Peripheral hyperacuity: isoeccentric bisection is better than radial bisection

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Performance of three-dot bisection was determined as a function of orientation for a variety of feature separations and field meridians at eccentricities of 0–10 deg for two observers. The dot stimuli and separations were scaled in size to compensate for eccentricity. The precision of three-dot bisection was found to depend on the direction of test-feature offset. In the fovea, horizontal and vertical bisections were better than oblique bisections, while at eccentricities of 5–20 deg, isoeccentric (on a tangent to a circle of a given eccentricity) bisection was better than radial bisection. The direction of offset was more important than the orientation of the stimulus. Large separations showed a stronger effect than small separations. The anisotropy of bisection appears different from the meridional effect for resolution and is unlikely to be simply related to a local anisotropy of the cortical magnification factor.

INTRODUCTION

The oblique effect is well known in foveal vision.[1] In the periphery, the oblique effect gives way to a meridional effect in which the resolution of gratings and the suprathreshold visibility of gratings is best for gratings oriented radially with respect to the fovea.[2,3] In addition, curvature detection, a hyperacuity task in the fovea, also shows an oblique effect in the fovea but is best for curved lines lying along radial meridians in the periphery.[4] Both the oblique and the meridional effects have been shown to be of a nonoptical origin. Hyperacuity tasks appear to be limited by the extent of striate cortical representation both in the fovea and in the perifoveal field,[5,6] while contrast and resolution tasks seem to be limited by ganglion-cell density[7–9] and/or striate receptive-field size.[10] However, the anatomical or physiological basis for the meridional effect has been related to both retinal and cortical sources.[2–4] These include the elongation of the ganglion-cell receptive fields,[11] the orientational bias of cortical receptive fields,[12] and a possible anisotropy of the cortical magnification factor.[13]

Because the visual field is completely represented in the ocular dominance columns of each eye in layer 4c beta of the primary visual cortex, it has been hypothesized that cortical magnification is locally anisotropic in this layer; cortical magnification across the width of each column is half of that along the length of the column.[13] Since ocular-dominance columns appear to run along approximately isoeccentric contours, it has been suggested that this purported anisotropy may account for the meridional effect.[2,4] Such a model predicts a meridional effect of equal magnitude whether the stimulus is small enough to be represented within a single ocular-dominance stripe or whether it extends over several stripes (see Figs. 11b and 11c of Ref. 4). However, if differences in bisection performance were based on differences in resolution resulting from meridionally elongated ganglion-cell receptive fields or the orientational bias of cortical receptive fields, then these differences should be stronger for stimulus separations of less than a receptive-field diameter than for wider separations. Therefore measuring the dependence of bisection on the direction of offset at small and large separations serves to test whether the direction-dependent effect is compatible with either of these hypotheses. Contrary to both ideas, we found that the dependence on the direction of the test-feature offset was more pronounced for separations larger than optimum in comparison with separations smaller than optimum.

The curvature detection task is a two-dimensional task in that the direction of the bulge is orthogonal to the long axis of the stimulus. Thus Fahle's results[4] do not show whether performance of hyperacuity tasks depends on the orientation of the stimulus configuration or on the direction of stimulus displacement. To distinguish between these two possibilities, we chose a hyperacuity task, three-dot bisection, in which both the stimulus orientation and the offset direction are the same. Taken together, these two results show that the direction of test-feature offset was more important than the orientation of the stimulus configuration. This finding was further verified by performing a two-dimensional task, vernier alignment, at an eccentricity of 10 deg.

