

The Projection of the Visual Field Onto the Lateral Geniculate Nucleus of the Ferret

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ABSTRACT

The projection of the visual field onto the dorsal lateral geniculate nucleus (LGN) of the ferret was mapped electrophysiologically. The nucleus contains a single orderly map of the contralateral visual hemifield. The upper visual field is represented dorsally and rostrally in the nucleus; central fields are found in the medial and caudal sections of the LGN; and peripheral fields are represented most laterally. The ipsilateral eye is represented in laminae A1 and C1 up to eccentricities of 20–30°. Lines of projection run perpendicular to the laminar borders. The ferret LGN resembles that of the cat rotated approximately 110° clockwise in the sagittal plane, viewing the right nucleus from its lateral aspect; it differs from the cat in having a larger monocular segment.

Key words: visual system, retinal projections, visual field map

Ferrets (*Mustela putorius furo*) are small carnivores, similar in appearance to their close relative the mink (*Mustela vison*). Guillery and his colleagues have drawn attention to the ferret as a particularly useful experimental animal for studies of the visual system (Linden et al., '81). The ferret lateral geniculate nucleus (LGN) shows the typical carnivore pattern of lamination: laminae A, C, and C2 receive a projection from the contralateral eye, and laminae A1 and C1 receive an ipsilateral projection (Sanderson, '74; Linden et al., '81). The A laminae are further divided into two sublaminae, termed leaflets by Guillery ('71), that have been shown to represent a segregation of ON-center and OFF-center cells (Stryker and Zahs, '83). Because ferrets are born before the retinal afferents have segregated into the appropriate geniculate laminae, they are attractive animals for use in developmental studies (Linden et al., '81).

Before beginning our own studies on the development of the retinogeniculate pathway in ferrets, we have investigated some aspects of the organization of the LGN in adult animals. The following account describes the projection of the visual field onto the LGN. Some of these findings have previously appeared in abstract form (Zahs and Stryker, '82).

MATERIALS AND METHODS

Animals

Eleven normally pigmented adult ferrets, obtained from Marshall Farms, New Rose, New York, were used in these experiments. Eight of the animals were adult females (700–

900 g) and three were adult males (1,100 g). Six of these animals were used in anatomical studies to locate the LGN and label the retinal afferents. The remaining ferrets were used in the electrophysiological studies. Data from three of these animals on the stratification of ON and OFF responses in the LGN have previously been reported (Stryker and Zahs, '83).

Electrophysiological recording

Five ferrets were prepared for physiological recording by using techniques that are conventional for the cat visual system (Shatz and Stryker, '78). The ferrets were initially anesthetized with a mixture of acepromazine (0.04 mg/kg) and ketamine (40 mg/kg) injected intramuscularly. The femoral vein and the trachea were cannulated, and surgical anesthesia was subsequently maintained with thiopental sodium (20 mg/kg i.v.).

Animals were then placed in a modified kitten stereotaxic apparatus and the scalp, skull, and dura overlying the LGN were opened. In four ferrets, the skull was opened from Horsley-Clarke anterior-posterior coordinates –3.5 mm to +3.5 mm and lateral-medial coordinates 2.5 mm to 8.0 mm. The holes were made quite large to allow for variability in the location of the LGN between animals. In one ferret, electrode penetrations were made in the parasagittal plane, on an angle inclined 40–45° pointing anterior from vertical. In this animal, the skull was opened for 7 mm anterior to

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the tentorium, the lateral-medial edges of the opening being at Horsley-Clarke coordinates 2.0 and 8.0.

Following surgery, barbiturate infusion was discontinued and anesthesia was maintained by ventilating the ferret with 75% nitrous oxide, 25% oxygen at a rate and volume which maintained peak inspiratory pressure at 1.5 kPa and end-tidal carbon dioxide at 3.8–4.3%. Neuromuscular blockade was then induced with pancuronium bromide (0.1 mg/kg/hour) or gallamine triethiodide (10 mg/kg/hour). Atropine sulfate (0.08 mg i.m.) was administered every 12 hours during the course of the experiment in order to reduce the ferret's mucous discharge.

The nictitating membranes were retracted with phenylephrine hydrochloride, and atropine was used to paralyze accommodation and to dilate the pupils. Plastic contact lenses (2.7–2.9 mm base curve, plano) were fitted to focus the eyes on a tangent screen subtending 80° at a distance of 570 mm. The center of the screen was placed either directly in front of the ferret or at approximately 60° eccentricity. Focus was checked by retinoscopy and the most appropriate contact lenses were selected. The projections of the two optic discs were plotted on the tangent screen using a reversing beam ophthalmoscope.

Lacquered tungsten microelectrodes (Hubel, '57) were used to record multi-unit activity in the LGN. These electrodes had conical exposed tips tapering from 8 to 15 μm in diameter to a sharp point over 20–45 μm and impedances of 1.5–3.5 MΩ at 120 Hz. The electrodes were advanced rapidly for the first 500 μm after entering the brain, and in 100-μm steps thereafter. A hand-held light was used to plot receptive fields on the tangent screen, while LGN activity was assessed with an audio monitor. One or more electrolytic lesions were made along the course of each electrode penetration by passing -4 to -6 μA current for 4–6 seconds.

At the end of the recording sessions, the ferrets were deeply anesthetized with an intravenous injection of sodium pentothal and perfused through the heart with 0.9% saline followed by 10% formol saline. The heads were placed in the fixative overnight and blocks of brain containing the LGN were removed the next day. The blocks of tissue were sunk in 30% sucrose formalin before being embedded in a mixture of albumin and gelatin. Forty-micron sections were cut on a freezing microtome and sections containing the LGN were stained with cresyl violet. Three of the brains were cut coronally; the remaining two brains were cut sagittally. Camera lucida drawings were made of sections containing electrode tracks, and recording sites were assigned by referring to microdrive readings at the lesions and the entry point into the LGN. The brain of an additional ferret, not used for electrophysiological studies, was cut horizontally and stained with cresyl violet.

The receptive field position at each recording site was noted on the drawing. The location of each receptive field was expressed as two angles, azimuth and elevation, using a system of spherical polar coordinates (Bishop et al., '62). In order to calculate these angles, the fixation point for each eye had to be estimated. The fixation point elevation (i.e., the zero horizontal) was assumed to be the position of the smallest central receptive fields. The fixation point azimuth (the position of the vertical meridian at zero elevation) for each eye was calculated by the method of Sanderson and Sherman ('71). The horizontal distance (Y) from the optic disc to the vertical line passing through the fixation point is given by the expression

$$Y = \frac{A - F}{2}, \quad (1)$$

where A is equal to the separation of the optic discs' projections on the tangent screen. F, the mean receptive field separation on the tangent screen, was found by recording sites in the C laminae near the representation of the zero elevation where there was a response to stimulation of both eyes. The horizontal distances between the fields recorded for each eye at the same site in the LGN were averaged to give F.

Labelling the retinal afferents to the LGN

In three ferrets, retinal afferents to the LGN were labelled autoradiographically by intravitreal injections of 200–2,000 μCi ³H-proline (Amersham TRK.439, specific activity 40 Ci/mmol). The brains of two of these animals were sectioned in the coronal plane; the third brain was cut sagittally. Another LGN, cut in the sagittal plane, was labelled via an intravitreal injection of 0.25 mg wheat-germ agglutinin conjugated to horseradish peroxidase (WGA-HRP) (Sigma L-9008). One additional animal received a proline injection into one eye and an injection of WGA-HRP into the other eye. One series of parasagittal sections from this animal was tested for HRP with the TMB method (Mesulam, '78) and then stained with neutral red; a second series was exposed for autoradiography; and a third series was stained with cresyl violet.

Measurements of the volume of the LGN

Both labelled and Nissl-stained sections, taken at 120-μm intervals from two brains cut in the sagittal plane, were traced at a magnification of 60× in the camera lucida. The innervation volumes contralateral and ipsilateral to each of three labelled eyes were measured planimetrically, as was the total volume of the LGN (layers A, A1, C, C1, and C2). A correction for shrinkage was applied to the sections treated for HRP based on their size as compared to the adjacent Nissl-stained sections. No correction was applied to the measurements on Nissl-stained or autoradiographically labelled sections to relate them to the size *in vivo*.

