985 Fig. 9).

Nearby contours have a strong influence on one’s ability to make spatial discriminations. The masking effects of nearby contours have been noted in letter acuity (Flom et al., 1963a; Bouma, 1970), tilt judgements (Andriessen and Bouma, 1976; Westheimer et

account for this is that these eyes had undetected eccentric fixation of small magnitude so that the stimulus was in fact nonfoveal, however, while repetitive gratings improve vernier thresholds slightly (white P) they are still poorer than those of the normal observers. The hypothesis we prefer, is that strabismic amblyopia represents a central deficit and therefore each eye is affected (although not to the same degree). This notion will be considered in more detail in the discussion.

The extent of amblyopia and spatial interference in peripheral vision

Amblyopia is generally considered to most profoundly affect the visual acuity of the central visual field (Chevasse, 1939; Burian, 1967). This appears to be true also for vernier acuity (Levi and Klein, 1982b). With respect to spatial interference, Fig. 6 shows the effects of flanks on vernier thresholds for each eye of anisometropic amblyope J.M. with foveal viewing and at 2.5’, 5’ and 10’ in the lower visual field. The left most symbols show the unflanked thresholds for each eye. Note that foveally, the unflanked threshold of the amblyopic eye is approximately 3 times higher than that of the preferred eye, whereas at 10’ the two eyes are essentially identical. This can be more clearly seen in the inset which plots the amblyopic loss (ratio of the amblyopic:preferred eyes unflanked thresholds) as a function of eccentricity. It is also of interest to note that the amblyopic fovea shows both an unflanked threshold, and a spatial interference function similar to that obtained at 2.5’ in the normal periphery; whereas by 10’ the unflanked thresholds and spatial interference functions of the two eyes are quite similar.

**DISCUSSION**

The basic results of these experiments were: (1) for both strabismic and anisometropic amblyopes, as in normal vision (both central and peripheral), spatial interference “scales” to the unflanked vernier threshold, being strongest when the interfering contours are about 30 times the unflanked threshold distance, (2) for the amblyopic eyes of anisometropic amblyopes, grating and vernier acuity are affected similarly, (3) for the amblyopic eyes of strabismic amblyopes, as in the normal periphery vernier acuity is degraded to a greater extent than grating acuity, (4) the preferred eyes of strabismic but not anisometropic amblyopes have poorer vernier acuity than both the normal control observers and the preferred eyes of anisometropic amblyopes.

**Spatial interference**

Nearby contours have a strong influence on one’s ability to make spatial discriminations. The masking effects of nearby contours have been noted in letter acuity (Flom et al., 1963a; Bouma, 1970), tilt judgements (Andriessen and Bouma, 1976; Westheimer et
In normal foveal vision, these interference effects both in visual acuity and in hyperacuity are strongest when the interfering contours are at 2-4' from the target. Moreover, spatial interference occurs under dichoptic conditions both for letter acuity (Flom et al., 1963b) and for vernier acuity (Westheimer and Hauske, 1975; Levi et al., 1985) strongly suggesting that these interactions are central. In degraded vision (periphery and amblyopia) the extent of interference "scales" to the unflanked acuity value (Flom et al., 1963a; Levi et al., 1985; present paper). Thus, these spatial interactions in letter acuity and vernier acuity likely share a common basis. It has been suggested (Westheimer, 1981; Westheimer and McKee, 1977) that position coding requires a processing zone of several minutes of arc foveally and correspondingly larger (in proportion to the threshold) in the periphery.

