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Morphology, Central Projections, and Dendritic Field Orientation of Retinal Ganglion Cells in the Ferret

DAGMAR J. VITEK, JEFFREY D. SCHALL, AND AUDIE G. LEVENTHAL
Department of Anatomy, The University of Utah, School of Medicine, Salt Lake City, Utah 84132

ABSTRACT

Retinal ganglion cells were studied in pigmented ferrets that received small electrophoretic injections of horseradish peroxidase (HRP) into the dorsal lateral geniculate nucleus (LGNd) or optic tract. Ferret retina contains a number of types of retinal ganglion cells of which the relative cell body sizes, dendritic field structures, and central projections correspond closely to those of retinal ganglion cell types in the cat. Ferret retina contains about the same proportion of alphalike cells, a lower proportion of betalike cells, and thus a high proportion of other types of ganglion cells than cat retina. Ferret retina has a visual streak and somewhat weaker area centralis than cat retina. Changes in ganglion cell morphology associated with eccentricity are less pronounced in the ferret than in the cat. The adult ferret retina is about 12.5 mm in diameter, and the nasotemporal division is about 2.7 mm from the temporal margin. Interestingly, virtually all alpha cells in the pigmented ferrets studied projected contralaterally. Studies of infant ferrets indicate that 4 days after birth (P4) the area of ferret retina is 25% that of the adult. The neonatal ferret retina contains numerous small, densely packed cells in the presumptive ganglion cell layer. At P4 these cells appear to be uniformly distributed across the retina. The area centralis and visual streak are not obvious as late as 8 days after birth.

Key words: dendritic morphology, alpha cell, beta cell, newborn ferret, contralateral alpha cell projection

In recent years it has become clear that mammalian retina contains a variety of ganglion cell types with different receptive field properties, morphologies, retinal distributions, central projections, and developmental histories. This work has greatly facilitated our understanding of the visual pathways (reviewed in Rodieck, '79; Stone et al., '79; Lennie, '80). We have studied retinal ganglion cells in the ferret (*Mustela putorius furo*) in order to extend our knowledge of mammalian retina and to provide necessary background information for future studies of the ferret's visual pathways. The ferret is a carnivore and its visual system is remarkably similar to that of the cat, the species whose visual system has been studied the most intensively. Compared to the cat, however, the ferret is born at a very early stage, only 42 days after conception. At this time the ferret's lateral geniculate nucleus (LGNd) is as mature as the cat's is more than 3 weeks before birth (Linden et al., '81). The ferret, thus, offers advantages over the cat for studies of retinal development. This report describes the cell body sizes, dendritic field structures, and some of the central projections of the different classes of ganglion cells in retina of the pigmented ferret. The immature nature of the retina in the neonatal ferret is also described.

MATERIALS AND METHODS

Subjects

A total of eleven adult ferrets and four ferret kits provided data for this study.

Surgery

Nembutal was administered intraperitoneally to induce anesthesia and intravenously to maintain it. The animal's head was positioned in a stereotaxic apparatus and the skin, bone, and dura mater covering the appropriate regions were removed. The cortex was protected by a 4% solution of agar in saline. Body temperature was monitored continuously with a rectal thermistor and maintained automatically at 37–38°C.

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Neosynephrine was used to retract the nictitating membranes and atropine was employed to dilate the pupils. The corneas were protected from desiccation with zero-power contact lenses and the optic discs and area centrales were projected onto a tangent screen located 1.14 m from the animal's retina.

Electrophysiological recording

Prior to all horseradish peroxidase (HRP) injections, electrode penetrations were made into the brain in order to locate the LGNd or optic tract. Multiple- and single-unit activity was recorded with low-impedance (1–3 MΩ) microcapillary electrodes filled with 4 M NaCl. Neuronal responses were amplified conventionally, displayed on the oscilloscope, and monitored by ear.

Electrophoretic injection

Once a satisfactory site was located, the electrode was removed and a microcapillary electrode containing approximately 10% HRP in Tris HCl buffer (pH 8.6) was lowered into the appropriate region. The correct position was confirmed by recording with this electrode prior to all injections. Typically, HRP was injected using currents of $+3\mu A$ (1.5 seconds on, 0.5 seconds off) for a period of 2–3 hours (Leventhal, '82).

Multiple HRP injections (four or five) were made into the optic tract about 3 mm from the optic chiasm. In all animals injections were closely spaced and made across the mediolateral extent of the optic tract. Each injection was begun in the ventral part of the optic tract and the electrode was withdrawn slowly until, at the end of the injection, the electrode was in the dorsal portion of the optic tract. Injections into the optic tract made in this fashion expose the entire optic tract to HRP. This is necessary since fibers of different diameter are segregated within the optic tract (Guillery et al., '82).

Histology and histochemistry

Animals were maintained approximately 40 hours following HRP injections. They were then anesthetized and perfused through the heart with 600 ml of 35°C solution of 1% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer at pH 7.4, followed by 500 ml of 35°C lactated Ringer's containing 5% dextrose. Brains were removed and the portions containing the injection sites were blocked and stored for 2–4 days in a 30% sucrose solution and then frozen-sectioned at 50 μm. Sections were collected in 0.1 M Tris HCl buffer (pH 7.4), treated for 20 minutes in 0.1 M Tris buffer containing 0.03% p-phenylenediamine dihydrochloride, 0.06% pyrocatechol, and 0.02% H_2O_2 (PPD-PC reagent), and transferred back into 0.1 M Tris HCl buffer.

Whole retinae were removed and treated immediately after the perfusion. All retinae were rinsed in Tris buffer (pH 7.4) for 5 minutes, incubated in cobalt chloride in Tris buffer for 20 minutes at 35°C, rinsed in Tris buffer at 35°C for 5 minutes, rinsed in phosphate buffer at 35°C for 5 minutes, pretreated in the PPD-PC reagent (without H_2O_2) at 35°C for 15 minutes, treated with fresh PPD-PC reagent (with H_2O_2) at 35°C for 20 minutes, and rinsed in phosphate buffer for 30 minutes.

Cell body and dendritic field measurements

The cell bodies and dendritic fields of labeled ganglion cells were measured under the microscope using a calibrated eyepiece graticule and 40× planapochromat oil immersion objective. For each cell, soma diameter was recorded as the mean of its longer and shorter axes. The long axis of each dendritic field was measured for the diameter. In all cases, the person making the measurements was unaware of the area to which the labeled cells projected.

