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The distribution of preferred orientations in the peripheral visual field

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Abstract

Orientation discrimination was measured for line targets in the fovea and in locations along four meridians (vertical, horizontal, 45° and 135°) in the peripheral visual field. In all locations, the performance for vertical and horizontal contours was on average almost twice as good as for oblique ones. In addition, especially in peripheral locations along oblique meridians, thresholds tend to be better for radially-oriented contours compared to tangential ones. These effects are robust to length of the test lines and to small changes in position and cannot therefore be due to cortical singularities (pinwheels). The results suggest that the advantage of horizontal and vertical contours, as well as possibly of radial ones, is a manifestation of a characteristic structural property of the organization of the visual pathway.

Keywords: Oblique effect; Radial/tangential anisotropy; Peripheral visual field; Cortical pinwheels

1. Introduction

There is abundant evidence that in foveal vision contours of not all orientations are processed equally: the horizontal and vertical are favored. Specifically, horizontal and vertical contours have better orientation discrimination thresholds and to some extent also vernier acuity (Westheimer & Beard, 1998 which also reviews the literature as does Regan, 1999). There has been speculation whether the concentric organization of the visual system, with its progressive reduction in sensitivity as the distance from the fovea increases, manifests itself in a radial/tangential preference in the retinal periphery, so that contours collinear with the fovea have better performance than their orthogonals, i.e., contours with a tangential orientation. The layout of the oculomotor system, based on the coordinates defined by the system of Listing, could possibly provide some guidance here.

A consequence of Listing's law of eye movements is the following (Westheimer, 1981). If one considers the sheaf of lines of all possible orientations intersecting in the fixation point, the only foveally-imaged line segment that has remained in its original orientation when the movement has been completed is the one lying in the meridian of motion, i.e., where the axis of rotation defining the motion is normal to that meridional plane. Thus when the eye has moved into a tertiary position, [1] viz. one reached by rotation around an axis that is neither vertical nor horizontal, lines of all other orientations, including the horizontal and vertical, are now imaged with a torsional angle. In other words, there is orientational invariance only for stimuli lying in the retinal meridians along which the eye movement takes place. It would be of interest, therefore, if in the retinal periphery there is a better orientation discrimination for lines lying in these radial meridians, i.e., that are collinear with the fovea, rather than the horizontal/vertical directions that are favored in the center of the visual field. A recent study addressing this question (Davey & Zanker, 1998) is therefore important. Moreover, the results of these authors suggest that there is an oblique effect in orientation discrimination also in the periphery of the visual field, not fully in agreement with Vandenbussche, Vogels, and Orban (1986) who found an oblique effect only for eccentricities up to about 10° and

[1] Fixating a point straight ahead with the head erect places the eye in the primary position. Looking along the horizontal or the vertical meridians in the visual field places it in secondary positions. All positions within the four quadrants of the visual field are called tertiary.

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essentially none in the more distant periphery. The question of orientation discrimination in various meridians and retinal locations is here re-examined.

2. Methods

The sensitivity of normal human observers for differences in line orientation was measured in the fovea and also in various locations in the periphery of the visual field while the eye maintained central fixation. The locations were equidistant from the fovea and situated along the horizontal (0°/180°), vertical (90°/270°), and the two principal oblique (45°/225° and 135°/315°) meridians. Line lengths were 20 arcmin in the fovea, 1° at 9° eccentricity and 2° at 18°–20° eccentricity. As will be shown later, line length is not a significant issue. In each location, thresholds were obtained for four line orientations, horizontal, vertical, 45° and 135°. Earlier research (Westheimer, 1996) revealed that position clues of the line-ends are not utilized in orientation discrimination. Because it cannot be assumed that observers had reached their optimal performance, each observer was given sufficient training to stabilize thresholds. Once this had been achieved, approximately three sessions of 150 trials each, in each of the four meridians, were obtained in each of eight locations in the periphery. Observer GW also served as a subject for a second set at a different eccentricity. Four to six runs were obtained on each experimental day, so that the data represents a good cross section of the observer's performance throughout the study. Both JM and AL, undergraduate biology students, were at the outset unaware of the purpose of experiments. They, as also observer GW, had normal visual functions for the purpose of the experiment. Except for a set of monocular thresholds to ensure their concordance, observation was binocular throughout and all positions in the visual field were outside the blind spot.