RESULTS

Anatomy

Laminar structure. The pattern of geniculate lamination which has been described for several species of carnivores (Sanderson, '71, cat; Sanderson, '74, mustelids, racoon, fox) is also found in the ferret (Sanderson, '74; Linden et al., '81). Progressing from the outside (nearest the optic tract) to the inside of the LGN, one first encounters the C laminae: lamina C3, which does not receive a retinal input, is outermost, followed by contralaterally innervated C2, ipsilaterally innervated C1, and contralaterally innervated lamina C. Lamina A1, which receives the majority of the uncrossed retinal input to the LGN, is found just inside lamina C in the medial part of the nucleus. Contralaterally innervated lamina A is the innermost layer, found adjacent to lamina A1 in the binocular portion of the nucleus and just inside lamina C in the more laterally placed monocular segment.

This laminar organization is easily seen in parasagittal and horizontal sections through the nucleus. The coronal plane is parallel to the plane of the laminae over much of the nucleus, making the arrangement of the laminae ob-

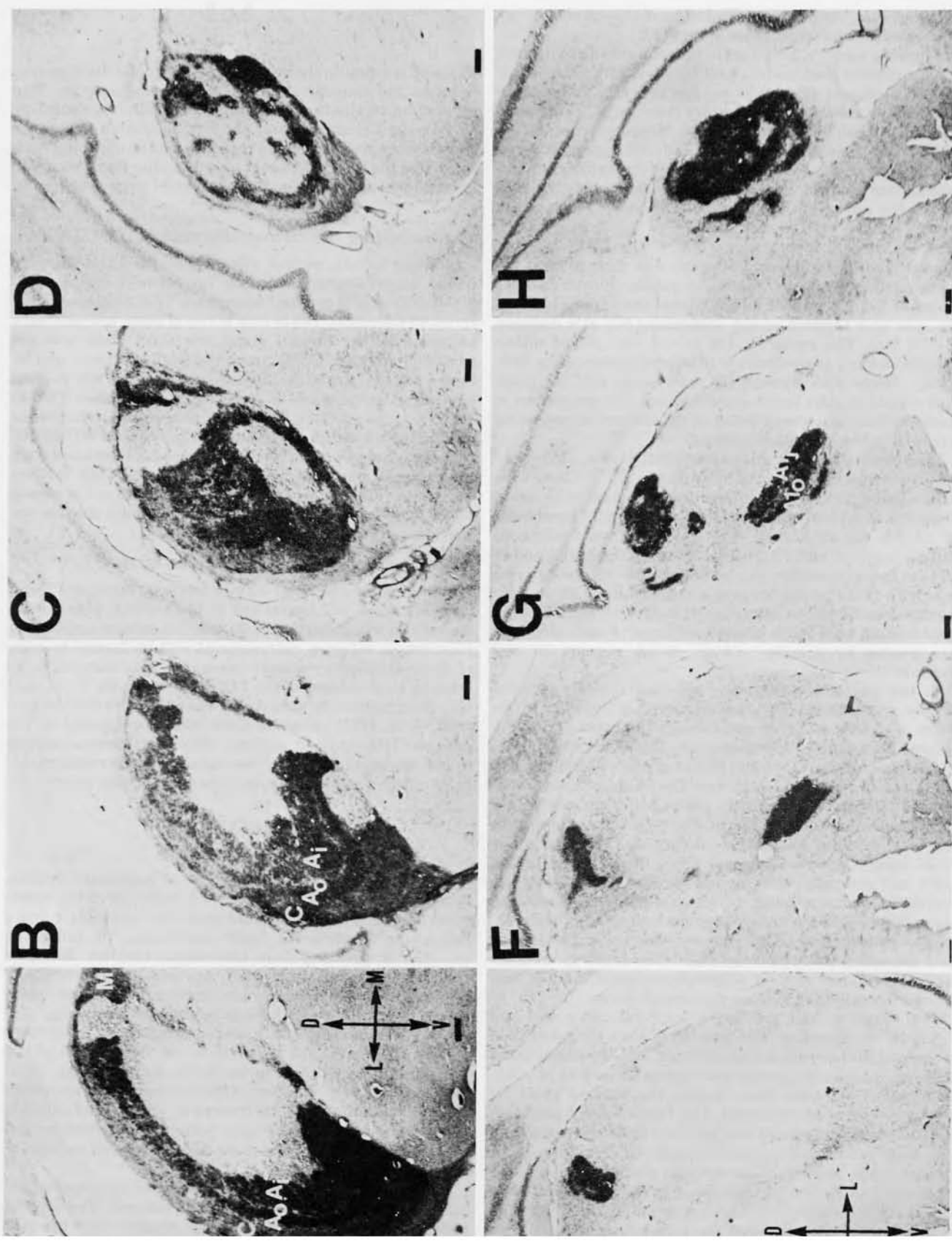


Figure 1

scure in coronal section. However, as this plane is useful for viewing the topographic organization of the nucleus, the pattern of innervation seen in coronal section will be described (Fig. 1).

The projections of the two eyes, as revealed by the anterograde transport of ^3H -proline, are shown in Figure 1. The anterior part of the LGN is shaped like the capital letter "C" when viewed in coronal section (Fig. 1A). Here the nucleus receives afferents mainly from the contralateral eye, with only a small patch at the dorsomedial edge of the LGN receiving ipsilateral input (Fig. 1F). The laminar structure of the LGN is clear only in the most rostral sections when the nucleus is cut coronally. As seen in Figure 1A, the outer rim of the nucleus is made up of the C laminae (Linden et al., '81). A sublamination of the A laminae, termed "leaflets" by Guillery ('71), is visible over much of the nucleus in this section. In more caudal sections, the ipsilateral projection can be seen to expand from the medial edge of the nucleus. At its posterior pole, the LGN appears as an oval-shaped sheet in coronal section. The majority of the ipsilateral input to the LGN is found here. Lamina A1, which receives this ipsilateral input, may also be divided into leaflets, although the boundaries between the leaflets are obscure in coronal section.

The laminar structure of the LGN is most easily seen in parasagittal views of the nucleus (Fig. 2). In autoradiographically labelled sections, the subdivision of the laminae into leaflets is apparent, especially in the ventral half of the nucleus. In some labelled sections, it is possible to resolve the C laminae into components (Fig. 2D). Label in the perigeniculate nucleus (PGN) contralateral to the injected eye (Fig. 2C,D) has been previously noted (Linden et al., '81). These authors believe this label represents fibres of passage entering lamina A rostrally or traversing the PGN on their way to other diencephalic or mesencephalic nuclei. In the case illustrated here, however, much of the perigeniculate labelling may be transneuronal because the animal survived longer than 1 week after the injection.

Contralateral to the injected eye, narrow bridges of label can be seen to connect lamina A with lamina C (Fig. 2D). Several such bridges were also observed in the doubly labelled animal; they passed through thick parts of the lamina and were not merely features of its ragged edge. Figure 3 illustrates that ipsilateral-eye afferents are excluded from lamina A1 within these contralateral-eye bridges. Thus the retinal afferents serving the two eyes remain complementary rather than overlapping, even in the presence of such disruptions of the ordinary geniculate laminar structure. Ipsilateral-eye bridges through lamina C connecting laminae A1 and C1 were also observed complementary to gaps in the contralateral terminal field (not illustrated).

Volume of LGN. The total volumes occupied by the laminar LGN (including the interlaminar plexuses), measured on both sides of two animals in Nissl-stained parasagittal sections taken at 120- μm intervals, were 2.87 and 3.15 mm^3 in one 795-g female and 4.14 and 4.80 mm^3 in another 796-

g female. In the animal in which one eye was labelled with WGA-HRP, the ipsilateral projection occupied 11% of this volume; the contralateral projection occupied 76%; and the balance (13%) appeared not to be innervated by either eye (interlaminar plexus, lamina C3, blood vessels, etc.). In the doubly labelled animal, the projection from the WGA-HRP-labelled eye occupied 7% of the geniculate volume ipsilaterally and 70% contralaterally; while the projection from the autoradiographically labelled eye occupied 12% of the LGN ipsilaterally and 76% contralaterally. Thus, 82% and 83% of the two sides of the LGN were occupied by labelled terminal fields. The ipsilateral eye's terminal field appears to occupy only a fifth or less of the volume occupied by that of the contralateral eye.

Measurements of the volumes innervated by the two eyes in the binocular segment were also obtained from the double-labelled geniculates. The binocular portion of each section was defined by drawing lines perpendicular to the laminar borders at the dorsal and ventral edges of lamina A1. On the right side, the binocular segment, measured on Nissl-stained sections, occupied 1.96 mm^3 , or 41%, of the total volume of the LGN. Terminals from the contralateral (autoradiographically labelled) eye occupied 1.26 mm^3 in the binocular segment, while terminals from the ipsilateral (WGA-HRP-labelled) eye occupied 0.34 mm^3 . On the left side, the binocular segment consisted of 1.67 mm^3 , or 40%, of the LGN. The terminal field of the contralateral (WGA-HRP-labelled) eye occupied 0.93 mm^3 in the binocular segment, while that of the ipsilateral (autoradiographically labelled) eye occupied 0.49 mm^3 .

