Multiple Projection of the Visual Field to the Medial Portion of the Dorsal Lateral Geniculate Nucleus and the Adjacent Nuclei of the Thalamus of the Cat

W. J. KINSTON, M. A. VADAS AND P. O. BISHOP [1]
Brain Research Unit, Department of Physiology, University of Sydney, Sydney, Australia

ABSTRACT   The organization in the cat of the projection of the visual field onto the medial part of the central half of dorsal lateral geniculate nucleus (LGNd), the medial interlaminar nucleus (MIN) and the posterior nucleus of the thalamus (PN) has been studied by systematically plotting the receptive fields of single units isolated in the nuclei by tungsten microelectrodes. Using a grid of verticals (azimuth) and horizontals (elevation), projection maps were prepared by locating the recording sites of the units in serial histological sections. We have plotted three separate but related topographical projections of the visual field, one in each nucleus. Particular attention was paid to the projection of the visual axis in the LGNd. With the possible exception of the upper periphery, the whole of the visual field is represented in the MIN, the topographical organization with respect to azimuths being the mirror-image of that in the LGNd. There were very few binocularly activated units in the MIN and no evidence was found of a laminar segregation of crossed and uncrossed optic tract terminals. The topographical projection onto the PN resembled that in the MIN except that the upper visual field was even more restricted and the organization of azimuth values was again reversed such that the central visual field projected inferomedially and the peripheral field dorsolaterally. In all three nuclei a naso-temporal overlap was found with receptive fields located across the midline in the ipsilateral hemifield for about 2° in the case of LGNd units and 6° or more in the case of the MIN and PN. Some observations are made on visually active units in the lateral posterior nucleus of the thalamus and the pulvinar, many responding binocularly.

As early as 1927 Overbosch had examined the topographical projection of the retina on the lateral geniculate nucleus in the cat using anatomical methods. However the first precise, though still partial, description of the projection of the visual field on the nucleus of this animal was made by Bishop, Kozak, Levick and Vakkur ('62) who systematically plotted the visual directions of receptive fields of single geniculate neurons. While they described the main features of the projection, the complexities of the posteromedial aspect of the nucleus remained largely unexplored. Seneviratne and Whitteridge ('62) and Bishop ('65), while recording the activity of single units in the lateral geniculate nucleus found a second mirror-image representation of the visual field at the medial edge of the nucleus in a part which they assumed to be identical with the medial interlaminar nucleus (MIN). Much earlier the MIN had been identified in the cat by

Thuma ('28) and so named because it seemed continuous with, and similar to, the central interlaminar nucleus (CIN). The latter comprises the two layers of scattered large cells between the laminae of the main dorsal nucleus. The MIN was later described in detail by Hayhow ('58) who first clearly established the nucleus as receiving optic tract terminals. He thought the pattern of terminal degeneration which follows unilateral eye nucleation gave evidence of a trilaminated organization of the cells. While he recognized its relation to the CIN, Hayhow nevertheless considered the MIN as a relatively independent accessory pars dorsalis. As mentioned above electrophysiological studies first brought to light the possibility that there was a separate topographically organized projection of the retina on the MIN. These electrophysio-

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[1] Present address: Department of Physiology, John Curtin School of Medical Research, Australian National University, Canberra, A.C.T., Australia.

logical observations have subsequently been confirmed by anatomical studies (Garey, '65; Stone and Hansen, '66; Laties and Sprague, '66; Garey and Powell, '68). Degeneration following focal retinal lesions makes it clear that the MIN receives a topographical projection from the retina independent of that to the dorsal lateral geniculate nucleus (LGNd) and that it is anatomically a cellular entity distinct from the central interlaminar nucleus.