Ganglion cell density

The procedures used to determine the distribution of retinal ganglion cells in ferret retina as well as the criteria used to differentiate ganglion cells from glial cells have been described previously (Stone, '78; Leventhal, '82).

Dendritic field analysis

Camera lucida drawings were made of well-filled cells across the retina. Each drawing was then traced onto a digitizing tablet interfaced to a PDP 11/23 computer. The high resolution of the digitizing tablet (0.005 inches) allowed an accurate representation of the dendritic field to be made. Only the presumed postsynaptic dendritic segments ramifying in the inner plexiform layer (IPL) were considered in the analysis of orientation. The cell body and proximal trunk dendrites were excluded since electron microscopic studies indicate that these support virtually no synapses (Kolb, '79; Stevens et al., '80).

The center of the dendritic field was computed by summing the X, Y coordinates of all points representing dendrites arborizing in the IPL. Vectors were drawn from that center to each point comprised in the dendritic field. The angle of the vector was measured from the vertical nasotemporal division of the retina. This was determined from the distribution of labeled ganglion cells resulting from HRP injections into the LGNd or optic tract. The vectors were then added; the angle of the resultant vector gave the orientation of the dendritic field. The length of the resultant could range from 0 to 1; it is a measure of how oriented the dendritic field is and has been termed *orientation bias*. An orientation bias of 0 describes a circular, unoriented dendritic field. This measure of dendritic field orientation bias is comparable to the one used by Levick and Thibos ('82) to describe the physiological orientation bias of retinal ganglion cells.

RESULTS

Ganglion cell types in ferret retina

In the cat, ganglion cells can be classified as alpha, beta, gamma (Boycott and Wässle, '74), and epsilon (Leventhal et al., '80). There are also some ganglion cells that do not clearly fit into any of these groups (Farmer and Rodieck, '82; Rowe and Dreher, '82; Leventhal, '82). These cells have been divided into two heterogeneous groups and are referred to as g1 and g2 cells (Leventhal, '82). Ferret retina contains a number of classes of ganglion cells whose morphology and central projections are very much like those of cell types in cat retina. Given these similarities, we refer to them according to the nomenclature for cat retinal ganglion cells. We recognize, of course, that homologies between corresponding classes in the cat and the ferret may or may not exist. Examples of the types of cells we have seen in the ferret are shown in Figures 1 and 2.

Ferret alphalike cells have the largest cell bodies and coarsest axons of all classes of ferret ganglion cells. Their dendritic fields are large and consist of coarse main dendrites that branch repeatedly. Ferret betalike cells have medium-sized cell bodies and medium-gauge axons. Their dendrites branch profusely over a very small region, and

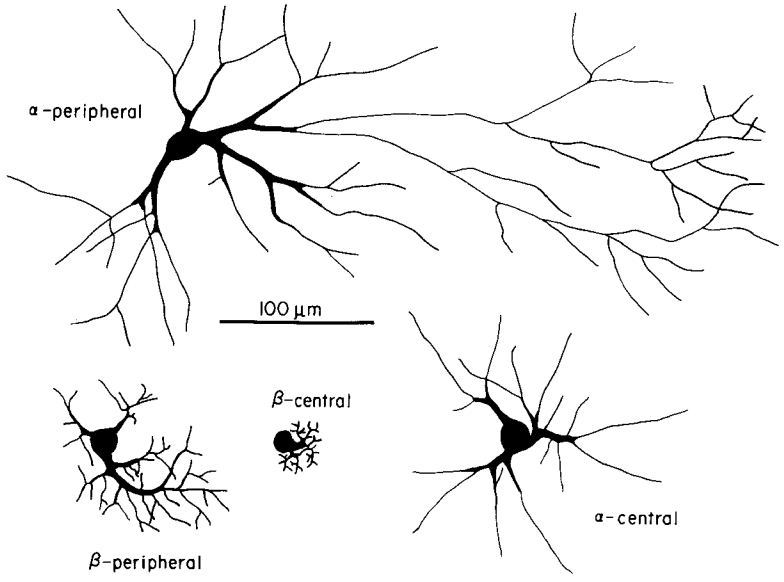


Fig. 1. Camera lucida drawings of alpha and beta cells in the ferret. Central cells are less than 1 mm from the center of the area centralis; peripheral cells are 3–5 mm from the area centralis.

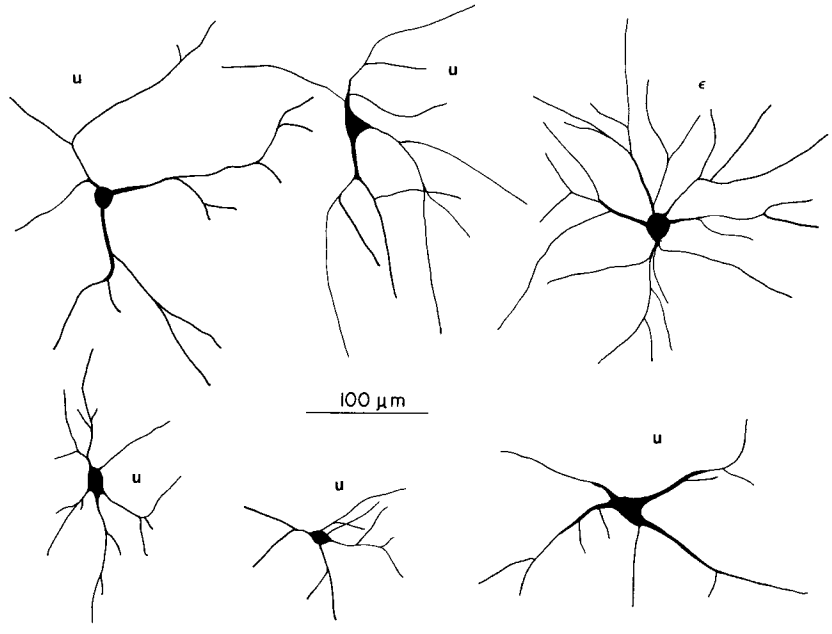


Fig. 2. Camera lucida drawings of epsilon and unclassified cells. All cells are 3–5 mm from the area centralis. The techniques employed are likely not to have stained completely the dendritic fields of ganglion cells having small cell bodies.

their dendritic fields are smaller than those of any other class in the ferret. Ferret epsilonlike cells have medium-sized cell bodies, fine- to medium-gauge axons, and large dendritic fields. They typically have medium-gauge main dendrites which branch less profusely than those of alpha or beta cells and taper gradually with distance from the cell body.