METHODS

The precision of bisecting the space between two reference dots was compared at selected separations in the horizontal, vertical, and oblique (315-deg) meridians of the inferior temporal quadrant of the visual field. Each observer was tested monocularly at one or more separations: (1) smaller and (2) larger than the optimum. For observer YY the foveal separations were 2 and 10 arcmin, and for observer DL they were 2.3, 4.6, and 16.13 arcmin. The reference dots were on continuously, while the test dot was flashed for 150 msec. In order to make the cortical representation of our perifoveal stimuli comparable with the foveal stimulus, we scaled our foveal separations and the size of the dot stimuli in the perifoveal field by moving the observer closer by the factor 1 + E/0.77 deg, where E is the eccentricity in degrees, as

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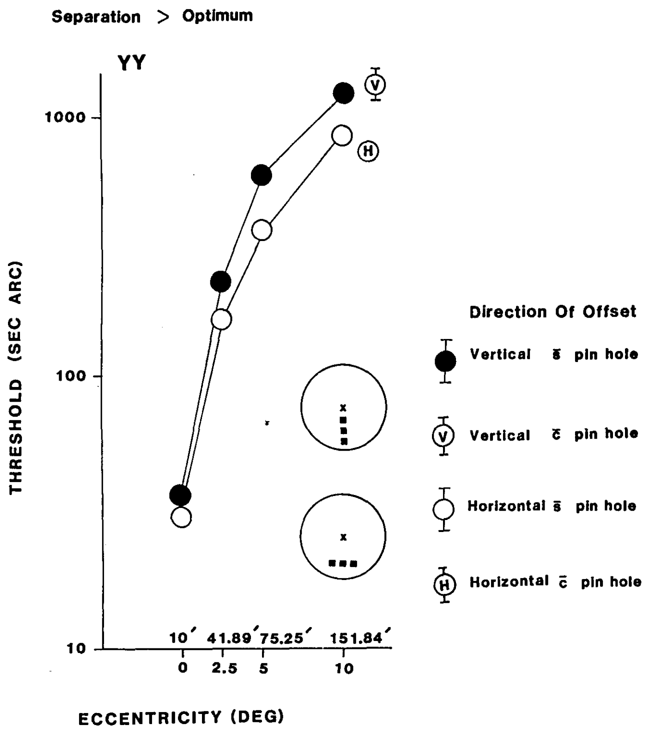
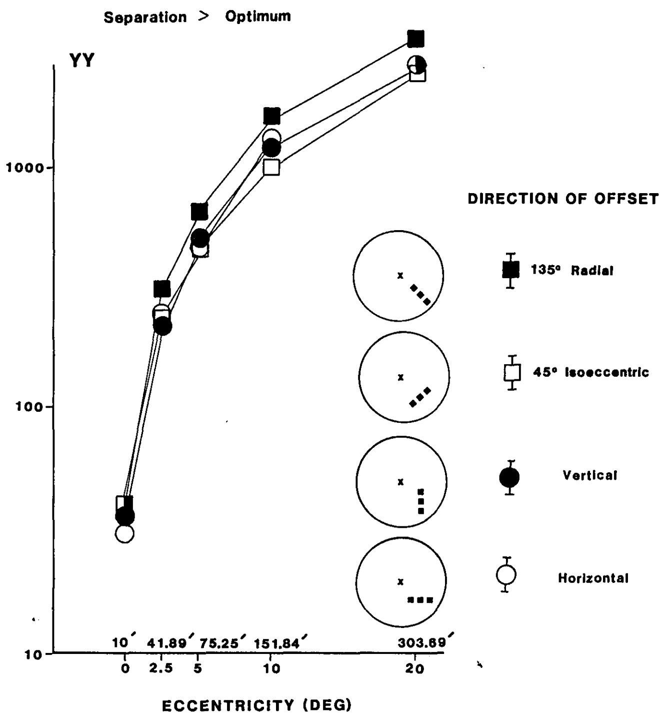
discussed in our preceding paper.[6] The stimuli were clearly visible at all eccentricities, although the more peripheral stimuli were brighter because of our method of scaling.

