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Alpha and beta cells projecting from retina to lamina A of the lateral geniculate nucleus in normal cats, monocularly deprived cats, and young kittens

C.-F. Hsiao and S. Murray Sherman

Department of Neurobiology and Behavior, State University of New York at Stony Brook, Stony Brook, NY 11794–5230, USA

Summary. We strictly limited small injection of horseradish peroxidase (HRP) to lamina A of the lateral geniculate nucleus of cats. This was done to label retrogradely only the alpha (Y) and beta (X) classes of retinal ganglion cell. Eighty-six such injections at a range of matched eccentricities were made bilaterally in 9 normal adult cats, 7 cats reared from birth to adulthood with monocular lid suture, and 9 normal kittens at 4 weeks of age; 5348 alpha and beta cells were retrogradely labeled from these injections. Quantitative measurements were made from these labeled cells and compared among 4 experimental conditions, these being normal adult retinas, the nondeprived and deprived retinas of lid sutured cats, and the retinas of kittens. Each injection led to a similar relative ratio of labeled alpha and beta cells (typically 5–15% alpha cells) that did not differ significantly among the experimental conditions, but further analysis suggested a slight dimunition of labeled alpha cells in deprived retinas. Because the larger arbors of retinogeniculate Y axons are more likely to penetrate small geniculate HRP injection sites from eccentric locations than would be the case for the more restricted arbors of X axons, a normal tendency resulted for the peripheral halo of zones of retrograde labeling to be dominated by alpha cells. Thus a more accurate reflection of the relative numbers of labeled alpha and beta cells would result from considering only the core of zones of retrograde labeling. When this is done, deprived retinas exhibited relatively fewer labeled alpha cells than did normal, nondeprived, or kitten retinas. This may relate to prior observations (Sur et al. 1982) that abnormally few Y axons from the derpived retina innervate lamina A. No statistically significant differences in alpha or beta cell size were seen among normal, nondeprived, and deprived retinas, although both of these cell types in the kittens were equally smaller than their normal adult counterparts. This is particularly interesting in view of the postnatal growth of retinogeniculate axon arbors (Sur et al. 1984). The results are not surprising for alpha cells, since retinogeniculate Y axon arbors grow considerably after 4 weeks of age, but they are surprising for beta cells, since retinogeniculate arbors of X axons *decrease* after 4 weeks of age. This suggests no clear, general relationship between soma size and the extent of a cell's axonal arbor. Overall, these results suggest that no dramatic abnormalities due to rearing with monocular suture are evident at the level of the retina, although subtle effects can be demonstrated there (see also Leventhal and Hirsch 1983). The most peripheral site in the visual system at which such dramatic effects have been documented thus seems to be at the level of retinogeniculate innervation.

Key words: Visual development – Visual deprivation – Retina – Lateral geniculate nucleus – Retinogeniculate cells – X and Y cells

Offprint requests to: S.M. Sherman (address see above)

Introduction

Although the abnormalities that develop postnatally during monocular deprivation in cats have been intensively studied for the past 20 years (reviewed in Movshon and Van Sluyters 1981; Sherman and Spear 1982; Sherman 1985a), the details of the underlying mechanisms for these abnormalities have proved elusive. A crucial piece of evidence for the elucidation of these mechanisms is the determination of the

most peripheral site within the visual system (i.e., the site that is the fewest synapses removed from the photoreceptors) at which deprivation-induced abnormalities can be discerned. Such knowledge is needed to deduce the mechanisms of the primary developmental abnormalities, because many of the abnormalities at more central sites may be secondary to those at more peripheral sites (for details and caveats of this line of reasoning, see Sherman and Spear 1982).

Earlier evidence suggested that the most peripheral site of these abnormalities is the striate cortex (Wiesel and Hubel 1963, 1965), but more recent studies have pushed this location more peripherally to at least laminae A and A1 of the lateral geniculate nucleus. Normally, these laminae contain two classes of relay cell, called X and Y cells, which in turn are respectively innervated by retinal X and Y cells to form two parallel X and Y pathways from retina to cortex. In cats reared with monocular deprivation, retinal afferents from the deprived eye fail to form normal arbors in laminae A and A1 (Sur et al. 1982); the X arbors become abnormally large while the Y arbors remain underdeveloped. The cells in deprived laminae A and A1 (i.e., laminae receiving retinal afferents from the deprived eye) fail to develop normally, perhaps because of the abnormally developed retinogeniculate arbors (Friedlander et al. 1982; Sur et al. 1982), and this is particularly true for the Y cells (reviewed in Sherman and Spear 1982; Sherman 1985a, b).

In contrast to these abnormalities that have been documented for deprived geniculate laminae, retinal ganglion cells of the deprived eye seem to develop normal morphology and physiology (Sherman and Stone 1973; Kratz et al. 1979; Cleland et al. 1980). Sur et al. (1982) described normal response properties and soma morphology even for those X and Y retinal ganglion cells that gave rise to abnormal retinogeniculate arbors. If indeed deprived retinal ganglion cells develop normally while their retinogeniculate arbors and postsynaptic geniculate cells develop abnormally, then retinogeniculate circuitry is a likely candidate for a primary site of deprivation-induced abnormalities.

A recent report, however, has suggested that these retinal ganglion cells may be subtly abnormal. Leventhal and Hirsch (1983) used retrograde transport of horseradish peroxidase (HRP) to identify the population of retinal ganglion cells projecting to the lateral geniculate nucleus in monocularly deprived cats. These ganglion cells included both alpha and beta cells, which are the morphological counterparts of Y and X cells, respectively (Boycott and Wässle 1974; Saito 1983; Stanford and Sherman 1984). Leventhal and Hirsch (1983) reported that deprived ganglion cells, both alpha and beta, were slightly smaller than their normal counterparts. Because Sur et al. (1982) were able to label for measurement the somata of only a few retinal ganglion cells with abnormal retinogeniculate arbors, these authors may well have missed the small abnormalities in soma size reported by Leventhal and Hirsch (1983).

A confirmation and extension of the observations of Leventhal and Hirsch (1983) is needed to establish more precisely the morphological abnormalities of deprived retinal ganglion cells that project to the lateral geniculate nucleus. We thus studied the distribution and morphology of retinal ganglion cells retrogradely labeled from small HRP injections limited to lamina A of normal and monocularly deprived cats. By limiting these injections to lamina A, we could ensure that only X and Y cells would be labeled in retina (Stone et al. 1979; Leventhal 1982; Sherman and Spear 1982; Wässle 1982; Rodieck and Brening 1983; Sherman 1985a). These small injections also should fail to label a class of deprived Y cells whose retinogeniculate arbors fail to innervate lamina A despite normal innervation of lamina C (Sur et al. 1982). The injections of Leventhal and Hirsch (1983) may not have been sufficiently small to avoid labeling the somata giving rise to these abnormal axon arbors. Finally, since many features of deprived retinogeniculate arbors resemble those of 3–4 week old normal kittens (Sur et al. 1982, 1984), we extended this analysis to such young kittens.

Material and methods

Subjects

Data were obtained from 9 normal adult cats, 7 monocularly deprived cats raised to adulthood (i.e., > 9 months postnatal), and 9 normal kittens at 4 weeks of age. Normal adult cats of 2–4 kg body weight and indeterminate age were obtained from licensed suppliers. The remainder were born and raised in our closed breeding colony. Each of the monocularly deprived cats had the lids of one eye sutured closed under halothane anesthesia at 7–10 days postnatal, which was just before natural eye opening, and was maintained in this condition until the final acute experiment in adulthood. These cats were inspected at regular intervals (daily at first and several times per week thereafter) to ensure that no openings appeared in the sutured lids that might expose the cornea.

HRP injections

The animals were prepared for HRP injections under aseptic conditions. We anesthetized each with sodium pentobarbital given intraperitoneally at an initial loading dose of 50 mg/kg. Supplementary doses were given as needed during the HRP injection procedures (described below). The animal was then placed into a

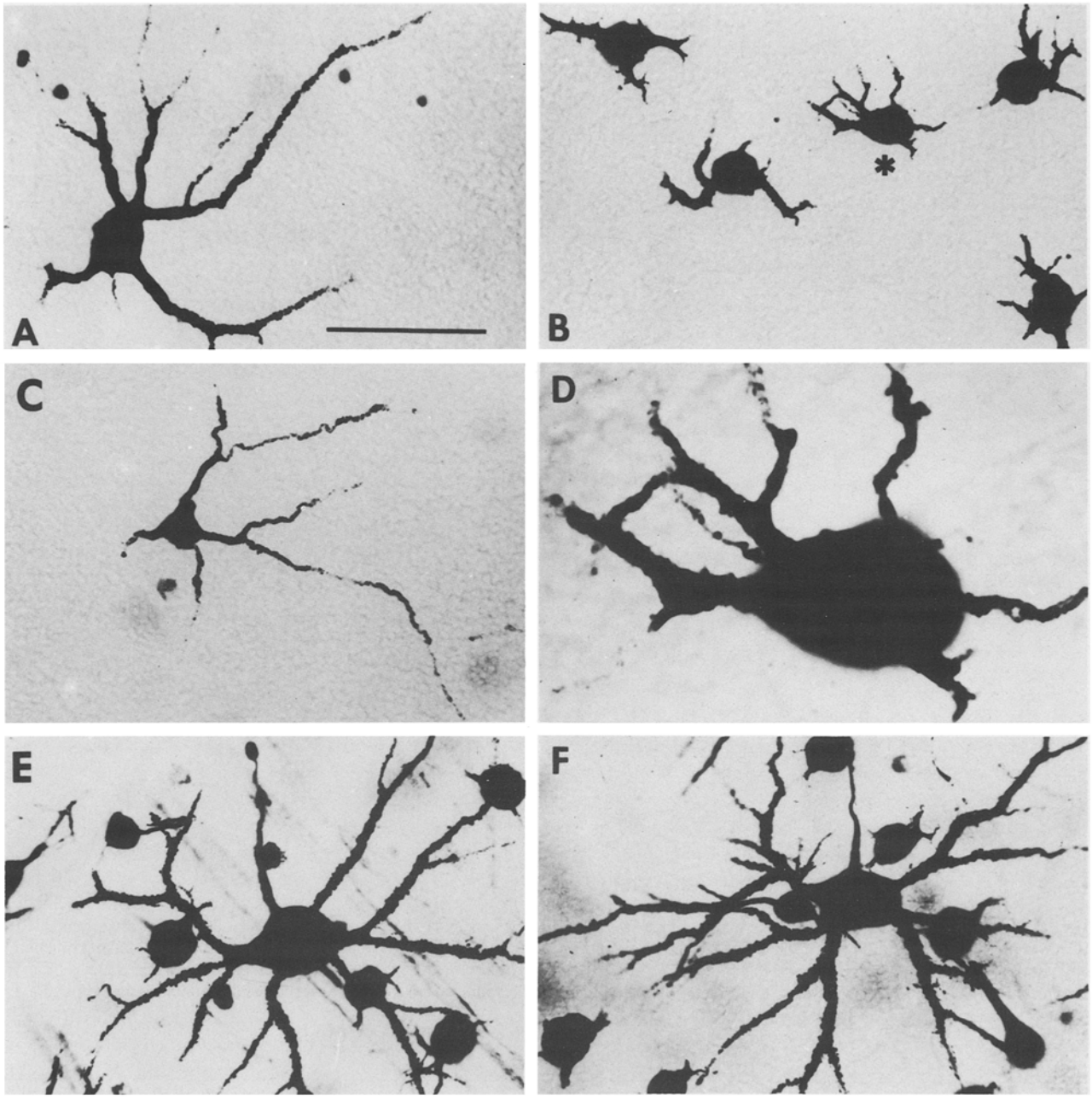

Fig. 1A–F. Photomicrographs of retrogradely labeled retinal ganglion cells following injections of HRP into the lateral geniculate nucleus. All are located between 5° and 15° from the area centralis. The scale in **A** represents 100 μm and applies as well to all panels except **D**, for which it represents 25 μm. **A–D** represent labeling after large injections into the lateral geniculate nucleus, whereas **E** and **F** represent labeling after a small injection limited to lamina A (see text for details). **A**: Alpha cell. **B**: Beta cells. The cell just above the asterisk is shown in higher power in **D**. **C**: Gamma cell. **E,F**: Views of an alpha cell surrounded by presumed beta cells