Some labeled ganglion cells in our material did not fit into the three classes described above. These cells resemble the g1 and g2 cells described in the cat (Leventhal et al., '85). These cells are referred to here as unclassified. All ganglion cells having cell bodies between 8 and 20 μm which cannot be considered beta or epsilon cells are included in the unclassified group. Cells which resemble the gamma cells illustrated by Boycott and Wässle ('74) are also included in this group. The cell body and dendritic field diameters of the different types of ganglion cells in ferret retina are plotted in Figure 3.

Distribution of ganglion cells in ferret retina

Figure 4 shows the density of ganglion cells in different parts of ferret retina. The distribution of all ganglion cells

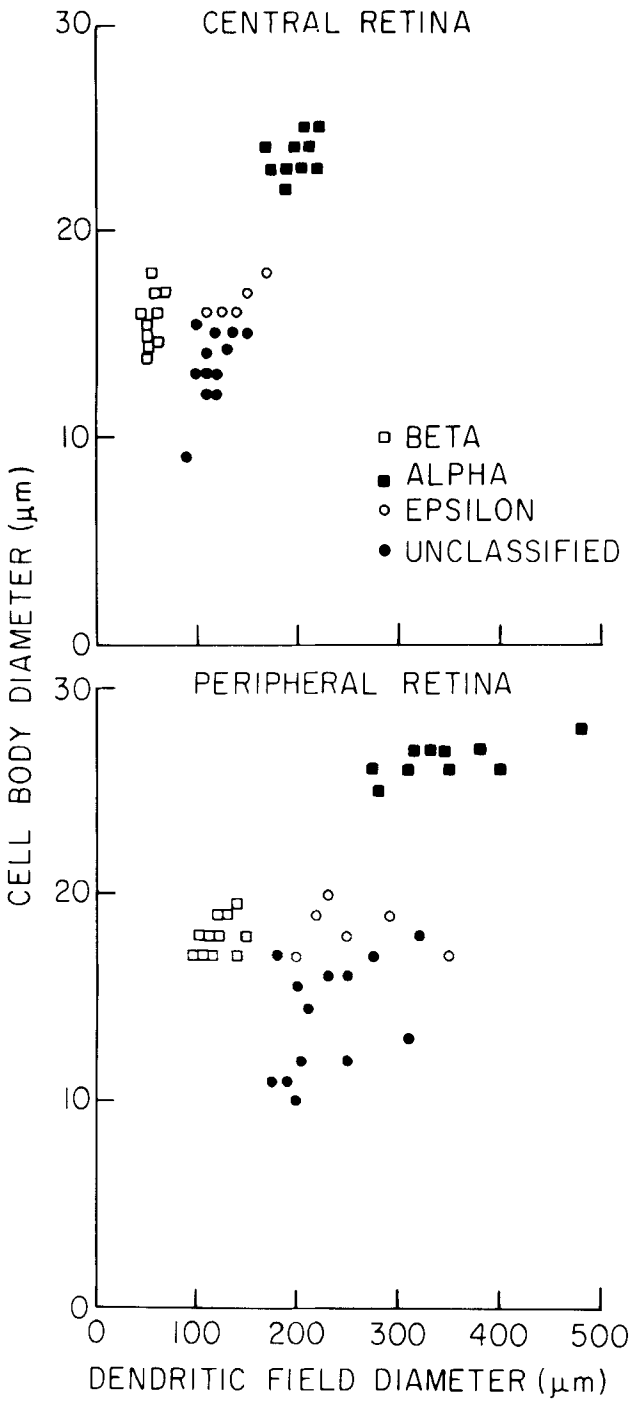


Fig. 3. Cell body and dendritic field diameters of alpha, beta, epsilon, and unclassified cells in central (<1 mm from the area centralis) and peripheral (5–6 mm from the area centralis) regions of ferret retina. The techniques employed are probably not staining the fine-caliber distal dendrites of small ganglion cells. Thus, the dendritic field diameter of cell types other than alpha and beta may be larger than our measurements indicate.

and large alpha ganglion cells are shown separately. The peak density of ganglion cells in ferret retina (the area centralis) is about 5,200 cells/mm^2 and occurs about 2.7 mm from the temporal margin. The center of the area centralis is roughly 2.6 mm from the center of the optic disk. The peak density of large cells is about 75 cells/mm^2. The density of ganglion cells in the ferret area centralis is, therefore, about half that in the cat area centralis (Stone, '78). Ganglion cell density decreases more rapidly temporal than nasal to the area centralis. The density of ganglion cells is higher along the horizontal than other retinal meridians, indicating that a visual streak is a feature of ferret retina. The density of cells in the visual streak of the ferret, even in the far nasal periphery, is over 3000 cells/mm^2.

The nasotemporal division of ferret retina

The distributions of ganglion cells in the ipsilateral and contralateral retinae labeled by multiple injections of HRP into the optic tract of an adult pigmented ferret can be seen in Figure 5. The "nasotemporal division" of ferret retina is about 2.7 mm (range 2.5–2.9 mm in four ferrets) from the temporal margin and passes through the area centralis. The nasotemporal division makes an angle of about 112° with the line connecting the centers of the area centralis and optic disk (Fig. 6).

In the cat, some of the ganglion cells in regions of retina temporal to the area centralis project contralaterally; the proportion of cells in temporal retina projecting contralaterally is higher for alpha cells and other types of cells than for beta cells (Stone et al., '78; Cooper and Pettigrew, '79; Leventhal, '82). A similar situation exists in the ferret. The labeled cells in contralateral temporal retina were alpha cells and other types, but not beta cells. It is noteworthy and rather surprising that all of the labeled alpha cells in temporal retina in this ferret (Figure 5) were observed in the eye contralateral to the injection. This suggests that virtually all alpha cells project contralaterally. Injections into the optic tracts of two other ferrets also provided no evidence for a significant ipsilateral alpha cell projection.

The distribution of ipsilaterally and contralaterally projecting ganglion cells in the two retinae of a ferret that received multiple HRP injections into the LGNd are shown in Figure 7. The injection sites in this animal were centered in the A laminae but involved all layers of the LGNd and the medial interlaminar nucleus (MIN). The line of decussation is evident and, as following optic tract injections, passes through the center of the area centralis. A substantial number of cells in the contralateral temporal retina were again labeled; these were alpha cells and other types. Few, if any, beta cells in temporal retina projected contralaterally to the LGNd in this ferret.