Observer YY was tested at eccentricities of 0–10 deg in all three meridians and, in addition, at an eccentricity of 20 deg along the oblique meridian only. For observer DL, performance was determined at eccentricities of 0–10 deg in the vertical meridian only. At each location in the field, the effect of the direction of offset (or orientation of the stimulus) was explored by aligning the reference dots so that they were horizontal or vertical. For the oblique meridian, testing was also carried out with the dots aligned on an approximately isoeccentric line and on radial lines centered on the fovea, with each pair of reference dots straddling the desired eccentricity. At each eccentricity, runs of different orientations were paired in an interleaved fashion to prevent spurious order effects. Since the dots were at slightly different eccentricities when they were lined up radially, thresholds for discrimination of test-dot displacement from midpoint toward the more central versus the more peripheral reference dot were also determined at an eccentricity of 10 deg for observer DL.



(a)



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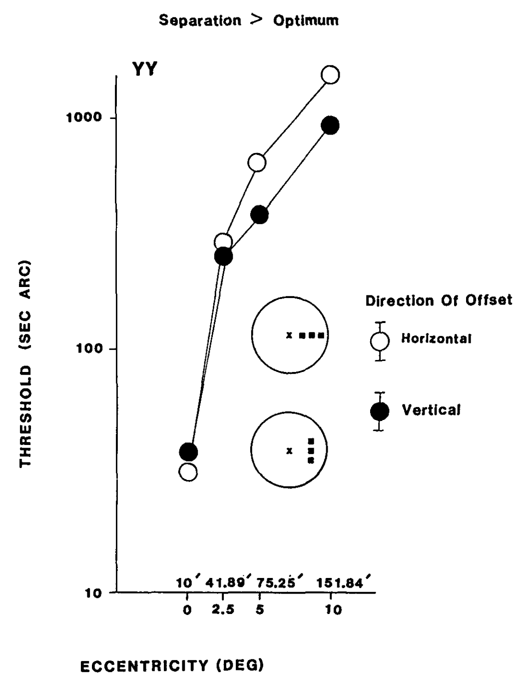

(b)

Fig. 1. Horizontal- and vertical-bisection thresholds for observer YY are plotted as a function of eccentricity from 0- to 10-deg eccentricity at a separation larger than optimum along (a) the inferior vertical meridian, (b) the temporal horizontal meridian, and (c) the inferior temporal oblique meridian. In addition to the horizontal and vertical thresholds, oblique thresholds are also shown for the oblique meridian up to 20-deg eccentricity. Inset shows schematic of stimulus (not drawn to scale). Where error bars are not shown, they are smaller than the size of the symbols. The values of the separations are indicated above the abscissa.