stereotaxic device facing a frontal tangent screen. All pressure points were infiltrated with 1% procaine. Topical application of atropine and neosynephrine was used to dilate the pupils and retract the nictitating membranes; zero-power contact lenses were then placed over the corneas. We exposed the bone on top of the skull and made small craniotomies over each lateral geniculate nucleus. Following the HRP injections, the scalp wounds were sutured, and the animal was removed from the stereotaxic apparatus for an additional 48 h survival period. During this period, antibiotics were administered to prevent infection, and low doses of barbiturate were given to keep the animal sedated and as comfortable as possible.

A glass micropipette was used both to record neural activity as well as to deliver HRP. The micropipette was filled with 7% HRP (Sigma type VI) in 0.2 *M* KCl and 0.05 *M* TRIS at a pH of 7.4. Its tip was then broken to produce an impedance across the tip of

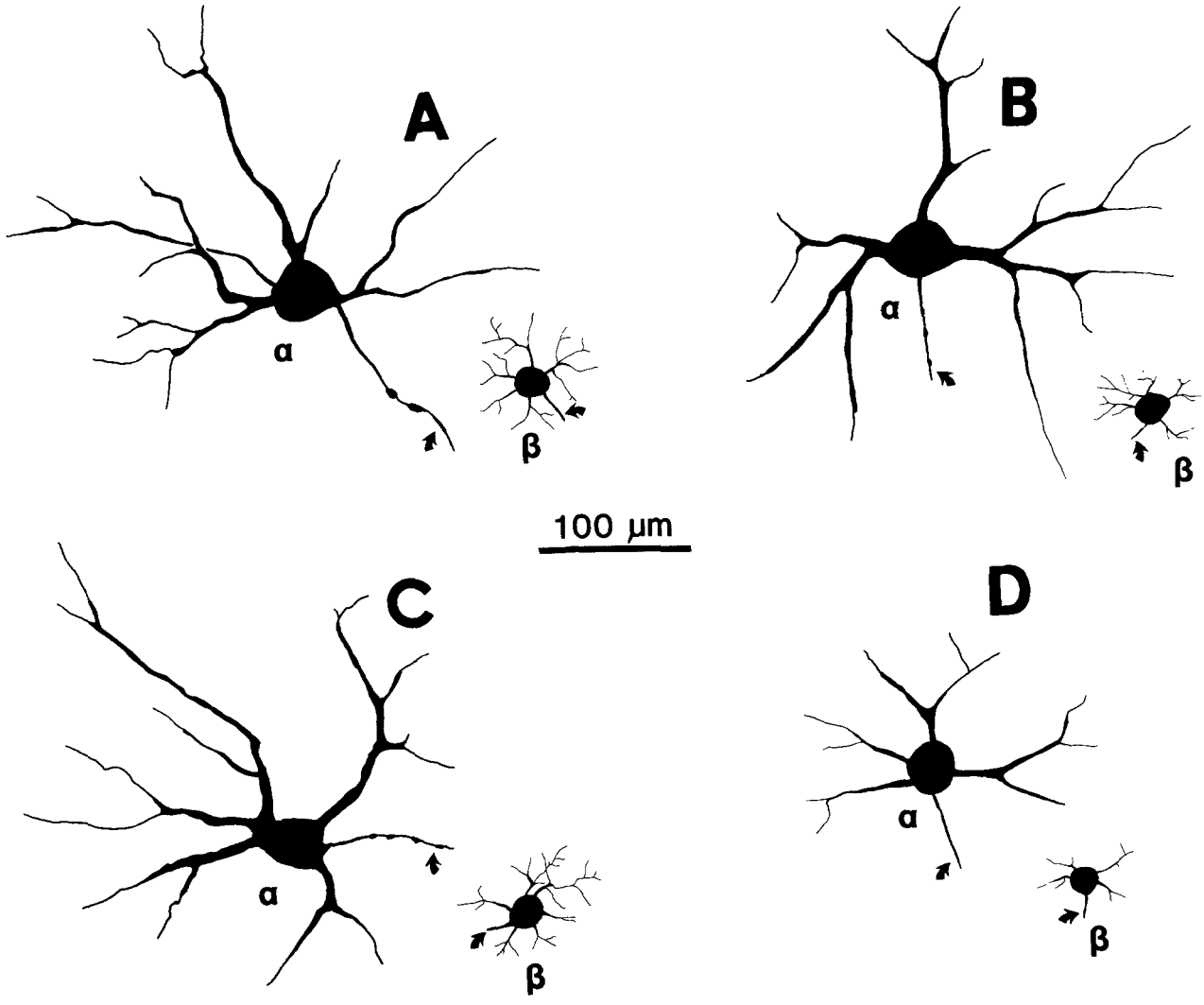

Fig. 2A–D. Tracings of 4 representative examples each of alpha and beta cells that were retrogradely labeled following small HRP injections into geniculate lamina A. Each cell is located in nasal retina between 10° and 15° from the area centralis. One alpha and one beta cell are separately identified for each of the four paired groups, and arrows indicate axons. **A** Examples from a normal adult retina. **B** Examples from the nondeprived retina of a monocularly deprived cat. **C** Examples from the deprived retina of a monocularly deprived cat. **D** Examples from a normal, 4-week-old kitten

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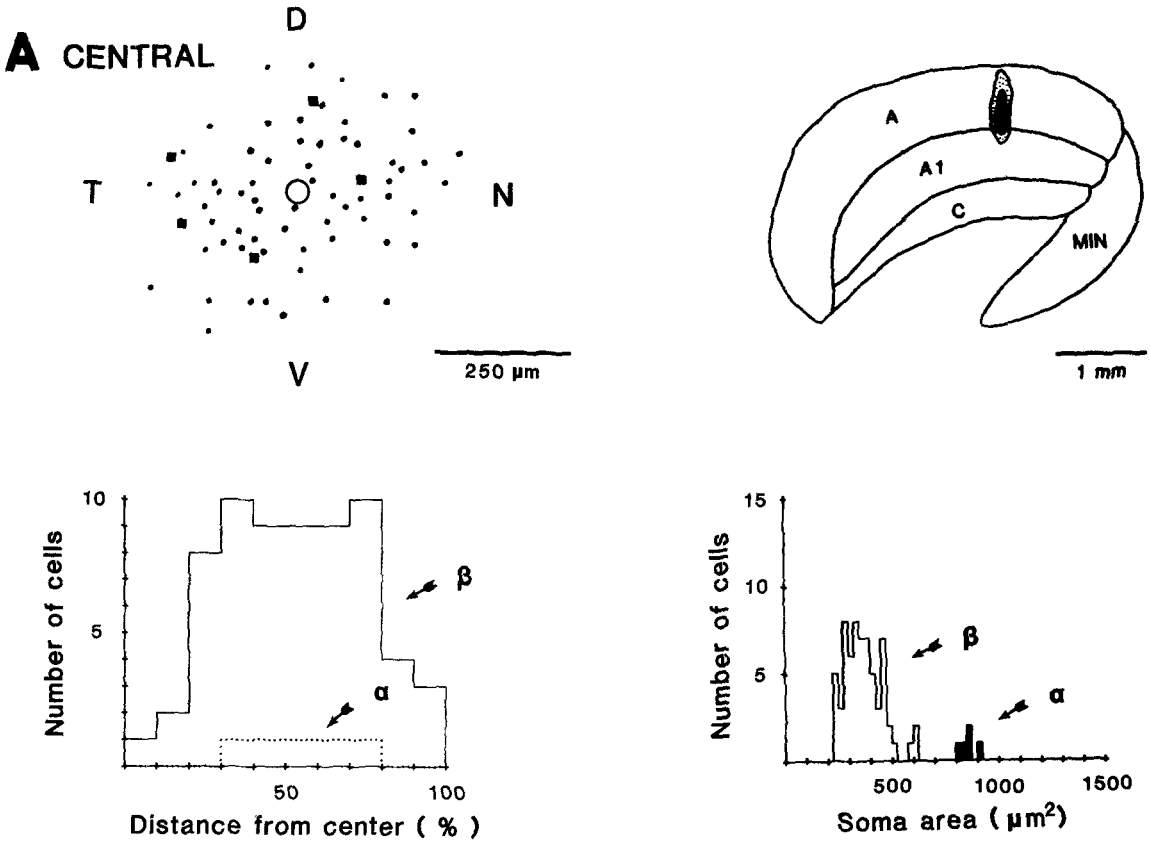
Fig. 3A and B. Representative examples of data base from small injections into geniculate lamina A of normal cats. All of retrogradely labeled cells are located in the nasal retina of the eye contralateral to the injection site. **A** Injection leading to labeling near area centralis. The *upper left* panel shows the zone of retrograde labeling, with 5 alpha and 65 beta cells. Thus 7.1% of the retrogradely labeled neurons are alpha cells. The circle denotes the center of the zone of labeling and is 4.1° from the area centralis. *D, N, V,* and *T* refer respectively to dorsal, nasal, ventral, and temporal directions in the retina. The *upper right* panel shows a drawing of a coronal section through the left lateral geniculate nucleus, including our interpretation of the visible HRP injection. In all cases, we attempted to distinguish between a relatively intense core zone (solid) and a fainter halo (stippled), but the distinctions were never clear and always a bit arbitrary. Our criteria for an injection adequately limited to lamina A do not depend greatly on the injection site (see *Materials and methods*), except to verify that lamina A rather than another region (e.g., lamina C or portions of the medial interlaminar nucleus) has been injected with HRP. The *lower left* panel shows a frequency histogram of the relative distance of each labeled cell from the center of the zone of labeling. The histogram is normalized to the most eccentric cell, which is given a value of 100%. The average of the alpha cell distances is equal to the beta cell average. The *lower right* panel shows a frequency histogram of the cross-sectional areas of the labeled alpha and beta cells. The average size of alpha cells is 857 μm^2 and of beta cells is 368 μm^2. **B** Injection of right lamina A leading to zone of labeling more distant from the area centralis; panels and conventions as in **A**. The center of the labeling zone is 26° from the area centralis. Of the retrogradely labeled cells (10 alpha and 70 beta), 12.5% are alpha cells. The average of the alpha cell relative distances from the center of the zone of labeling is 1.2 times greater than is the beta cell average. The average size of alpha cells is 1069 μm^2 and of beta cells is 479 μm^2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Soma area (µm²)

Fig. 3

roughly 1 MΩ at 200 Hz. We recorded visually driven neural responses through the micropipette as we lowered it through one of the craniotomies towards the lateral geniculate nucleus. We used small spots of light flashed on or moved across the tangent screen to determine the ocular dominance of these responses as well as the visual field locations of effective visual stimuli. We plotted retinal landmarks repeatedly as needed by the method of Fernald and Chase (1971) in order to relate these visual field locations to retinal co-ordinates. With the aid of Sanderson's (1971) maps, we could then translate this to fairly precise locations within the lateral geniculate nucleus, including the dorsal and ventral borders of lamina A or A1.

