VERNIER ACUITY, CROWDING AND CORTICAL MAGNIFICATION*

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Abstract—When a vernier target is flanked by optimally positioned lines, foveal vernier discrimination is strongly degraded (Westheimer and Hauske, 1975). We confirmed this observation (Experiment I) and have mapped out a 2 dimensional "perceptive field" for crowding in the fovea using a 2 dot target (Experiment II). Crowding was also measured in peripheral vision, using either small flanking dots as masks (Experiment III), or using repetitive vernier gratings (Experiment IV). The results showed that when scaled in proportion to recent estimates of the cortical magnification factor, vernier acuity is as good in the periphery as it is centrally. Both centrally and peripherally, there appears to be a psychophysical processing module which we term a "perceptive hypercolumn". At all eccentricities vernier thresholds were found to be approximately 1/40 of the size of a perceptive hypercolumn and were elevated if interfering contours are present in the same (or adjacent) hypercolumns.

Vernier acuity   Spatial interference   Hyperacuity   Periphery   Cortical magnification

INTRODUCTION

When a vernier target is flanked by a pair of optimally positioned lines, foveal offset discrimination is strongly degraded (Westheimer and Hauske, 1975). Such interference effects are ubiquitous in spatial vision, and have been demonstrated to occur for foveal targets in tilt judgements (Westheimer *et al.*, 1976; Andriessen and Bouma, 1976), stereopsis (Butler and Westheimer, 1978) and letter acuity (Flom *et al.*, 1963b). Because spatial interference occurs also under dichoptic conditions (Flom *et al.*, 1963a; Westheimer and Hauske, 1975) it has been considered to reflect a central, neural inhibitory interaction. Spatial interference in Hyperacuity tasks is especially interesting because it operates over distances which are very large when compared to the accuracy of hyperacuity thresholds (Westheimer, 1981). Spatial interference is also evident in the finding that vernier discrimination is severely degraded at high spatial frequencies (Levi and Klein, 1982 a,b; 1983). Thus, an understanding of the neural interactions involved in spatial interference is important to any theory of hyperacuity (Westheimer, 1981; Barlow, 1981; Watt and Morgan, 1983). In the first experiment to be reported here, we have confirmed the results of Westheimer and Hauske (1975) in showing that the strongest interference occurs when flanks are 2-4 min from the target with foveal viewing. Spatial interference also occurs in 2 dot vernier discrimination. With these very localized stimuli, we have mapped

out a "perceptive field" for spatial interference both in the direction of the offset and in the orthogonal direction (Experiment II).

Spatial interference in the periphery

It is generally thought that spatial interference with letter acuity is especially strong in the periphery (Korte, 1923; Bouma, 1970; Lettvin, 1976; Banks *et al.*, 1979). For example, Bouma (1970) reported that for complete visual isolation of a letter presented at an eccentricity of E°, no other letter should be present within a distance of about $0.5 E^\circ$. Similar results occur for tilt judgements in the periphery (Andriessen and Bouma, 1976). Because vernier acuity is especially degraded in the periphery (Bourdon, 1902; Westheimer, 1982), it seemed likely that spatial interference with vernier acuity might be particularly strong in the periphery. Thus we explored spatial interference with vernier acuity (using long abutting targets) in the periphery (Experiment III). We find that vernier acuity for abutting targets is severely degraded in the periphery, falling off more rapidly than grating acuity. However, both foveally and peripherally, the functions relating vernier threshold elevation to the distance of the flanks peaks at a distance approximately 30 times the unflanked vernier threshold. Complete isolation occurs only when the flanks are about 60 times the unflanked threshold value. Thus spatial interference with vernier acuity in the periphery "scales" to the unflanked vernier threshold. Comparable "crowding" occurs with repetitive vernier gratings (Levi and Klein, 1982a, b; 1983) at high spatial frequencies (Experiment IV).

Cortical magnification and hyperacuity

It is of special interest to attempt to relate the decline in visual performance with eccentricity to changes in the anatomy and physiology of the visual system (Weymouth, 1958; Cowey and Rolls, 1974; Rovamo *et al.*, 1978; Koenderink *et al.* 1978; Drasdo, 1977; Virsu and Rovamo, 1979; Schwartz 1980, 1983). Our results, in agreement with Westheimer (1982) show that vernier acuity falls off faster with eccentricity than does grating acuity. The fall-off in vernier acuity is compatible with recent estimates of cortical magnification (Dow *et al.*, 1981; Tootell *et al.*, 1982; Van Essen *et al.*, 1984) while the decline in grating acuity is consistent with retinal factors. The present results show that when scaled to cortical magnification, vernier acuity over a wide range of spatial frequencies is the same in the periphery as it is foveally.

Fig. 2. Vernier threshold (± 1 SE) as a function of the distance of the flanks from the target for four observers.

EXPERIMENT I.
VERNIER ACUITY WITH LONG LINES: SPATIAL INTERFERENCE IN CENTRAL VISION

Methods and stimuli

An example of the stimulus is shown schematically in Fig. 1. The vernier stimulus consisted of two long (1.5°), thin (50"), bright (960 cd/m²), high contrast horizontal lines generated on the CRT of a computer (Commodore 2001 with green phosphor). The display was modified so that the vertical height could be shrunk, making it possible to precisely position the stimuli with high resolution in the vertical dimension (Klein and Levi, 1985). The left hand "reference" line was presented continuously. The test line was flashed for 250 msec in one of 5 positions. The observer's task was to judge whether the test line was above, below or aligned with the abutting reference line, and to rate their confidence by giving numbers from -2 to $+2$. Feedback as to the direction and magnitude of offset was given after each trial. Our psychophysical procedures have been described in detail elsewhere (Levi and Klein, 1983; Levi, Klein and Aitsebaomo, 1984). Thresholds for discrimination of the position of the test line were obtained by calculating a maximum likelihood estimate of the d' values for each stimulus and interpolating to a $d' = 0.675$ equivalent to the 75% correct level (e.g. Westheimer and Hauske, 1975).

The flanking contours were symmetrically placed at various distances from the reference line. These

flanks were presented continuously with the reference line. They were approximately 6% of the length of the reference and test lines. In order to minimize the possibility of a bisection cue, the flanks were adjacent to the reference line and did not extend to the test line as shown in Fig. 1. The flanks were 5.8 min long by 50" wide (the same width as the test and reference lines), and equal in brightness to the test and reference lines.

Three of the observers were the authors who were highly experienced and one observer was naive as to the purpose of the experiment. All observers had normal visual acuity and normal binocular vision. Testing was monocular with the nondominant eye patched via a black occluder. Data were collected in blocks of 125 trials, each preceded by 10-20 practice trials, with the spacing of the flanking lines varied between blocks. Each condition was repeated (in a different order) and the thresholds shown are the geometric mean of the threshold values determined from several (2-5) blocks.

Results

Figure 2 shows the basic phenomenon for the fovea of the four observers with normal binocular vision. Vernier thresholds are plotted as a function of the distance of the flanks (on log-log coordinates). The symbol closest to the ordinate shows the unflanked threshold for each observer. The elTect of the flanks was to elevate thresholds in a nonmonotonic fashion. For each observer the strongest interference occurred when the flanks were about 2-3 minutes away from the reference line. At this point, the thresholds were elevated approximately 3 fold. Moving the flanks closer or further from the reference line resulted in a lowering of threshold, so that when the flanks were 5-8 min away, thresholds returned to the unflanked baseline value. This interference function is in direct agreement with the results of Westheimer and Hauske (1975).