Electrophysiological mapping

The following sequence of events was often encountered in a vertical penetration. Upon entering the LGN, the electrode first passed through an area of high spontaneous activity. Histology later showed this region to be the C laminae. The unit clusters here could frequently be driven by both eyes, depending on the eccentricity of the receptive field, and were usually responsive to both the onset and offset of a spot flashed in the center of the receptive field. The electrode would remain in this region for a variable distance, typically 200–400 μm . As the electrode was advanced out of the C laminae, the quality of the response would change, becoming extremely tonic, from one eye only, and of one center-type. The center-type could change during the course of the penetration. Penetrations in the rostro-medial part of the LGN often passed through the PGN. When the electrode was in the PGN, responses sounded less vigorous and unit clusters were binocularly driven. In the most rostral penetrations, the electrode never reentered the LGN. More caudally, the electrode would travel through the PGN for 800–1,000 μm and then return to the LGN. Finally, as the lower border of the LGN was reached, the receptive fields might be in either eye, and the boundaries of the fields were less distinct.

In the most medial penetrations, our electrode sometimes entered the medial interlaminar nucleus (MIN). Recording sites in the MIN were characterized by large receptive fields, the borders of which were difficult to define with flashing or moving spots of light. No attempt was made to study the topographic organization of the MIN.

The zero elevation and optic disc projection. As noted in Materials and Methods, we estimated the elevation of the fixation point from the position of the smallest receptive fields. Figure 4A shows the entire complement of contralat-

Fig. 1. Autoradiographs shown in brightfield of a series of coronal sections through the LGN. Upper row (A–D): sections contralateral to an eye in which the vitreous humor had been injected with ^3H -proline. Lower row (E–H): sections ipsilateral to the injected eye sections progress from rostral to caudal moving from left to right within each row. The sections have been lightly stained with cresyl violet. A_i, inner leaflet of lamina A; A_o, outer leaflet of lamina A; A1_i and A1_o, inner and outer leaflets of lamina A1; C, C laminae; M, medial interlaminar nucleus. Scale bar = 200 μm . The orientation of the sections A–D is shown in A; orientation of E–H is shown in E.

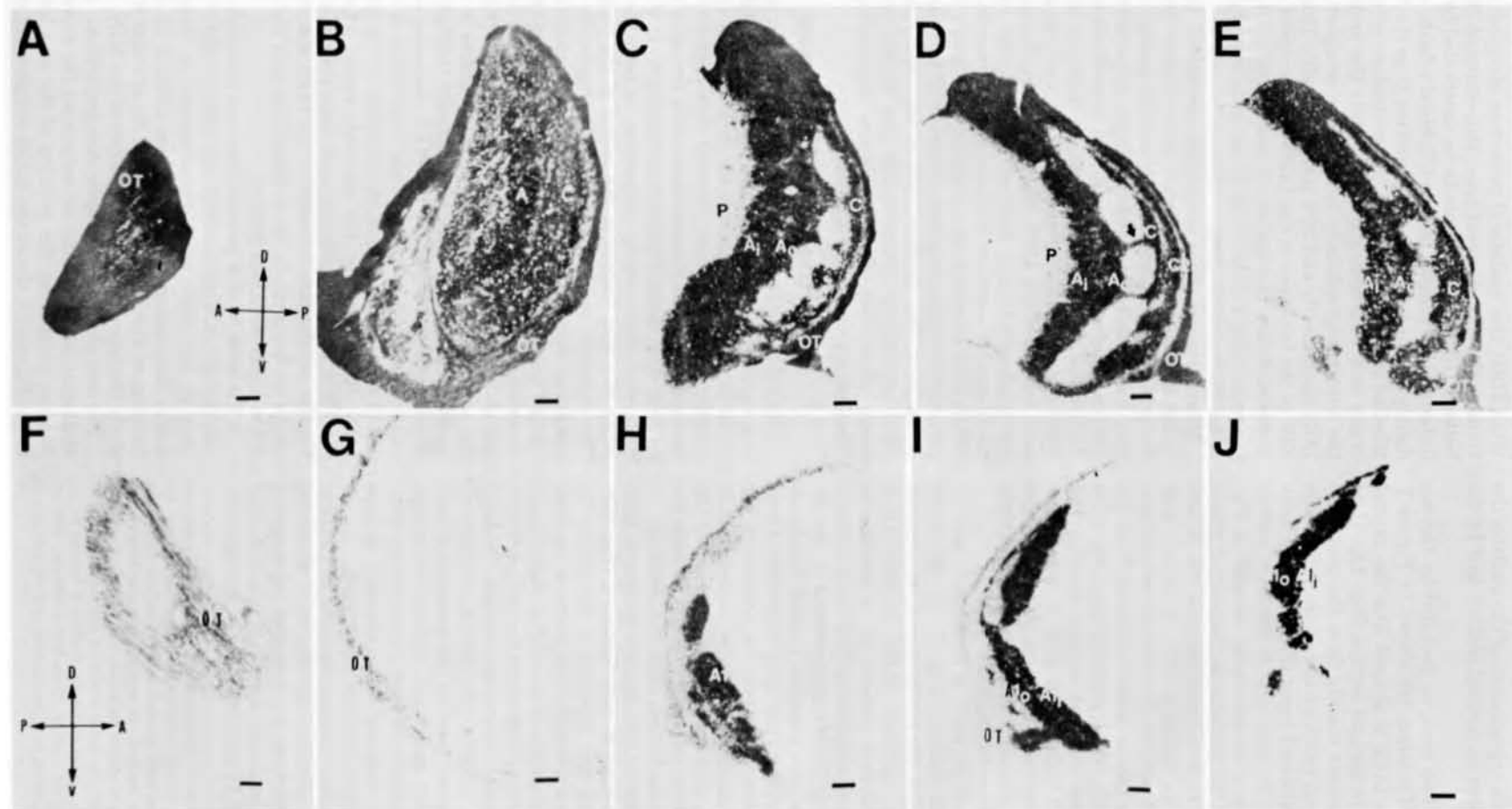


Fig. 2. Autoradiographs of a series of parasagittal sections through the LGN. Upper row (A-E): sections contralateral to an eye which had been injected with ^3H -proline. Lower row (F-J): sections ipsilateral to the injected eye sections progress from lateral to medial moving from left to right within each row. A_o , outer leaflet of lamina A; A_i , inner leaflet of lamina A; $A1_o$,

outer leaflet of lamina A1; $A1_i$, inner leaflet of lamina A1; C, C laminae; OT, optic tract; P, perigeniculate nucleus. Scale bar = 200 μm . The orientation of sections A-E is shown in A, that of F-J is shown in F. The arrow in (D) points to one of the bridges of label between lamina A and lamina C.

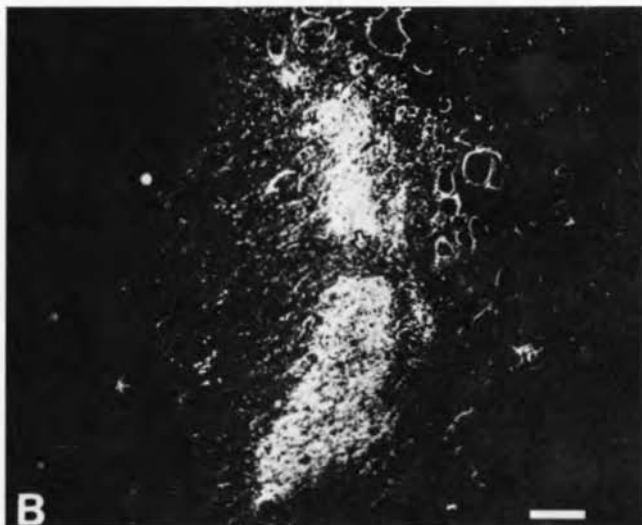


Fig. 3. Serial parasagittal sections through the LGN of the double-labelled ferret in which the contralateral eye had been injected with WGA-HRP and the ipsilateral eye with ^3H -proline. A. Section reacted with TMB method to make WGA-HRP label visible, then stained with neutral red, and photographed in darkfield. Note bridge of label through lamina A1

connecting laminae A and C. B. Section exposed for autoradiography and photographed in darkfield. Note that the terminal field of the proline-labelled eye excludes the bridge across lamina A1 visible in A. Scale bar = 200 μm . Other conventions as in Figure 2.