To date there has been no systematic study of the projection of the visual field either onto the medial portion of the LGNd in the cat or onto the adjacent nuclei of the lateral thalamus. The present paper aims to remedy this deficiency. We have paid particular attention to the projection of the visual axis onto the LGNd and the details of the projection of the visual field onto the MIN. In addition we have established that the posterior nucleus of the thalamus (PN) also receives a separate and distinct topographical projection of the visual field. We have also made some preliminary observations on the pulvinar and lateral posterior nucleus of the thalamus both of which have at various times been implicated as visual centers.

The posterior nucleus was first differentiated from the pulvinar in the carnivore by Rioch ('29) and subsequently described in the cat by Ingram, Hannett and Ranson ('32) as a wedge-shaped mass of cells lying in the angle between the two geniculate bodies. Using the terminology of the latter authors, the form and general relations of the nucleus have been well illustrated by Jimenez-Castellanos ('49), Jasper and Ajmone-Marsen ('54) and Laties and Sprague ('66). Although recognised for many years as a distinct nucleus, the PN, as an entity, has either been largely ignored by the experimentalists or tacitly included with other thalamic nuclei. Laties and Sprague ('66) however make it clear that this nucleus does not receive terminals from the optic tract (cf. also, Hayhow, '58; Singleton and Peele, '65; Garey and Powell, '68). The PN probably has its principal input by relay from the lateral geniculate nucleus (cf. reviews by Meikle and Sprague, '64; Buser and Bignall, '67). The evidence on this point is however difficult to evaluate because reference is rarely

made to the PN and when discussing this region authors commonly use expressions such as "structures just medial to the lateral geniculate nucleus."

Terminology and Abbreviations

The term dorsal lateral geniculate nucleus is usually used to include the medial interlaminar nucleus. In view of the distinctive nature of the latter nucleus however it is more convenient to exclude it from the dorsal nucleus. The following are the abbrevations used in this paper:

LGNd, the dorsal lateral geniculate nucleus excluding the MIN
LGNv, the ventral lateral geniculate nucleus
MIN, the medial interlaminar nucleus
CIN, the central interlaminar nucleus
PN, the posterior nucleus of the thalamus
LP, the lateral-posterior nucleus of the thalamus
Pul, pulvinar
OT, optic tract

METHODS

Cats (36 in number; 2.5–4 Kg weight) were anaesthetized by one of three different methods:

1. Ether for the initial surgical preparation followed by N_2O/O_2 (70%/30%) for the duration of the experimental procedures.

2. Sodium pentobarbitone (Sagatal, May and Baker; 25 mg/Kg injected intraperitoneally) during the initial procedures followed by a continuous intravenous infusion of sodium pentobarbitone (1.34 mg/kg per hour) for the duration of the experiment.

3. Chloralose (70 mg/kg) injected intraperitoneally in aqueous solution followed by intravenous injections of chloralose in carbowax (20 mg/kg) every two hours.

The headholder aligned the cat's head with respect to Horsley-Clarke (H–C) reference planes in such a way as not to obstruct the visual field. Under these circumstances the visual axes of the paralyzed eyes are inclined at an angle of 12.5° to the H–C horizontal (Bishop, Kozak and Vakkur, '62b). (In experiments subsequent to those reported here, analysis has been greatly simplified by tilting the H–C horizontal of the stereotaxic apparatus 12.5° so as to make the visual axis approximately horizontal.) A craniotomy about 1 cm² was made over the region of the left lateral

geniculate nucleus and the dura removed. A wall of acrylic dental cement was placed around the craniotomy but spaced some little distance back from the actual opening. The hollow thus formed was filled with a gel of 5% agar in saline to diminish brain pulsations. The thoracic cage was suspended by a clamp attached to a vertebral spine. The cat's temperature was maintained at 38.5°C by means of an electric heating blanket controlled by a rectal thermistor. The corneas were protected with plastic contact lenses of zero power. The eye lids and nictitating membranes were retracted with phenylephrine (10%) and the pupils dilated with atropine. A small tangent screen attached to the perimeter arm was located at 0.5 meter in front of the nodal points and the eyes were focussed on it by means of lenses determined by retinoscopy. Positive lenses (1 to 4D) were generally required.