REFERENCE (CONTINUOUS)

—   TEST (FLASHED)

Fig. 1. Schematic of the stimulus. The lefthand (reference) line was presented continuously. The righthand (test) line was flashed for 250 msec. The flanks, which were presented at different distances from the target were also presented continuously.
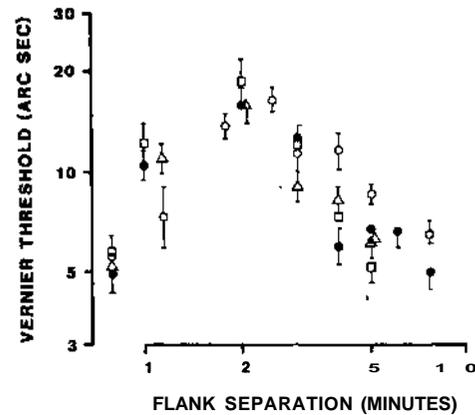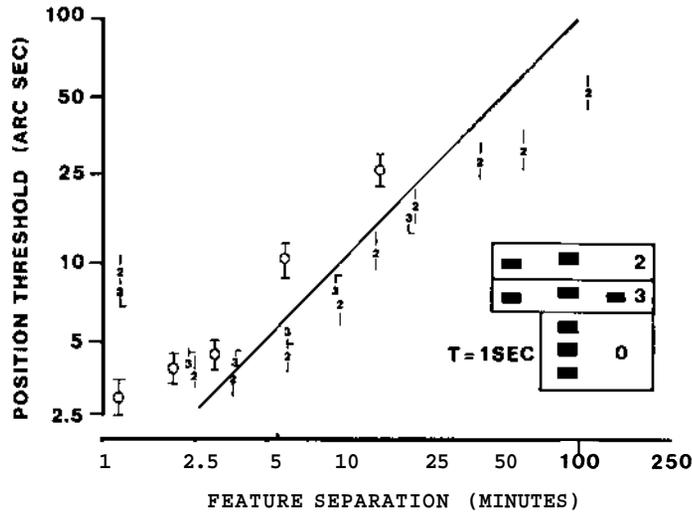
Fig. 3. Position thresholds are plotted as a function of feature separation for 2-dot vernier (2's), 3-dot vernier (3's) and 3-dot bisection (0's) for observer DL. For the 3-dot tasks, separation is specified between the center dot and one of the outer dots. The error bars show ± 1 SE. The solid line has a slope of 1 and is plotted for a Weber fraction = 1/60.

EXPERIMENT II.
VERNIER ACUITY WITH DOTS: A "PERCEPTIVE FIELD" FOR SPATIAL INTERFERENCE

Methods and stimuli

In order to explore interference effects with more localized stimuli, vernier acuity was measured using 2 small bright rectangles (14" high by 1.21′ long). These stimuli appeared as 2 small bright dots. As in Experiment I, one "dot" was presented continuously, and served as a reference. The "test" dot was flashed on for 1 sec in one of 5 positions. The observers' task, as in the previous experiment, was to judge whether the test dot was above, below or aligned with the reference dot, and to rate their confidence. The flanks were identical in size and brightness to the reference dot, and were presented continuously.

The first author served as the main observer for this experiment, however all of the main results have been replicated in other observers and under different luminance levels (Klein and Levi, 1984). Viewing was binocular.

Results

Figure 3 shows the dependence of vernier thresholds on the separation between the centers of the dots (with no flanks). The 2's are the data for the two dot stimulus. The 3's show that the addition of a second reference equally spaced on the other side of the test does not significantly alter the vernier thresholds. Note that at separations of 2.5′–6′ the thresholds are very low. At both smaller and larger separations, thresholds increase. At small separations the increase is caused by blurring. At larger separations thresholds increase, being approximately 1/70 of the feature separation (i.e. equivalent to a constant orientation threshold of about 0.8 deg). The effects of flanking

targets in the direction of the vernier offset was explored by placing the flanks symmetrically on each side of the reference dot, at different distances.

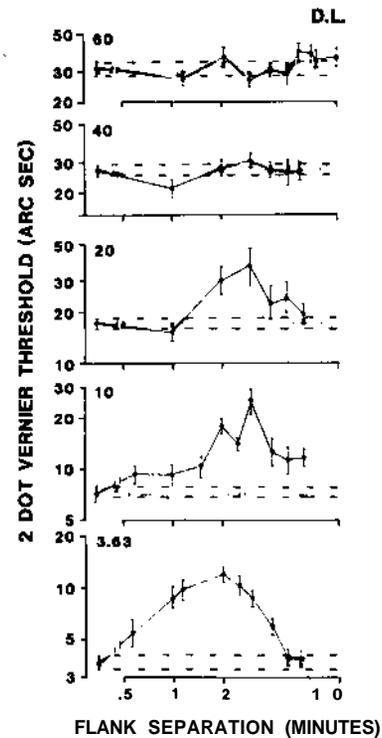Figure 4 shows the effects of flanks on 2-dot vernier thresholds. Each curve represents a different feature

Fig. 4. 2-Dot vernier threshold as a function of the distance of the flanks in the direction of vernier offset. Each graph shows a different feature separation indicated (in minutes of arc) by the number at the top left of each curve. The leftmost datum and hatched line shows the unflanked threshold and its standard error. Observer D.L.

separation. For each curve the leftmost symbol and hatched line shows the unflanked threshold and its standard error. For widely separated targets, flanks do not significantly elevate vernier thresholds; however for separations of 20′ or less, strong threshold elevation is seen when the flanks are 2′–3′ from the reference dot. The 3.63′ curve resembles closely the data of the previous experiment with abutting lines in showing a 3-4 fold threshold elevation when the flanks are at 2′ from the reference. Interestingly, with the flanks at 2′, eliminating the reference dot, gives approximately the same threshold. Under these conditions the observer uses the strategy of bisecting the flanks to make the position judgements.

These results clearly demonstrate that flanking contours *in the direction of the vernier offset* and at an optimal distance, strongly mask vernier discrimination. What are the properties of spatial interference in the orthogonal direction?

In order to examine this question, we measured 2 dot vernier discrimination for optimally spaced targets (3.63′) and placed the flanking dots at a variety of locations, both in the direction of offset and orthogonal to it. Figure 5 shows a few examples of the data. Each curve shows flanks at a fixed distance in the direction of offset. The abscissa is the distance of the flanks from the reference dot in the direction orthogonal to the offset. Thus at 0, the flanks are symmetrically placed about the reference (as shown in the schematic stimulus in Fig. 5). At +3.63′, the flanks surround the test dot (at the distance indicated in the upper left hand corner of each curve). The hatched lines, show the unflanked threshold and its standard error. The results show clearly that spatial interference with vernier discrimination is strongest when the flanks are lined up with the reference dot. The effect of the flanks diminishes not only as the flanks are moved away from both the reference and test dots (i.e. negative numbers in Fig. 5), but also, surprisingly, when the flanks are moved toward the test dot. The data at +3.63 are with (continuously viewed) flanks on either side of the (flashed) test dot. For all flank separations about the test dot there is negligible threshold elevation. The explanation for this surprising rinding is quite simple. When the flashed test dot was flanked, the observer was able to use a different cue to spatial location, viz. bisection. We have shown previously with long lines that bisection can result in remarkably low position thresholds (Klein and Levi, 1985). The open circles in Fig. 3 show that 3-*dot* bisection is also very good. For large separations, the thresholds are approximately 1/30 of the feature separation, and at small separations (<2′) bisection thresholds are lower than vernier thresholds. Thus, with flanks symmetrically placed at 2′, the bisection cue could result in position thresholds of about 4", as shown in Fig. 5.

Figure 6 shows the "perceptive field" for spatial interference. Two dot vernier thresholds (separation 3.63′) were measured with flanks in 70 different

locations both in the direction of offset and in the orthogonal direction (30 of these points are shown in Fig. 5). Figure 6 summarizes the data (representing approximately 18,000 trials) in the form of a contour plot of iso-threshold elevation lines. The contour lines are at thresholds of 3.0, 2.5, 2.0 and 1.5 times the unflanked threshold. This contour plot demonstrates clearly that: (1) The strongest inhibition is extremely localized in both directions. (2) The visual system is capable of using more than one cue for position; thus, where a bisection strategy can be used (with the flanks in the plane of the test dot) threshold elevation is insignificant. (3) Thresholds are elevated by 50% or more in a square area 9′ on a side, centered at the midpoint of the test-reference pair. (4) The perceptive field exhibits a marked asymmetry about the test-reference pair. It is important to keep in mind that our stimulus configuration is asymmetric in that the test dot was flashed, while the reference and Hanks were on continuously and more importantly, the two flanking dots were always symmetric with respect to the reference dot but not the test dot. This
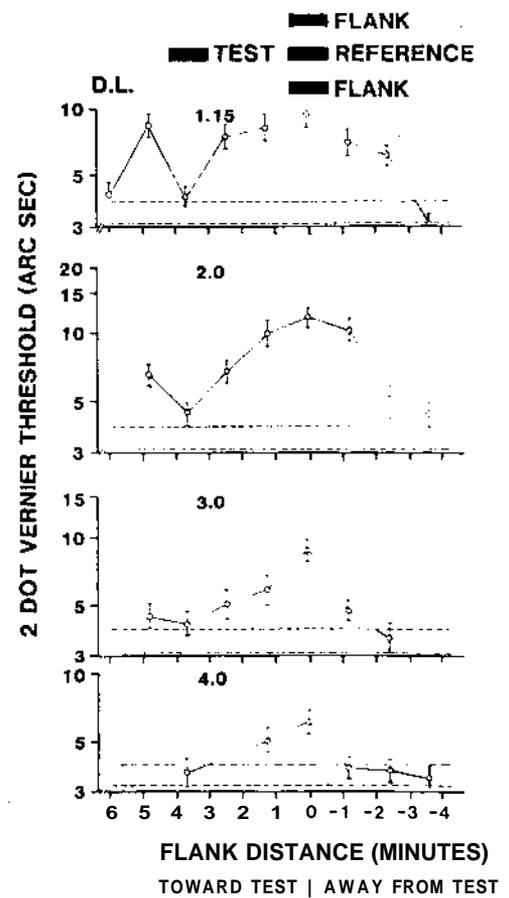