In one of the normal adults, HRP was iontophoresed with > 10 microamp square-wave depolarizing pulses at several overlapping positions along a projection line to involve all of the geniculate laminae and the optic tract. This was done to produce retrograde labeling of the maximum number of retinogeniculate somata. In each of the other cats, much smaller injections were attempted by iontophoresing HRP from the micropipette with square-wave current pulses of 5–10 μA at 1 Hz for 10 min. For these injections, the electrode tip was placed within the upper half of lamina A, and HRP was iontophoresed into 2–3 well separated sites within lamina A of each hemisphere.

We sought to limit our HRP injections to lamina A, because this lamina receives retinal input from only X and Y cells (Stone et al. 1979; Leventhal 1982; Sherman and Spear 1982; Wässle 1982; Rodieck and Brening 1983; Sherman 1985a), and we wished to ensure that our HRP injections labeled only X and Y retinal ganglion cells. Although lamina A1 also receives only X and Y input from retina, we avoided label of this lamina in order to prevent the spread of HRP into other geniculate regions (e.g., the C-laminae). Such spread would contaminate our results by also labeling other retinal ganglion cell types, such as W cells (Leventhal 1982; Rowe and Dreher 1982) and perhaps even retinal axons in the optic tract projecting to targets other than the lateral geniculate nucleus. By limiting our HRP injections to lamina A, we can be certain that only retinogeniculate X and Y axons were labeled.

Previous studies (e.g., Holländer and Vanegas 1977; Vanegas et al. 1978; Mesulam and Rosene 1979) as well as our own observations convinced us that we could not rely on the size of the injection zone as visualized in our histological material to verify that only axons in lamina A would retrogradely transport HRP. Instead, we adopted a criterion based on the distribution of retrogradely labeled retinal ganglion cells. We accepted data only from injection sites that produced retrograde labeling of ganglion cells limited to the contralateral nasal retina and not found in the ipsilateral temporal retina. Labeled cells in the appropriate region of the ipsilateral temporal retina indicate that HRP was transported from retinal axons reaching lamina A1. If so, then we cannot be certain that every retrogradely labeled cell in either retina is an X or Y cell, since we cannot rule out the possibility that the HRP injection extended down into the C-laminae or even into the optic tract. Data from such injection sites were not analyzed in detail.

Histological procedures

After the postinjection survival period, the animals were given an overdose of barbiturate and perfused transcardially with heparinized saline followed by a fixative solution (2% glutaraldehyde and 1% paraformaldehyde buffered to pH 7.4). A portion of the brain containing both lateral geniculate nuclei was stereotaxically removed and placed overnight in a solution of 30% sucrose and 0.1 *M* phosphate buffered to pH 7.4. The eyes were also removed, and the caudal half of each eye, which contained the retinas, was placed overnight in a solution of 30% sucrose and 0.1 *M* phosphate buffered to pH 7.4. The lateral geniculate nuclei were then coronally sectioned on a Vibratome at 100 μm, and flat mount preparations were made from the retinas. We reacted the geniculate sections and retinas with O-dianisidine to visualize the presence of HRP (deOlmos 1977).

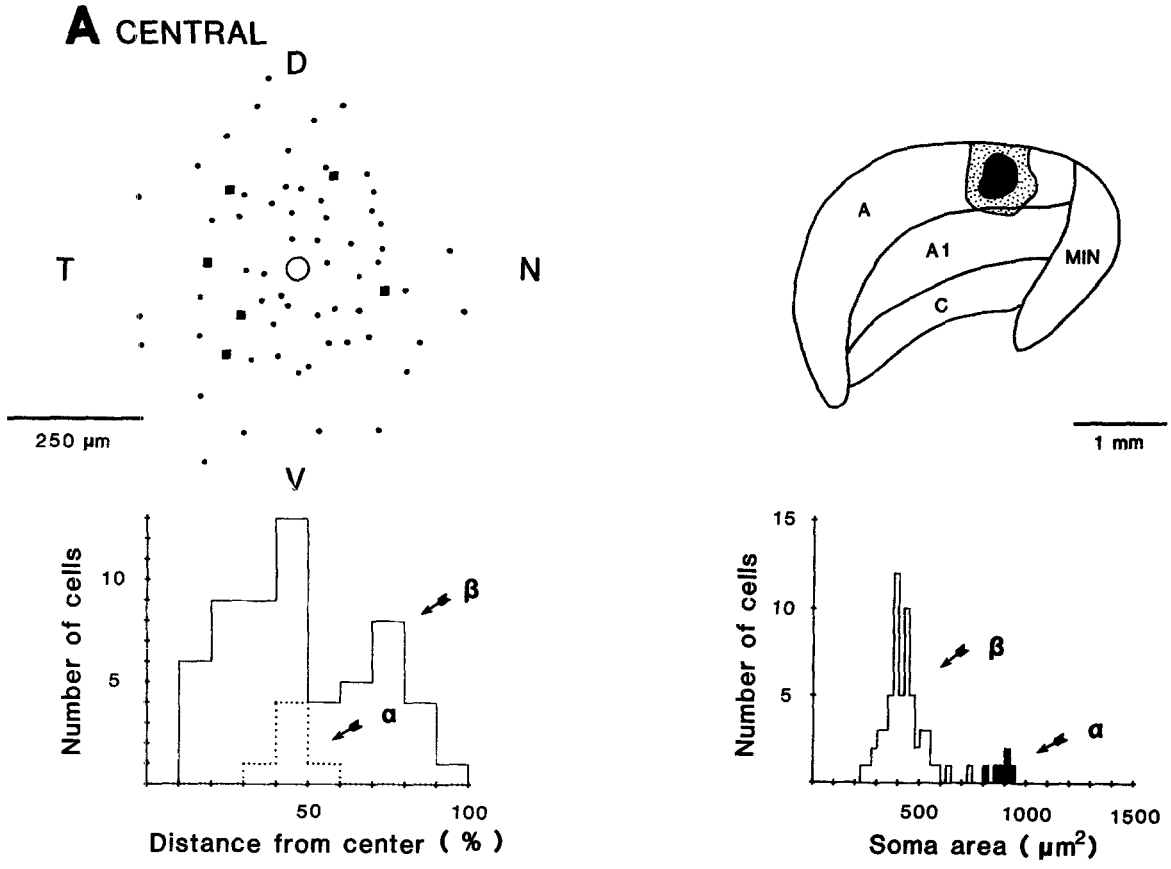
Labeled retinal ganglion cells were drawn at roughly 1000x with the aid of a drawing tube attached to a microscope and a 100x oil-immersion objective (N.A. of 1.32). We used a planimeter on these drawings to measure the cross-sectional area of each labeled soma. After the labeled cells were drawn, we counterstained the retina with cresyl violet to observe the other retinal ganglion cell somata and to permit a clear visualization of the area centralis. We measured the linear distance between each labeled ganglion cell and the center of the area centralis. This was converted to degrees of visual angle by the use of published data available for both adult cats and kittens (Bishop et al. 1962; Olson and Freeman 1980).

Data analysis and statistics

Quantitative analysis of retrogradely labeled cells was performed only on cases that met our criteria for HRP injections limited to lamina A. For these cases, we classified each labeled cell as alpha or beta (see *Results* for details) and measured their soma sizes. We also used the following procedures to determine the location of the geometric center of the zone of retrogradely labeled retinal ganglion cells (expressed in degrees of visual angle from the area centralis) and to derive a measure of the relative locations among the labeled cells. For each zone of retrograde labeling, the azimuth and elevation of each cell relative to the middle of the area centralis was determined, and the mean of these values was computed. The mean azimuth and elevation was then taken as the center of the zone of retrograde labeling. Relative locations among the labeled cells were then determined by computing the distance between each cell and the center of the zone of labeling, calculating the average of these distances separately for alpha and beta cells, and computing the alpha-to-beta ratio of these averages. This provides a measure of the relative location within the zone of labeling of the two cell classes.

To avoid sampling artifacts due to potential variation in these parameters with eccentricity from the area centralis and across animals, we adopted the following two protocols. First, comparisons were made only among groups of cells with comparable eccentricities. For this analysis, we grouped injections into 4