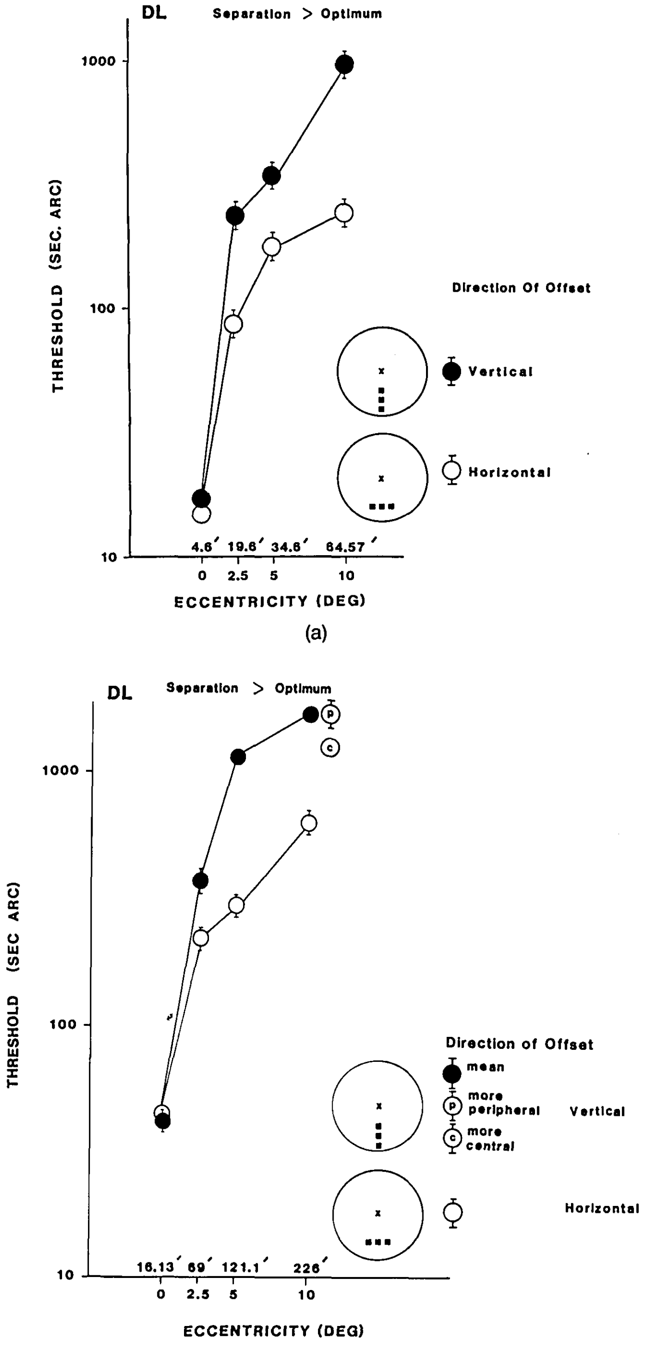

Fig. 2. Horizontal- and vertical-bisection thresholds for observer DL are plotted as a function of eccentricity from 0- to 10-deg eccentricity at separations (a) slightly larger than and (b) much larger than optimum for the inferior vertical meridian. In (b) the thresholds for a displacement in the more central versus the more peripheral direction are shown for radial bisection at 10 deg.

The methods and procedures are identical to those described in our preceding paper.[6]

RESULTS

The results obtained at a variety of separations and meridians are shown on the graphs of threshold as a function of eccentricity under each condition (Figs. 1–3). In the fovea, oblique bisection thresholds were slightly worse than the vertical and horizontal thresholds [Fig. 1(c)]. For observer YY, horizontal-bisection thresholds were slightly better than vertical-bisection thresholds for separations both smaller and larger than optimum (Figs. 1 and 3). For observer DL there was little difference between foveal horizontal and vertical bisection at separations larger than optimum [Figs. 2(a) and 2(b)], but for separations smaller than the optimum his vertical threshold was lower [Fig. 3(b)].

Outside the fovea, performance of isoeccentric bisection was better than that of radial bisection along all three meridians and for all separations (Figs. 1–3). The horizontal