Fig. 5. 2-Dot vernier threshold (feature separation 3.63′) as a function of the distance of the flanks from the (continuously viewed) reference dot in the direction *orthogonal* to the offset. Each curve shows flanks at a fixed distance (indicated in minutes of arc by the number at the top of each curve) in the direction of the offset. The hatched line shows the unflanked threshold ± SE. Observer D.L.
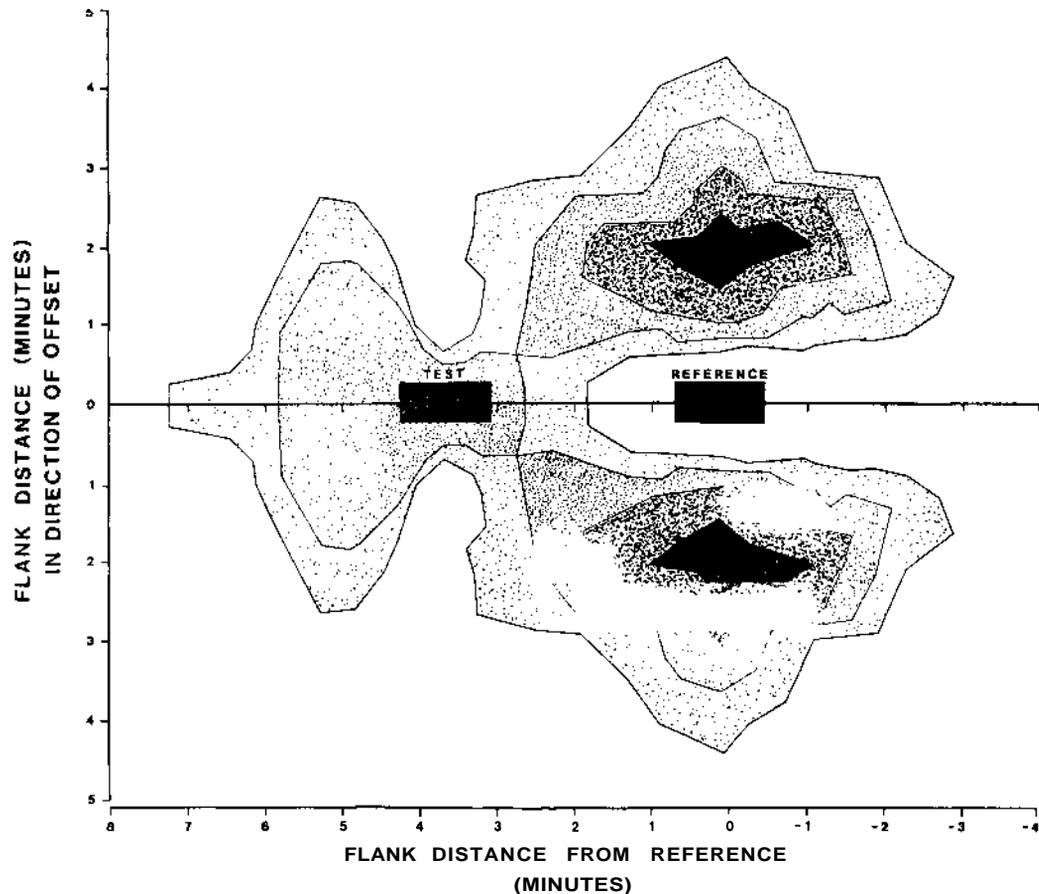
J

Fig. 6. A "perceptive field" for spatial interference. Flanking dots were placed in 72 locations both in the direction of offset, and in the orthogonal direction. This figure summarizes the data in the form of a contour plot of the iso-threshold elevation lines. Contour lines are at thresholds of 3.0, 2.5, 2.0 and 1.5 times the unflanked threshold. The greatest threshold elevation is shown by the darkest shading. Observer **D.L.**

asymmetry in the stimulus configuration is undoubtedly the source of the asymmetry in the "perceptive field".

Williams and Essock (1985) have recently found similar results using a small rectangular background as the masking stimulus. The main difference between our results and theirs occurred when the flanks were adjacent to the test dot. Our stimulus configuration provided a strong bisection cue, whereas the stimulus of Williams and Essock (1985) had only a weak bisection cue.

Spatial interference under dichoptic conditions

In order to determine the site of spatial interference Westheimer and Hauske (1975) performed a dichoptic experiment. They placed the vernier stimulus in one eye, and the flanks in the other. Under these conditions, they reported that spatial interference was strong. We have replicated this finding. This was done by polarizing the stimuli so that one eye saw the test and reference dots (separated by 6′) and the other eye saw the flanks. In order to avoid the strong rivalry effects encountered in our standard conditions, it was necessary to briefly flash (150 msec)

both the test and reference dots, while the flanks remained continuously visible. A border, seen with both eyes, served as a fusion lock. Under these conditions, the threshold with no flanks was 8″. When flanks were placed at 2.6′ from the target (but in the other eye) the threshold was elevated by a factor of two (16″ $\pm$ 2.4″). Placing the flanks in the same eye gave a threshold of 19″ $\pm$ 3″. Thus, interference is about as strong dichoptically as monocularly. Placing the flanks 6′ from the target (either in the same eye, or in the fellow eye) gave thresholds equal to the unflanked condition.

EXPERIMENT III.
SPATIAL INTERFERENCE IN THE PERIPHERY

Methods and stimuli

The basic experiment involved determining vernier thresholds as a function of the separation of the flanks in the fovea, and at 2.5°, 5° and 10° in the lower visual field. The stimuli and methods were essentially those used in Experiment I. For peripheral viewing, the stimulus dimensions were "scaled" in proportion to the grating acuity values typical of

each retinal locus (Westheimer, 1979). This was accomplished by keeping the physical stimulus the same at all eccentricities and varying the viewing distance according to $d = d_f/ + E/2.5$) where E is the eccentricity in degrees and d_f is the distance used for foveal viewing. Thus for $E = 2.5°$ the height, width and length of the stimulus was doubled with respect to the foveal values, by halving the viewing distance (Levi *el al.*, 1984).

Two highly practiced observers participated in the periphery experiments. One observer was one of the authors (P.A.) who had normal binocular vision and normal visual acuity in each eye. The second observer (J.M.) was an anisometropic amblyope, with corrected to normal vision in his nonamblyopic eye. For both observers testing was monocular with the non-dominant eye patched via a black occluder. Since the periphery is highly susceptible to the effects of practice (Saugstad and Lie, 1964; Johnson and Leibowitz, 1974; Fendick and Westheimer, 1983) the observers were given extensive practice (> 6000 trials) distributed across eccentricity, prior to the final data collection.

Acuity was also measured for square wave gratings at each eccentricity using the same CRT display and using the method of adjustment.