Fig. 4A and B. Representative examples of data base from small injections into nondeprived geniculate lamina A of monocularly deprived cats, with labeling of the nasal retina in the contralateral, nondeprived eye; conventions as in Fig. 3. **A** Injection of left lamina A, leading to central zone of retinal labeling, the middle of which is 4.7° from the area centralis. Of the retrogradely labeled cells (6 alpha and 59 beta), 9.2% are alpha cells. The average of the alpha cell relative distances from the center of the zone of labeling is 0.9 times as large as the beta cell average. The average size of alpha cells is 894 μm^2 and of beta cells is 422 μm^2. **B** Injection of right lamina A, leading to peripheral zone of retinal labeling, the middle of which is 25° from the area centralis. Of the retrogradely labeled cells (20 alpha and 144 beta), 12.0% are alpha cells. The average of the alpha cell relative distances from the center of the zone of labeling is 1.2 times greater than is the beta cell average. The average size of alpha cells is 1024 μm^2 and of beta cells is 493 μm^2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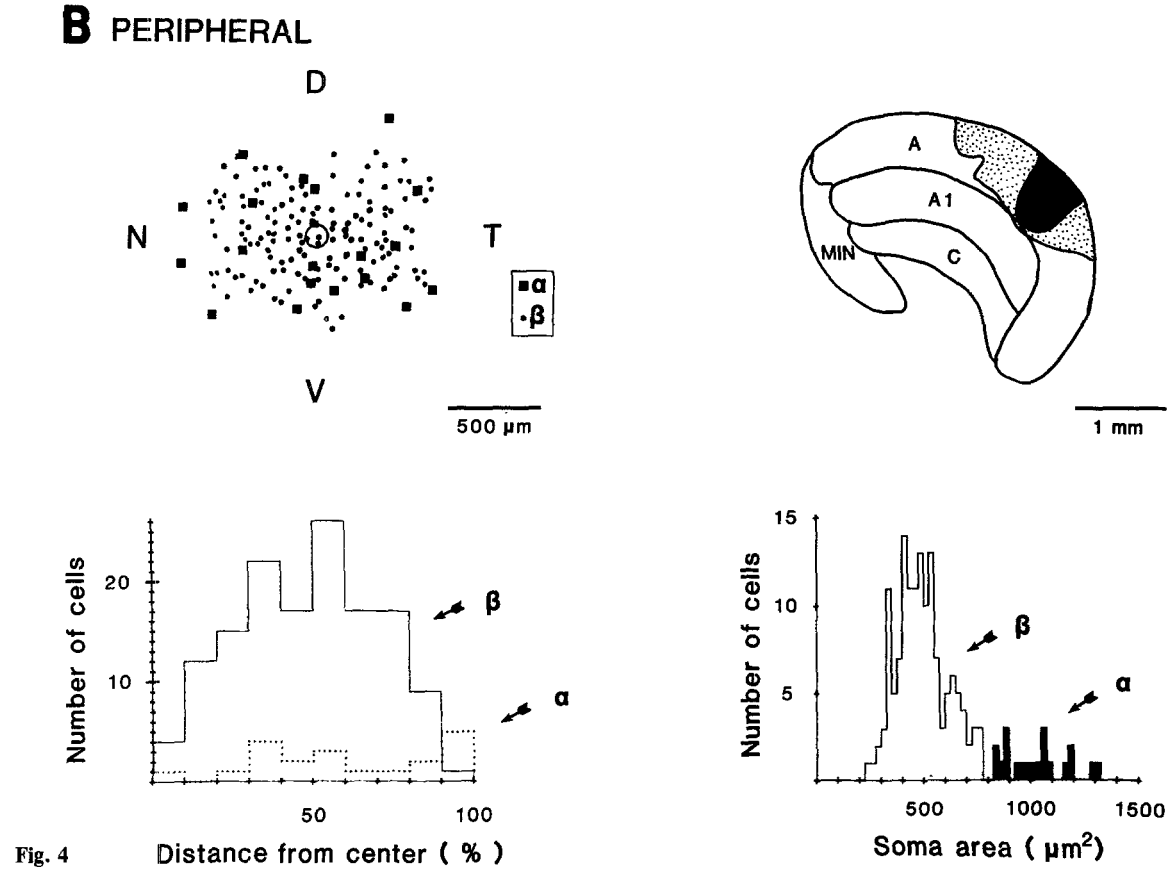
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Soma area (µm²)

Fig. 4

eccentricity ranges for the locations of the centers of zones of retrograde labeling; 0–5°, 5–10°, 10–15°, and > 15° (see *Results* for details). Since HRP injections in each cat were well spaced, each retina had only one set of labeled cells at a given eccentricity range. Because we sould accurately place the injection micropipette within the retinotopic map of lamina A, we could ensure that labeled cells with comparable eccentricities were available in most cats. Second, we reduced the data from each injection site to a single value for each parameter. Our reduced data for cells retrogradely labeled from each HRP injection site consisted of the eccentricity from the area centralis of the center of the zone of retinal labeling, the number of labeled cells, the percentage of the total that were alpha and beta cells, the average soma size of each class, and the abovementioned measure of the relative location of each class. Statistical comparisons among animals were made only from these values. Occasionally, a comparable eccentricity was labeled in each retina of normal cats and kittens. For ease of exposition in *Results*, we regard each injection as producing a single set of reduced values for analysis. Statistically, it made no difference whether the values for comparable eccentricities in the two retinas of normal cats and kittens were treated in this manner as independent observations or whether they were averaged before comparison across animals.

Unless otherwise noted, the Mann-Whitney U-test was used for all statistical comparisons.

Results

Our data base derives from more than 100 HRP injections placed into the lateral geniculate nuclei of 25 cats and kittens. Of these, a subset of 86 injections that labeled 5348 retinal ganglion cells were selected for quantitative analysis. Quantitative measurements of individual, retrogradely labeled cells were limited to their location and soma size (see *Materials and methods.)*.We made no attempt to quantify aspects of dendritic structure, because it was clear that even our best retrograde labeling did not completely label a ganglion cell's dendritic arbor (cf. Saito 1983; Stanford and Sherman 1984).

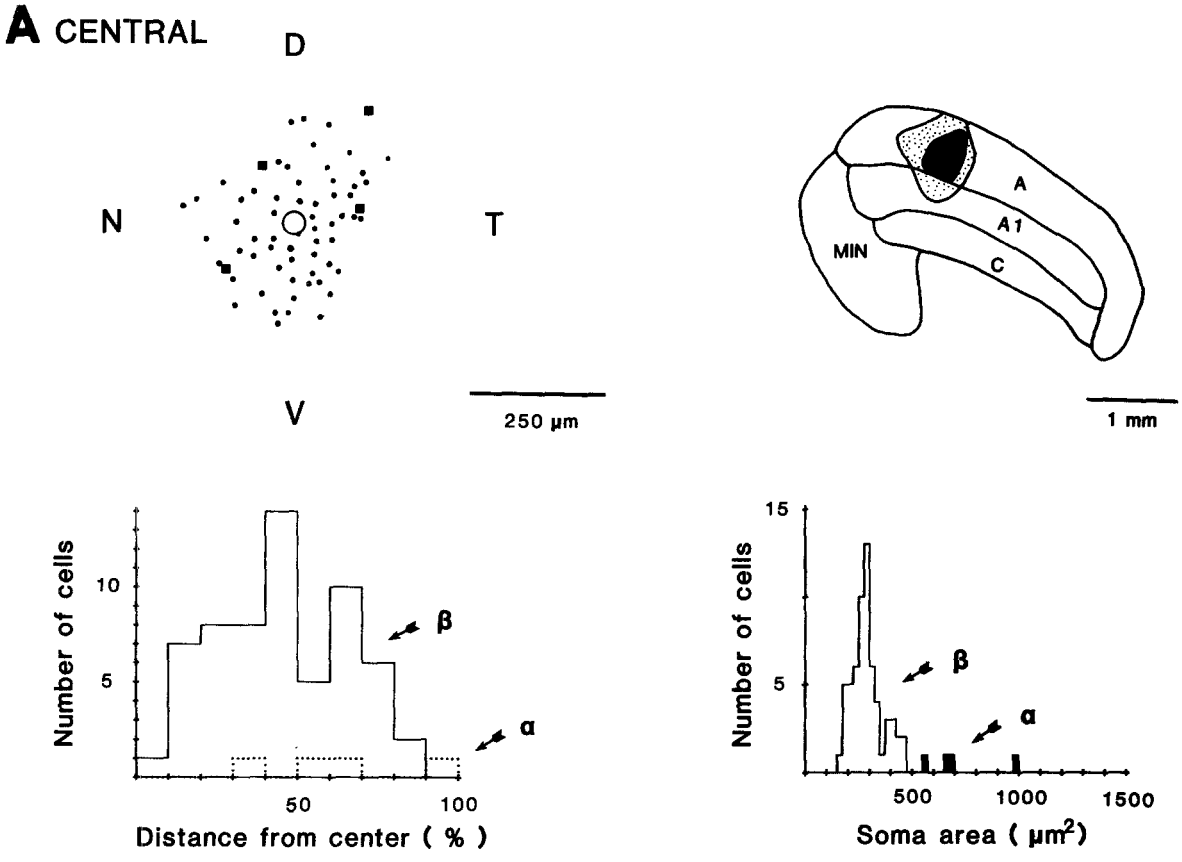
Classes of labeled retinal ganglion cells

Large injections. We made no quantitative measurements of labeled retinal ganglion cells from the one normal cat in which large injections of HRP were placed into the lateral geniculate nucleus. However, this cat provided examples of all of the major cell classes previously described with similar techniques (Boycott and Wässle 1974; Stone and Clarke 1980; Leventhal 1982). These included alpha, beta, and gamma cells, plus other cell types (e.g., delta and epsilon cells). The alpha and beta cells are Y and X, respectively, while the others appear to be various subtypes of the W class (Boycott and Wässle 1974; Leventhal 1982; Saito 1983; Stanford and Sherman 1984; reviewed in Stone et al. 1979; Sherman and Spear 1982; Wässle 1982; Rodieck and Brening 1983; Sherman 1985a). Figure 1 shows representative examples of well labeled alpha, beta and gamma cells. The alpha cells were particularly easy to identify due to their large somata, thick axons and dendrites, and extensive dendritic arbors. Beta cells, which had medium sized somata and axon diameters, were chiefly characterized by their small but densely branched dendritic arbors. Gamma and other cell types had small-to-medium sized somata, thin axons, and sparse, but often far-reaching dendritic arbors amanting from thin dendrites. In addition to finding many examples of each of these morphological classes from this cat, we also encountered many labeled ganglion cells that could not be classified, because of labeling that was either too faint or not sufficiently transported into the dendritic tree. However, the large size of alpha cell bodies made their identification straightforward even when poorly labeled; difficulty in identification of poorly labeled neurons was limited to distinguishing among beta, gamma and other cell types.

In the other cats, several injections intended only for lamina A extended to other laminae, as evidenced by labeled cells in corresponding regions of the ipsilateral temporal retina. Although cells labeled from these injections were not quantitatively examined, we often found examples of types other than alpha and beta cells as well as poorly labeled cells. As noted below, this differs from the appearance of cells labeled from restricted injections.

Small injections. After small injections limited to lamina A, the zone of labeled cells in the contralateral nasal retina exhibited a characteristic appearance. The zone of labeling was relatively sharply

Fig. 5A and B. Representative examples of data base from small injections into deprived geniculate lamina A of monocularly deprived cats, with labeling of the nasal retina in the contralateral, deprived eye; conventions as in Fig. 3. **A** Injection of right lamina A, leading to central zone of retinal labeling, the middle of which is 3.5° from the area centralis. Of the retrogradely labeled cells (4 alpha and 61 beta), 6.2% are alpha cells. The average of the alpha cell relative distances from the center of the zone of labeling is 1.4 times greater than is the beta cell average. The average size of alpha cells is 725 μm^2 and of beta cells is 292 μm^2. **B** Injection of right lamina A, leading to peripheral zone of retinal labeling, the middle of which is 22° from the area centralis. Of the retrogradely labeled cells (11 alpha and 82 beta), 12.6% are alpha cells. The average of the alpha cell relative distances from the center of the zone of labeling is 1.4 times greater than is the beta cell average. The average size of alpha cells is 999 μm^2 and of beta cells is 405 μm^2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Soma area (µm²)

Fig. 5

defined and contained well labeled cells. Faintly labeled cells were exceedingly rare (< 1%) and are not further considered here. The dark labeling enhanced the sharpness of the labeled zone's boundaries and contrasted with labeling from larger injections for which the transition between clearly labeled and unlabeled cells gradually passed through more faintly labeled neurons.