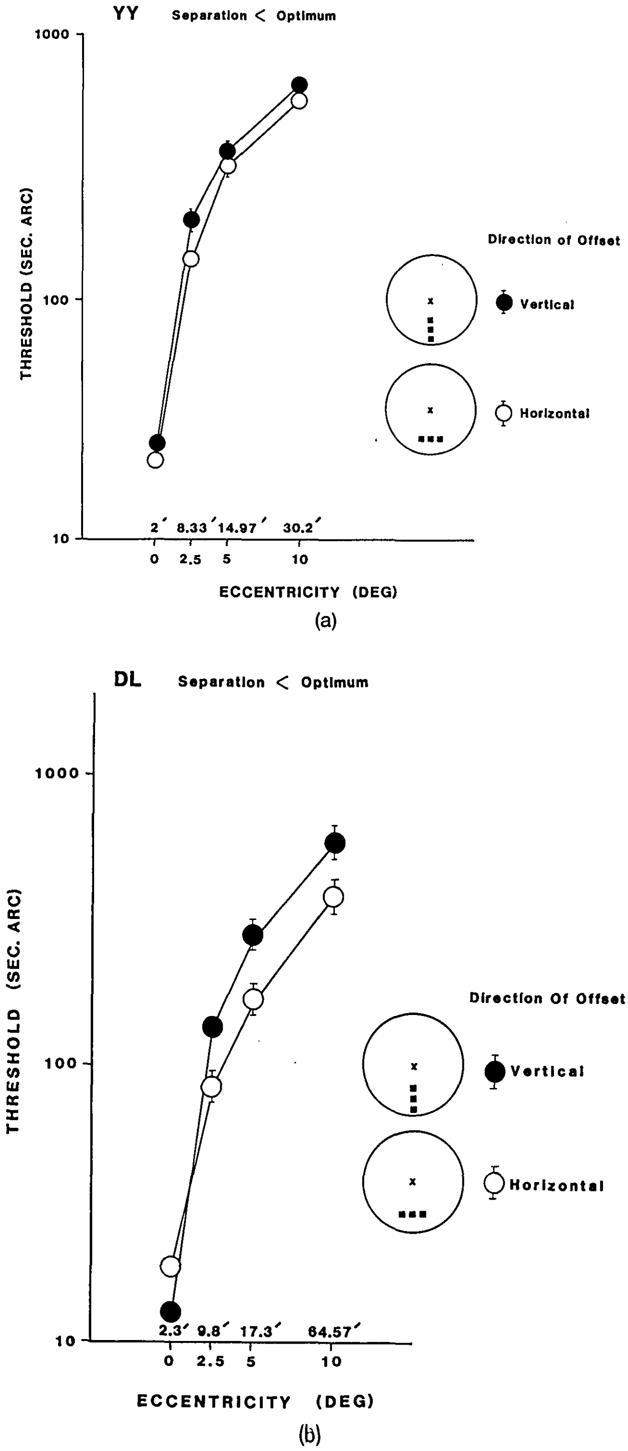

Fig. 3. Horizontal- and vertical-bisection thresholds are plotted as a function of eccentricity from 0- to 10-deg eccentricity at a separation smaller than optimum for observers (a) YY and (b) DL.