Results

Figure 7 shows data at four retinal loci (foveal, and 2.5°, 5° and 10° in the lower visual field) for P.A. and J.M. There are several points of interest here. (1) The unflanked thresholds are markedly elevated with increasing eccentricity. This fall-off will be considered in the next section. (2) Spatial interference extends over greater distances in the periphery than in the fovea. Thus, the peak interference, and the distance over which thresholds are elevated with respect to the baseline, shift systematically to greater distances with increasing eccentricity. (3) In the periphery, the interference function has the same shape on these log -log coordinates. Thus, the interference effect appears to scale in accord with the unflanked threshold value at each retinal locus. This can be seen in Fig. 8 where the unflanked thresholds at each eccentricity are plotted against the flank distance at which (1) the interference function peaked (circles) and (2) the threshold fell to $1/e$ of its value at the peak (triangles). The dashed line is a theoretical line with a slope of 1. This would be expected if the interference "scaled" to the unflanked threshold value. The actual slopes obtained for the peak and $1/e$ data (1.09 ± 0.062 and 1.08 ± 0.08 respectively) were compatible with a slope of 1 suggesting that the threshold values and interference effects are linearly related. Thus when scaled to the unflanked threshold at each peripheral retinal site, the extent of interference is identical to that observed at the fovea. Both foveally and peripherally, peak interference occurs when the flanks are about 25-30 times the unflanked threshold distance and there is still significant interference when the flanks are 50-60 times the threshold distance away.

The linear relationship between the extent of spatial interference and the (unflanked) peripheral vernier threshold is at first glance surprising. Many spatial acuity tasks are known to be subject to spatial interference; however, these effects are often considered to be stronger and/or more extensive in the periphery (e.g. Bouma, 1970). The present results suggest that interference effects with vernier acuity are in fact more or less homogeneous across the central 10°; however, the "scale" changes.
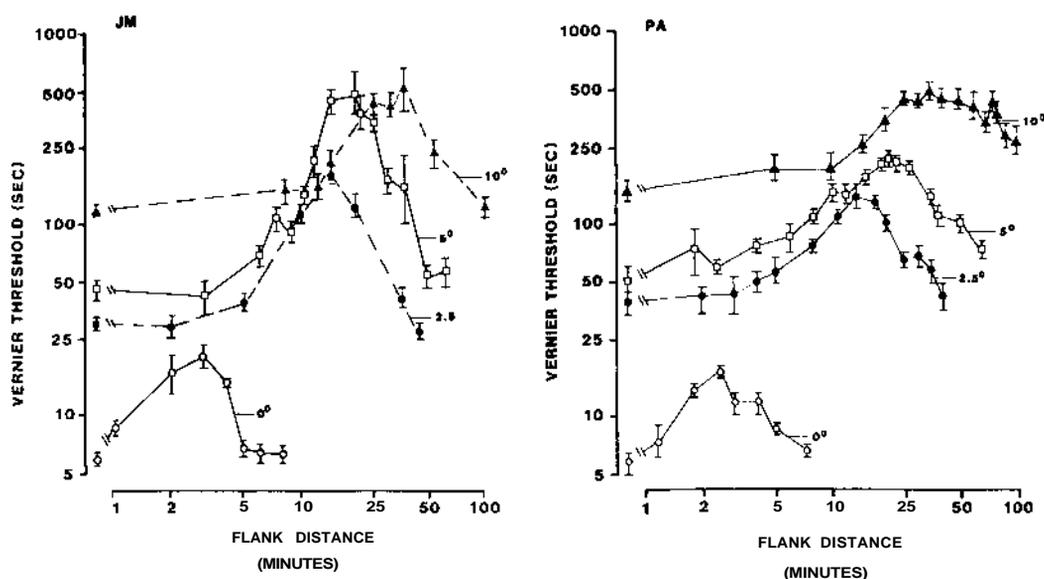

Fig. 7. Vernier threshold as a function of flank separation at 0°, 2.5", 5" and 10 in the lower visual field. Unflanked thresholds for each eccentricity are shown by the symbols nearest the ordinate. Observers J.M. and P.A.

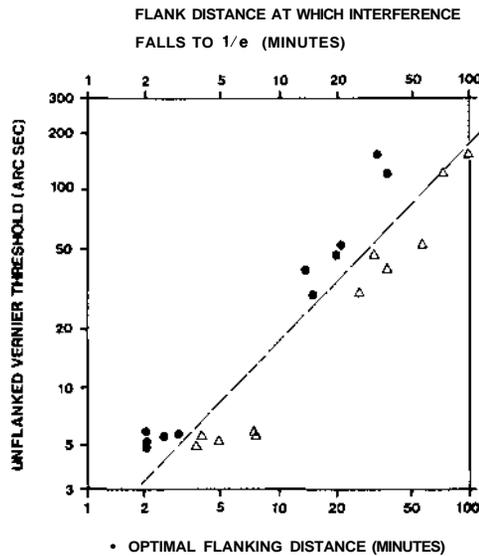FLANK DISTANCE AT WHICH INTERFERENCE
FALLS TO 1/e (MINUTES)

Fig. 8. The unflanked vernier thresholds obtained with foveal viewing (Fig. 2 for each of 4 observers) and at 2.5°, 5 and 10 in the lower visual field (J.M. and P.A. from Fig. 7) are plotted against the distance at which the flanks raised threshold maximally (circles), and the distance at which thresholds fell to √e of their maximal value (triangles). The dashed line has a slope of 1.

The present results also help clarify the relationship between interference and resolution. Foveally, interference effects occur maximally when the flanks are at about 2 to 3′—about an octave below the resolution limit. As has been previously reported (Westheimer, 1982) vernier acuity falls off more rapidly in the periphery than does grating resolution. Figure 9 shows how unflanked vernier acuity and grating acuity covary foveally, and at 2.5, 5 and 10° in the lower visual field for the two observers (on log-log coordinates).

The dashed line has a slope of 1—which would be expected if vernier and grating acuity showed a similar decline in the periphery. The data show that in fact vernier acuity declines more rapidly than does grating acuity in the periphery; however, at each eccentricity, vernier acuity remains better than grating acuity. With respect to interference effects, the results show that interference is strongest at about two to three times the resolution limit foveally, but at 5 deg, interference is optimal at about 20′ i.e. about 7 to 8 times the resolution limit and at 10° interference is strongest at about 10 times the resolution limit. Thus, interference with vernier acuity seems to be a property of the mechanisms involved in vernier discrimination, and is distinct from the resolution capacity. These results are somewhat analogous to our finding in strabismic amblyopes (Levi and Klein, 1982a, b). In those experiments, strabismic amblyopes, when tested with repetitive vernier gratings showed a decoupling between vernier acuity and grating acuity, with their vernier acuity being more degraded than their grating acuity. For normal observers with foveal viewing, vernier acuity was degraded when the interline separation was within a factor of two to three of the cutoff spatial frequency. In strabismic amblyopes this "crowding" occurred at interline separations well below their cutoff spatial frequency (a factor of 4 to 10).

The fourth experiment was undertaken with two aims in mind (1) to test whether this "crowding" of vernier acuity at high spatial frequencies is analogous to the spatial interference effects described above and (2) to ask what sets the scale for vernier acuity in the periphery.

EXPERIMENT IV.
VERNIER ACUITY WITH GRATINGS IN CENTRAL AND PERIPHERAL VISION

The problem of scaling

There has been over a long period of time, a strong interest in attempting to relate variations in visual performance with eccentricity, to changes in the anatomy and physiology of the visual system (e.g. Weymouth, 1958; Cowey and Rolls, 1974; Drasdo, 1977; Rovamo et al., 1978). For a variety of resolution tasks, the retinal periphery performs as well as central vision when the stimulus size is "scaled" in proportion to the inverse of the linear cone density at each eccentricity (Weymouth, 1958; Koenderink et al., 1978; Rovamo et al., 1978; Virsu and Rovamo, 1979; Virsu, 1983; Wilson, 1970). This scaling factor has frequently been characterized as the "cortical magnification" factor which corresponds to the linear extent of cortex (in mm) corresponding to one degree of visual angle. One notable exception to this scaling rule are the position acuities (vernier, phase and
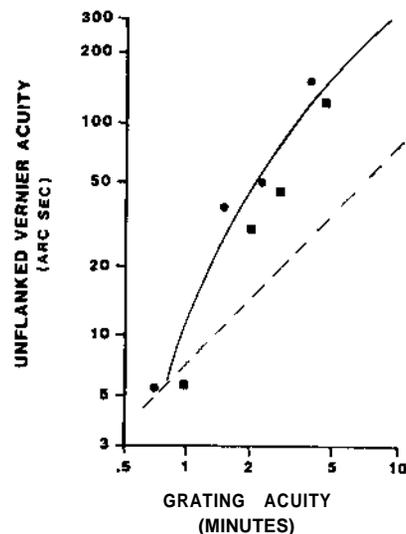
Fig. 9. Unflanked vernier thresholds vs grating acuity at 0°, 2.5°, 5 and 10 in the lower visual field for observers J.M. (squares) and P.A. (circles). The dashed line has a slope of 1. The solid line has the form $V = 0.7G - 0.3$ where V = vernier acuity and G = grating acuity.

stereopsis) which decline more rapidly with eccentricity than contrast sensitivity or grating acuity (Westheimer, 1982; Klein and Tyler, 1981; Stephenson and Braddick, 1983; Fendick and Westheimer, 1983). There are several possible accounts for the relatively sharp decline of position acuity in the periphery compared to grating acuity. One is that different psychophysical tasks may be processed in different cortical regions, each with its own magnification factor (Jamar *et al.*, 1984). Or the periphery may lack the specialized mechanism required for position acuity. The explanation preferred by us is that retinal and cortical factors can impose different limits on psychophysical performance. Some tasks (e.g. resolution) may be limited primarily by retinal factors (e.g. the blur-function of the eye; cone density etc.), while other tasks (e.g. position acuities) may be primarily limited by cortical processing (Westheimer, 1982; Barlow, 1979, 1981).