An analysis of Figure 7 again reveals a striking absence of labeled alpha cells in the ipsilateral temporal retina. This is especially surprising since many beta cells as well as other types of cells in temporal retina were labeled. The injection site must therefore have included the ipsilateral layers of the LGNd. Only one labeled cell in the ipsilateral temporal retina of this ferret could be identified as an alpha cell; this is the only ipsilaterally projecting alpha cell we have observed following any of our injections into the LGNd (six animals) or optic tract (three animals).

Ganglion cell size groups in ferret retina

The sizes of the cell bodies of ganglion cells labeled by HRP injections into the ferret's optic tract and LGNd are shown in Figure 8. In our material many cells have their dendritic fields well stained and thus the different morphological types can be identified. The mean cell body diameter of well-stained cells belonging to the different morphological types are indicated in the histograms. Means were based upon 20–30 well-stained examples of each type.

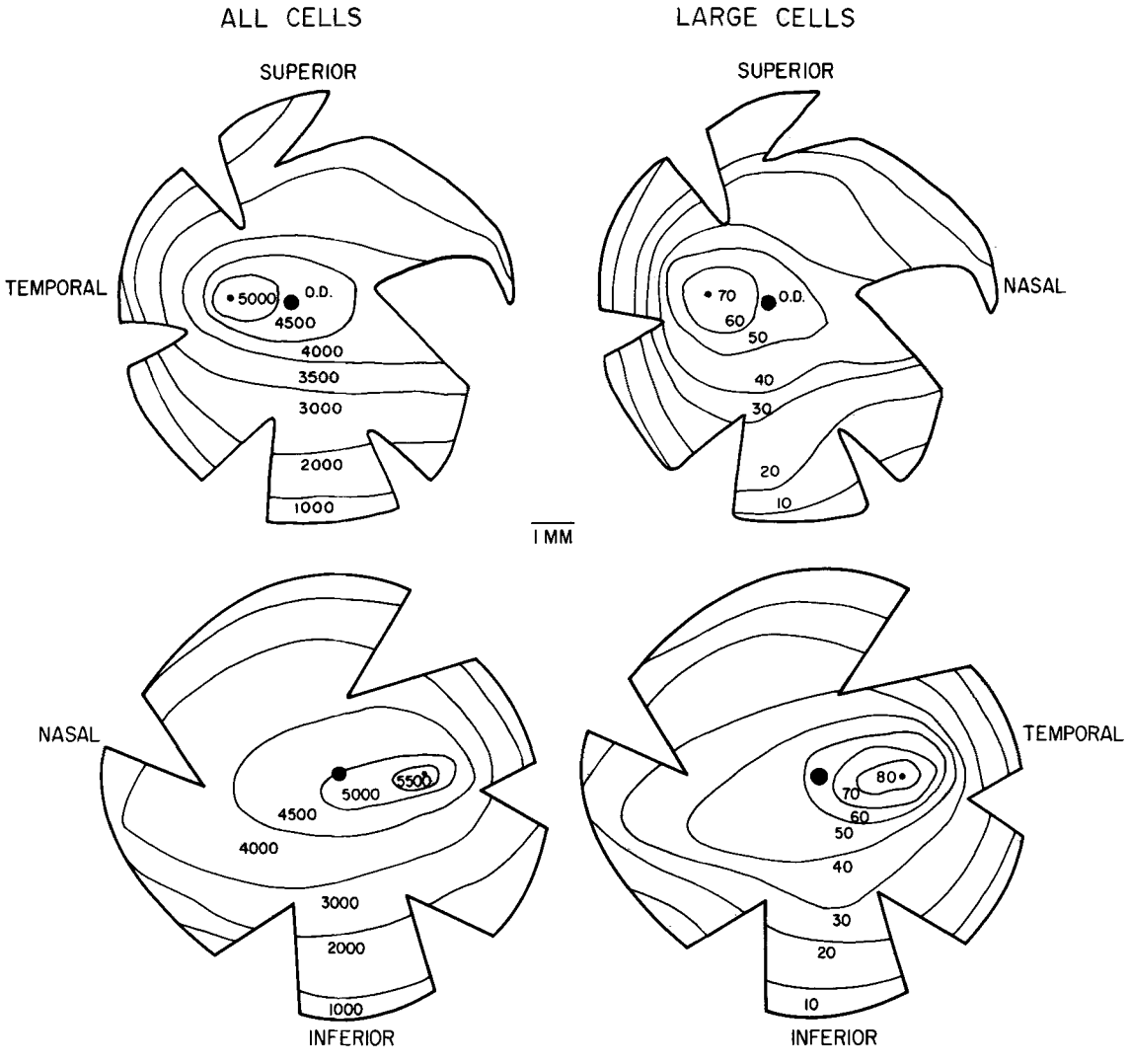


Fig. 4. Retinal ganglion cell density map of two ferret retinae. The distributions for all cells and large (alpha cells) are shown separately. The number of cells per mm^2 represented by each isodensity line is indicated.

The relative numbers of ganglion cells of different types labeled by optic tract injections differed somewhat in the cat and ferret. This is because ferret retina contains a higher relative proportion of cell types other than alpha and beta. In the cat it has been estimated using techniques identical to those employed here that about 40% of retinal ganglion cells are beta cells, 5% are alpha cells and the rest (55%) are other types (Leventhal, '82). Based upon the relative numbers of well-stained cells of the different types in our ferret retinae, we estimate that about 25% of ferret ganglion cells are betas, 3–4% are alphas, and the rest (72%) are other types. As in the cat, in the ferret injections of HRP centered in the A laminae label mainly alpha and beta cells. Relatively few of the smallest ganglion cells project to the ferret LGNd (Fig. 8). We have not yet made injections restricted to the A laminae in the ferret. Thus we do not know whether, as in the cat, only alpha and beta cells project to the ferret's A laminae.

In the cat, the cell bodies of HRP-stained retinal ganglion cells range in size from 9 to 46 μm. In the ferret, cells range in size from 8 to 28 μm. The smaller size of ferret ganglion cells mainly reflects the fact that large- and medium-sized cells in the ferret are smaller than their counterparts in the cat. For example, in peripheral cat retina alpha, beta, and epsilon cells average 42, 26, and 25 μm in diameter, respectively, while peripherally located alpha, beta, and epsilon cells average 24, 16, and 16 μm in diameter, respectively in ferret retina. It is also our impression that the axons of alpha and beta cells are finer than those of alpha and beta cells in the cat. In the ferret, even the coarsest axons, those of alpha cells, are only about 1 μm in diameter. Since accurate measurements of axon diameter are not possible using the light microscope, no quantitative analysis was attempted.