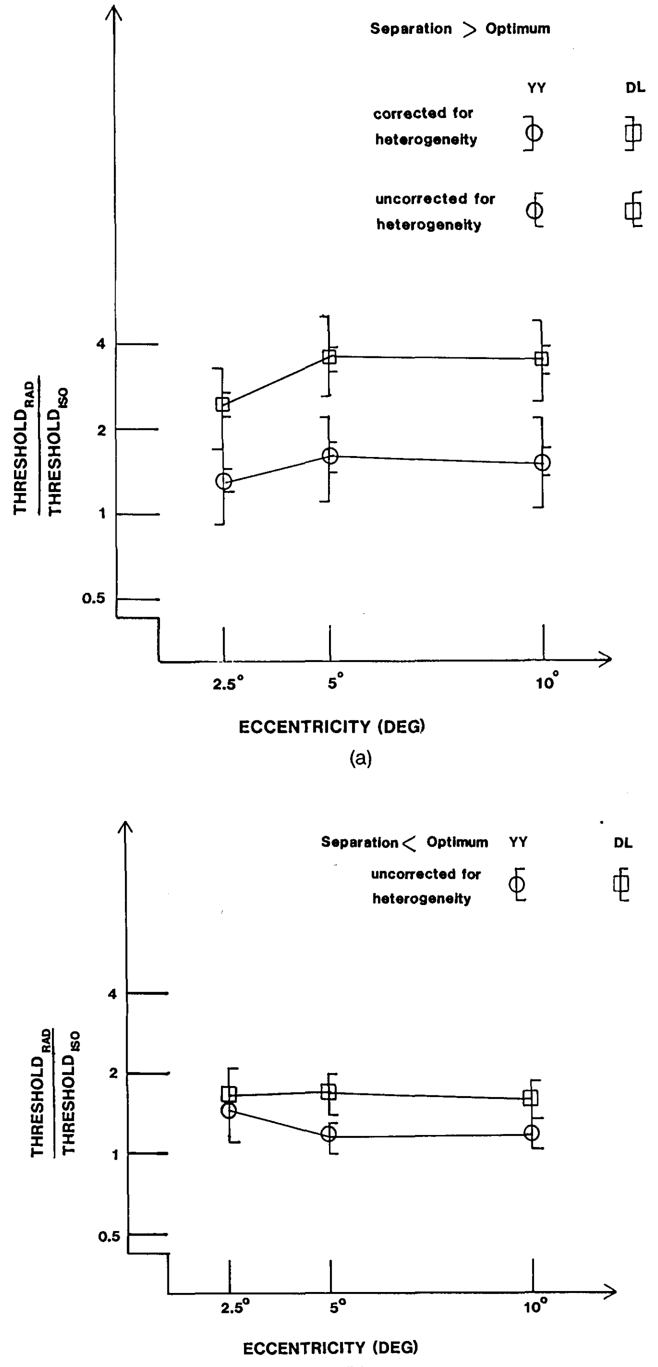

Fig. 4. The ratios of radial-to-isoeccentric bisection thresholds averaged across conditions for each observer are plotted as a function of eccentricity from 2.5 to 10 deg for separations (a) larger than and (b) smaller than optimum. The larger error bars reflect the heterogeneity of the data.

stimulus was bisected more easily along the vertical meridian from 2.5- to 10-deg eccentricity [Figs. 1(a), 2, and 3], whereas along the horizontal meridian, vertical bisection was better [Fig. 1(b)]. In each case the best direction of offset was isoeccentric rather than radial. Along the oblique meridian, oblique isoeccentric bisection was best, oblique radial bisection was worst, and horizontal and vertical bisections were intermediate at eccentricities of 5 to 20 deg. However, at 2.5 deg, vertical bisection was slightly better than isoeccentric bisection. The ratio of the radial to isoeccentric thresholds was smallest at 2.5-deg eccentricity for both observers (Fig. 4). Observers YY and DL showed ratios that were approximately constant for eccentricities greater than 2.5 deg [Figs. 4(a) and 4(b)].

The ratio of radial-to-isoeccentric bisection thresholds was found to be greater for separations larger than the optimum [Figs. 1, 2, and 4(a)], in comparison with separations smaller than the optimum [Figs. 3 and 4(b)], although observer DL always showed a more pronounced difference than observer YY. For the radial task at 10 deg, the precision of bisection for an offset of the test dot directed toward the fovea is better than for an offset directed away from the fovea; however, thresholds in both directions were worse than the threshold obtained for dots aligned isoeccentrically [Fig. 2(b)].

These findings have been summarized by plotting the ratio of thresholds for isoeccentric offsets against thresholds for radial offsets of the test dot against the eccentricity of the viewing angle [Figs. 4(a) and 4(b)]. Because thresholds for separations larger [Fig. 4(a)] and smaller [Fig. 4(b)] than optimum at each eccentricity have been pooled across different meridians and separations for each observer, the heterogeneity of the data was taken into consideration by multiplying the standard errors with the reduced chi-squared factor (=square root of chi squared divided by the degrees of freedom). The original and compensated standard errors are shown for comparison (the latter were generally larger than the former). At separations both larger and smaller than optimum, bisection performance was significantly better for dots aligned isoeccentrically than for those aligned radially, although the effect was greater for separations larger than the optimum.

CONTROL EXPERIMENT: TWO-DOT SEPARATION DISCRIMINATION

It is possible that three-dot bisection is worse in the radial direction than in the isoeccentric direction simply because the observer ignores the more peripheral reference dot. The difference predicted from probability summation would be a square-root-of-2 factor. To test this idea, observer YY performed two-dot separation discrimination (a task that is identical to three-dot bisection except for the absence of one reference dot) for the isoeccentric versus the radial direction of offset at a separation of 153 min at 10 deg. The experimental procedure was unchanged except that the orientation of the stimulus was changed by turning the computer on its side instead of using a dove prism.