The two-interval forced choice psychophysical procedure was employed where trials, regularly occurring in intervals of three seconds, started with the presentation of a reference line at a fixed orientation to serve as a comparison stimulus. Its orientation remained constant during each run of 150 trials. It was followed, after a 600 ms pause, by the test line in the same location but in randomly one of seven orientations at equally-spaced intervals centered on the comparison in the usual procedure of the method of constant stimuli. Both the comparison and the test lasted 300 ms. In check experiments it was verified that results were similar when the duration was reduced to 100 ms. There are no difficulties for experienced observers to maintain steady fixation while reporting on peripheral visual experiences. In the interval between successive trials the observer pressed a computer mouse button to signal whether the test line appeared to have a more clockwise or counterclockwise orientation than the comparison. Data were analyzed by the method of probits, yielding a threshold (half the difference between the 25% and 75% responses on the psychometric curve) and its standard error. Because the standard errors were always less than 10% of the thresholds, they were usually omitted when plotting the data.

Targets were bright (≈40 cd/m^2) on a dark background in a darkened room, shown on a 15″ Sony monitor, controlled by a Pentium-based IBM-type computer. Programs written in the C language with anti-aliasing feature for oblique lines were run under DOS. Observation distances were 5 m or 75 cm, depending on whether conditions were foveal or peripheral. For peripheral vision, a fixation point was available on the monitor as needed for the particular location being tested.

3. Results

Fig. 1 depicts the orientation discrimination threshold for a foveally-seen line, as a function of the base orientation. It illustrates the well-known oblique effect: performance is better for horizontal and vertical contours than oblique ones. All observers exhibit such an oblique effect and, as it will be seen below, it is present not only in the fovea but also in all other locations in the visual field that were tested.

The experiments were now repeated in eight other locations in the visual field, with the observer maintaining central fixation. That is, the observer now had to discriminate whether a test line shown in this retinal location differed in orientation from that of the immediately

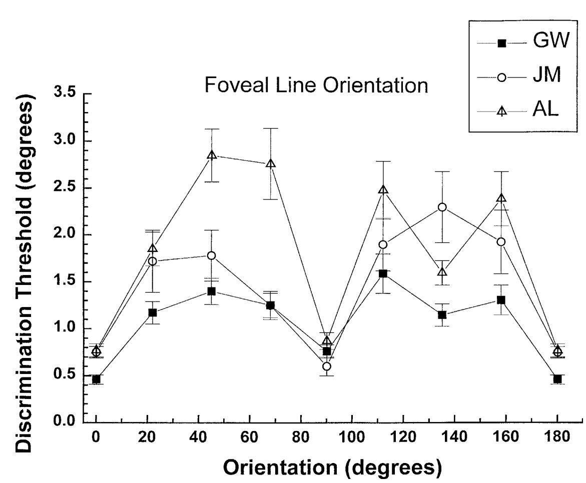

Fig. 1. Orientation discrimination thresholds for 20 arcmin foveal lines as function of base orientation. Exposure duration 300 ms. All three observers have much better performance for vertically and horizontally-oriented lines than oblique ones, that is they manifest a prominent oblique effect.

preceding comparison line. In each location, four orientations were tested, the horizontal, the vertical and two obliques. Each of the eight locations was equidistant from the fovea and chosen so that one of the four orientations of the test line was aligned with the fovea, i.e., was radially oriented. For observers AL and JM the eccentricity was 20°. For observer GW in addition to results at 18°, a full set of results is shown for a smaller eccentricity, 9°. The data for the three observers are shown in Figs. 2–4. Corresponding to each location there are four lines representative of the direction of the test line. In the figures, line lengths are *inversely* proportional to the orientation discrimination threshold and the dashed circle represents the mean of the four meridians. In all observers and visual field locations the horizontal and vertical thresholds are without exception better than those in the oblique meridians (Table 1), the overall ratio being 0.53 ± 0.12. Thus it is clear that the superiority of these directions is maintained regardless of the location in the visual field.