Hubel and Wiesel (1974) first suggested that the striate cortex consists of a large number of repeating modules (hypercolumns), each of which carries out a highly stereotyped analysis of the inputs from a small region of the visual field. Each hypercolumn consists of a pair of ocular dominance columns and a complete set of orientation columns. In humans, a hypercolumn is roughly 2 mm in extent (i.e. 2 \times 10^2 \text{mm}) the dimension of an ocular dominance column; Hitchcock and Hickey, 1980). Daniel and Whitteridge (1969) coined the term "magnification factor" (\(M\)), to describe the extent of cortical surface (in mm) devoted to a unit portion in visual space (in degrees). They, and other workers (Hubel and Wiesel, 1974; Dow et al., 1981; Tootell et al., 1982; Van Essen et al., 1984) have demonstrated that the cortical magnification factor is greatest in the foveal representation and falls off rapidly with eccentricity. Foveally, a human ocular dominance column represents about 4 min of visual space, and correspondingly larger areas with increasing eccentricity. In the preceding paper (Levi et al., 1985) we demonstrated that both centrally and peripherally "crowding" in vernier acuity occurs when the interline spacing, expressed in units of cortical distance, is smaller than one ocular dominance column (< 1 mm). Thus, the intriguing notion, first suggested by Barlow (1981; but see Westheimer, 1982b) is that the processing zone required for optimal hyperacuity has its anatomical basis in the modular organization of the visual cortex. How does such a notion hold up in the light of the present experiments? Although little is known about the specific effects of early strabismus and/or anisometropia on the pattern of columns in the cortex, in monkeys, monocular deprivation has a dramatic impact. Early lid suture leads to shrunken and interrupted columns for the deprived eye, and widening of the columns for the experienced eye (Hubel et al., 1977). It is plausible that the reduced cortical input of the amblyopic eye per unit area of visual space would result in elevated thresholds and enlarged processing zones (much like the normal periphery). It has also been speculated that the increased cortical territory devoted to the preferred eye of an amblyope might be expected to result in increased visual sensitivity (Freeman and Bradley, 1980). Freeman and Bradley (1980) reported that the preferred eyes of a group of anisometropic amblyopes indeed had better vernier acuity than did a control.
group with normal vision in both eyes. Their observers were inexperienced in psychophysical observations. On the other hand, Johnson et al. (1982) found no significant difference in the vernier acuities of the dominant eyes of identical twins (only one of whom had monocular visual experience). In the present study, the preferred eyes of two highly practiced anisometropic amblyopes showed unflanked vernier acuities which were comparable to those of our normal observers (about 5°-6°). On the other hand all 6 observers with strabismus showed higher thresholds and a wider range of spatial interference with their preferred eyes. These results, and those of Westheimer (1982b) suggest that other factors in addition to the columnar organization (e.g. sampling, sensitivity ceiling etc., and the functional capacities of the neurons) should be considered in attempting to relate anatomy to visual sensitivity. At present it is also not clear how strabismus influences the size of ocular dominance columns. What is clear, is that the spatial extent of the processing modules for hyperthresholds and a wider range of spatial interference is proportional to the unflanked threshold in foveal vision, peripheral vision and amblyopic vision.

**Preferred eyes of strabismic amblyopes**

The results of the preferred eyes of the strabismic amblyopes are interesting. They resemble, in much milder form, the results of the amblyopic eyes or of the normal parafovea. Control experiments with artificial pupils (2.8 mm), long viewing durations (1 sec) and with the stimuli rotated by 90° suggest that neither abnormal accommodation nor retinal image motion due to unsteady fixation are likely to explain these data. Moreover, vernier acuity for briefly presented stimuli is not affected by retinal image motion (Westheimer and McKee, 1975). We cannot entirely rule out the possibility that these observers possessed minute, undetected eccentric fixation; however each had 20/20 or better Snellen acuity and appeared to be capable of central fixation with visuoscopy. For several observers we also measured vernier acuity with repetitive gratings. For normal observers the addition of a row of optimally spaced lines improves vernier acuity slightly (possibly due to probability summation—see Fig. 11 preceding article). Similar results were obtained with the preferred eye of a strabismic amblyope i.e. a small improvement in vernier acuity with repetitive gratings which were consistent with the improvements shown by normal observers. However, the threshold of the preferred eye of the strabismic amblyope remained poorer than those of the normal observers. Thus, small amounts of eccentric fixation, if present, are unlikely to account for these findings.

This is by no means the first report of mild abnormalities of the preferred eyes of strabismics. For example, unsteady fixation (Hermann and Priestley, 1965; Schor and Hallmark, 1978) and irregular tracking (von Noorden and Mackensen, 1962; Fukai et al., 1976; Schor and Levi, 1980) have been reported to occur in amblyopes with strabismus when fixating with their preferred eyes. Interestingly, Fukai et al. (1976) reported oculomotor anomalies in the preferred eyes of about 90° of strabismic amblyopes, but in only 6° of amblyopes without strabismus (i.e. anisometropes). These oculomotor anomalies of the preferred eyes of strabismic amblyopes have been recently confirmed by Bedell and Flom (1984). They showed that several oculomotor abnormalities co-exist, and attributed them to a central deficit responsible for the abnormal eye movements of both eyes. Sensory deficits have also been previously noted in the preferred eyes of strabismic amblyopes (Kandel et al., 1977; Kelly et al., 1984). In the present study, we think it unlikely that eccentric fixation or oculomotor anomalies are responsible for the deficits in vernier acuity, and our forced-choice methodology eliminates criterion effects. Bedell and Flom (1984) suggested the simple hypothesis that there are central deficits in the cortex of individuals with strabismic amblyopia which influence the performance of each eye. Interestingly, physiological evidence exists for such deficits in the cortex of cats reared with experimental strabismus (Chino et al., 1983) and in cortical evoked potentials of humans (Srebro, 1983).