Changes in morphology associated with eccentricity

In the cat the morphologies of alpha and beta cells change dramatically with increasing distances from the area centralis (Boycott and Wässle, '74; Leventhal, '82). In the ferret changes in morphology associated with eccentricity are less pronounced. Alpha and beta cells within the ferret's area centralis are, on average, about 23 and 15 μm in diameter, respectively, while alpha and beta cells in the far periphery are only slightly larger, on average about 26 and 18 μm in diameter, respectively (Fig. 3). The dendritic fields of alpha and beta cells within the ferret's area centralis are rarely

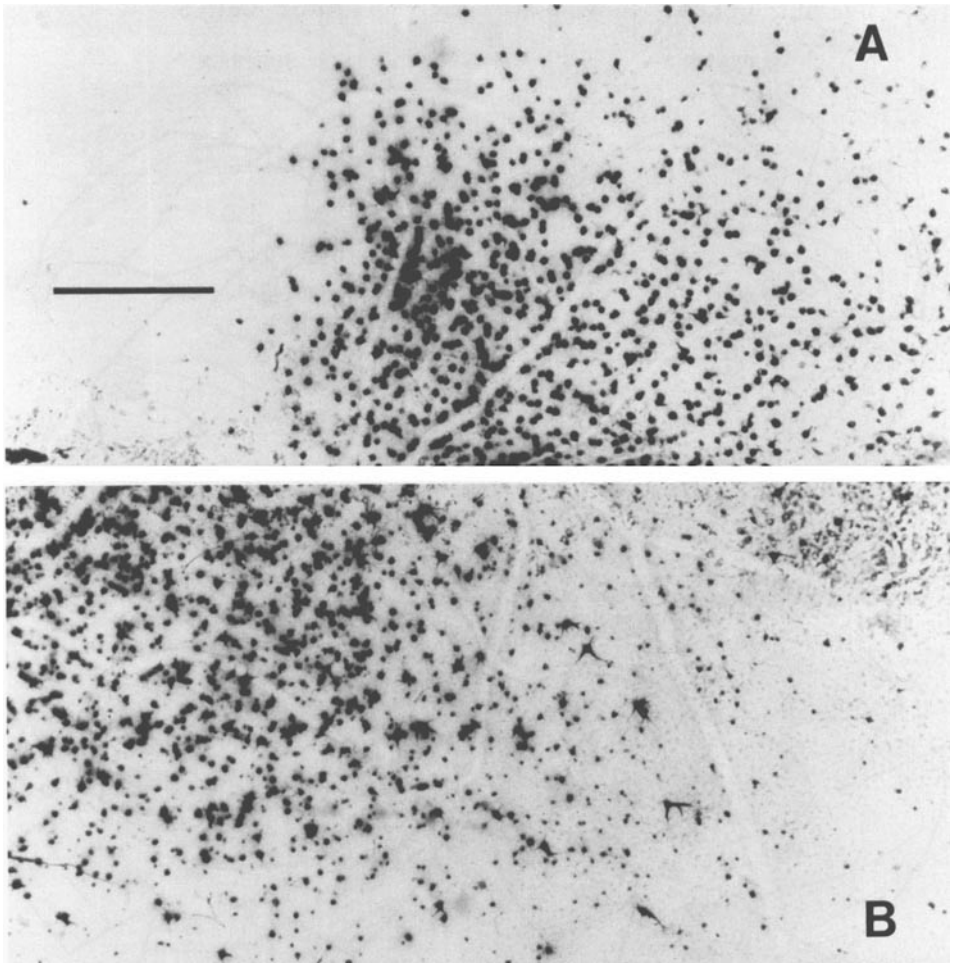


Fig. 5. Photomicrographs of the ipsilateral (A) and contralateral (B) retinae of a pigmented ferret that received multiple HRP injections into the optic tract. Notice that no alpha cells were labeled in the ipsilateral retina. Scale bar = .5 mm.

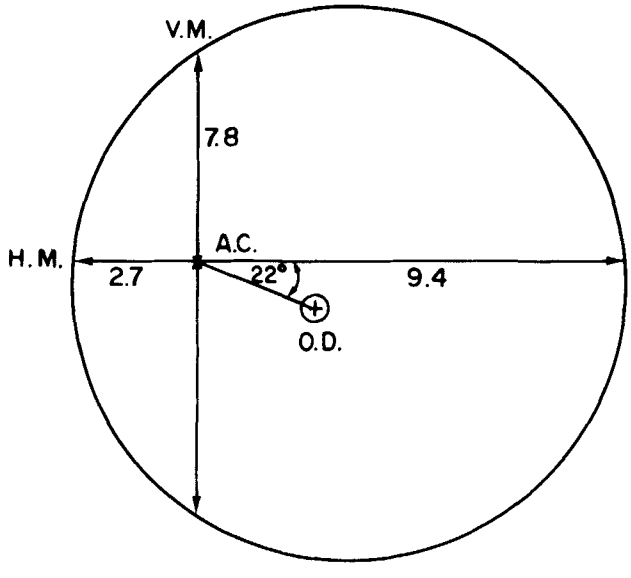


Fig. 6. Schematic drawing of adult ferret retinae illustrating the relative positions of the area centralis (A.C.), optic disc (O.D.), and nasotemporal division.

smaller than 175 and 50 μm in diameter, respectively, while in the far periphery alpha and beta cell dendritic fields are rarely larger than 500 and 175 μm, respectively (Fig. 3). The cell bodies and dendritic fields of alpha and beta cells within the ferret's area centralis are, thus, as large or larger than those of alpha and beta cells in the cat's area centralis while in the periphery alpha and beta are smaller than cat alpha and beta cells.

Dendritic field orientation of ferret retinal ganglion cells

In the cat most retinal ganglion cells of all types have oriented dendritic fields. A cell's dendritic field orientation is related to its position on the retina (Leventhal and Schall, '83). The dendritic fields of all types of cat retinal ganglion cells are oriented radially, i.e., like the spokes of a wheel having the area centralis at the hub. A similar situation exists in the ferret.

The distribution of the orientation biases of a sample of alpha cells is shown in Figure 9. Since a bias of 0.1 or greater (Levick and Thibos, '82; Leventhal and Schall, '83) indicates a significant degree of orientation, these results indicate that about 85% of the alpha cells are oriented.