It has been widely accepted that magnification of the foveal representations in the cortex and in the retina are approximately equal (Drasdo, 1977; Rovamo *et al.*, 1978). However, recent physiological and anatomical evidence suggests that cortical magnification of the foveola is considerably higher than previously estimated, and that emphasis on central vision is far greater in the cortex than in the retina (Malpeli and Baker, 1975; Dow *et al.*, 1981; Tootell *et al.*, 1982; Van Essen *et al.*, 1984) or in the LGN (Connolly and Van Essen, 1984).

The inverse of the cortical magnification factor, M^{-1} (the number of degrees of visual space/mm of cortex) rises approximately linearly with eccentricity (Daniel and Whitteridge, 1961; Hubel and Wiesel, 1974; Dow *et al.*, 1981) as do many spatial acuities (Weymouth, 1958; Genter *et al.*, 1981). Figure 10 replots the physiological data from Dow *et al.*'s two monkeys. This figure shows the inverse of cortical magnification (in deg/mm) as a function of eccentricity on linear coordinates. For each monkey it can be seen that M^{-1} rises approximately linearly with eccentricity. This rise takes the form $M^{-1} = k(E + X)$ where E = eccentricity and k = slope. The lines, fit independently to the data of each monkey by nonlinear regression, have been extended to intersect the X axis at approximately $E = -0.77°$. This X axis intercept is a scale free factor which can be used to summarize the variation of anatomical, physiological or psychophysical factors with eccentricity by a single parameter. X shows at what eccentricity the foveal value will double. Table 1 provides the values of X for M^{-1} as well as for CD^{-1} (inverse of cone density) and a variety of psychophysical tasks. Many previous investigators have assumed that the value of X for M^{-1} was approximately 2.5-3.5, like that for CD^{-1} (Rovamo *et al.*, 1978; Drasdo, 1977; Sakitt and Barlow, 1982); however, our analysis of the data of Dow *et al.* (1981) sugget X should be about 0.77. Thus, their data on M^{-1}, measured very close to the fovea, suggests that the cortical representation of the fovea is magnified three to four times compared to the retinal representation. Interestingly, the results of Daniel and Whitteridge (1961) shown by the stars in Fig. 10 are consistent with Dow *et*.'s results, as are the recent results of Tootell *el al.* (1982), and Van Essen *et al.* (1984).

To test this new version of cortical magnification, vernier acuity was measured at several eccentricities
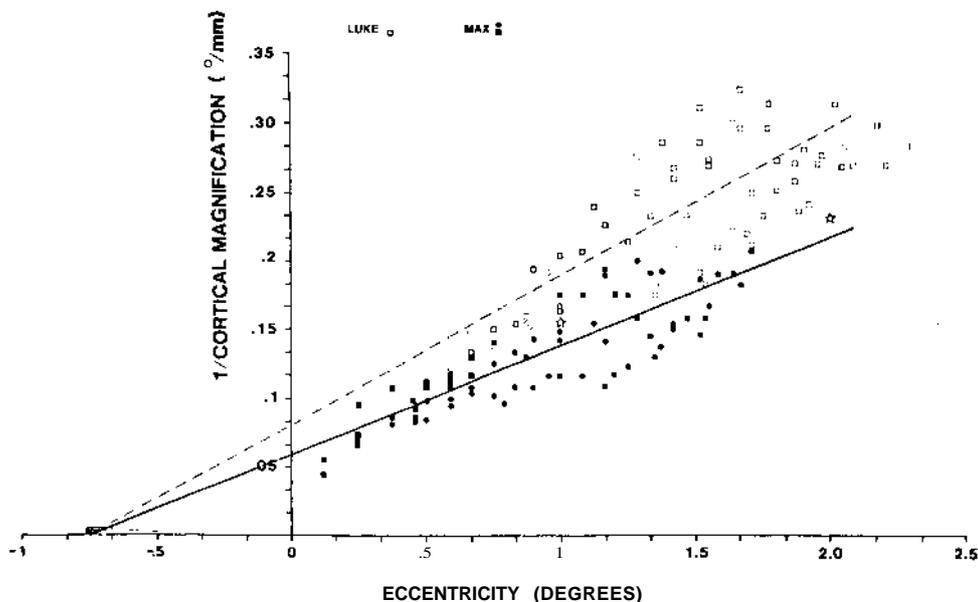

Fig. 10. Inverse cortical magnification (deg/mm) vs eccentricity for the 2 rhesus monkeys of Dow *et al.* (1981). The straight lines were (it to the data of each monkey independently via linear regression. The stars are data from Daniel and Whitteridge (1961).

Table 1

Dependent variable	Investigator(s)	X-intercept (deg)	
Cortical mag. factor^{-1}	Dow *et al.*	0.77 ±0.1 (Max)*	
		0.76 + 0.25 (Luke)	
Cortical mag. factor^{-1}	Tootell *et al.*	0.97	
Cortical mag. factor^{-1}	Van Essen *et al.*	0.82	
Cone density^{-1}	Rolls and Cowey	0–2.5	2.31[a]
	(macaque)	0-5°	2.35
		0-10°	3.2
	Osterberg	0–2.5°	1.7
	(human)	0–5	2.05
		0-10°	2.9
Grating acuity	Present study	3.0 + 0.24 (J.M.)	
		2.2 ± 0.07 (P.A.)	
Grating acuity	Westheimer	2.6 ± 0.6 (X)	
Vernier acuity	Present study	0.77 ±0.05 (J.M.)	
		0.62 ±0.08 (P.A.)	
Stereoacuity	Fendick and Westheimer	0.74 ±0.08 (X)	
Phase discrimination†	Klein and Tyler	0.77 ±0.25 (X)	
Unreferenced motion‡	Levi *et al.*	5.6 ±0.67 (P.A.)	
Relative motion	Levi *et al.*	1.05 ±0.18 (P.A.)	

The error bars equal one standard error obtained by nonlinear regression. The regression is nonlinear since the Y intercept is the product of X and k.
[a]The decline of cone density with eccentricity is not linear. Therefore the X-intercept depends upon the eccentricity to which it is measured.
*The data for each of Dow *et al.*'s monkeys are presented.
†The task was to center a thin dark line on the peak of a cosine grating. The phase threshold at each eccentricity was measured.
‡Detection thresholds for motion.

with several spatial frequencies. Abutting stimuli were utilized to ensure that the judgements were based upon very localized cues.