Bar graphs were constructed giving the ratio of the radial to the tangential threshold for each orientation and location. A value less than unity signifies that a line in this position collinear with the fovea has better orientation discrimination than one orthogonal to it. The

AL

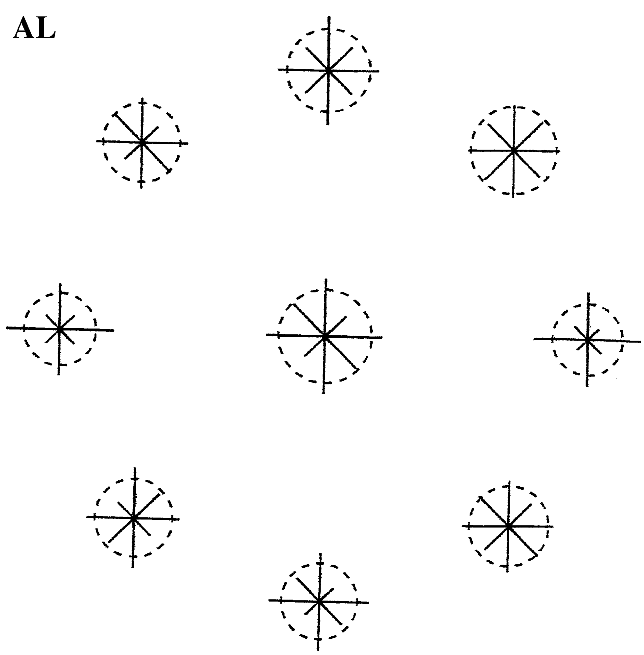

Fig. 2. Orientation discrimination for lines of four basic orientations (horizontal, 45°, vertical, 135°) in the fovea (center) and eight peripheral locations, 20° from fovea along the horizontal, vertical and two principal oblique meridians. Here the reciprocals of thresholds are shown; the longer the lines the better the performance. The dashed circle indicates the mean sensitivity for the four meridians at the location. These data are drawn to scale. Exposure duration 300 ms; peripheral line length, 2°. Observer AL. Regardless of location, the orientation of vertical and horizontal contours is discriminated better than that of oblique ones. There also is a tendency for radial contours to be favored over their orthogonals.

JM

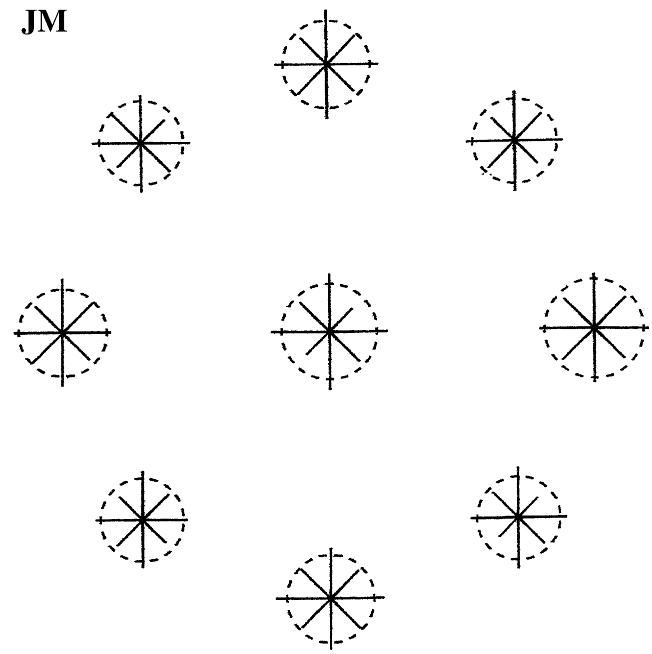

Fig. 3. Data like those in Fig. 2 for observer JM.

