Retinal Ganglion Cell Dendritic Fields in Old-World Monkeys are Oriented Radially

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We analyzed the dendritic field morphology of 297 ganglion cells from peripheral regions of monkey retina. Most of the dendritic fields were elongated, and there was a significant tendency for the dendritic fields to be oriented radially, i.e., like the spokes of a wheel with the fovea at the hub. An overrepresentation of radial orientations in the peripheral retina of primates might explain why humans are best able to detect stimuli which are oriented radially using peripheral vision[10,28,32].

INTRODUCTION

Neurons in primate and feline visual cortex have been characterized by their orientation selectivity[12,13]. Recently, however, it has been found that cells in the dorsal lateral geniculate nucleus (LGNd) of cat[8,34] and monkey[15] are sensitive to stimulus orientation. Cat retinal ganglion cells are also orientation sensitive; most cells outside the area centralis prefer stimuli which are oriented radially, i.e. oriented parallel to the line connecting the cell with the area centralis[20]. Since most cat retinal ganglion cell dendritic fields outside of the area centralis are elongated and oriented radially, the structure of a ganglion cell's dendritic field probably confers upon the cell its orientation sensitivity[18].

The overrepresentation of radial orientations established in cat retina appears preserved in the LGNd[34] and visual cortex[16,19,29]. Psychophysical studies have shown that humans, using peripheral vision, are best able to perceive stimuli which are oriented radially[10,28,32]. We were therefore interested to determine if, as in the cat, the dendritic fields of monkey retinal ganglion cells are oriented radially.

MATERIALS AND METHODS

Ganglion cells were sampled from 5 *Macaca mulatta* retinas. The dendritic fields of the cells were visualized following horseradish peroxidase (HRP) injections into the optic nerve or LGNd. The procedures for the demonstration of HRP have been presented previously[17,26]. The quality of filling appeared comparable to that seen with Golgi stains, as shown in Fig. 1. The cells were drawn at magnifications of ×400, ×630 and ×1000, and were classified as either P-beta (or B) or P-alpha (or A) types[17,25]. The dendritic fields of all P-beta and many P-alpha ganglion cells within 4 mm of the center of the fovea are smaller than 30 μm[25]. The morphology of such small dendritic fields cannot be accurately analyzed using the light microscope; consequently, we were forced to restrict our analysis to cells lying more than 4 mm from the center of the fovea. The methods used to determine the orientations of ganglion cell dendritic fields and the relationships between dendritic field orientation and retinal position have been described elsewhere[18,27], as have the specific statistical tests employed to analyze our data[2].
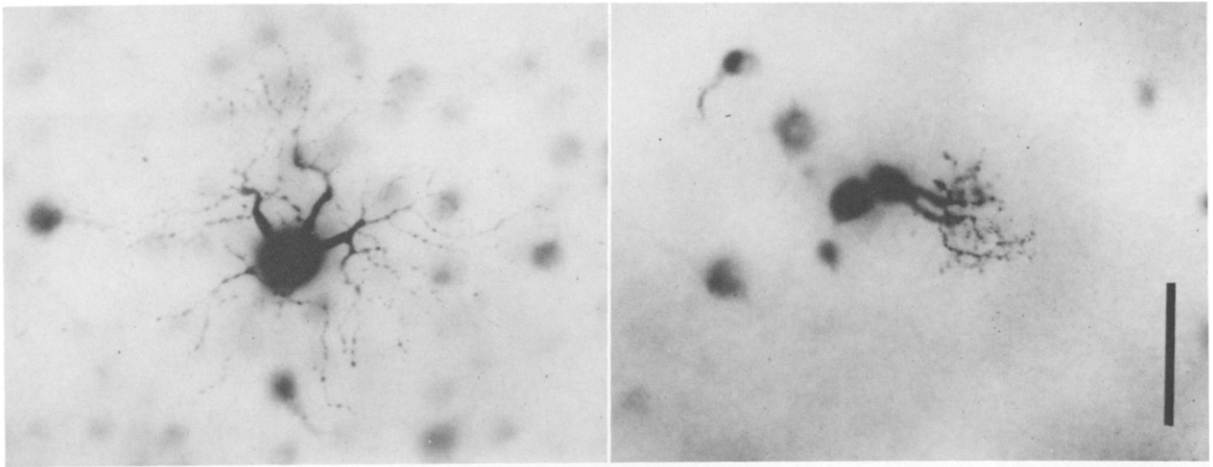
Fig. 1. Photomicrographs of an HRP-filled P-alpha/A (left) and P-beta/B (right) ganglion cell. The scale bar measures 50 μm. The P-alpha cell was located 8.9 mm from the center of the fovea. The P-beta cell was located 4.3 mm from the center of the fovea. A computer replication of this P-beta cell is presented in Fig. 2 with the analysis of the orientation of its dendritic field.