Figure 10 presents the differences between the dendritic field orientations of alpha cells and their polar angles on

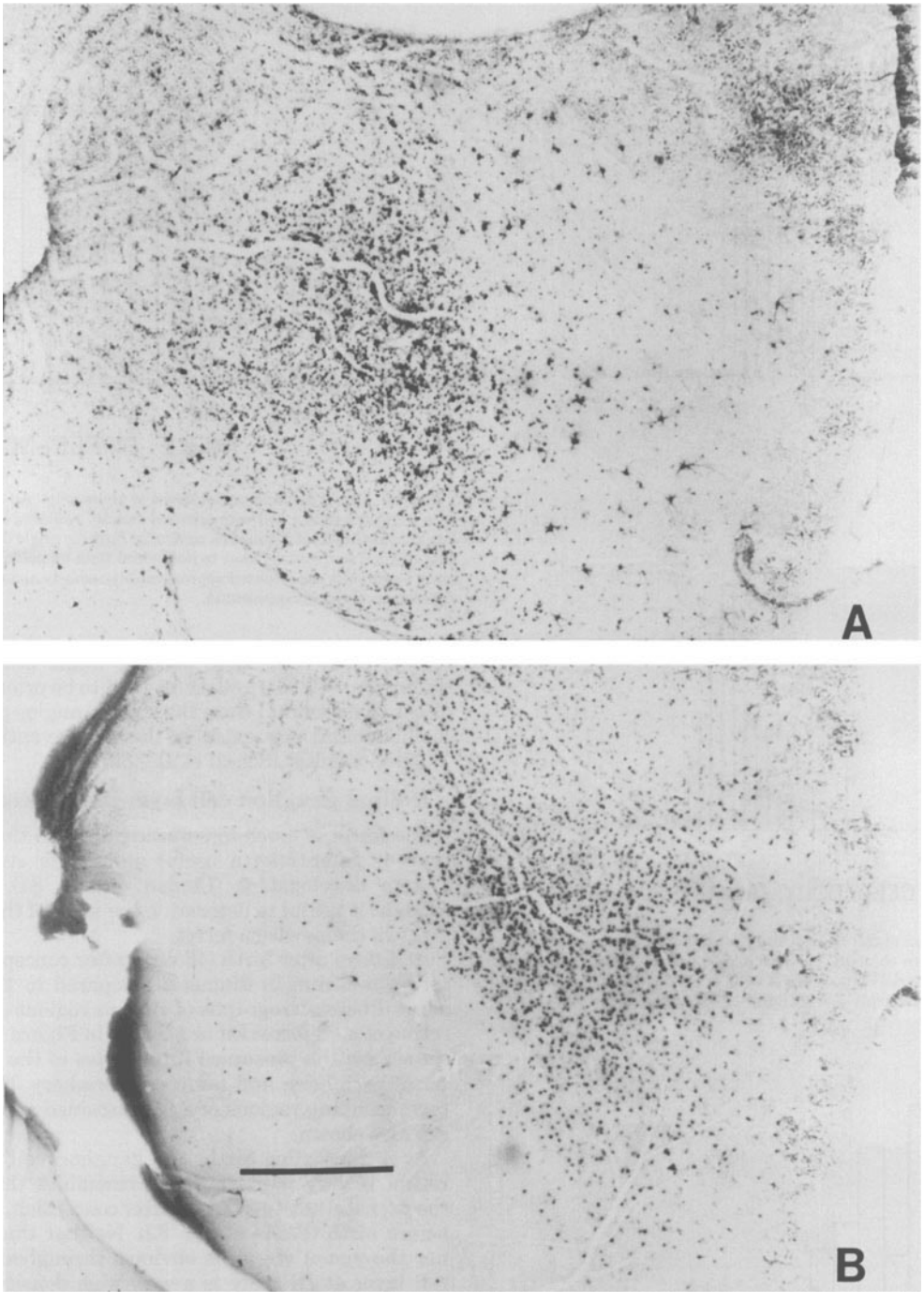


Fig. 7. Photomicrographs of the ipsilateral (B) and contralateral (A) retinae of a pigmented ferret that received multiple HRP injections into the LGNd. Again notice that virtually no alpha cells were labeled in the ipsilateral retina. Scale bar = 1 mm.

the retina. An angle difference of 0° indicates that a cell is oriented radially, e.g., a cell located on the horizontal meridian (polar angle of 0°) with a dendritic field orientation of 0°. An angle difference of 90° or −90° indicates that a cell is oriented tangentially, e.g., in a cell with a horizontal dendritic field on the vertical meridian. It is evident that most cells in ferret retina have small angle differences and thus are oriented radially (V test, $U = 5.1$; $P < .001$).

In the histogram in Figure 10, positive angle differences (0° to +90°) indicate cells whose dendritic fields are oriented closer to horizontal than their polar angles predict. For example, a cell with a dendritic field orientation of 30° which is located 45° off of the horizontal meridian has an angle difference of +15°. Conversely, negative angle differences (0° to −90°) indicate cells which are oriented closer to vertical than their polar angles predict. Clearly, in ferret

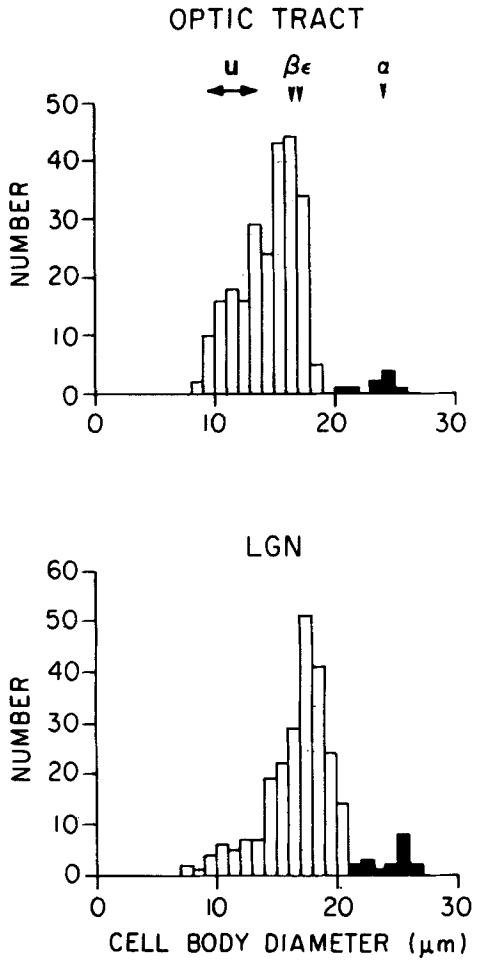


Fig. 8. Distribution of cell body sizes of retinal ganglion cells labeled by injections of HRP into the optic tract (top) and LGNd (bottom). The mean cell body diameters of different types of cells are indicated above the histograms. Notice that relatively few of the smallest cells project to the LGNd.