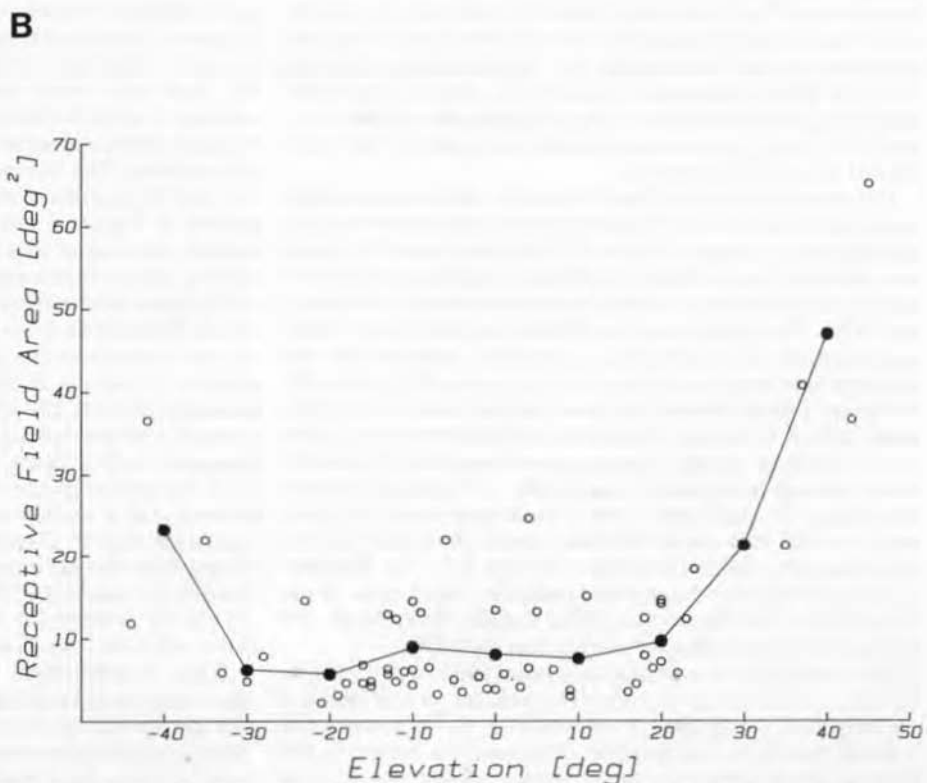
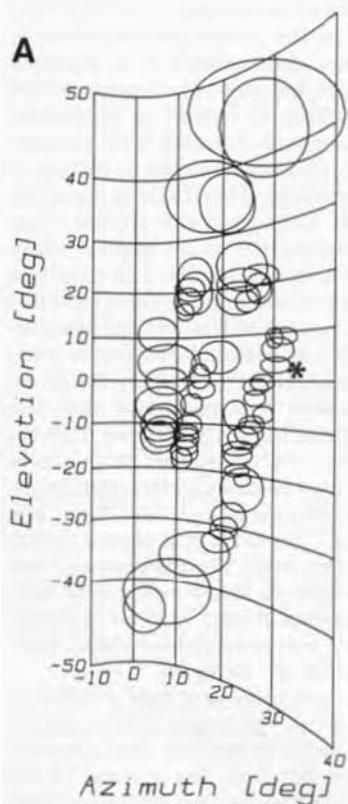


Fig. 4. All receptive fields within the central 30° of azimuth recorded through the contralateral eye of one animal. Ellipses indicate the relative sizes of the receptive field centers. The projection of the right optic disc is marked by the asterisk. These data were obtained from the same experi-

ment illustrated in Figures 7 and 8. B. Receptive field area (deg^2) versus elevation (deg) for the fields shown in A. Each open circle represents a receptive field from A. Closed circles represent the average area of the receptive fields found at the elevation indicated ± 5 deg.

eral eye receptive fields plotted in the central 30° in one experiment. The projection of the right optic disc, plotted with a reversing beam ophthalmoscope, is also shown in this figure. In this experiment, receptive field size did not differ appreciably between elevations -30° and +20°. Very small receptive fields were found at the fixation point elevation illustrated (3° below the optic disc projection), consistent with the observation that the smallest fields were centered 3°, 4°, and 4° below the optic disc projection in other mapping experiments. The horizontal separation between the projection of the optic disc and the fixation point was 33° in the case illustrated. This distance was found to be 32, 33, and 28° in the three additional experiments mentioned above.

This figure also illustrates a finding consistent in other experiments: that the most medial receptive fields recorded within the LGN were located farther from a vertical line passing through the fixation point in the upper visual field than in the lower visual field. Penetrations medial to those containing the receptive fields illustrated were found to be outside the LGN. A line connecting the most medial receptive fields within the LGN formed an angle of between 10 and 20° with the vertical in different experiments.

Coronal plane findings. Results of a typical experiment are shown in Figure 5. Five penetrations can be seen in this coronal section from the posterior LGN. Lesions mark the lower boundary of the LGN in all but the most medial penetration. Here the upper lesion was made 100 μ m below the border of the nucleus. The two most medial tracks are each marked with two lesions. Cells recorded along the two lateral tracks had receptive fields driven from the contralateral eye. The three more medial tracks are in ipsilaterally innervated lamina A1. As the electrode travelled downward in the LGN, receptive field elevations decreased and the fields progressed toward the vertical meridian. More peripheral receptive fields mapped more laterally in the LGN, while more central fields were recorded at more medial sites in the nucleus.

The results from the three ferrets in which the penetrations were viewed in the coronal plane are summarized in the projection maps of Figure 6. The data from 306 receptive fields in four animals have been superimposed on five representative sections across the anteroposterior extent of the LGN. The maps from the different animals were made as consistent with each other as possible. Isoazimuths and isoelevations were drawn by connecting recording sites with receptive fields having the same azimuths or elevations, respectively. Following the method of Sanderson ('71), scatter in azimuth values along a penetration was ignored if there was no net change in azimuth. In drawing isoelevation lines, interpolations were sometimes made. (For example, a 10° line might be drawn between recording sites with receptive field elevations of 9° and 11°.) The Horsley-Clarke coordinates have been assigned relative to those obtained in the animal (an 830-g female) from which the largest number of receptive fields was recorded.

The isoazimuth lines, seen in coronal section, are curved, so that an electrode penetration parallel to the midline encountered a progression of receptive fields toward the vertical meridian. Isoelevation lines are also curved in the coronal plane, beginning at the medial edge of the nucleus and arcing ventrolaterally. In general, peripheral fields are represented in the rostralateral part of the LGN, while central fields are represented in the caudal and medial parts of the nucleus. There is an expanded representation of the central visual field in the caudal LGN.

The vertical meridian is represented near the medial border of the LGN. In the most caudal coronal sections, receptive fields with small negative azimuths were found in the lower visual field at the medial border of the nucleus. The representation of the vertical meridian is slightly lateral to the medial border in these sections. The horizontal meridian is found in the more dorsal part of the LGN. While superior receptive fields were recorded in the rostral LGN, most of the nucleus is devoted to the inferior half of the visual field.

Sagittal plane findings. In an additional experiment, the LGN was sectioned parasagittally after electrophysiological mapping. Figure 7 shows these sections, tracings from which are aligned with the mapping data in Figure 8. Receptive fields recorded in the PGN are included. Although the quality of the responses changed when the electrode passed from LGN to PGN, progress in the receptive field positions was continuous between the two nuclei.

Isoelevations appear as lines oriented normal to the geniculate laminae when viewed in parasagittal section. Higher elevations are represented dorsally in the nucleus. The parasagittal plane is inconvenient for viewing isoazimuths; it is not possible to follow an isoazimuth from superior to inferior visual world within a single parasagittal plane. Fields with the same azimuth values are found in a series of parasagittal sections, occurring higher in the nucleus in more medial planes. This observation is consistent with the outward bowing of the isoazimuth lines seen in coronal section. Within a single parasagittal plane, receptive fields with higher azimuth values are found rostrally.

The relationship of the isoelevation lines to the geniculate laminae is easily seen in the parasagittal sections of Figure 8. Isoazimuth lines are also expected to be oriented normal to the laminar borders, but this relationship would be clear only when the nucleus is viewed in horizontal section. Figure 9A shows a horizontal section from another animal taken approximately midway from top to bottom of the nucleus. The laminar structure of the LGN is apparent in this Nissl-stained section. Data from the animal illustrated in Figure 8 are superimposed on an appropriately scaled drawing of this section in Figure 9B. The numbers shown on this figure represent the azimuth values recorded at the zero isoelevation line in each of ten vertical penetrations. Isoazimuth lines (drawn as dashed lines) can be seen to run normal to the geniculate laminae. Only fields recorded in lamina A are shown; it is presumed that the isoazimuth lines are continuous between laminae. The expanded representation of the central visual field is also apparent in this figure. It should be stressed that this figure is a composite of the electrophysiological data from one animal and a section through the LGN of a second ferret, intended only to illustrate the angle the isoazimuth lines make with the laminar borders. In the drawing (Fig. 9B), lamina A1 appears to lie opposite lamina A as far laterally as the 45° isoazimuth. In fact, receptive fields in lamina A1 have not been found beyond the 30° azimuth.