After these small injections, two distinct cell types were always seen (Fig. 2). One consisted of alpha cells, which could clearly be identified on the basis of their large somata, thick axons, and thick dendrites that often could be followed into extensive arbors. The other type consisted of smaller somata, thinner axons and dendrites, and, when sufficiently well-labeled, small, dense dendritic arbors. Many of these smaller cells did not exhibit such well-labeled dendrites, and on the basis of labeled somata and proximal dendrites alone, one cannot confidently distinguish between beta cells on the one hand and additional cell types, such as gamma, delta, or epsilon cells, on the other (cf. Leventhal 1982). However, because the HRP injections were limited to lamina A, to which only X or beta cells among the smaller ganglion cells project (Stone et al. 1979; Leventhal 1982; Sherman and Spear 1982; Wässle 1982; Rodieck and Brening 1983; Sherman 1985a), we are fairly confident that all of these labeled cells with smaller somata are X or beta cells. Two other observations are consistent with this conclusion. First, among all of the smaller cells with well-labeled dendritic arbors, each was clearly a beta cell. Second, the axons of the smaller, labeled cells seemed too thick to be associated with these other cell types, as evident from reference to our material from larger HRP injections that retrogradely labeled these other cell types.

Data base for quantitative analysis

Our data base for quantitative comparisons among the cats consists only of those injection sites that failed to label cells in temporal retina. Figures 3–6 provide typical examples of such limited injection sites for normal cats (Fig. 3), for the nondeprived eye of monocularly deprived cats (Fig. 4), for the deprived eye of these cats (Fig. 5), and for normal 4-week-old kittens (Fig. 6). These illustrate the resultant zones of retrogradely labeled retinal ganglion cells, the histological appearance of the injection site, and quantitative analysis of the labeled cells; the figure legends indicate the reduced data for these examples that exemplify the data used for statistical comparisons among the groups of experimental animals. As noted in *Materials and methods*, our criterion for injections limited to lamina A depends upon the pattern of retrograde labeling in the retina and not upon the appearance of the injection sites. Indeed, some injections appeared to spill across into lamina A1 (e.g., Fig. 3A), but they did not label cells in the ipsilateral temporal retina. Except for the one normal cat in which small HRP injections were not attempted, each hemisphere of each cat contained at least one injection limited to lamina A. We analyzed data from 86 such injection sites: 16 in normal cats; 31 in the monocularly deprived cats, including 16 for the nondeprived retina and 15 for the deprived retina; and 39 for the 4 week old kittens. Figure 7 summarizes features of those HRP injections limited to lamina A, including: the retinal locations of the retrogradely labeled cells (Fig. 7A), the number of injections for each type of animal and within each eccentricity range (Fig. 7B), and the distribution of the numbers of labeled ganglion cells related to each of these HRP injections (Fig. 7C). Figure 7B represents the groupings used for statistical analysis.

Relative numbers of labeled alpha and beta cells

Figure 8 summarizes the percentage of alpha cells retrogradely labeled from HRP injections into lamina A. This percentage is shown both as a function of eccentricity for each injection (Fig. 8A) as well as for injections within each eccentricity range (Fig. 8B). The percentage of labeled beta cells can also be simply derived from Fig. 8 as the alpha percentage subtracted from 100%. In accord with

Fig. 6A and B. Representative examples of data base from small injections into geniculate lamina A of normal, 4-week-old kittens; conventions as in Fig. 3. All of the retrogradely labeled cells are located in the nasal retina of the eye contralateral to the injection site. **A** Injection of right lamina A, leading to central zone of retinal labeling, the middle of which is 1.6° from the area centralis. Of the retrogradely labeled cells (4 alpha and 61 beta), 6.2% are alpha cells. The average of the alpha cell relative distances from the center of the zone of labeling is equal to the beta cell average. The average size of alpha cells is 505 μm^2 and of beta cells is 234 μm^2. **B** Injection of left lamina A, leading to peripheral zone of retinal labeling, the middle of which is 22° from the area centralis. Of the retrogradely labeled cells (7 alpha and 56 beta), 11.1% are alpha cells. The average of the alpha cell relative distances from the center of the zone of labeling is 1.6 times greater than is the beta cell average. The average size of alpha cells is 862 μm^2 and of beta cells is 378 μm^2

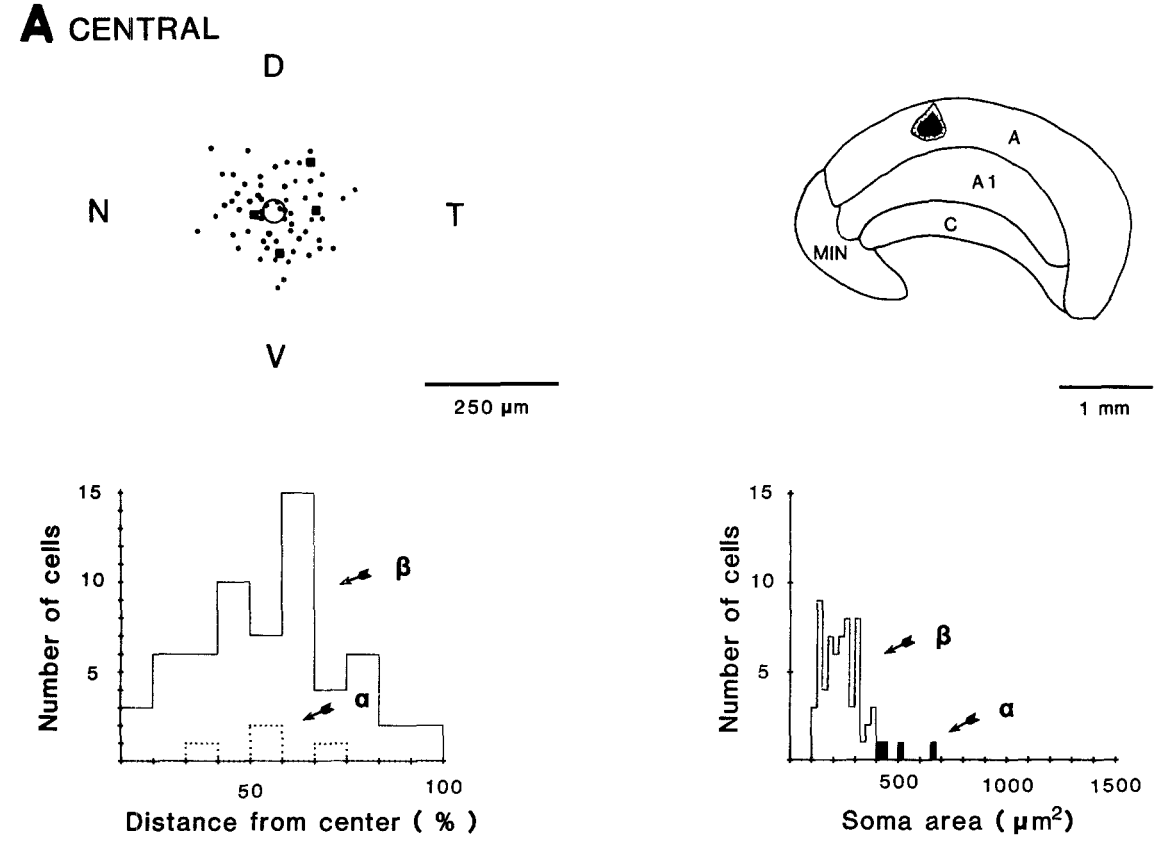
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Fig. 6

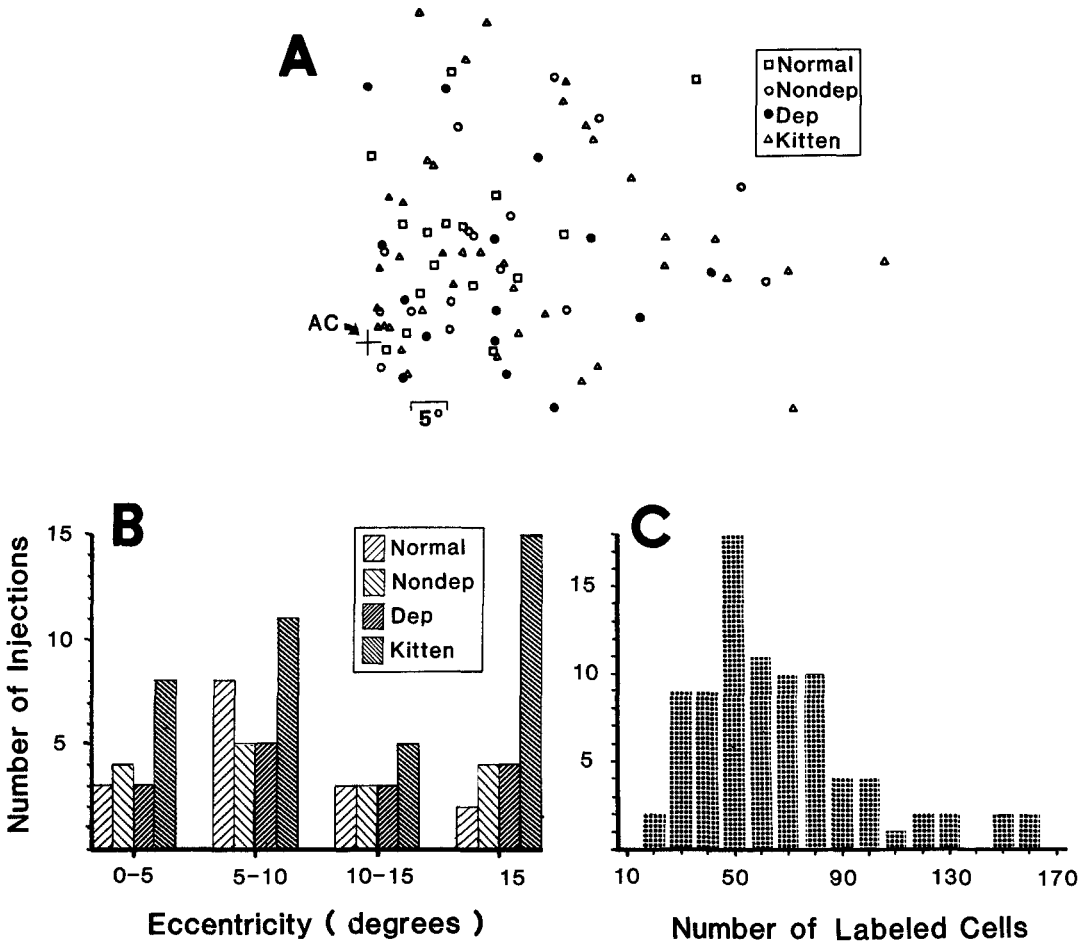

Fig. 7A–C. Summary of data base for quantitative analysis. This is based on retrograde labeling of retinal ganglion cells from HRP injections limited to lamina A. **A** Location of the center of each zone of retrograde labeling relative to the area centralis (**AC**). Nasal retina is to the right of the area centralis and superior retina is above it. As can be seen, all of the zones of labeling are located in nasal retina and are separately illustrated for the various experimental conditions. Data from these injections are further illustrated in Figs. 8–12. **B** Grouping of the data from **A** into the various eccentricity ranges. **C** Frequency distribution of the number of retrogradely labeled retinal ganglion cells from the sites summarized in **A**

previous reports (Fukuda and Stone 1974; Stone et al. 1979; Leventhal 1982; Wässle 1982), we observed a systematic increase in the relative ratio of labeled alpha cells with increasing eccentricity (Fig. 8). Neither the percentage of alpha cells nor its relationship with eccentricity differed significantly ($p > 0.1$) between any two of the experimental subject groupings (normal adult cats, nondeprived and deprived eyes of monocularly deprived cats, and young kittens).