Methods and stimuli

The vernier stimuli consisted of two rows of vertical lines on a dark background with a horizontal offset between the upper and lower rows, presented for 250 msec on the CRT of a computer (see inset, Fig. 11). Thresholds were measured in the fovea and at 2.5°, 5° and 10° in the lower visual field of the two highly practiced observers who participated in the previous experiment. Viewing was monocular. For peripheral viewing the stimulus dimensions were "scaled" in proportion to . This was accomplished by keeping the physical stimulus the same at all eccentricities and varying the viewing distance according to $d = d_f/(+ E/0.77)$ where E is the eccentricity in degrees and d_f is the distance used for foveal viewing. Thus, at each eccentricity, the dimensions of each screen element (pixel) were scaled in height,
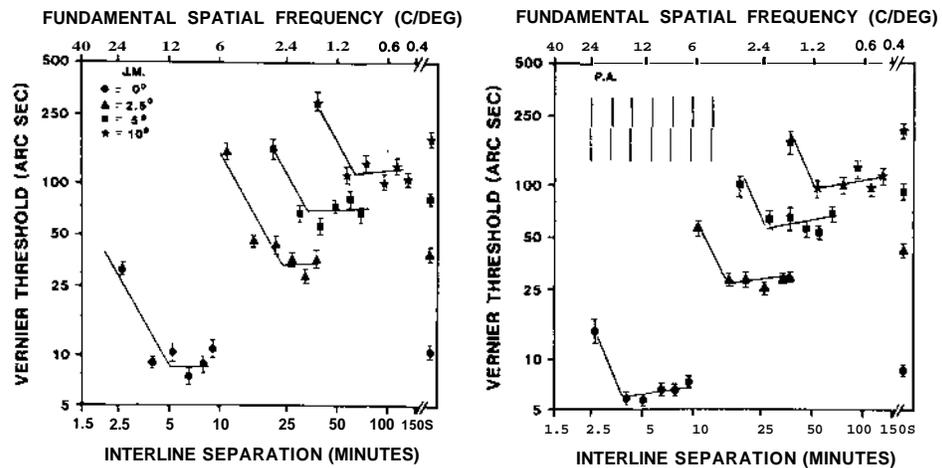

Fig. 11. Vernier thresholds as a function of interline separation at 0 . 2.5 . 5 and 10 for J.M. and **P.A.** The inset shows the repetitive vernier target schematically. At each eccentricity the stimulus size was scaled according to M^{-1}. The S shows vernier thresholds for classical vernier targets (i.e. single lines).

width, spacing etc. to provide equal cortical valence. For foveal viewing the lines were 12.5′ long, and thin (10″). Edge effects were minimized by giving the lines at the ends random offsets. In order to avoid the ambiguities which can occur with repetitive stimuli, the offsets used never exceeded one fourth of the interline separation.

The psychophysical procedures were identical to those in the previous experiments.

Results

Figure 11 shows how vernier thresholds vary as a function of the interline separation (I/spatial frequency) at each retinal locus. Foveally, thresholds are approximately invariant with large interline separations, but increase sharply at small separations (high spatial frequencies; Levi and Klein, 1982a, b). Similar functions are obtained peripherally; however the thresholds are much higher than in the fovea, and the sharp increase in thresholds occurs at much larger separations. The thresholds for single vertical lines, and the interline distances at which thresholds begin to rise, are similar to the data of Experiment III. Because of the repetitive nature of these stimuli, the thresholds continue to rise as the interline separation is made smaller. The data of the periphery are reminiscent of the results of strabismic amblyopes (Levi and Klein, 1982a, b) in that vernier acuity and grating acuity are decoupled, with vernier acuity falling off more rapidly than grating acuity. This can be seen in Fig. 12, which shows the *relative* rise in the optimal vernier threshold and grating acuity threshold at each retinal locus. In this normalized plot, it is of interest to note that vernier thresholds covary with Dow *et al.*'s (1981) estimate of M^{-1} (solid line). Grating acuity thresholds on the other hand rise 3-4 times slower. It is of interest also to note that the variation in *human* cortical magnification factor in the lower visual field is compatible with monkey cortical magnification, and with the present vernier data. The *X*'s in Fig. 12 are estimates of human cortical magnification in the lower visual field made by Cowey and Rolls (1974). They calculated *M* using information provided by Brindley and Lewin (1968), who plotted the distribution of phosphenes evoked by stimulation of the visual cortex in a human patient with electrodes implanted on the visual cortex at known distances. Our analysis of their data (from Fig. 2, method I) suggests that the variation in human *M* with eccentricity is similar to that of monkey *M*. For their data within the central 10°, the *X* intercept is 0.8 (albeit with a large error bar, ±0.9). Table 1 summarizes the results of a number of studies of variations in visual capacity with eccentricity, by giving the *X* axis intercepts. Our analysis suggests that those capacities for which the fovea is highly specialized i.e. the hyperacuities (stereopsis, vernier, relative motion and phase discrimination)* rise in threshold with eccentricity like ^{1}, while resolution (e.g. grating acuity) shows a slower rise with eccentricity. This may reflect the fact that resolution is limited by retinal factors (viz, the line spread function of the eye, the variation in cone density, and the size of the receptive fields of retinal ganglion cells). Interestingly, *unreferenced* motion falls off very little in the periphery. The large *X* intercept for unreferenced motion may be a consequence *not* of peripheral specialization for motion, but because of a floor effect for detecting motion with no nearby reference (Levi *et al.*, 1984).

Figure 13 presents the vernier data of Fig. 11 but now the abscissa is the interline spacing in cortical units (mm of cortex; lower abscissa) or cortical spatial frequency (upper abscissa). Similarly the left hand ordinate is now also expressed in terms of threshold vernier offset in mm of cortex.

The specific values for the axes of Fig. 13 are based upon the assumption that the mean human foveal magnification (M) is 15 mm/degree (Cowey and Rolls, 1974). This is in good agreement with other recent estimates of foveal *M* in monkeys (Dow *et al.*, 1981; Tootell *et al.*, 1982; Van Essen *et al.*, 1984) which are on the order of 10–12 mm/deg. Since human striate cortex is about twice as large as that of rhesus monkeys (Schwartz, 1980), and their visual capabilities are similar with respect to visual field coordinates, human foveal *M* should be approximately *2* times bigger than that of rhesus. Thus we have assumed a foveal *M* = 15mm/deg (i.e. 1 mm of cortex = 4′ of visual field foveally); however, the specific value chosen for foveal *M* is not critical. What is important, is the *relative* change in *M* with eccentricity. If our scaling procedure was appropriate, then at each eccentricity each screen element (pixel) would stimulate an equal *cortical* distance. For example, foveally each pixel subtended 0.16′ or 0.04 mm of cortex. At 10° each pixel subtended 2.3′, but an *equal* cortical distance. In Fig. 13, the left hand ordinate then represents the threshold offset in cortical distance, while the abscissa represents the interline spacings (which ranged from 16 to 72 pixels at all eccentricities) in terms of cortical spatial frequency or distance. (The mathematical formula for obtaining cortical mm is given in the discussion.) When the data of Fig. 11 are replotted in terms of cortical distances, the widely disparate functions obtained at each eccentricity collapse to a more or less unitary function, suggesting that when scaled according to M^{-1} vernier discrimination is *as good* in the periphery as it is foveally. Moreover, in units of cortical distance, vernier thresholds are less than 0.05 mm regardless of eccentricity and are degraded when the interline spacing is < 1 mm.

As noted previously, many peripheral thresholds

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*It should be noted however that the stimulus size in the stereopsis, relative motion and phase discrimination experiments were inappropriately scaled to CD^{-1} rather than M^{-1}.