Lines of projection. The maps indicate that a point in the visual world projects to a line running perpendicular to the geniculate laminae. In order to confirm this, penetrations inclined approximately 40° from the vertical in the sagittal plane were made in two ferrets. Two of these oblique penetrations are shown in Figure 10. The upper penetration is nearly perpendicular to the geniculate laminae and is approximately along a line of projection. The receptive field positions change relatively little along this penetration, compared with the progress in receptive fields encountered

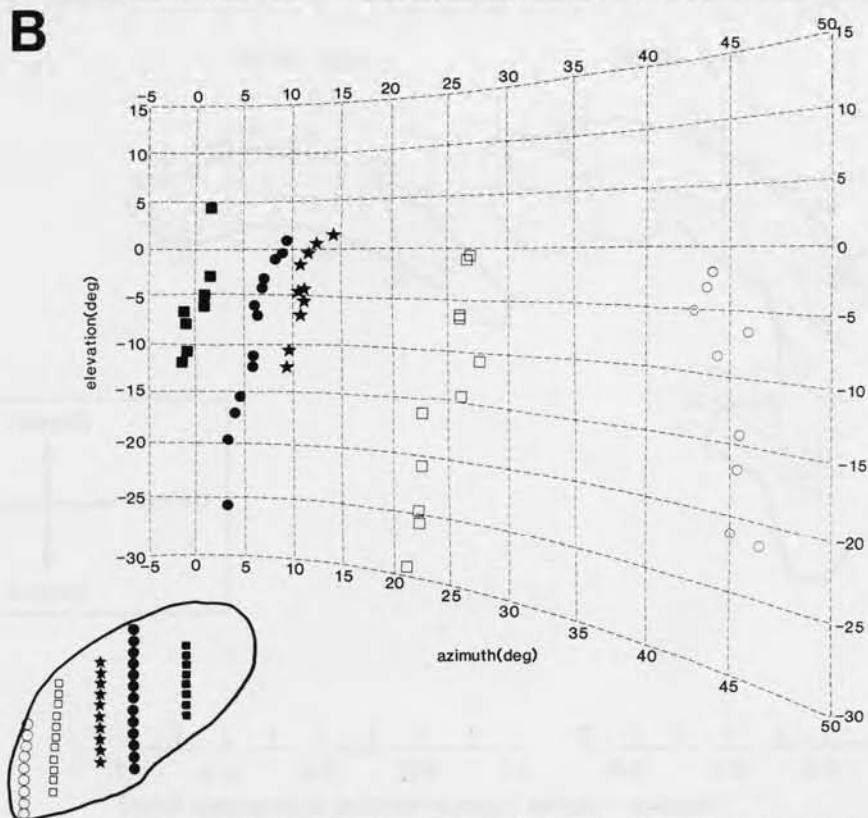
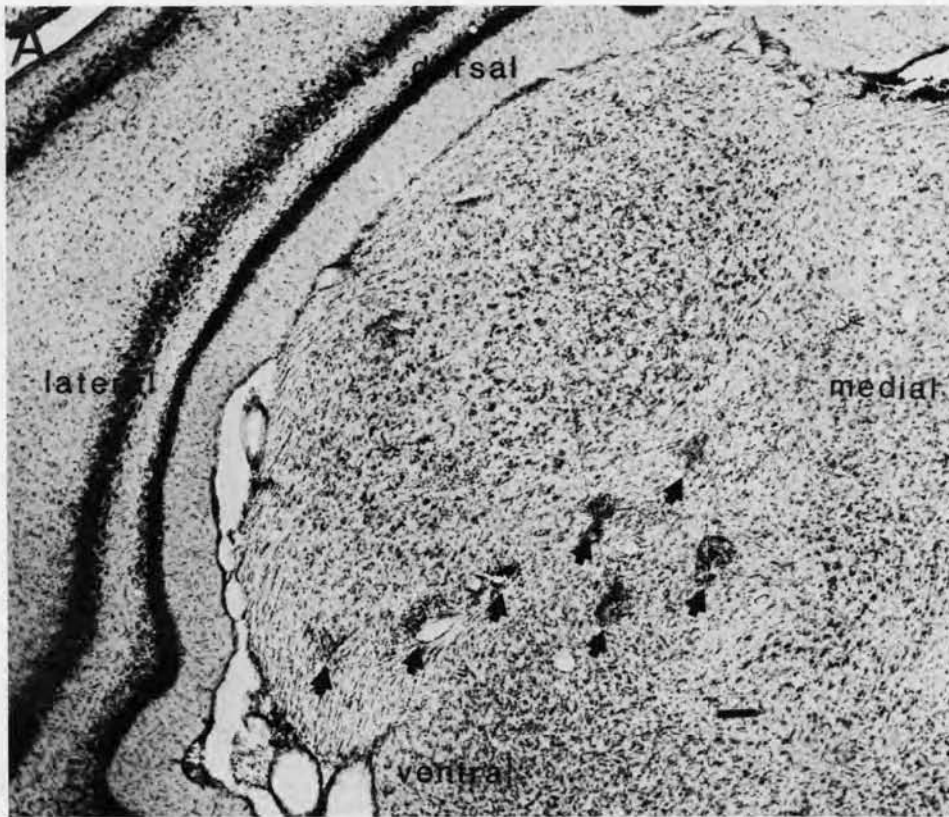


Fig. 5. A. Five penetrations through a single coronal plane in the LGN seen in a Nissl-stained section. A lesion (marked by arrows) marks the end of each penetration. The two most medial penetrations are each marked by two lesions. Scale bar = 100 μ m. B. Locations of the receptive fields recorded along the penetrations through the section shown in A. Open symbols mark

sites where fields were recorded from the contralateral eye; filled symbols mark sites where fields were recorded from the ipsilateral eye. As the electrode moved downward in the LGN, the receptive fields moved down. The symbols correspond to those marking the LGN site at which the field was mapped (inset).