Soma sizes of alpha and beta cells

Figures 9 and 10 summarize the size distributions of labeled alpha and beta cells among different animals. Figure 9 shows the entire data base, and Fig. 10 shows the same data divided into the eccentricity groupings for statistical analysis. In all animals, the mean sizes of both alpha and beta cells increase with increasing eccentricity (Figs. 9A, B and 10A, B), a phenomenon that has been previously documented for normal cats (Boycott and Wässle 1974; Fukuda and Stone 1974; Leventhal 1982). We also measured the mean ratio of alpha to beta cell body sizes for each injection and found a slight decrease in this ratio with increasing eccentricity (Figs. 9C and 10C).

We found no reliable differences among the adult animals, which includes normal adults and both eyes of monocularly deprived cats, in the sizes of these cells ($p > 0.1$), in the alpha to beta ratio of these soma sizes ($p > 0.1$), or in the relationship between soma size and eccentricity ($p > 0.1$). Our data thus do not provide independent support for the conclu-

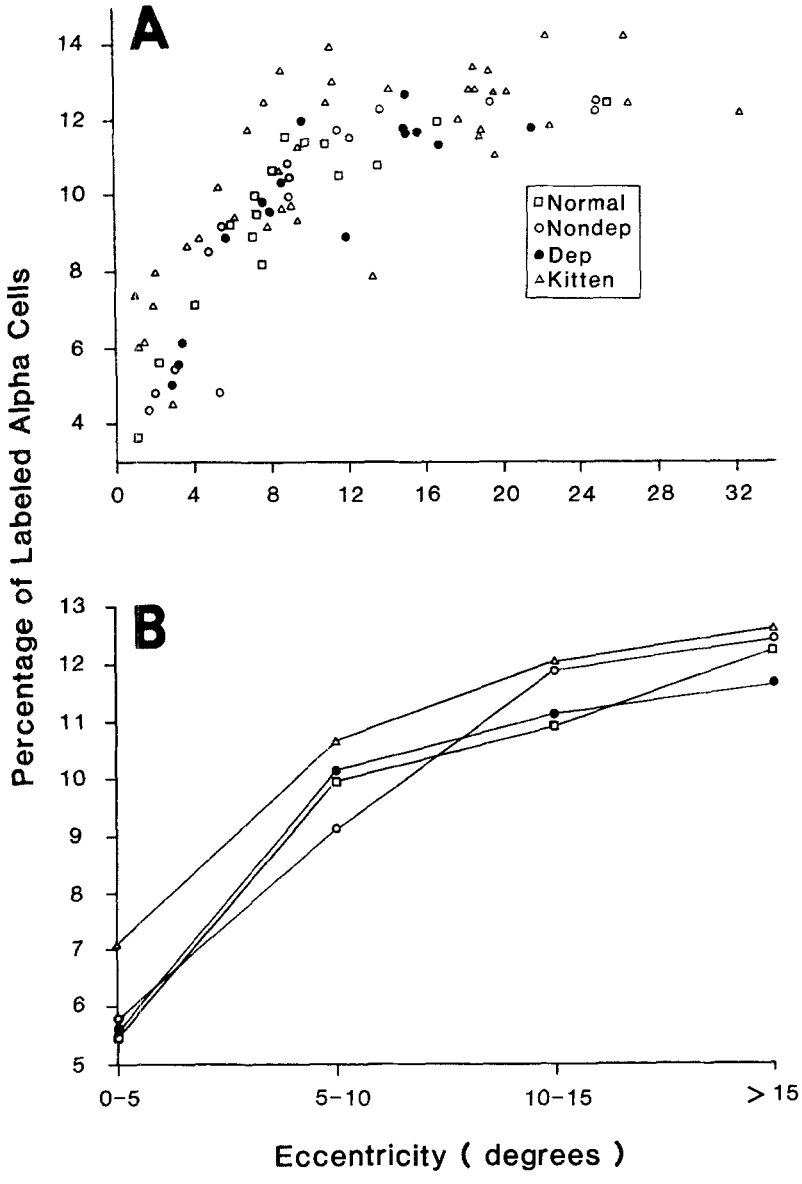

Fig. 8A and B. Relative percentage of retrogradely labeled alpha cells as a function of eccentricity. A percentage is shown for each of the labeled zones summarized in Fig. 7, and eccentricity refers to the distance from the area centralis to the center of the zone of retrograde labeling. The percentage of labeled beta cells for each point is simply 100% minus the alpha cell percentage shown. **A** Distribution of percentages for each injection site. **B** Distribution of mean percentages for each eccentricity group. No statistically significant differences were seen in this parameter amoung the various experimental conditions. For clarity of illustration and because parametric statistical tests were not employed, bars for the standard error of the mean are not depicted; they are as follows from lowest (0°–5°) to highest (> 15°) eccentricity groupings: Normal eyes – 0.8%, 0.4%, 0.2%, 0.2%; Nondeprived eyes – 0.8%, 1.0%, 0.2%, 0.1%; Deprived eyes – 0.3%, 0.5%, 0.9%, 0.1%; Kitten eyes – 0.5%, 0.4%, 1.0%, 0.2%

sions of Leventhal and Hirsch (1983). However, except for the most central eccentricity group, our data do reveal a trend that is consistent with the Leventhal and Hirsch (1983) claim, since the mean values of the population of alpha and beta cells are smaller in deprived retinas than they are in normal or nondeprived retinas (Fig. 10A, B). Furthermore, we found that both alpha and beta cells in kittens were generally smaller than normal (for alpha cells, $p < 0.02$ or less at each eccentricity group and $p < 0.001$ for all eccentricities combined; for beta cells, $p < 0.05$ or less at all eccentricity group except 0–5°, for which no significant difference between normal adults and kittens was seen, and $p < 0.01$ for all eccentricities combined). The ratio of alpha to beta soma sizes is not abnormal in kittens ($p > 0.1$), which indicates that alpha and beta cells are equally small at 4 weeks of age. This probably reflects a generally incomplete growth of retinal ganglion cells in these kittens.

Relative location of labeled alpha and beta cells

For each of the HRP injection sites limited to lamina A, the center of the zone of retrogradely labeled retinal ganglion cells was determined, and the mean distance from each labeled alpha and beta cell to this center was calculated (see *Materials and methods*). Figure 11 summarizes part of the data from these injections and illustrates the positive correlation between these distances for alpha and beta cells

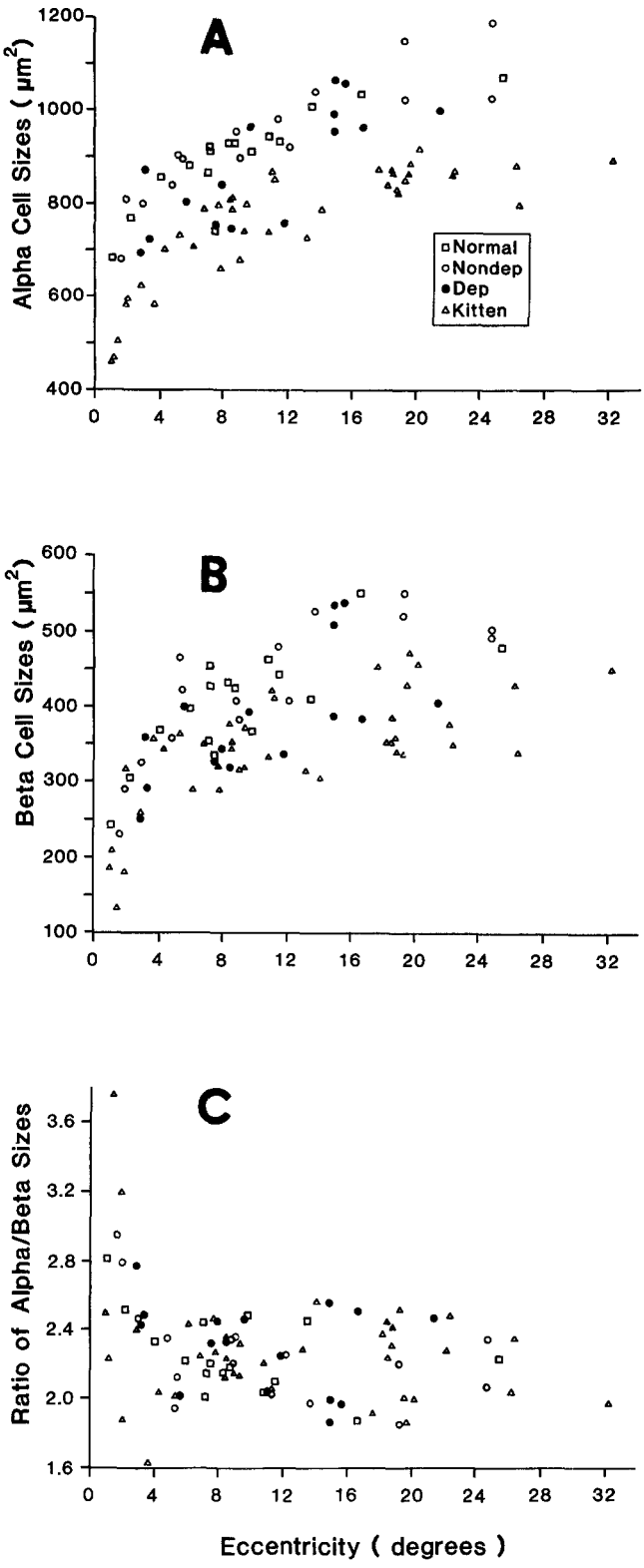

Fig. 9A–C. Soma sizes of retrogradely labeled alpha and beta cells as a function of retinal eccentricity. Sizes represent cross-sectional area, and one mean value is represented for each of the injections summarized in Fig. 7. **A** Sizes of alpha cells. **B** Sizes of beta cells. **C** Ratios of the mean alpha size to the mean beta size for each injection

($r = +0.88$; $N = 86$; $p < 0.001$). It is also evident from Fig. 11 that, for each type of experimental animal and at each eccentricity range, these distances tend to be larger for alpha than for beta cells ($p < 0.001$ on paired t-tests). This means that labeled alpha cells tend to be located nearer the periphery of the zone of labeling, while beta cells are more concentrated in the center; there is, however, considerable overlap in these distances for alpha and beta cells for nearly every injection.