Within the central 10 cone density is approximately equal to ganglion cell density (Weymouth, 1958).
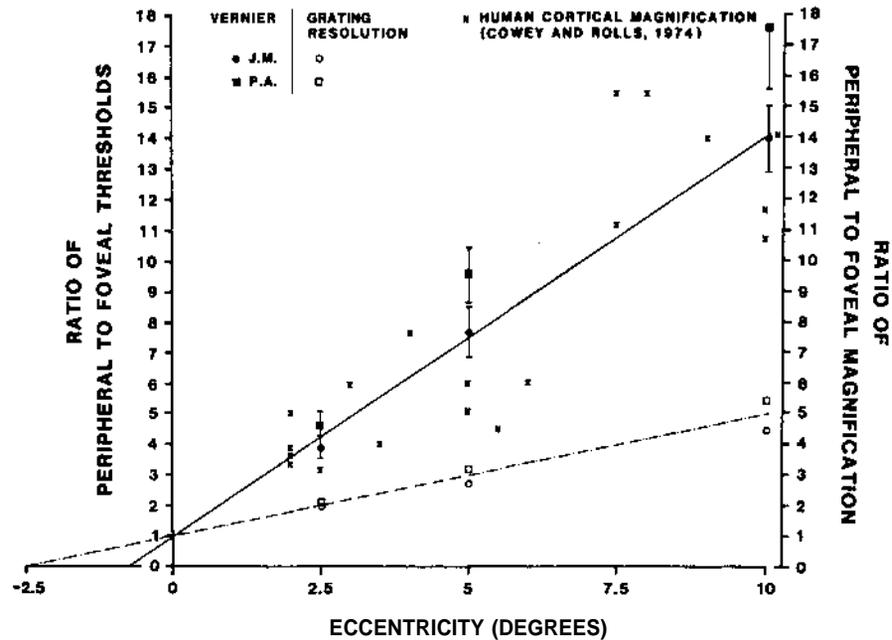
Fig. 12. The ratio of peripheral to foveal thresholds for optimal vernier acuity (solid symbols) and for grating acuity (open symbols) for J.M. and P.A. The solid line shows the ratio of peripheral to foveal I   from Dow *et al.* (1981). The dot-dashed lines shows the ratio of peripheral to foveal CD   from Rolls and Cowey (1970). The X's are estimates of human cortical magnification in the lower field from Cowey and Rolls (1974).
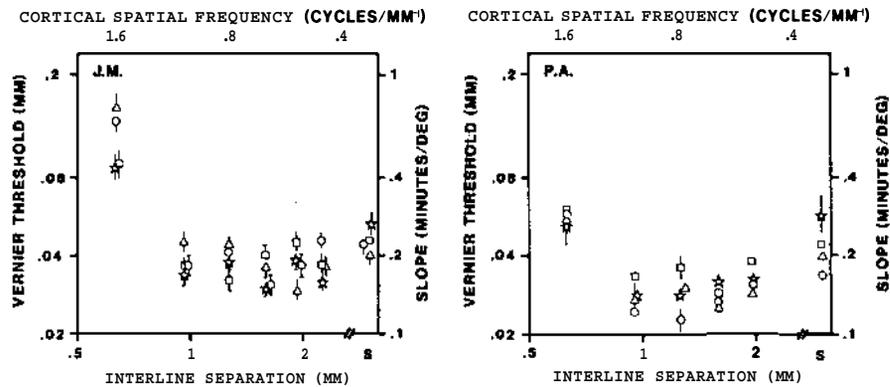

Fig. 13. The data of Fig. 11 are replotted here. Now the interline spacing (lower abscissa) or fundamental spatial frequency (upper abscissa) are in units of cortical distance. Similarly, the threshold vernier offset at each eccentricity is expressed in units of cortical distance. When plotted in this way, the widely disparate curves of Fig. 11 collapse to a more or less unitary function. The righthand ordinate is the slope (i.e. the threshold expressed in minutes per degree of eccentricity). This provides a measure of the absolute diffculty of the task.

can be summarized by the equation Th = slope x $(E + X)$. In order to completely specify visual function in the periphery, *two* parameters are needed. One is X, which gives the difficulty of the task in the periphery *with respect to* the foveal threshold. The other is the slope (the threshold in minutes per degree of eccentricity) which provides a measure of the absolute difficulty of the task in the periphery. For vernier acuity, the slope is approximately 0.17 (righthand ordinate in Fig. 13); for grating acuity it is approximately 0.35 (present study; Wertheim, 1894; McKee and Nakayama, 1984). Thus, in absolute terms vernier acuity remains better in the periphery than grating acuity.

This study investigated spatial interference with vernier acuity in central and peripheral retina. The results showed that under a variety of conditions (abutting long lines; 2 dots), thresholds are stongly elevated by optimally placed flanks. Foveally and peripherally, flanking was strongest when the flanks were 25-30 times the unflanked threshold distance from the target. It seems surprising that a visual system which can discern positional information with a grain of a few arc seconds (foveally) is subject to interference over relatively large distances. The "perceptive-field" for interference in the fovea determined with closely spaced dots, was shown to be an elongated region extending about 4.5′ on either side of the stimulus in the direction of offset, and about 9′ in the orthogonal direction. Since these interfering effects occur under dichoptic conditions, they cannot be attributed to light scatter, blur or retinal effects, and it is likely that they are cortical. Moreover, these effects are also evident in the cortical potentials (VEPs) evoked by suprathreshold vernier offsets (Steinman *et al.*, 1985). Such interference effects are ubiquitous in spatial vision and occur for orientation discrimination (Westheimer *et al.*, 1976), stereopsis (Butler and Westheimer, 1978), Snellen acuity (Flom *et al.*, 1963b), as well as vernier acuity (Westheimer and Hauske, 1975 and the present study). Moreover, similar effects occur when a rectangular luminous background is added to a two dot vernier target (Williams *et al.*, 1983; Williams and Essock, 1985). These data, when considered in the light that hyperacuity information can be integrated over zones of several minutes of arc in the fovea (Westheimer and McKee, 1977), suggest that line position coding requires a processing zone of several minutes of arc (foveally), i.e. 20-40 times the positional threshold accuracy. Moreover, Westheimer and McKee (1975) showed that briefly exposed vernier stimuli were quite resistant to retinal image motion of less than about 4″/sec. Thus, during the integration time of 1/50 sec, the stimulus would travel over a distance of at least 30 times the vernier threshold distance measured (Barlow, 1981).

Why is it that a visual system capable of discerning position with an accuracy of a few arc seconds, is susceptible to interference from stimuli 30 times further away? In the flanking experiments of Westheimer and Hauske (1975) and the present study, with foveal viewing, at the peak of the function relating flank distance to threshold, a vernier offset of 18″ produces the same effect as an offset of 6″ with no flanks. One interpretation is that the flanks "repel" the dot or line with the offset. Watt (1984) has pointed out that this is precisely what happens to the peaks and troughs in the second derivative of the optically and neurally blurred stimulus. The data of the periphery however, suggest that optical or retinal blurring has a minimal effect and that the size of the

zone of interference is "linked" to the unflanked threshold. It is interesting to note that the results of Experiment IV (shown in *cortical* units in Fig. 13) suggest that crowding occurs when the interline separation is less than 1 mm. This cortical distance corresponds reasonably well with the dimension of a human cortical ocular dominance column (Hitchcock and Hickey, 1980). Thus, we conjecture that interference may occur only when the interfering stimuli fall within the same (or adjacent) cortical ocular dominance column(s) as the target. This notion is similar to the suggestion of Barlow (1981), and is discussed further in the next section.

In the normal periphery, vernier acuity falls off about 3-4 times faster than grating acuity (relative to fovea). Since the optimal flanking distance scales to the (unflanked) vernier acuity, in the periphery the interfering targets are widely spaced with respect to the resolution limit. Analogous results occurred with repetitive vernier gratings; thus, in the periphery, as was the case for strabismic amblyopes (Levi and Klein, 1982a, b) "crowding" occurred at spatial frequencies well below the resolution limit. The subsequent paper (Levi and Klein, 1985) shows that crowding of vernier acuity in strabismic amblyopes, like the normal periphery, occurs at distances proportional to the unflanked thresholds.