GW

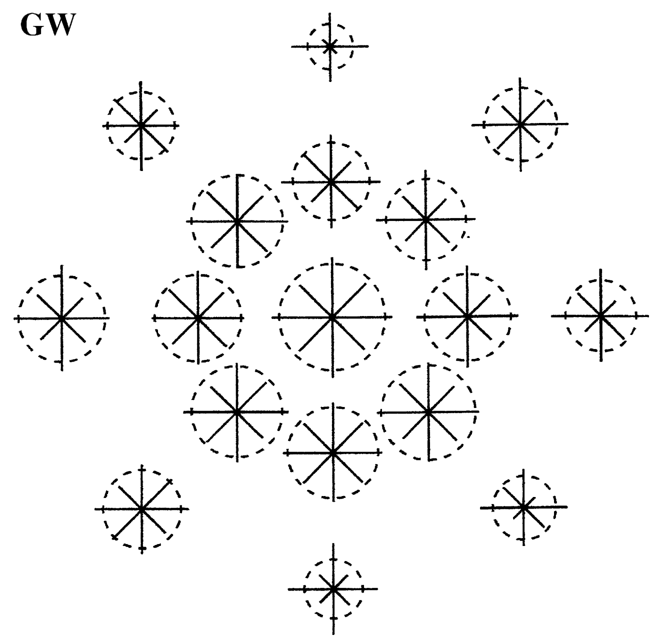

Fig. 4. This figure is similar to that in Fig. 2. The data in the outer ring represent findings at an eccentricity of 18° with a 2° test line and, in addition, a second set of data is shown for locations with only 9° eccentricity and test-line length 1°. Observer GW.

evidence for a radial/tangential organization is not as compelling as the superiority of the cardinal, i.e., horizontal and vertical directions, but there is nevertheless some indication of it. In many locations in the peripheral visual field, contours aligned with the fovea show better orientation discrimination than their orthogonals. This is particularly prominent in the locations lying in

Table 1
Orientation discrimination for line targets cardinal thresholds/oblique thresholds

Location in visual field (meridian)	Observer and eccentricity			
	AL 20°	JM 20°	GW 18°	GW 9°
0	0.35	0.59	0.44	0.68
45	0.59	0.60	0.60	0.60
90	0.39	0.49	0.53	0.49
135	0.82	0.55	0.53	0.48
180	0.30	0.54	0.45	0.44
225	0.70	0.46	0.57	0.56
270	0.38	0.53	0.52	0.70
315	0.46	0.60	0.70	0.58

Overall ratio for all observers and positions 0.53 ± 0.12.

the 45° and 135° meridians in the visual field (Fig. 5A), but for some of the observers also in the horizontal and vertical locations (Fig. 5B). To the extent the ratio is less than unity it demonstrates a grain running through the visual field favoring this kind of organization; it overlays the inbuilt horizontal/vertical predisposition.

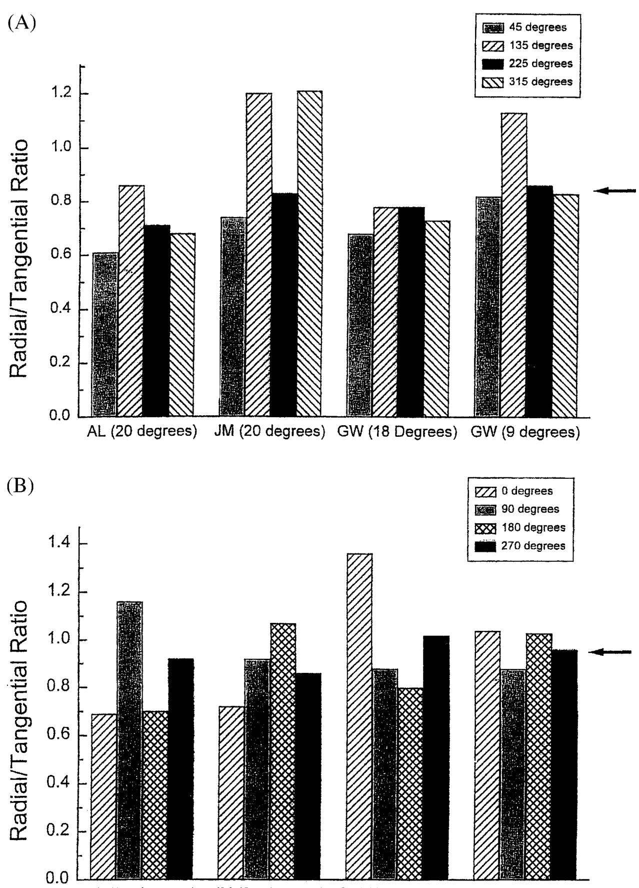

Fig. 5. Bar graphs showing the ratio of the radial to the tangential thresholds in all observations, separately those lying in the 45°, 135°, 225° and 315° locations (A) and those in the up, down, right and left locations in the visual field (B). The mean ratio, given by the pointer in the right margin, is 0.83 for the former and approximately unity for the latter.