We found that the threshold for two-dot separation discrimination was 558 ± 43 sec for an isoeccentric offset and 1158 ± 149 sec for a radial offset. Because two-dot separation discrimination shows a direction anisotropy like three-dot bisection, the anisotropy cannot simply be due to the more peripheral reference dot's being ignored the three-dot bisection task.

CONTROL EXPERIMENT: ORIENTATION VERSUS DIRECTION

For three-dot bisection, the direction of the test-dot offset is along a line that includes the reference stimuli. This is in contrast to three-dot vernier alignment in which the reference dots are oriented perpendicularly to the direction of

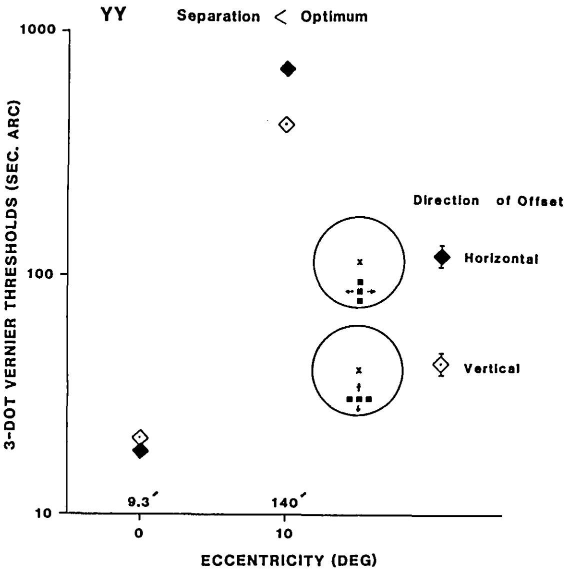

Fig. 5. Horizontal and vertical vernier thresholds are plotted at 0- and 10-deg eccentricity at a separation smaller than optimum for observer YY. The error bars are smaller than the size of the symbols.

test-dot offset. In order to test whether the orientation of the stimulus configuration or the direction of offset determines threshold, three-dot vernier acuity was measured in observer YY. A separation of 9.26 arcmin was used in the fovea for dots that were aligned vertically and horizontally. This measurement was repeated with the scaled separation of 140 arcmin at 10-deg eccentricity along the inferior vertical meridian.

Three-dot vernier acuity (each data point is the weighted mean of 4–5 runs) for observer YY was shown to be better at an eccentricity of 10 deg for vertically aligned dots that were horizontally offset than for horizontally aligned dots that were vertically offset, whereas in the fovea the thresholds were not significantly different (Fig. 5). Thus our results together with Fahle's[4] results show that the perifoveal hyperacuity threshold was dependent on the direction of the test-feature offset rather than on the orientation of stimulus configuration.

CONTROL EXPERIMENT: OPTICS

To test whether the dependence of the test dot on the direction of offset in the perifoveal field could be attributed to peripheral optics, e.g., astigmatism, a double-aperture pinhole was used for a separation of 151.84 arcmin at 10 deg along the inferior vertical meridian. The foveal aperture was 1 mm in diameter, while the peripheral one was 2 mm in diameter, to obtain good peripheral optical image quality. The double-aperture pinhole was positioned so that, when the 1-mm opening was occluded, the fixation mark could not be seen but the dot stimuli would still be visible, while the opposite occurred when the 2-mm aperture was covered.

When the double-aperture pinhole was used, the horizontal-bisection offset continued to give better thresholds than the vertical offset [Fig. 1(a)]. Therefore the dependence of the bisection task on the orientation of the test feature offset in the perifoveal field cannot be attributed to a degradation of image quality. Other experiments have also shown that the quality of peripheral optics remains good up to an eccentricity of 20 deg.[14] We conclude that, like the meridional effect in resolution[2,3] and in curvature detection,[4] the direction-dependent effect of our results cannot be explained by peripheral optics.