RESULTS

Fig. 2 shows the computer representation and dendritic field orientation analysis of a P-alpha and a P-beta cell. We calculated the orientation biases of 297 dendritic fields. Orientation bias can range from 0 to 1; a value of 0 describes a perfectly circular dendritic field. It has been shown previously both physiologically[20] and anatomically[18] that an orientation bias of 0.1 or greater indicates a significant degree of orientation. Using this criterion, 90% of the monkey ganglion cells we sampled had significantly oriented dendritic fields, as shown in Fig. 3.

To ascertain whether the orientation of each dendritic field is related to its position on the retina, we calculated the angle difference between the orientation of each oriented dendritic field and the polar angle of the line connecting it to the center of the fovea. Angle differences can range from +90° to -90°; an angle difference of 0° describes a dendritic field which is oriented exactly radially. If the orientation of a dendritic field was more horizontal than its polar angle, then its angle difference was positive. For example, a cell with a polar angle of 45° oriented at 30° had a positive angle difference of 15°. Conversely, if the deviation was towards vertical, then the angle difference was negative.

Although all orientations were represented in each area of retina, overall, as shown in Fig. 4, there was a statistically significant tendency for ganglion cells outside of central retina to have dendritic fields which are oriented approximately radially (n = 269, U = 4.38, $P < 0.0005$, mean angle difference = +18°). This is true for both P-alpha (n = 77, U = 1.98, $P < 0.025$, mean angle difference = +9°) and P-beta (n = 192, U = 3.99, $P < 0.0005$, mean angle difference = +21°)-type ganglion cells. The positive mean angle differences indicate that, as has been reported for the cat[18], most cells are oriented more horizontally than their polar angles.

The tendency for dendritic fields to be oriented radially in monkey, as in cat retina, varied with meridian. Cells within 22.5° of the horizontal meridian exhibited a stronger tendency to be oriented radially than did cells within 22.5° of the oblique (45° and 135°) or vertical meridians; the distribution of angle differences for cells near the horizontal meridian differed significantly from the distributions for cells subserving other meridians (Watson $U^2 = 0.35$, $P < 0.005$, comparing horizontal to vertical angle difference distributions). The tendency for dendritic fields to be oriented radially did not vary with eccentricity more than 4 mm from the fovea.