Figure 12 shows how these relationships vary with eccentricity. There is a tendency for these distances to increase with increasing eccentricity (Fig. 12A, B). However, the alpha to beta ratio of these distances remains relatively constant with eccentricity, implying that these labeled zones vary only in scale (Fig. 12C, D). This may simply be a reflection of a reduced magnification factor with increased eccentricity (Sanderson 1971). That is, the same sized HRP injection in a more eccentric retinotopic location in lamina A would label retinogeniculate axons representing a larger visual field area, meaning a larger spread in labeled retinal ganglion cells, than it would in a more central retinotopic location.

The most interesting result from this analysis is the one obvious abnormality seen in the deprived retinas. The alpha to beta ratios of distances from labeled cells to the center of the zone of labeling is larger for the deprived than for the normal retinas ($p < 0.02$ or less for each eccentricity group and $p < 0.001$ for all eccentricities combined). No differences in this measure were found among normal, nondeprived, or kitten retinas ($p > 0.1$). Whether this abnormality seen in labeled zones of the deprived retinas is due to widely scattered alpha cells rather than to beta cells being particularly concentrated near the center of these zones cannot at present be determined.

Discussion

We identified alpha and beta cells in the retinas of normal cats, monocularly deprived cats, and young kittens by retrogarde labeling from small injections of HRP placed into lamina A of the lateral geniculate nucleus. Nearly all of the measures we made of these cells from deprived retinas of the monocularly deprived cats were remarkably normal. These measures include soma sizes and numbers of labeled cells. However, the one abnormality that was detected in deprived retinas relates to the relative locations of labeled alpha and beta cells. The only sign of immaturity noted in the kitten retinas was the small soma sizes of alpha and beta cells.

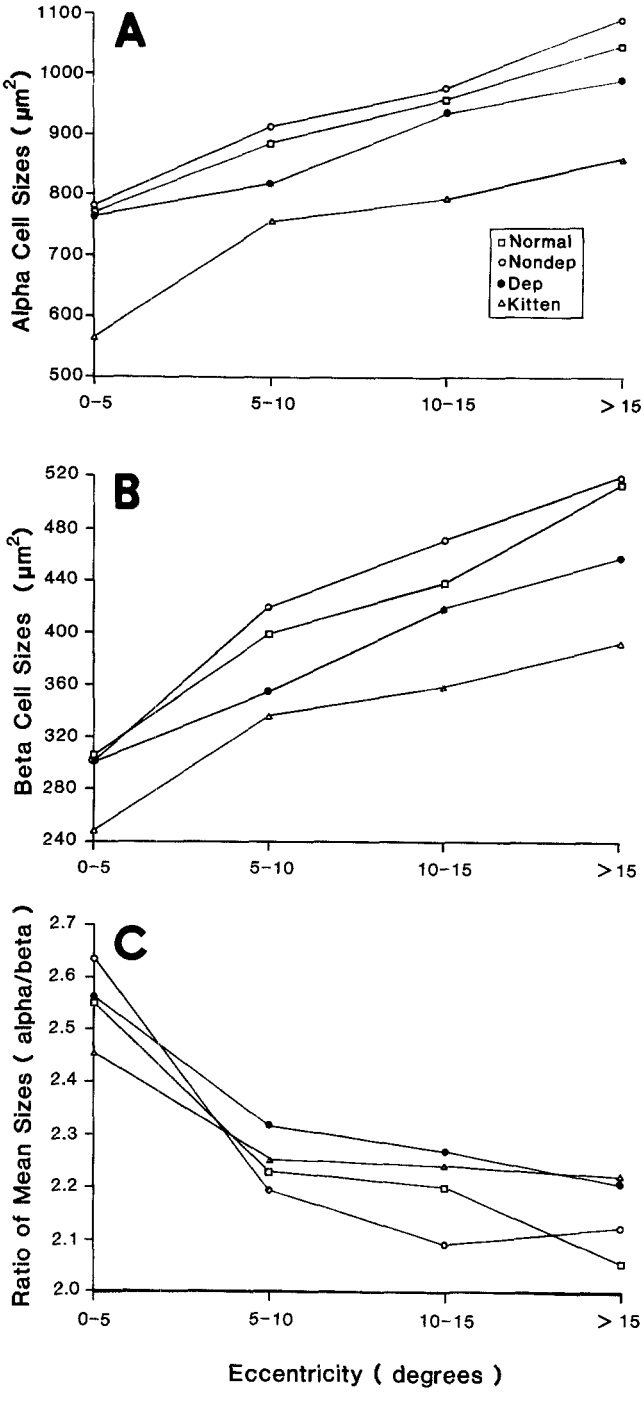

Fig. 10A–C. Same data as in Fig. 9, but illustrating the means for each eccentricity group. **A** Sizes of alpha cells. Cells in the kitten are smaller than are cells in the normal adult ($p < 0.02$ or less for each eccentricity group and $p < 0.001$ for all eccentricities combined), but no statistically significant differences were seen among three adult experimental conditions at any eccentricity. The standard errrors of the mean are, from the lowest to the highest eccentricity groupings: Normal – 41 μm², 21 μm², 20 μm², 13 μm²; Nondeprived – 30 μm², 10 μm², 28 μm², 37 μm²; Deprived – 44 μm², 35 μm², 75 μm², 21 μm²; Kitten – 27 μm², 16 μm², 26 μm², 7 μm². **B** Sizes of beta cells. Again, the kitten cells are abnormally small ($p < 0.05$ or less for each eccentricity group except 0–5°, for which the difference between kittens and normal adults is not statistically significant, and $p < 0.01$ for all eccentricities combined). No differences were seen among the adult experimental conditions. The standard errors of the mean are: Normal – 30 μm², 14 μm², 12 μm², 25 μm²; Nondeprived – 24 μm², 12 μm², 28 μm², 11 μm²; Deprived – 26 μm², 15 μm², 48 μm², 33 μm²; Kitten – 28 μm², 9 μm², 22 μm², 13 μm². **C** Ratios of the mean alpha size to the mean beta size. No statistically significant differences were seen among the experimental conditions, which suggests that alpha and beta cells are equally immature with regard to soma size in the kittens. The standard error of each of the means is 0.1 except for the mean for kittens value at 0°–5° eccentricity, which has a standard error of 0.2

Relative locations of labeled alpha and beta cells

Normal retinas. Alpha and beta cells are distributed in fairly orderly mosaic patterns within the retina (Wässle 1982), and the retinotopic map within lamina A is quite precise (Sanderson 1971). In lamina A of normal cats, however, terminal arbors from retinal X axons are considerably more limited in extent than are those from retinal Y axons (Sur and Sherman 1982; Bowling and Michael 1984). As is illustrated schematically by Fig. 13, it thus follows that small HRP injections into lamina A would label more Y arbors whose main terminal fields were relatively distant from the injection site than would be the case for the more compact X arbors. This, in turn, would result in a relative over-representation of retrogradely labeled alpha cells in a peripheral halo of the zone of labeling (Fig. 13), which might account for our observation that labeled alpha cells lie more distant from the center of the zone of labeling than do the beta cells. It also follows that only the central portion of the zone of labeling accurately reflects the relative number of labeled alpha and beta cells.

This over-representation would be the same absolute size regardless of the size of the injection. Consequently, the larger the injection, which leads to more labeled alpha and beta cells, the smaller the resultant overestimate in the relative alpha to beta ratio for cells projecting to lamina A. We thus conclude that the percentage of labeled alpha cells derived from Fig. 8 is artifactually high. Indeed, our estimates for the relative alpha cell percentage projecting to lamina A does seem slightly high compared to other estimates of this percentage based on larger injections of HRP into the lateral geniculate nucleus (Illing and Wässle 1981; Leventhal 1982).

Deprived retinas. Although the relative numbers of labeled alpha and beta cells were the same in all groups of experimental animals (Fig. 8), this was because the deprived retinas had relatively more

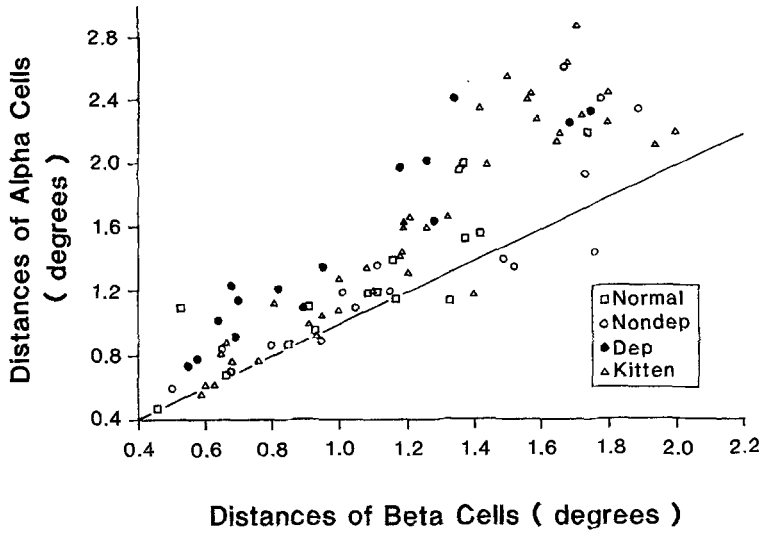

Fig. 11. Scatter plot of the mean distances from the center of the zone of retrograde labeling for labeled alpha and beta cells. This is shown for each injection summarized in Fig. 7. A center of each zone of labeling was determined, and the distance between this center and each labeled cell was measured. For each injection, a mean distance was then calculated separately for the alpha and beta cells. A close correlation exists between these means for alpha and beta cells, and no obvious difference was detected in this relationship among the different experimental conditions. A line of slope 1 is also indicated