DISCUSSION

We found that three-dot bisection is slightly but significantly better for a test-feature offset directed along an isoeccentric axis than along a radial axis for eccentricities of 5–20 deg. The direction-dependent anisotropy of bisection in the perifoveal field is similar to the meridional effect in grating resolution[2,3] in that the best resolution and discrimination are achieved for separations or offsets along the isoeccentric direction while the worst occur along the radial direction.

Our results showed a stronger anisotropy at large separations, where the dots would be separated by many receptive fields in both radial and isoeccentric directions, and a weaker anisotropy at small separations, where the dots might fall within a single receptive field in the radial direction. It is difficult to explain this by using the orientation-dependent differences in the resolving capacities of the elliptical receptive fields of ganglion cells[11] or the orientation bias of cortical cells.[12] However, because the periphery is undersampled,[15] it is possible that better performance for isoeccentric offsets may result from a more efficient sampling of the stimulus along isoeccentric contours[16] owing to a slightly higher density of receptive fields along isoeccentric contours than along radial contours.

Because ocular-dominance columns appear to run along approximately isoeccentric contours, it has been hypothesized that an anisotropy of cortical magnification in layer 4*c* of the striate cortex could account for the meridional effect.[2,4] Such a model predicts a meridional effect of equal magnitude for short as well as long curved lines[4] that is equivalent to a small versus large separation in our bisection task. However, we found that the anisotropy for bisection was weaker for small separations than for large separations. This hypothesis also depends on the assumption that hyperacuity is processed in the granular layer of the striate cortex, where the monocular inputs remain segregated. Such an assumption is questionable in light of studies that show that vernier acuity can be masked dichoptically[17,5] and that for large feature separations dichoptic vernier acuity is equivalent to monocular vernier acuity.[18] Unfortunately, anatomical and physiological studies[19,20] are not accurate enough to resolve this issue. However, our results do not rule out the idea that this directional-dependent effect of bisection is related to the columnar organization of the cortex, e.g., performance may be better for offsets that do not cross the boundaries of ocular-dominance columns. Hyperacuity tasks appear to be processed in psychophysical modules: limited spatial compartments in which features are localized relative to one another.[21] The extent of these modules appears to be approximately constant in cortical units, 0.1 E^* (the effective eccentricity), where E^* = E (the eccentricity in degrees) + 0.77 deg.[5,6] Our results support the idea that processing of stimuli within a module is different from processing of stimuli that fall into different modules.[5,6]

If the threshold elevation of bisection in the radial direction resulted from a difference in spatial interference exerted by the more central versus the more peripheral dot, performance of vernier acuity would be also worse for radially aligned reference dots. Similarly, the tuning of spatial filters to lower frequencies with eccentricity[22] would predict that the tuning of the filters responding to the two reference dots might differ significantly in the radial case but not in the isoeccentric case. Our results contradict both ideas; in the vernier task, performance was worse not when the reference dots were radial but when they were isoeccentric.

Since the thresholds for the radial and isoeccentric directions were determined for paired separations, our results imply that the change of bisection performance with eccentricity is steeper for radially directed offsets than for isoeccentrically directed offsets.

In conclusion, we found that three-dot bisection is dependent on the direction of test-feature offset. In the fovea, horizontal and vertical bisections are better than oblique bisections, whereas at eccentricities of 5–20 deg isoeccentric bisection is better than radial bisection. By comparing the performance of vernier acuity with bisection, this effect was shown to depend on the direction of offset rather than the orientation of the stimulus. This anisotropy was more pronounced for large than for small separations. Our results suggest that the dependence of bisection on the test-feature direction is different from the meridional effect for resolution[2,3] or a local anisotropy of the cortical magnification factor.[13] Instead, we suggest that this anisotropy may be related to a more efficient sampling of the stimulus along isoeccentric contours than along radial contours[16] or to a difference in the processing of offsets that cross the boundaries of ocular-dominance columns versus that of offsets that do not. Finally, the magnitude of the anisotropy may depend on a difference in the processing of stimuli that fall within a psychophysical module versus that of stimuli that fall into different modules.[5,6]

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