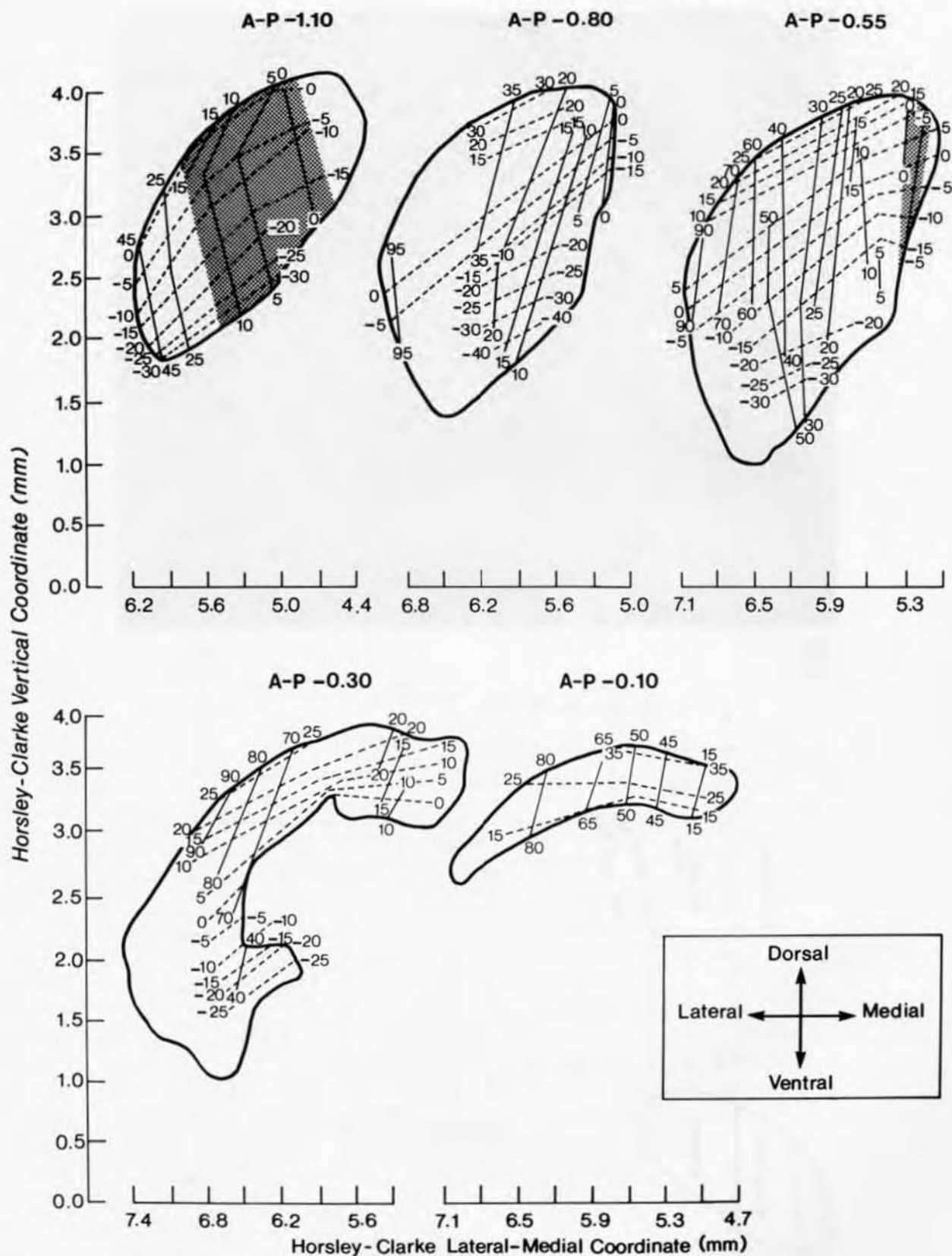


Fig. 6. The visual field projected onto coronal sections of the LGN. Data from 306 receptive fields recorded in four animals have been superimposed on five representative sections across the anteroposterior extent of the LGN. Solid lines, isoazimuths; dashed lines, isoelevations; shaded areas, fields recorded in the ipsilateral eye. The number above each section gives the Horsley-Clarke A-P coordinate of the section.

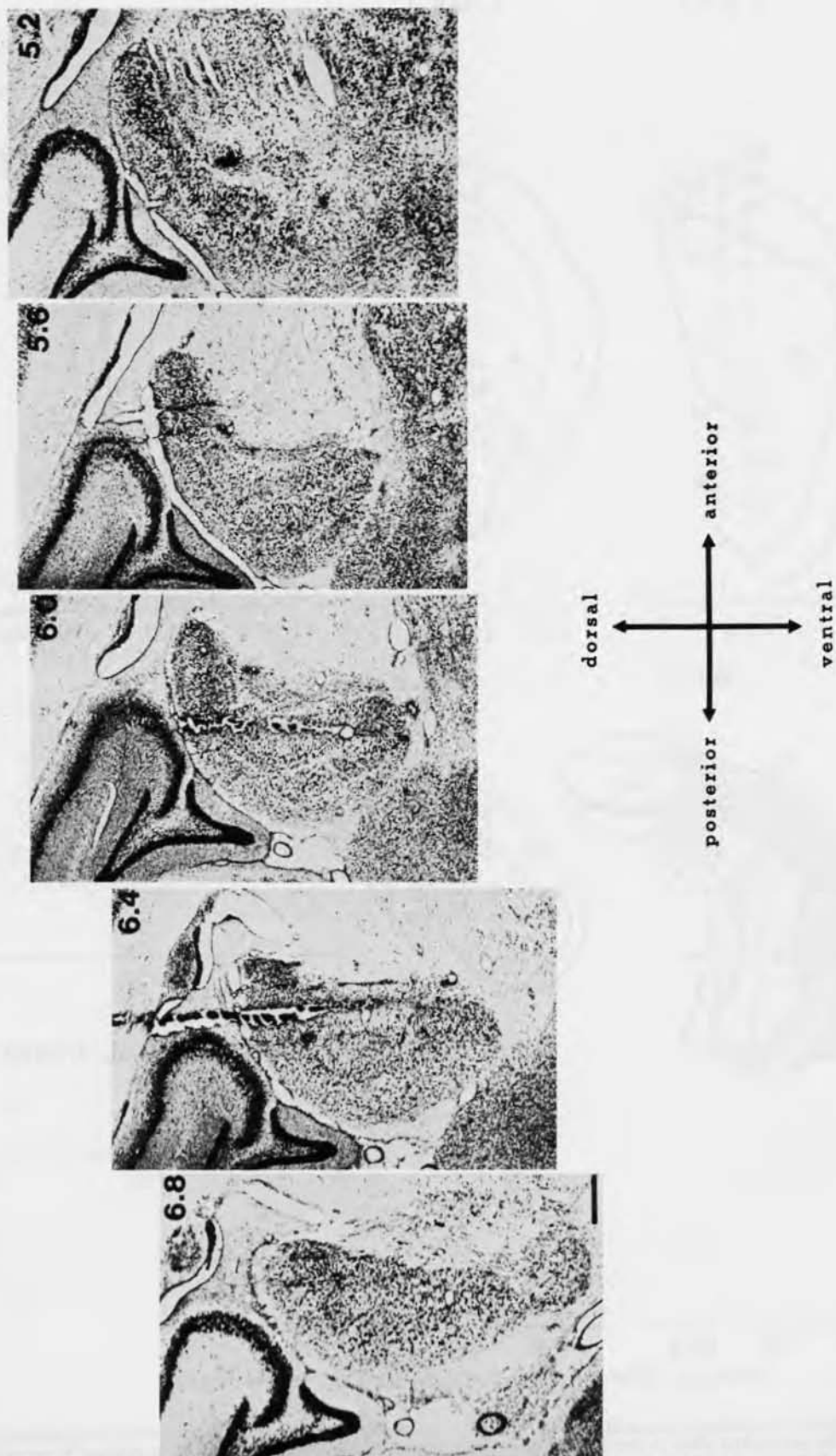


Fig. 7. Parasagittal sections from the LGN of a single animal, containing the penetrations from which the maps in Figure 8 were obtained. The sections have been stained by a Nissl method. The numbers in the upper right corners give the lateral-medial coordinate of the section. The figure is arranged to reflect the relative vertical position of the sections. Scale bar = 500 μ m.