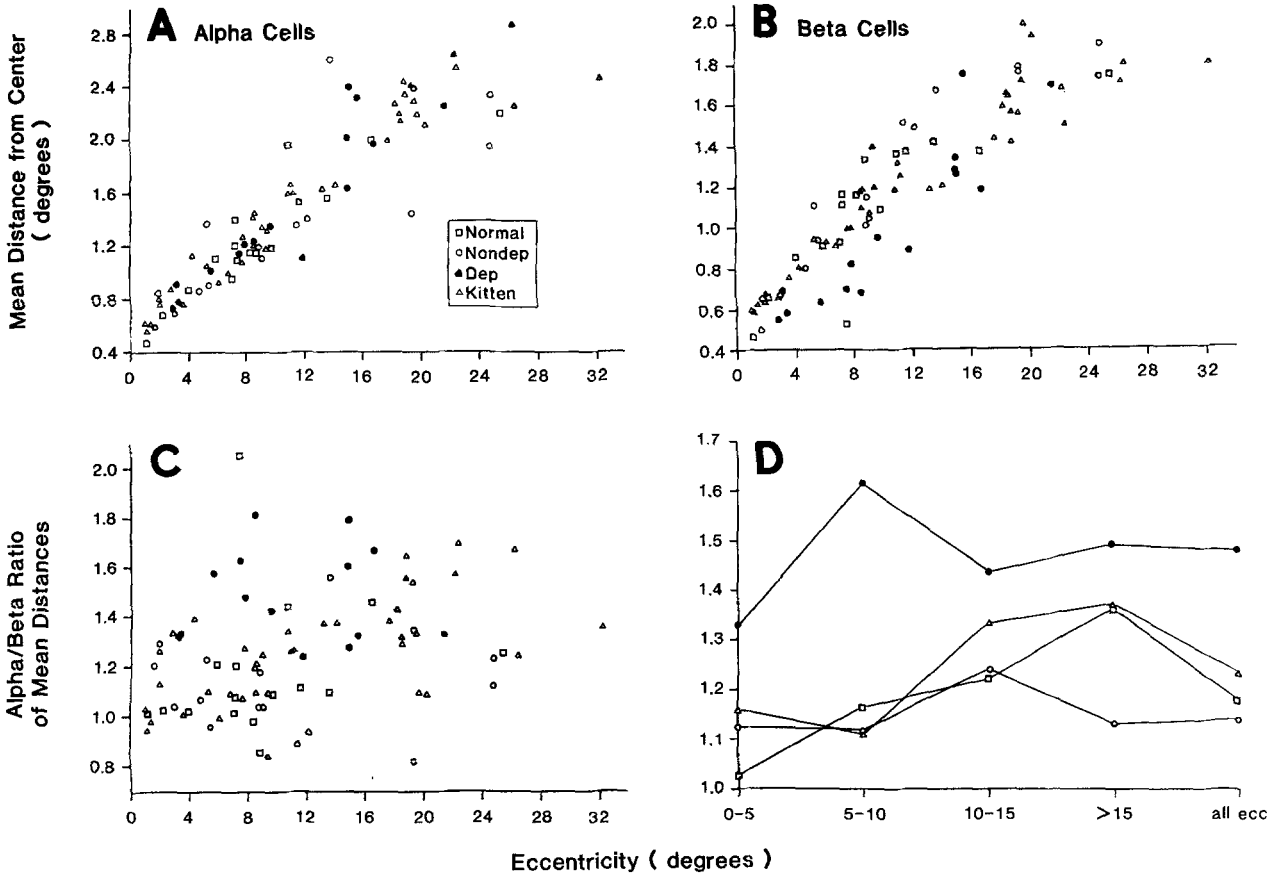

Fig. 12A–D. Mean distances of retrogradely labeled cells from the center of the zone of labeling as a function of retinal eccentricity. Each of the injections summarized in Fig. 7 is included. **A** Alpha cells. **B** Beta cells. **C** Ratios of the mean alpha cell distances to the mean beta cell distances size for each injection. **D** Same ratios as in **C**, but organized into eccentricity groups with one mean per group for each of the experimental conditions. This ratio is greater for the deprived retinas of monocularly deprived cats than for normal retinas ($p < 0.02$ or less at each eccentricity group and $p < 0.001$ for all eccentricities combined). Thus, for the deprived retinas, labeled alpha cells are abnormally scattered compared to labeled beta cells. No such differences were seen among normal, nondeprived, and kitten retinas. Each of the standard errors of the means is 0.1 or less

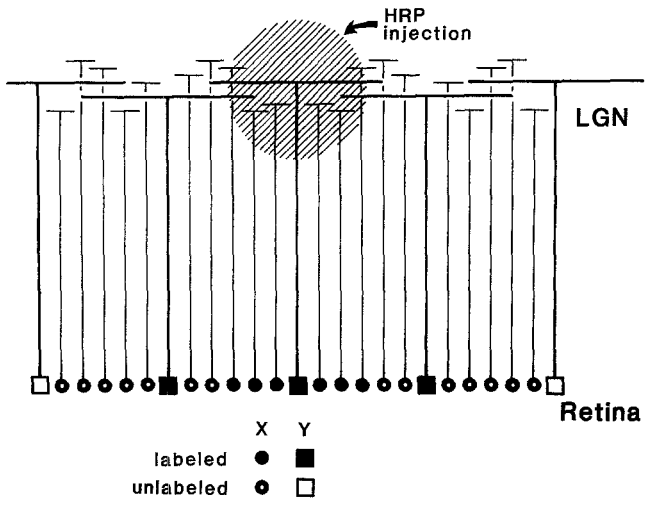

Fig. 13. Schematic diagram illustrating the consequence of different extents of X and Y retinogeniculate arbors on retrograde labeling of their somata in the retina. The much larger extents of Y arbors in the lateral geniculate nucleus (*LGN*) allow them to obtain HRP for retrograde transport from much farther afield than is the case for X arbors. If the retinotopic map is approximately equal in precision for X and Y arbors, an assumption supported by the available data, the result will be an over-representation of retrogradely labeled Y cells around the periphery of the zone of retrograde labeling in the retina

alpha cells located near the periphery and correspondingly fewer near the center of zones of labeling than was the case in normal, nondeprived, or kitten retinas (Fig. 12D). Unfortunately, it is most difficult to interpret this deprivation-induced change in retinogeniculate projections, and it must be emphasized that the differences illustrated in Fig. 12D, while statistically significant, are not large.

One plausible interpretation follows directly from the line of reasoning described above for normal retinas. Since the central zone of retrograde labeling in the retina provides the most accurate estimate of the actual number of alpha cells relative to beta cells (see Fig. 13), and since these zones in deprived retinas have abnormally few alpha cells (see Fig. 12D), it may be that fewer than normal alpha cells project to lamina A from the deprived eye. Indeed, some Y axons from the deprived retina of monocularly deprived cats fail to innervate the contralateral lamina A (Sur et al. 1982), a situation never seen normally (Sur and Sherman 1982; Bowling and Michael 1984). Other deprived Y axons often meander through lamina A for considerable distances despite emitting only a sparse arbor (Sur et al. 1982 and unpublished observations). This latter group of Y axons might retrogradely transport injected HRP despite their small terminal arbors, and their meandering courses that represent relatively imprecise retinotopic fidelity could then explain the tendency for alpha cells to be frequently located in the periphery of labeled zones in the deprived retinas. However, Leventhal and Hirsch (1983) reported no deprivation-induced alteration in the numbers of labeled alpha and beta cells following relatively large HRP injections into the lateral geniculate nucleus. This is consistent with our interpretation only if the injections of Leventhal and Hirsch (1983) labeled those deprived Y axons that innervated lamina C but not lamina A (Sur et al. 1982). This, in turn, would suggest that the deprivation has no effect on development of Y or alpha cells in the nasal retina or on their axons invading lamina C, but only affects the development of their arbors in lamina A where they must compete for terminal space with retinal X axons (Sur et al. 1982, 1984; Sherman 1985b). While all of the available evidence is consistent when viewed from this perspective, we emphasize that the new data presented in this paper provide only weak and indirect additional support for a failure of Y axons to innervate lamina A.

Soma sizes of labeled alpha and beta cells

Normal cats. The sizes of labeled alpha and beta cells in normal cats is well within the range of those reported in prior studies that used similar techniques (Fukuda and Stone 1974; Illing and Wässle 1981; Leventhal 1982). The relationship between soma size and eccentricity for these cells also matches that described previously (Fukuda and Stone 1974; Leventhal 1982).

Deprived retinas. Most past studies of deprived retinal ganglion cells have emphasized their apparently normal morphology and physiology (Sherman and Stone 1973; Kratz et al. 1979; Cleland et al. 1980). Recently, however, Leventhal and Hirsch (1983) reported abnormalities among these cells with regard to cell size. These authors concluded that, relative to their counterparts in normal or nondeprived retinas, deprived alpha and beta cells were 11.7% and 17.4% smaller, respectively. They reported these differences for both nasal and temporal retinas of the deprived eye. We found no support for this soma size abnormality, at least for the nasal retina, but it must be remembered that the effect claimed by Leventhal and Hirsch (1983) is rather subtle. It does seem safe to conclude that, if there is any deprivation-induced abnormality in the sizes of retinal ganglion cell bodies, it must be quite a small abnormality indeed.

At least two differences exist between our study and that of Leventhal and Hirsch (1983), either of

which could account for the different conclusions reached. First, different sizes of HRP injection were placed in the lateral geniculate nucleus. Because ours were limited to lamina A while theirs were not, we would not have sampled potentially smaller cells projecting from nasal retina to other regions. For instance, deprived Y axons that fail to innervate lamina A might have smaller somata than those that do. Although Sur et al. (1982) found no evidence for this, their data base was quite limited. It is more difficult to explain why different sized injections should affect the sample of labeled beta cells, although the possibility cannot yet be ruled out that some deprived X axons from smaller somata also fail to innervate lamina A. Second, the subtle differences reported by Leventhal and Hirsch (1983) might require a large sample to detect. Because of their larger HRP injections, these authors labeled many more alpha and beta cells for measurement than we did.

Kitten retinas. In normal 4-week-old kittens, labeled alpha and beta cells bodies are smaller than their counterparts in normal adults by roughly the same degree (Figs. 9 and 10). This is interesting in the context of the postnatal development of retinal X and Y arbors in lamina A (Sur et al. 1984). At 4 weeks of age, X arbors are considerably larger with more terminal boutons than in adulthood, while Y arbors are smaller with fewer boutons. Hence alpha cell bodies grow in synchrony with their geniculate axon arbors, which is hardly surprising, but as beta cell bodies grow, their geniculate axon arbors shrink, which is most surprising. This challenges the conventional view that soma size and axon arbor development are closely correlated (e.g., LeVay et al. 1980), a challenge already posed by the observation that abnormally large or small retinogeniculate axon arbors are not associated with obviously abnormal soma sizes among the axons' parent cells (Sur et al. 1982).

Conclusions

We failed to obtain any independent, direct evidence of developmental abnormalities among retinal ganglion cells of cats monocularly deprived from birth. Our data, however, are limited to those alpha and beta cells that innervate lamina A. Although we were unable to confirm prior claims (Leventhal and Hirsch 1983) that deprived retinal ganglion cells grow less than normal, our data indicate trends consistent with this view. We found some evidence of a subtle abnormality in the relative location of retrogradely labeled alpha and beta cells that suggests a slight reduction in the strength of the alpha cell projection to lamina A, a conclusion consistent with previously published observations (Sur et al. 1982). In view of evidence of fairly dramatic abnormalities in deprived retinogeniculate arbors (Friedlander et al. 1982; Sur et al. 1982), it seems reasonable to conclude that retinogeniculate circuitry represents the most peripheral site in the visual system at which visual deprivation leads to *pronounced* developmental anomalies. Finally, both our failure to find evidence of striking soma size changes for deprived alpha and beta cells in view of the alterations seen in their retinogeniculate arbors (Sur et al. 1982) as well as our present evidence that the beta cell bodies grow during a postnatal period when their retinogeniculate axon arbors shrink (Sur et al. 1984) suggest that no clear-cut relationship exists between the development of a cell's soma and its axon arbor.

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