**Strabismic vs anisometropic amblyopia**

Functional amblyopia is most commonly associated with strabismus, anisometropia or both, each of these factors occurring with approximately equal frequency (Schapero, 1971). The performance of strabismic and anisometropic amblyopes differ in a variety of respects in terms of their clinical characteristics (Irvine, 1948; Duke-Elder, 1973), prognosis (Kivlin and Flynn, 1981) and psychophysical performance (Hess et al., 1980; Hess and Bradley, 1980; Levi and Klein, 1982a,b; 1983; Flom et al., 1982; Bedell and Flom, 1983; Sireteanu and Fronius, 1981). The present study, and our previous experiments (Levi and Klein, 1982a,b; 1983) suggest that anisometropic amblyopes (without constant strabismus) show similar losses in vernier acuity and grating resolution, whereas strabismic amblyopes show greater losses for vernier than for grating resolution. Because these differences in psychophysical performance are not accounted for on the basis of eccentric fixation or anomalous eye movements (Levi and Klein, 1982a,b; 1983) it is likely that they reflect different neural bases for strabismic and anisometropic amblyopia. What follows below are some speculations regarding the factors which may limit the performance of anisometropic and strabismic amblyopes.

**Sampling the visual image**

The visual image is sampled by an array of cortical receptive fields of various sizes, shapes and orientations. Sakitt and Barlow (1982) have proposed an elegant model for the early stages of cortical processing of form information. We speculate that the
processing module for hyperacuity, like the anatomical modules described by Hubel and Wiesel (1974), contain much of the necessary machinery for analyzing a small area of space. Two important considerations for encoding the visual image are the sizes of the cortical receptive fields and their spacing. We assume that each module consists of receptive fields of various sizes. Figure 7(a) (top) shows very schematically three Mexican hat operators which have spatial frequency tuning given by: \( f^3 \exp(-f) \) (the properties of these functions are described in detail in Klein and Levi, 1985: however any center surround receptive field could be used). The receptive fields shown represent the smallest mechanisms and have a peak spatial frequency of 30 c/deg and a bandwidth of 1.5 octaves (giving a cutoff spatial frequency equal to about 60 c/deg). In space these receptive fields have a center excitatory area equal to 1'. The spatial sampling is at 1 min intervals. *The second row of Fig. 7(a) shows 3 similar operators, but twice the size (2' centers) and spaced at 2' intervals. Since these larger receptive fields have a cutoff at half the spatial frequency of the 1' mechanisms, the spatial sampling interval can be doubled, while maintaining the same efficiency as the smaller mechanisms. The effect of binocular competition induced by the monocular defocus which occurs in anisometropia (Copps, 1944; Jampolsky et al., 1955) might be expected to eliminate the smallest receptive fields but should not affect either the sensitivity or spatial sampling of the larger receptive fields. Thus, the reduced vernier and grating acuity of anisometropic amblyopes can be readily understood in terms of the sensitivity of high spatial frequency mechanisms.

The bottom row of Fig. 7(a) shows the same three (2') receptive fields but sampled at 4' intervals. Thus an image viewed through this array would be undersampled in space. This decoupling of receptive field size and spacing is consistent with what happens in the periphery, where cortical receptive field size changes less with eccentricity than does cortical magnification (Dow et al., 1981; Van Essen et al., 1984). It is likely that grating acuity is limited primarily by the filtering properties (optical and neural) of the visual system. If on the other hand, vernier acuity depends upon both filtering and spatial sampling (Snyder, 1982), then this simple model might account for the decoupling of grating acuity and vernier acuity in peripheral vision.