We determined the point on the retina about which the ganglion cell dendritic fields are oriented. This was accomplished by finding the point on the retina about which the mean squared deviation of the dendritic field orientations was minimal[27]. The signifi-
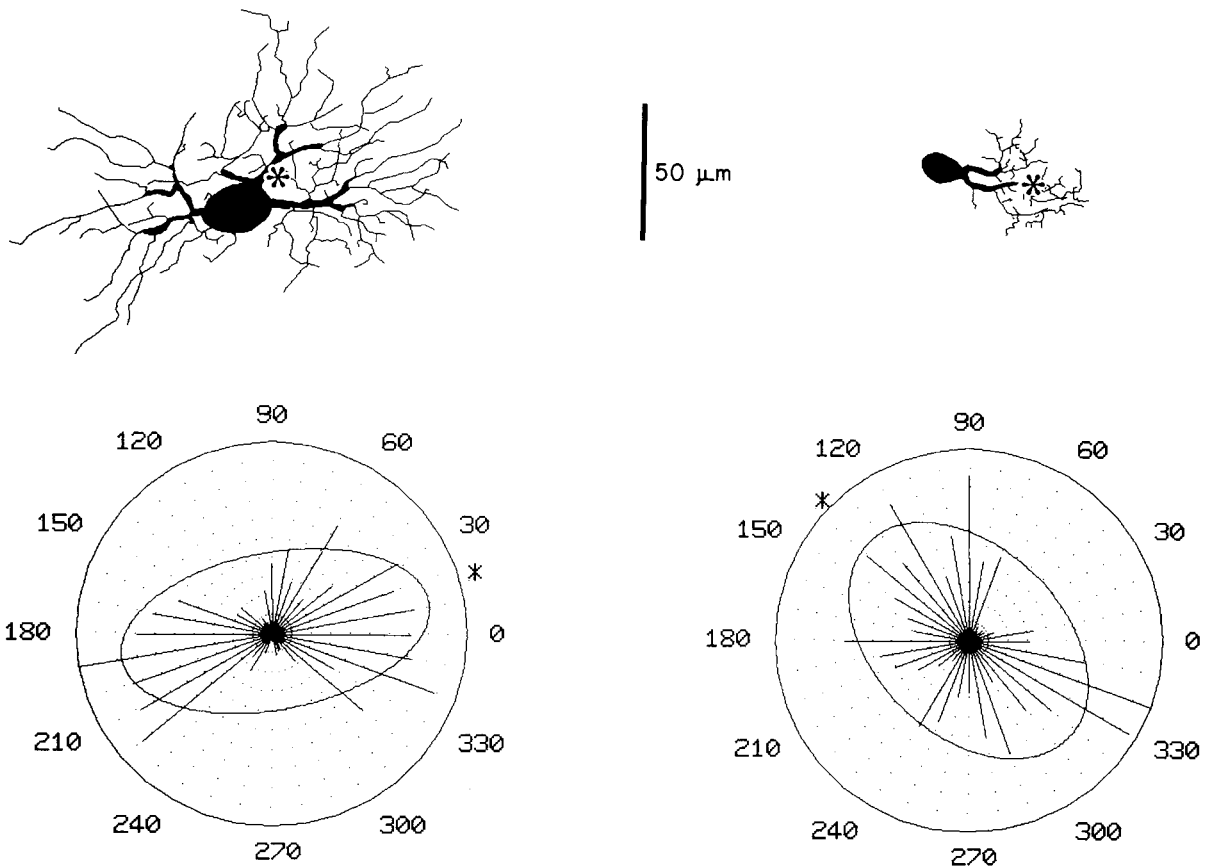
Fig. 2. Computer representation and orientation analysis of a P-alpha/A (left) and a P-beta/B (right) cell. The scale bar corresponds to 50 μm and is aligned parallel to the vertical meridian of the retina. The asterisk within the dendritic field is situated at the geometric center of the dendritic field. The circular histograms represent the density of dendrites within the dendritic field; the center of the histogram corresponds to the center of the dendritic field. The lines emanating from the center of the histogram are proportional in length to the density of dendrites in the given direction. The asterisk denotes the orientation of the dendritic field calculated by a vector summation algorithm[18]. For each cell studied, an ellipse was also fitted to the points comprising the dendritic field. The inclination of the major axis of the ellipse provides another measure of orientation. The ratio of the lengths of the long and short axes of the ellipse reflects the elongation of the dendritic field. The P-alpha cell shown was located 8.3 mm from the center of the fovea, and had a polar angle of 16° from the horizontal meridian. Its dendritic field had an orientation bias of 0.32, an ellipse axes ratio of 2.0 and was oriented at 26°. The angle difference of this cell was –10°; thus, this dendritic field was oriented nearly radially. The P-beta cell was located 4.3 mm from the center of the fovea and had a polar angle of 158°. Its dendritic field had an orientation bias of 0.24, an ellipse axes ratio of 1.5 and was oriented at 139°.

cantly oriented P-alpha cells were oriented about a point 1.7 mm temporal and 1.2 mm inferior to the center of the fovea. The significantly oriented P-beta cells were oriented about a point 0.5 mm temporal and 1.8 mm superior to the center of the fovea.

DISCUSSION

We have provided evidence that the dendritic fields of most P-alpha and P-beta ganglion cells are elongated in regions of macaque retina more than 4 mm from the center of the fovea. There was a significant tendency for the elongated dendritic fields to be oriented radially with respect to the fovea. The dendritic fields are not oriented about the optic disk. The dendritic fields of a small sample of ganglion cells in human retina have been studied, and most are also oriented radially with respect to the fovea[27].
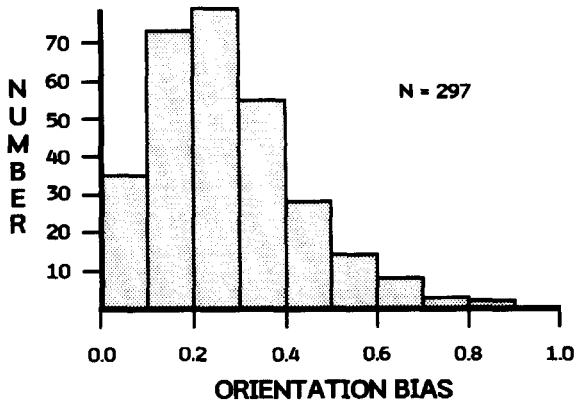
Fig. 3. Orientation biases of all monkey ganglion cells analyzed. Orientation bias reflects the elongation of a dendritic field. The values can range from 0 to 1; a perfectly circular dendritic field has an orientation bias of 0.0. It is evident that most retinal ganglion cells in the old world monkey have elongated dendritic fields. An orientation bias of 0.1 appears to be a reasonable cut-off between oriented and unoriented dendritic fields[18,20]. Accordingly, 90% of the ganglion cells we sampled had significantly oriented dendritic fields.