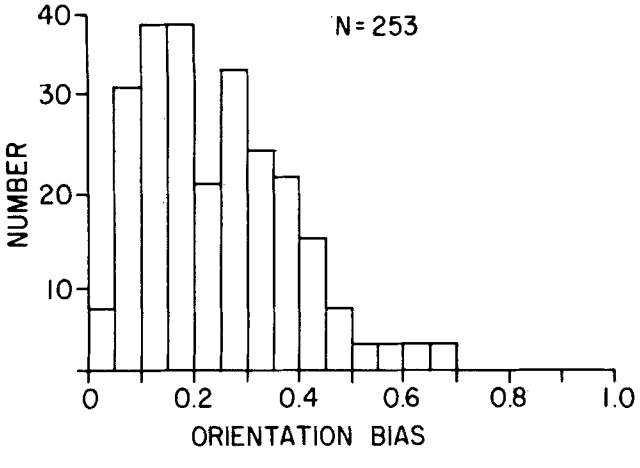


Fig. 9. Dendritic field orientation biases of alpha cells. Orientation biases range from 0 to 1 with 0 being unoriented. Notice that most cells have oriented dendritic fields.

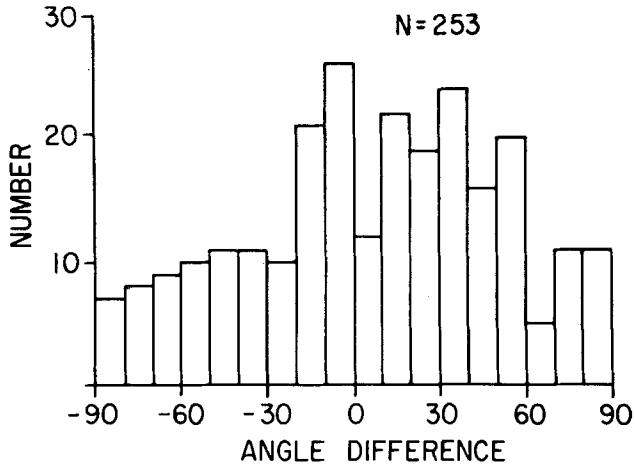


Fig. 10. Dendritic field orientations of alpha cells. An angle difference of zero indicates that a cell was oriented exactly radially, i.e., parallel to the line connecting it with the area centralis. Positive angle differences indicate that the cell is oriented closer to horizontal than its polar angle. Notice that most alpha cells are oriented approximately radially and that positive angle differences are overrepresented.

retina, most cells have positive angle differences (mean difference = +15°) and, thus, tend to be oriented somewhat closer to horizontal than their polar angles predict. A similar horizontal bias exists in the cat (Leventhal and Schall, '83) and monkey (Schall et al., '85).

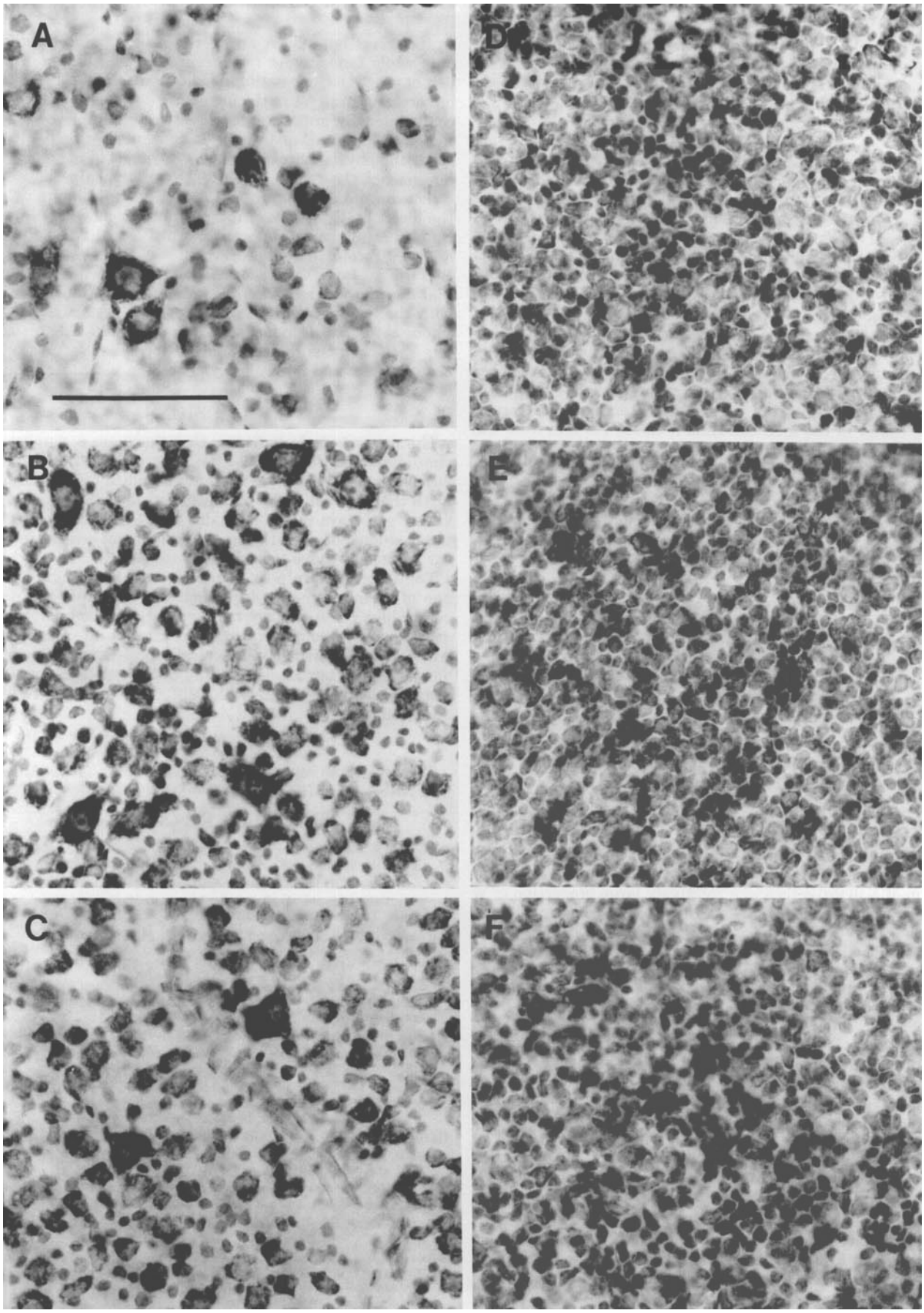
Retinal ganglion cell layer in the neonatal ferret

The ferret is much less mature at birth than the cat and, thus, is potentially a useful animal for studies of visual system development (Linden et al., '81). We therefore thought it useful to determine the state of the ganglion cell layer in the newborn ferret.