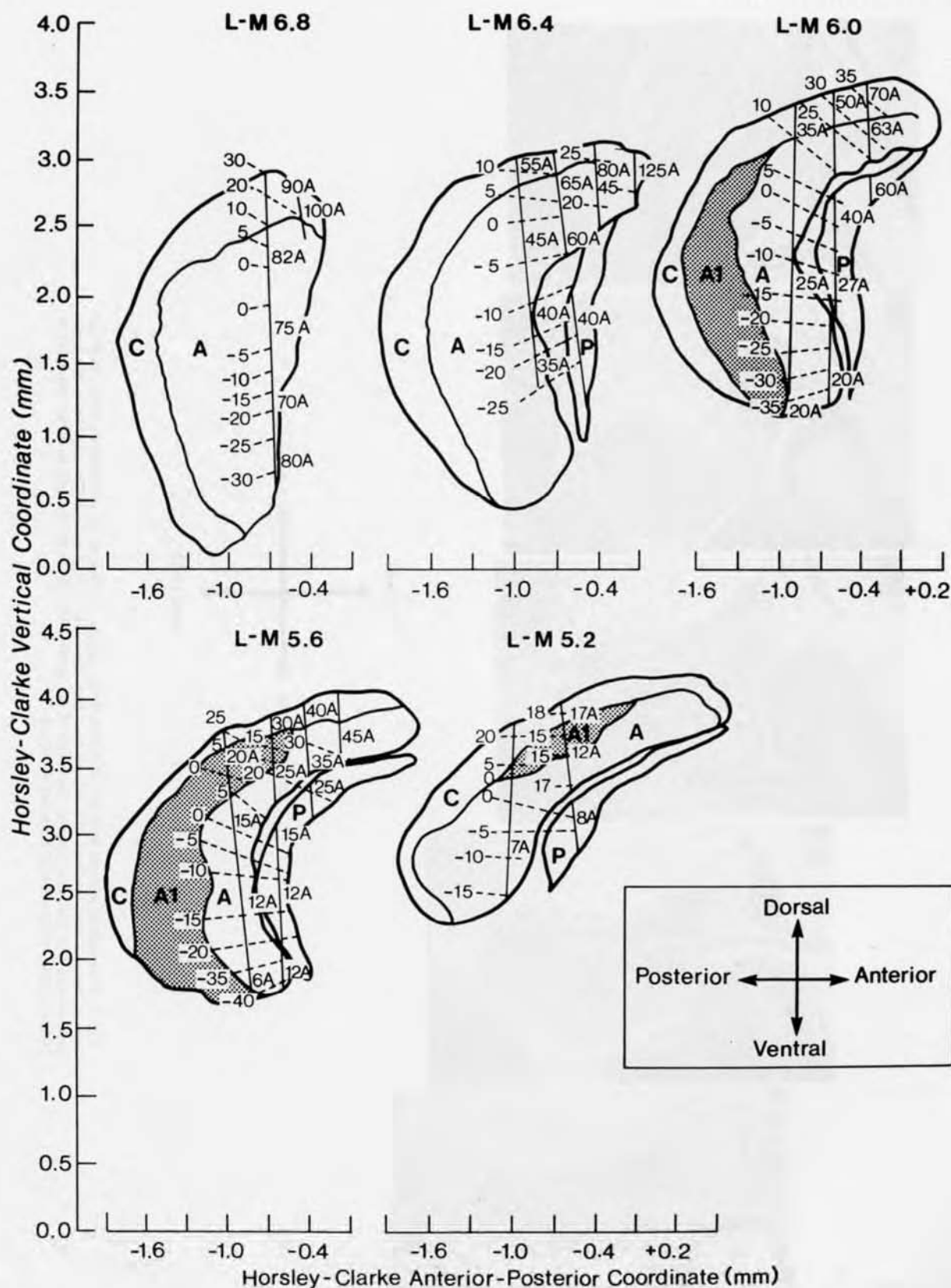


Fig. 8. The visual field projected onto parasagittal sections of the LGN. Five rows of penetrations in the parasagittal plane yielded 247 receptive fields in the LGN and PGN. Data were obtained from a single animal. Isoazimuths, solid lines whose values are postscripted with "A"; isoeleva-

tions, dashed lines; shaded areas, fields recorded in the ipsilateral eye; A, LGN lamina A; A1, LGN lamina A1; C, C laminae; P, perigeniculate nucleus. The number above each section gives the Horsley-Clarke lateral-medial coordinate of the section.

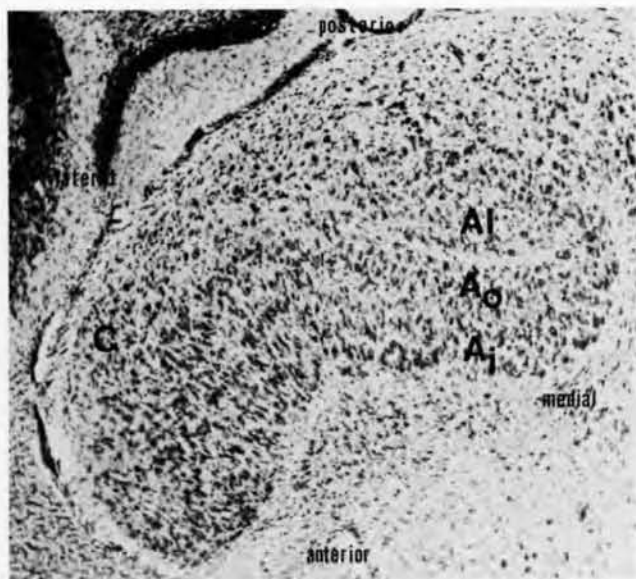
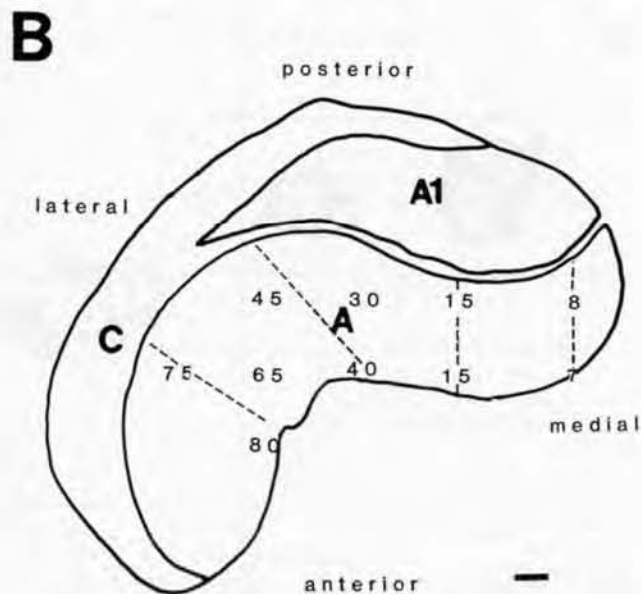


Fig. 9. A. Horizontal section approximately midway from top to bottom in the LGN. This section has been stained by a Nissl method. A₁, inner leaflet of lamina A; A₀, outer leaflet of lamina A; A₁, lamina A₁; C, C laminae. B. Azimuth values recorded along the zero elevation in the exper-



iment illustrated in Figure 7 have been superimposed on a drawing of the section in A. Dashed lines, isoazimuths; A, lamina A; A₁, lamina A₁; C, C laminae. Scale bar = 100 μ m.

in the lower penetration. The 10° jump in elevation recorded when the electrode passed from lamina A₁ to lamina A does not reflect an error in correcting for misalignment of the eyes; no such discontinuity is observed in crossing from contralaterally innervated lamina C to lamina A₁.

Extent of visual field. The range of azimuths encountered for the contralateral eye was from -2° to +125°, while elevations ranged from -45° to +45°. It is likely that more inferior fields are represented in the ferret LGN. We were unable to map the most ventral portion of the LGN, as our stereotaxic apparatus obscured the most inferior visual field. Fields of the ipsilateral eye had azimuths ranging from -5° to +30°. Elevations of receptive fields for sites in lamina A₁ ranged from +15° to -25°.

DISCUSSION

The LGN of the ferret contains a single orderly map of the contralateral visual hemifield. Microelectrode recordings of multiunit activity in the LGN reveal that the upper visual field is represented dorsally and rostrally in the nucleus, central receptive fields are found in the medial and caudal sections of the LGN, and peripheral fields are represented in the lateral LGN.

Comparison with cat

The organization of the ferret LGN may be compared to that of the more widely studied cat LGN: the ferret map would become like the cat map if the ferret's right LGN were rotated approximately 110° clockwise, as viewed from its medial aspect, in a parasagittal plane. (Compare Fig. 6 of Sanderson, 1971, with Fig. 8 here.) The ferret, having more laterally placed eyes, does not have as large a binocular representation of the visual field as does the cat. The volume of ipsilaterally innervated territory was between an eighth and a fifth of that innervated by the contralateral

eye. Ipsilateral recording sites in lamina A₁ had receptive fields with azimuths as far as 30° from the vertical meridian in the upper visual fields, and as far as 20° at the horizontal meridian, a much less extensive ipsilateral representation than in the cat. Ipsilateral sites in the cat LGN have been reported to have azimuths as far as 40° from the vertical meridian (Sanderson, '71). The visual field map is continuous between the LGN and PGN in the ferret, as in the cat (Sanderson, '71). Although sublamination of the A laminae into leaflets has not been described in the cat, a partial stratification of OFF responses has been reported (Bowling, '83). As in the ferret (Stryker and Zahs, '83) and the mink (LeVay and McConnell, '82), OFF responses are concentrated in the outer (nearer the optic tract) half of the geniculate laminae.

Planes of section

The three standard planes of section are each useful for observing some aspect of geniculate organization. Although the laminar organization of the nucleus is obscure in coronal section, this plane is the most useful for viewing the pattern of isoazimuth and isoelevation lines representing a large part of the visual field. Lamination is easily seen when the LGN is sectioned parasagittally or horizontally. The parasagittal plane is also the most useful for observing the pattern of isoelevation lines relative to the laminae. Isoazimuths are oriented normal to the laminar boundaries when the nucleus is viewed in horizontal section. However, this plane is not useful for histological reconstruction after electrophysiological studies.

Orienting the neurophysiologist

The summary map presented in Figure 6 and the data from the experiment illustrated in Figure 7 should aid in locating the position of a site being recorded in the LGN.