Once the horizontal, vertical and oblique data have been assembled, mean orientation discrimination can be calculated in each of the peripheral locations. They show a surprising scatter; locations in equivalent positions of eccentricity can differ by as much as a factor of 1.5. The results were obtained in field positions that had problems associated neither with the blind spot nor with excessive eccentricity. Nor did they depend on ocularity, because monocularly-determined thresholds did not differ from the binocular ones on which this study is based.

4. Discussion

Although primate retinal ganglion cells have been shown to have oriented dendritic (Schall, Perry, & Leventhal, 1986) and receptive (Passaglia, Troy, Rüttiger, & Lee, 2002) fields, the processing of contour orientation is a cortical phenomenon. Even then, orientation discrimination thresholds are at least an order of magnitude smaller than the receptive field orientation tuning of cells in the primary visual cortex and hence speak for substrates possibly even more remote from the geniculate input the cortex. It is, therefore, unlikely that our results have a retinal origin. In fact there is some support for the conjecture, first proposed by Bouma and Andriessen (1968), that the oblique effect in orientation discrimination has its origin in the distribution of preferred orientation of neurons in the primary visual cortex. Two primate studies designed to investigate this (Celebrini, Thorpe, Trotter, & Imbrie, 1993; DeValois, Yund, & Hepler, 1982) both report more neurons selective for horizontal and vertical orientations than for oblique ones. It is also of interest to note, that in the region of the primate visual cortex dedicated to the perifovea there is a higher of representation of neurons with radially-oriented receptive fields in the upper layers (Bauer & Dow, 1989).

There have been discussions recently concerning cortical anisotropies associated with the orientation columns, especially the pinwheel structure that is a necessary consequence of folding three dimensions (two dimensions of position in the visual field, plus the segregation into contour orientation) into the two dimensional surface of the cortex (Bonhoeffer & Grinvald, 1993).

Two experiments were performed to ascertain the extent to which singularities like pinwheels might have influenced our findings. In one experiment, observer AL measured the orientation discrimination for radial and tangentially oriented lines in one retinal location as a function of line length. The results, Fig. 6, reveal a smooth change of both mean threshold and radial/tangential ratio as the test line increases in length from 1° to 3° of visual angle. The improvement in threshold with increasing line length is in accord with previous findings (Vandenbussche et al., 1986; Westheimer, 1982); the radial/tangential ratio follows along.

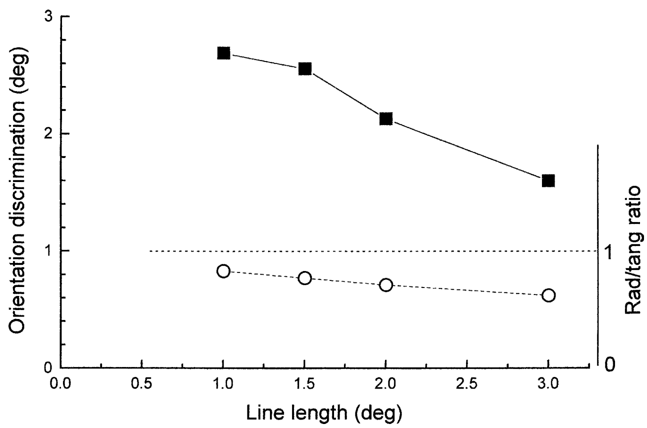

Fig. 6. Performance as a function of test-line length for observer AL in a single 20° peripheral location (up and to the right). Orientation discrimination improves with line length, the radial/tangential ratio remains well below unity throughout.

In the second experiment, performed by both AL and GW, the data for one retinal location were replicated in two adjacent locations, differing by 2°. This distance was predicated by the estimate (A. Das, personal communication) that the spatial extent of the pinwheels is of the order of the receptive field diameter of neurons in the primary visual cortex, which in the alert primate is less than 1° for bright line stimuli in the near periphery (Kapadia, Westheimer, & Gilbert, 1999, Fig. 1a). Thresholds were substantially invariant with small shifts in location, and did not reveal any differences in performance in neighboring parts of the visual field. The results in this study therefore suggest that the vertical/horizontal vs. oblique anisotropy, and perhaps the radial vs. tangential one as well, constitute a characteristic structural property of the visual system.

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