At 4 days after birth (46 days after conception) the ferret retina is 6 mm in diameter compared to 12.5 mm in the adult. Photomicrographs of various regions of Nissl-stained retina of a P4 ferret kit are shown in Figure 11. The regions shown are the presumed future sites of the area centralis, nasal periphery, and temporal periphery. For comparison, corresponding regions of a Nissl-stained adult ferret retina are also shown.

At 4 days after birth, the ganglion cell layer of ferret retina is very immature and resembles that reported for the prenatal cat 46–50 days after conception, almost 3 weeks before birth (Stone et al., '82). Neither the area centralis nor the visual streak is obvious; throughout the ganglion cell layer at P4 there is a very high density of small cells (Fig. 11). While there are obviously many more cells in the ganglion cell layer of the neonate than the adult, we hesitate to try to count them since the ganglion cell layer is indistinct and it is not clear to us which cells will mature

Fig. 11. Photomicrographs of thionin-stained retinae of adult (left) and 4-day-old (P4) ferret kits. Regions of far temporal retina (A, D), the area centralis region (B, E) and far nasal retina (C, F) are shown. At P4, ferret retina is very immature and contains numerous small cells throughout the ganglion cell layer. The area centralis (B) and visual streak (C) are not yet obvious.


A
D
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into retinal ganglion cells. We have also looked at the Nissl-stained retinae of 8-day-old ferret kits; our observations do not differ significantly from those reported above for 4-day-old ferret kits.

DISCUSSION

The present results indicate that ferret retina contains a number of different types of retinal ganglion cells. The relative cell body sizes, dendritic field structures, and projections of these types are similar to those of the different classes of cat retinal ganglion cells.

Despite these similarities, there are some notable differences between cat and ferret retina. Compared to cat retina (Stone, '78) ferret retina contains a relatively weak area centralis; the visual streak is a more prominent feature of ferret retina. A strong visual streak is typical of mammals with laterally directed eyes such as the rabbit (Provis, '79). The ferret's eyes are directed more laterally than the cats and our injections into the optic tract indicate that only about 2.7 mm of retina projects ipsilaterally in the ferret; the center of the area centralis is about 2.6 mm from the center of the optic disk.

Overall, ferret retinal ganglion cell types are somewhat smaller than their counterparts in the cat. Our impression is that their axons are also finer, indicating that the axonal conduction velocities of the different types of ferret cells will prove to be slower than those of their counterparts in the cat.

Ferret retina is smaller than cat retina. After correcting for the smaller size of ferret retina, the dendritic fields of ferret alpha and beta cells within the area centralis appear to subtend two to three times as many degrees of visual angle as do alpha and beta cells in the cat area centralis. In peripheral ferret retina the dendritic fields of alpha and beta cells subtend about 1.5 times as many degrees of visual angle as do cat alpha and beta cells. Thus, the receptive field centers of retinal ganglion cells are likely to be substantially larger in the ferret than in the cat.

Compared to the cat, ferret retina contains a lower proportion of beta cells and a higher proportion of cell types other than alpha. If the same relationships between structure and function which exist in the cat (see Rodieck, '79; Stone et al., '79; Lennie, '80, for review) exist in the ferret, then ferret retina should contain a relatively low proportion of X (beta) cells and a relatively large proportion of W (epsilon and unclassified) cells. In view of this it is interesting to note that the parvocellular C laminae of the LGNd are especially well developed in the ferret (Linden et al., '81). These layers receive inputs from W cells but not X and Y cells in the cat (Wilson et al., '76; Cleland et al., '76).

Is there an exclusively contralateral Y cell projection in the ferret?

In the normal cat some of the cells in temporal retina project contralaterally. These contralaterally projecting cells tend to be alpha cells and other types of cells, not beta cells (Stone et al., '78; Cooper and Pettigrew, '79; Leventhal, '82). A similar situation exists in the ferret. However, in the ferret but not in the cat virtually all alpha cells in temporal retina appear to project contralaterally. Since cat alpha cells are Y cells (Cleland et al., '75), there may be no ipsilaterally projecting Y cells in the ferret.

A completely crossed Y cell projection in the ferret suggests a number of studies which should enhance our understanding of the mammalian visual pathways. As in the cat in the ferret laminae A and C receive contralateral afferents while laminae A1 receives ipsilateral afferents (Linden et al., '81). Our results indicate that alpha cells do not project to lamina A1 in the ferret. We do not know whether contralaterally projecting ferret alpha cells project to lamina A, to lamina C or to both. It is of interest therefore to study the physiological classes of relay cells in the different laminae of the ferret LGNd. The relationships between structure and function in the A laminae and lamina C of the ferret LGNd is also of interest. In the cat, these layers contain a number of different morphological types having different receptive field properties.

In the cat layer 4a of area 17 and area 18 contains binocular neurons and receives predominantly Y cell inputs from both the ipsilateral and contralateral layers of the LGNd (Stone et al., '79). If in fact there are no ipsilaterally projecting Y cells in the ferret, then the topography, functional organization, and binocularity of cells in visual cortex are of interest.

CONCLUSIONS

The present study indicates that there are a number of similarities between retinal ganglion cells in the cat and ferret. The ferret's retina is, however, much less mature at birth than the cat's. The immature state of the retina and visual pathways in the neonatal ferret should allow postnatal studies of visual system development which, in the cat or monkey, have to be done *in utero*.

The ferret's usefulness is enhanced by the finding that one of its major morphological classes of retinal ganglion cells (alpha cells) does not appear to project ipsilaterally. A comparison of the ipsilateral and contralateral visual pathways in ferrets with no ipsilaterally projecting alpha cells should add to our understanding of the relative contributions to visual function of the different classes of retinal ganglion cells.

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