This picture could also apply to the results of strabismic amblyopes. The notion of spatial undersampling in strabismic amblyopes has some appeal. Undersampling can result from a reduction in the number of mechanisms [as illustrated in Fig. 7(a), bottom row], and also from aberrant position labeling (scrambling) of the mechanisms. For example, nonuniformities in sampling could account for many of the reported spatial distortions reported to occur in strabismic amblyopes (Hess et al., 1978, Bedell and Flom, 1983). Moreover, spatial undersampling in the absence of changes in the sensitivity of the filters could account for some strabismic amblyopes showing near normal contrast sensitivity but demonstrating reduced vernier acuity (Levi and Klein, 1982a,b) or spatial distortions (Hess et al., 1978).

Strabismic amblyopia occurs in individuals who have one eye continuously turned early in life. One consequence is that since accommodation is controlled by the fixing eye under binocular conditions, the foveal image of the deviating eye may be out of focus some of the time (Ikeda and Wright, 1974; von Noorden, 1977). A second consequence is that corresponding points in the two retinas receive different stimuli. Thus abnormal binocular interaction (suppression) probably plays an important role in the development of strabismic amblyopia (Wiesel, 1982; von Noorden, 1977). It is likely that binocular interaction in strabismus has a different form and field dependence than that resulting from anisometropia (Sireteanu and Fronius, 1981; Jampolsky, 1955) and that this abnormal binocular interaction results in alterations in the sampling characteristics of the deviated eye. Our working hypothesis is that alterations in both filtering and sampling properties may contribute to the psychophysical losses observed in strabismic amblyopes. The strong resemblance between the data of strabismic amblyopes and the normal periphery suggest that spatial sampling may be more strongly affected in strabismics. Moreover, the finding that strabismic amblyopes show marked disturbances in spatial localization for widely separated (low spatial frequency) targets (Levi and Klein, 1983; Bedell and Flom, 1983) suggest that strabismic amblyopia cannot simply be accounted for on the basis of blur or other retinal factors.

Thus, the effects of amblyopia may be to: (1) reduce the proportion of functional inputs to the cortex (2) decrease the sensitivity of mechanisms with small receptive fields and/or (3) alter the distribution of functional connections. The results may be a visual system which closely resembles the normal periphery (to be discussed below).

The effects of amblyopia on the extent of the processing module

Figure 7(b) shows the arrangement of the processing modules as a function of eccentricity. Here the vertical axis is in mm of cortex, each 1 mm module being approximately equal to the size of one normal human ocular dominance column (Hitchcock and Hickey, 1980) or a psychophysical spatial pro-

*For 60 c/deg cutoff the Nyquist sample spacing would be 0.5'. However, for any multisize receptive field model the Nyquist sample spacing of the smallest receptive field is larger than the Nyquist limit (Sakitt and Barlow, 1982; Burt and Adelson, 1983). In our qualitative scheme the precise sampling interval is not critical.
Fig. 7. (a) Schematic illustration of the notions of spatial filtering and spatial sampling. The top row shows 3 small hypothetical cortical 'Mexican hat' receptive fields with a peak spatial frequency of 30 c/deg, a cut-off spatial frequency of 60 c/deg, and a spatial sampling interval of 1' in accord with sampling theory (see text). The second row shows receptive fields of twice the size and sampled at twice the interval (also in accord with sampling theory). In anisometropic amblyopia the effect of binocular competition induced by monocular defocus should not affect either the sensitivity or spatial sampling of the larger receptive fields. The bottom row shows spatial undersampling. Here the same 3 receptive fields as shown above are now sampled at 4' intervals. We hypothesize that spatial undersampling may play an important role in the dramatic fall-off of vernier acuity in the normal periphery and in strabismic amblyopia. (b) Schematic illustration of cortical magnification and its relationship to strabismic amblyopia. Each heavily outlined box represents a normal 1 mm cortical processing module and the scattering of the centers of the receptive fields within it. At each eccentricity the spatial extent of the module is scaled in proportion to M^{-1}. Each stippled box represents a hypothetical processing unit for a strabismic amblyope. The zone of scattering of receptive field centers has been increased by a constant. This increases scatter a lot at 0°, but proportionally less with increasing eccentricity.
cessing unit (Barlow, 1981; Levi et al., 1985) in normal humans. The horizontal axis is eccentricity. The horizontal extent of each box represents the spatial extent of each 1 mm processing module. The heavily outlined boxes represent the normal visual system. The smallest box at the origin was constructed to extend approximately 4°, i.e. the size of a foveal spatial processing module, and consistent with $M = 13$ mm/deg at the fovea (see preceding paper).