Cortical magnification and hyperacuity

The results of Experiment IV suggest that (1) vernier acuity remains better than grating acuity in the periphery; (2) when "scaled" in proportion to recent estimates of the cortical magnification factor (Dow *et al.*, 1981; Tootell *et al.*, 1982; Van Essen *et al.*, 1984), vernier acuity is as good in the periphery as it is centrally. This result is surprising since position acuities (vernier, phase and stereopsis) have generally been considered to be especially poor in the periphery. Our analysis suggests that relative position can be made equally visible at any eccentricity by scaling according to M. That the scaling factor for position acuity is different than for grating acuity may simply reflect the fact that resolution is limited by retinal processes, while position acuity is limited by cortical processes. Thus, vernier acuity, stereoacuity and phase acuity all have X intercepts (Table 1) compatible with Dow *et al.*'s estimate of cortical magnification. The close match between the psychophysical results, and the cortical magnification data of Dow *et al.* (1981) is quite striking, and perhaps to some extent serendipitous since there is likely considerable within species (as well as interspecies) variation in size of striate cortex (Van Essen *et al.*, 1984). What is clear is that the relative change in magnification from fovea to periphery, is considerably different in the cortex than it is in the retina and LGN (Van Essen *et al.*, 1984; Connolly and Van Essen, 1984). Moreover, while the relative fall-off of grating acuity in the periphery may be consistent with retinal limitations, the decline of position acuities seems to
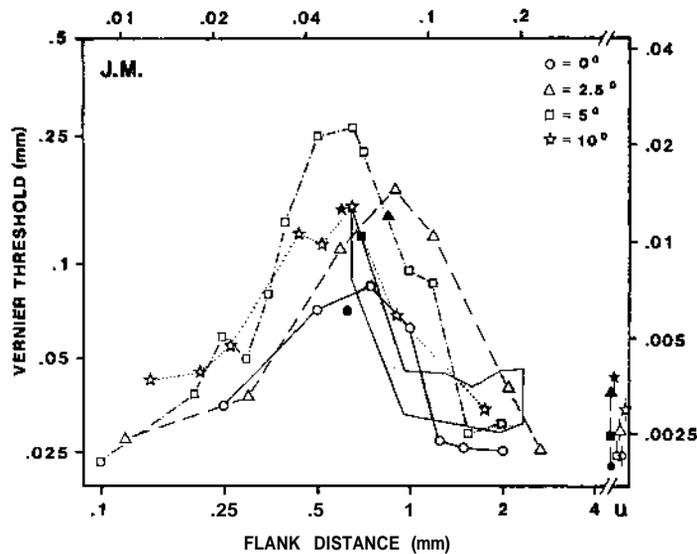
Fig. 14. The open symbols replot the data of J.M. from Fig. 7, in units of cortical distance and effective eccentricity. The U shows the unflanked vernier threshold at each retinal locus. Solid symbols show the unflanked thresholds and the peaks, for P.A. (also from Fig. 7). The stippled region is the range of thresholds at each eccentricity for J.M. obtained with repetitive vernier gratings (from Fig. 13).

be consistent with cortical anatomy. Similar conclusions have been reached by Fahle (personal communication).

To a good approximation†, many properties of peripheral vision can be summarized by the relationship $y = kE^*$, where $E^* = E + X$ is the *effective eccentricity* with X 0.8 deg for cortical processing and X 2.5 deg for retinal processing (Table 1). The slope k depends upon the task specified by y. For the inverse magnification factor M^{-1} (deg/mm) there are large individual variations in the size of striate cortex of both monkeys and humans (Van Essen *et al.*, 1984) and corresponding variations in the slope k. It seems likely that the size of the striate cortex varies a great deal more from individual to individual, than does its functional organization. Thus the slope k is inversely proportional to the square root of the area of the striate cortex (i.e. its linear size). For the rhesus monkey the slope k is approximately 0.12 mm (Dow *et al.*, 1981; Van Essen *et al.*, 1984). At the fovea this gives an inverse magnification $(M^{-1} = kX) = 0.096$ deg/mm or $M = 10.4$ mm/deg. The X value, which depends upon estimates of foveal or near foveal magnification hadn't been accurately studied until the recent work of Dow *et al.* (1981), Tootell *et al.* (1982), and Van Essen (1984). The fragile nature of the estimate of X can be demonstrated by noting that Dow's estimate of X — 0.3 deg is based on doing a linear regression to the pooled data of both monkeys. Our estimate of 0.8 deg is based on doing linear regressions to the data of each monkey separately. This value of 0.8 is consistent with the other recent estimates of X shown in Table

†The true variation in visual function with eccentricity is in fact exponential.

1 for cortical magnification, and with the value of X for a variety of hyperacuity tasks.

Figure 14 shows another application of cortical magnification scaling to the data of Experiment III for observer J.M. The lower and left axes are now labelled in cortical mm, using the formula M (deg/mm) $= 0.08E^*$. The slope value $k = 0.08$ mm^{-1} has been chosen to be about 0.7 times the value of the Rhesus monkey since the area of human visual cortex is about twice that of Rhesus (Schwartz, 1980). The upper and righthand axes are in units of the fraction of the effective eccentricity, E^*. Defining both the threshold and the flank distance as a fraction of effective eccentricity essentially eliminates the uncertainties associated with estimates based upon anatomical considerations and interspecies and individual variations.

The data plotted in Fig. 14 show the effect of a tiny mask on the vernier threshold at different eccentricities. As was pointed out in Results, the observer's viewing distance was inappropriately chosen for each eccentricity by using $X = 2.5$ deg rather than $X = 0.8$ deg (the experiments were done before we understood the difference between the retinal and the cortical scaling functions). The main effect of the inappropriate scaling while gathering data is that in the foveal condition the observer should have been further away, which would have made the lines shorter and thinner. But it is unlikely that shortening the lines would change the shape of the foveal data since the flank spacing and the threshold values are independent of the particular scaling factor X.

When the results of Experiment III are replotted according to cortical scaling $(X = 0.8$ deg), several points are notable: (1) The unflanked thresholds are about 0.0025 of the effective eccentricity. The con-

stancy of the threshold in cortical units provides further evidence that thresholds are proportional to effective eccentricity, $E + 0.8$. (2) Maximal masking occurs when the flanks are about $0.05E^*$ away from the test line. It is worth stressing that the data in the periphery makes it difficult to account for the effect of the mask in terms of optical or retinal factors since in the periphery the blur size is small compared to the extent of masking. (3) Masking becomes negligible when the flanks are more than $0.15E^*$ away. The masking locus is seen to be fairly independent of eccentricity-further evidence supporting the role of a cortical metric in controlling the effect of the masks. Bouma (1970) and Andriessen and Bouma (1976) found interference for letter identification and line tilt with flanks as far away as about $0.4E^*$. It is unclear why they found such a large extent of interference. (4) The magnitude of the masking varies somewhat. It is seen that there is about a three to four fold threshold elevation in the fovea, whereas the maximal threshold elevation is somewhat higher at 5 deg, suggesting that there may be slight departures from simple scaling. The solid symbols in Fig. 14 are the locations of the maximal masking data points and the unflanked data points of observer P.A. replotted from Fig. 7 onto the new axes. Both observers show similar results in these cortical distance units. (5) Also shown in Fig. 14 is a summary of Experiment IV (vernier gratings) in which the full range of J.M.'s data from Fig. 13 for the different eccentricities is replotted as the stippled region. For low spatial frequencies (Experiment IV) or large flank distances (Experiment III) the data of the two experiments are in good agreement. This is quite surprising considering that the stimuli differed with respect to: (i) their scaling (ii) orientation (vertical vs horizontal), (iii) temporal presentation (i.e. all lines flashed simultaneously in Experiment IV vs only the test line flashed in Experiment III, and (iv) the type of masking (i.e. repetitive long line vs a pair of tiny flanks). The vernier threshold gratings becomes degraded when the line separation is less than $0.08E^*$. It is noteworthy that the crowding in Experiment III occurred at a slightly wider separation than in Experiment IV.

Perceptive hypercolumns

We pointed out earlier (Experiment IV, Results) that spatial interference occurred when the interline distance was less than a cortical distance of about 1 mm, approximately the size of a human cortical ocular dominance column (Hitchcock and Hickey, 1980). Because of the uncertainties associated with estimates based upon cortical anatomy and physiology (Van Essen *el al.*, 1984) it is useful to define psychophysical spatial processing modules as suggested by Westheimer (1981). These modules subtend a few minutes in the fovea. Our data suggests that in peripheral vision these psychophysical modules scale to the eccentricity as do the anatomical modules termed hypercolumns. Figure 14 showed that mask-

ing occurs at a distance of about $0.1E^*$. We shall define this distance as the size of a "perceptive" hypercolumn. Since this measure is in spatial units it should be valid for both humans and monkeys (Schwartz, 1980) and should have less individual variability than a metric based upon cortical millimeters. In terms of perceptive hypercolumns, the results of Experiments III and IV can be summarized as: (a) The vernier threshold is approximately 1/40 of the size of a perceptive hypercolumn. (b) The vernier threshold will be elevated if interfering contours are present in the same or in adjacent hypercolumns. Since contrast sensitivity falls off more slowly in the periphery than does vernier acuity or other spatial discrimination tasks (e.g. Jamar *et al.*, 1984) these results present some difficulties for theories of hyperacuity based upon the contrast sensitivity function and its underlying filters unless additional assumptions are made regarding the variation of spatial sampling with eccentricity.

In summary, our analysis suggests that hyperacuity, when scaled to recent estimates of the cortical magnification factor is the same in the periphery as in the fovea. This does not preclude the possibility that the fovea has. in addition, special mechanisms and/or functions, not found in the periphery. The challenge with regard to cortical magnification theory is to find tasks which with appropriate scaling, the periphery cannot perform as well as the fovea.

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