These data imply that, as in the cat, ganglion cells at least in peripheral regions of primate retina are orientation-sensitive.

The distribution of the orientations of the ganglion cells in any spot of cat retina appears to be preserved
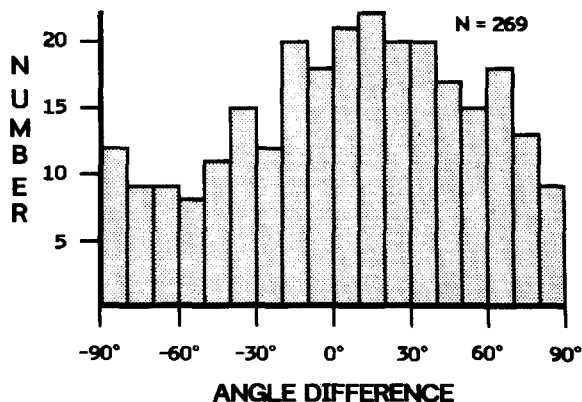

Fig. 4. Differences between dendritic field orientation and polar angle for oriented monkey ganglion cells. Dendritic fields which are oriented exactly radially have angle differences equal to 0°. If the dendritic field was oriented more horizontally than its polar angle on the retina, then the angle difference was positive. If a dendritic field was oriented more vertically than its polar angle, the angle difference was negative. It is evident that most monkey ganglion cell dendritic fields are oriented radially, although most cells are oriented more horizontally than their polar angles.

in the distribution of the preferred orientations of first-order cortical cells receiving input from that spot of retina[29]. In both retina and visual cortex of the cat, all orientations are represented, but there is an over-representation of cells which prefer orientations near radial. Consequently, it has been proposed that during development, the preferred orientations of retinal ganglion cells specify the orientation preferences of geniculate relay cells, which in turn specify the preferred orientations of the first-order cells in visual cortex on which they synapse[16,19,29]. While orientation specificity appears to be initiated in the retina, intracortical mechanisms greatly enhance the orientation selectivity of cortical neurons[3,7,24,30,31,33].

A noteworthy relation between retinal and cortical orientation specificity is evident in the monkey visual pathway. The dendritic fields of P-beta cells in central monkey retina are so small that they may receive input from single bipolar cells[5]. If there is no convergence on these ganglion cells, then they cannot be orientation-sensitive. Central P-alpha cells, on the other hand, have dendritic fields large enough to receive input from many bipolar cells[26]. The dendritic fields of most P-alpha cells which we have examined in the macular region are elongated; therefore, it is possible that they can be orientation-sensitive. Outside the fovea the dendritic fields of P-beta cells are large enough to receive input from many bipolar cells and so may be orientation-sensitive.

In regions of macaque striate cortex subserving central retina, cells in layer 4C-alpha are orientation-sensitive while cells in layer 4C-beta are not[4,6,9,11,21]. With increasing eccentricity, the proportion of orientation-sensitive cells in the cortex increases[21]. The input to layer 4C-alpha originates from the magnocellular layers of the LGNd, while that to 4C-beta originates from the parvocellular[14]. P-alpha ganglion cells project to the magnocellular LGNd layers, and P-beta ganglion cells, to the parvocellular[17,26]. Accordingly, ganglion cells which are probably orientation-sensitive, ultimately provide the input to orientation sensitive cortical cells, and ganglion cells which may not be orientation-sensitive provide the input to cortical cells which are not orientation-sensitive. It may be that the development of orientation specificity of neurons in layer 4C-alpha precedes the development of orientation specificity in other cortical layers in regions subserving central vision.

Recent psychophysical studies have shown that humans, using peripheral vision, detect radially oriented stimuli better than non-radially[10,28,32]. We would like to propose that the overrepresentation of radially oriented dendritic fields in peripheral retina is a possible explanation for this finding. If the distribution of the preferred orientations of the ganglion cells in each spot of primate retina is preserved in the visual cortex, then, as in the cat, more neurons in regions of primate visual cortex subserving the periphery will respond to radially oriented stimuli. The detection of a stimulus with a given orientation seems to be related to the number of cortical neurons which respond best to that orientation. In central vision, horizontal and vertical stimuli are detected better than oblique[1], and more neurons in primate striate cortex subserving central vision have horizontal- and vertical-preferred orientations[22,23]. An overrepresentation of radial orientations in the retina which is preserved in the visual cortex may, therefore, account for the ability to detect radially better than non-radially oriented stimuli.

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