At eccentricity the spatial extent of the module increases in proportion to $M^{-1}$ (i.e. the inverse of the cortical magnification factor; Daniel and Whitteridge, 1961) and has 50% overlap. Thus at 4°, the size of the module is 6 times larger than at the fovea. The stippled boxes represent the enlarged processing modules which are found in amblyopes (Figs 3, 4 and 6). There are several possible reasons why the size of the processing module is enlarged in the amblyopic eye. (1) In order to achieve a high signal to noise ratio, a large fixed number of neurons may be required (Sakitt and Barlow, 1982). The amblyopic loss of neurons in both strabismus and anisometropia would therefore necessitate a larger processing module. (2) The lack of fusion between the two eyes occurring in strabismus may cause an extra scattering of the receptive fields in the deviated eye (Petitgrew, 1974). Extending the zone of scattering by a constant [0.5 deg in Fig. 7(b)] would have the effect of increasing the relative size of the foveal processing module a lot, but would result in a proportionally smaller effect with increasing eccentricity. While this scheme is offered only as a tentative hypothesis, it seems plausible, and is open to direct physiological testing once a good animal model of strabismic amblyopia is found.

Peripheral vision and amblyopia

Analyses between the normal periphery and amblyopia have been made previously with respect to spatial summation (Flynn, 1967; Levi et al., 1981), contrast sensitivity (Katz et al., 1984), relative motion (Levi et al., 1984) and acuity (Flom et al., 1963a). On the other hand, it is now apparent that with appropriate scaling, the normal periphery performs many tasks similarly to the fovea. For example, when contrast sensitivity of the periphery is determined with stimuli scaled in proportion to the cone density of that retinal area, peak sensitivity “normalizes”. Similarly, vernier acuity and its associated crowding effects are similar in central and peripheral vision when scaled according to cortical magnification (Levi et al., 1985). It is only when comparing performance on two tasks with different scales (e.g. vernier and grating acuity) that one can distinguish central and peripheral vision. In comparing amblyopes’ grating acuity vs vernier acuity, anisometropes perform like blurred central vision, while strabismics perform like periphery. We suggest that the losses in anisometropic amblyopia can be understood in terms of the filtering properties of the visual system, whereas strabismic amblyopia may be a consequence of spatial undersampling.

In summary, it appears that comparing the performance properties of normal central and peripheral vision may provide useful insights into the visual limitations associated with amblyopia. The notions of spatial filtering and spatial sampling may provide a useful conceptual framework for understanding spatial vision both in normal and in amblyopic vision.

Note added in proof—In a recent article Bradley and Freeman (Vision Res. 25, 55-66, 1985) suggested that the loss in vernier acuity in both anisometropic and strabismic amblyopes could be accounted for on the basis of the reduced contrast sensitivity of the amblyopic eye. Their data on anisometropic amblyopes is in full agreement with our results. However, the results of their strabismics differ from our findings (present paper and Levi and Klein, 1982a,b). Figure 5 of the present paper shows that each of our strabismic observers has a vernier deficit which is two to eight times worse than the grating acuity deficit. We have measured the contrast sensitivity of several of these observers and find the CSF loss is also much too small to account for the vernier acuity loss. For example, J.V. shows a three-fold loss in contrast sensitivity (for example, see J.V.’s CSF in Levi et al., 1981).

We believe that the discrepant results can, in part, be accounted for on the basis that Bradley and Freeman measured thresholds for detection of the presence of a vernier offset while we measured thresholds for discrimination of the direction of the offset. We have noted previously (Levi and Klein, 1983) that strabismic amblyopes show more marked losses for discrimination of direction than for simple detection, particularly at high spatial frequencies. For example, J.V.’s amblyopic eye exhibited approximately a 50% lower threshold for detecting than for discriminating a vernier offset at middle spatial frequencies, increasing to a two-fold difference at high spatial frequencies. Similar results are obtained in peripheral vision (unpublished observations). A second difference between the two studies is that Bradley and Freeman used sinusoidal gratings whereas we used rectangular gratings. The 200% contrast of the fundamental spatial frequency of the rectangular gratings allowed us to measure vernier acuity at higher spatial frequencies where strabismic amblyopes showed the greatest losses in vernier acuity.

Acknowledgements—We thank Travett Robinson-Johnson for preparation of the manuscript, Joy Hirsch for ambylope-rusting, and Hugh Wilson and Tony Movshon for a helpful discussion.

REFERENCES


Vernier acuity, crowding and amblyopia