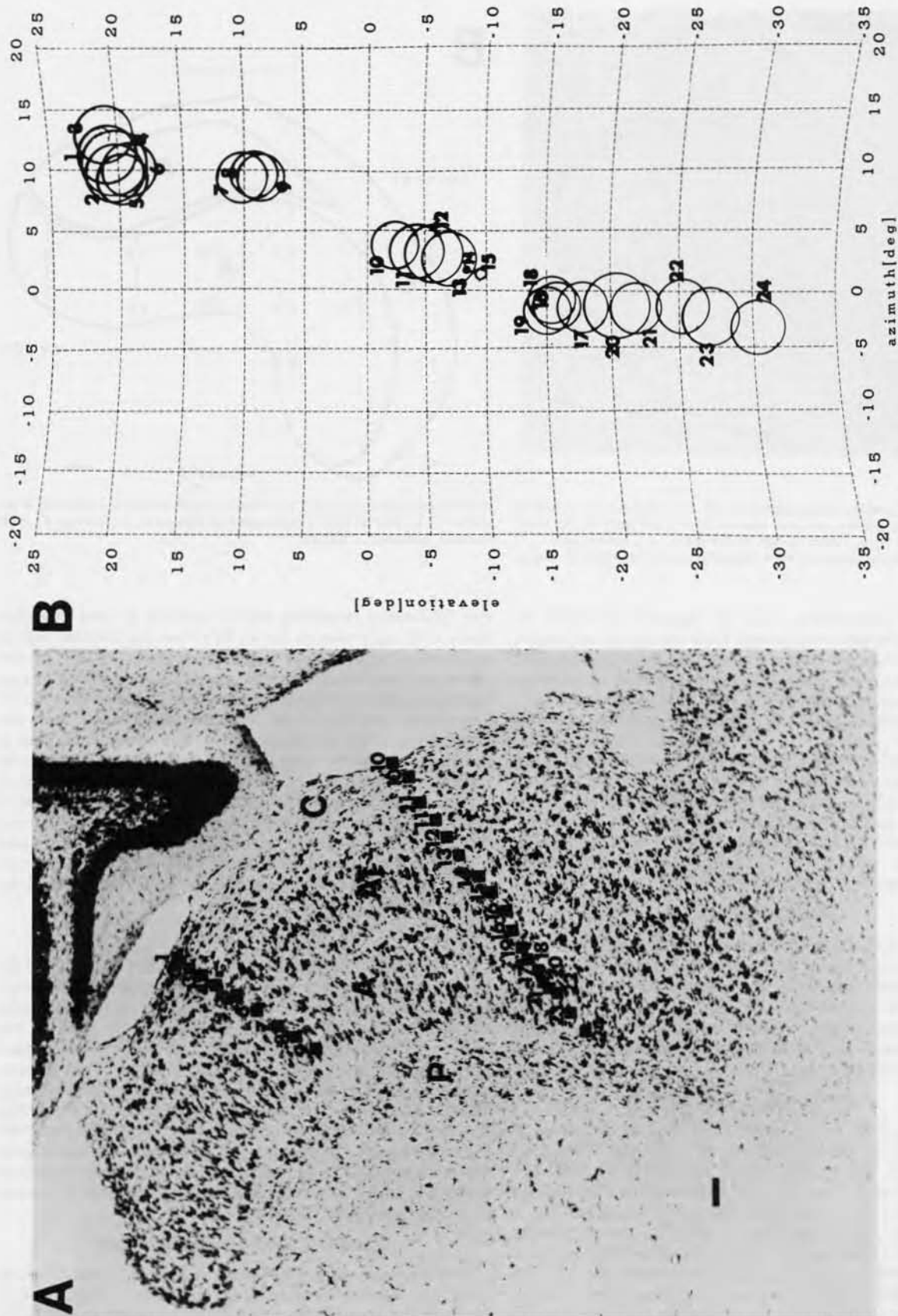


Fig. 10. Lines of projection run perpendicular to the geniculate laminae. in (B) were recorded. Dorsal is up, anterior is to the left in this section. B. A parasagittal section containing two penetrations angled approximately 40° from the vertical. The upper penetration falls approximately along a line of projection. Numbers indicate the sites from which the fields shown in (B) were recorded. Dorsal is up, anterior is to the left in this section. B. receptive field positions recorded at the sites marked on the section in A. Scale bar = 100 μ m.

Stereotaxic coordinates in these figures apply to female ferrets (700–800 g); we do not know by how much they would differ in the larger male animals. The precise position of the electrode along a line of projection may be determined by noting the eye preference and center-type of the receptive field. OFF-center receptive fields recorded through the ipsilateral eye are found in the outer leaflet of lamina A1 and ON-center ipsilateral fields map to the inner leaflet of A1. OFF-center contralateral fields are recorded in the outer leaflet of lamina A, and ON-center contralateral fields are found in the inner leaflet of lamina A (Stryker and Zahs, '83). The C laminae may be recognized by the high spontaneous activity recorded there. Optic tract fibres may contribute much of the high spontaneous activity evident in multi-unit recordings. Electrode penetrations located medial to the laminar LGN may encounter the medial interlaminar nucleus. Recording sites in the MIN are characterized by large multi-unit receptive fields, the borders of which are difficult to define using flashing or moving spots of light. The perigeniculate nucleus is located just rostral to the LGN. Although the visual field map is continuous between the LGN and the PGN, there should be no difficulty in determining when an electrode has passed from one nucleus to the other. Multi-unit responses recorded in the PGN are less vigorous than those recorded in the LGN, and responses in the PGN can be elicited through either eye.

Spatial and temporal response properties

As has been noted previously (Stryker and Zahs, '83), many cells in the A laminae often exhibited extremely tonic, X-like (Sherman, '82) responses to light stimuli flashed in their receptive fields. Other cells, usually encountered in the C laminae, had Y-like transient responses to such stimuli. Vitek et al. ('85) have found cells resembling the alpha, beta, and gamma cells of the cat in the ferret's retina. It is likely that, as in the cat, the different geniculate response properties reflect input from the different ganglion cell classes. The present mapping study, however, based primarily on multi-unit responses, sheds little light on the organization of these response properties within the LGN.

Retinal magnification and relation of the visual field meridians to the retinal axes

The optical magnification of the visual field onto the retina would be determined most directly by relating retinal recording sites to their receptive fields. In the absence of such information, we have estimated this value to be 12.4°/mm by comparing the angular separation between the optic disc projection and the estimated fixation point (31°) to the distance between the optic disc and area centralis measured on retinal whole mounts (2.4 mm and 2.8 mm, Cucchiario, '84; and 2.0 mm and 2.8 mm, Vitek et al., '85).

Our estimate of the elevation of the fixation point depends on the elevations of the smallest receptive fields. This estimate is subject to error because the size of central fields did not change dramatically with elevation (for example, see Fig. 4). However, our estimate of the fixation point elevation is supported by two observations. First, this determination of the zero elevation, in relation to the elevation of the projection of the optic disc, was consistent from animal to animal. Second, from an analysis of retinal whole-mounts retrogradely labelled by injections of HRP into the

LGN, Vitek et al. ('85) have demonstrated that in the ferret, as in the cat, the line connecting area centralis to the optic disc makes an angle of 112° with the line of decussation. The line connecting our estimate of the fixation point and the projection of the optic disc is inclined at 96° to the vertical. If this estimate of the fixation point is correct, then the results of Vitek et al. indicate that the line of decussation should be projected to an angle of 16° (112–96°) to the vertical. Such an inclined projection of the line of decussation is consistent with our finding that the most medial receptive fields within the LGN formed an angle of between 10 and 20° with the vertical (for example, see Fig. 4).

We have not been able to estimate the angle that the vertical meridian makes with a vertical line passing through the fixation point. To determine this would require measurement of the horizontal separation between the two receptive fields of binocular recording sites at extremes in the upper and lower fields. In these experiments focusing on the LGN, so few binocular receptive fields at extreme elevations were encountered that this determination was not possible.

Bridges

An unexpected finding in this and an earlier study (Stryker and Zahs, '83) was the occurrence of discontinuities in the ipsilateral projection onto lamina A1 and the contralateral projection onto lamina C. We were previously unable to determine whether such discontinuities were artifacts due to incomplete labelling of or damage to the retinal ganglion cells that would have supplied input to the unlabelled areas. In the present study, sections from the double-labelled animal allowed us to observe bridges of label from the contralateral eye spanning these gaps in the ipsilateral innervation of lamina A1. Similarly, bridges of label between laminae A1 and C1 were seen to fill the gaps in the contralateral innervation of lamina C. These findings make it clear that the results from single-labelled animals were not artifactual. Instead, genuine malformations of a smooth geniculate laminar pattern, reminiscent of, but much less pronounced than, those resulting from the Siamese and other pigment abnormalities (Guillery, '69; Guillery and Kaas, '71; Shatz, '77; Cucchiario and Guillery, '82), are a fairly common feature in the normally pigmented ferret.

Whatever the source of such irregularities in laminar pattern, the invariable outcome appears to be a strict segregation of the terminal fields of ipsilateral and contralateral eye afferents. Such an outcome suggests that the developmental mechanism responsible for the segregation of the two eyes' afferents operates more powerfully than any mechanism that tends to confine each eye's afferent terminals to particular laminae of the LGN.

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