Eye movements were almost entirely prevented by complete paralysis of the animal coupled with bilateral cervical sympathectomy (Rodieck, Pettigrew, Bishop and Nikara, '67). Paralysis was achieved by an initial intravenous injection of 80 mg gallamine triethiodide (Flaxedil; May and Baker) followed by a continuous intravenous infusion of Flaxedil (14 mg/hour) and d-tubocurarine (2.8 mg/hour) in normal saline (5.8 ml/hour). In later experiments (see Results) the initial paralysis was achieved by intravenous injection of 40 mg/kg Flaxedil followed by 200 μg/kg toxiferine with the paralysis being maintained by a continuous intravenous infusion of Flaxedil (25 mg/hour) and toxiferine (0.75 mg/hour) in normal saline (10 ml/hour). The paralysis entailed artificial respiration.

Single units were extracellularly recorded by tungsten microelectrodes made by a method based on that of Hubel ('57). It is difficult to determine the course of microelectrodes in brain sections unless the electrodes are straight and inserted along known (Horsley-Clarke) planes. Straight microelectrodes were produced by preliminary slight stretching of the heated tungsten wire. The general methods used in determining the projection of the visual fields were very similar to those of Bishop, Kozak, Levick and Vakkur ('62). The receptive fields were plotted on a small tangent screen borne on the arm of an adjustable perimeter (Kozak, Rodieck and Mears, '63). In this way the visual direction of the receptive fields was determined directly at the time of the experiment in terms of the two angles, azimuth and elevation, of the system of spherical polar coordinates described in detail by Bishop, Kozak and Vakkur ('62). The line of sight of the receptive field was taken as the line passing through the geometrical center of the field and the nodal point of the eye. The two angles of the coordinate system are defined as follows:

Azimuth is the angle between the projection of a given line of sight on the presumed fixation plane and the presumed visual axis (positive to the right, negative to the left of the visual axis).

Elevation is the angle between a given line of sight and the presumed fixation plane (positive upwards, negative downwards from the presumed fixation plane).

The perimeter arm was mounted on a lateral shift plate by which it was easy to make the center of curvature of the arm coincide with the nodal point of one or or other eye depending upon the laterality of the receptive field under study. In each experiment the perimeter arm was also adjusted so that the zeros of the azimuth and elevation scales coincided with the estimated direction of the visual axis for the particular eye.

At the end of each experiment the brain was perfused with 10% formalin in normal saline. After sufficient hardening in situ the brain was removed and placed in a specially-devised guillotine-like instrument. The latter enabled a block of tissue containing the relevant nuclei to be removed by sectioning the brain in appropriate H-C coronal planes. By having the anterior and posterior surfaces of the block cut accurately in H-C coronal planes, the subsequent histological sections could also be made in H-C coronal planes. In this way the microelectrode tracks were restricted to the minimum number of histological sections since, in the course of the experiment, the tracks had been carefully restricted to distinct coronal planes. The blocks were embedded in celloidin, sectioned at 30 μ and the sections deeply

stained with cresyl violet to display the course of the electrodes in relation to the various nuclei.

RESULTS

Figure 1, A and B shows an artist's impression of the shape and mutual relationships of the three nuclei (LGNd, MIN and PN) on the left side, the group being viewed from the anteromedial (A) and the inferomedial (B) aspects. The coronal sections (C and D), taken slightly behind the centre of the LGNd, show some of the relationships of the nuclei in more precise detail. Some idea of the dimensions of the nuclei is given by the semi-diagrammatic plan view in figure 2. However an accurate appreciation of their size and shape can only be obtained by studying serial sections in the three planes at right angles such as those provided by Laties and Sprague ('66) with respect to the LGNd and MIN. The latter is of irregular shape and, though broad in plan view because of its oblique position, is nevertheless relatively thin in the inferomedial to dorsolateral direction. The PN lies along and partly beneath the medial side of the MIN, the latter being distinguished by the large size of its cells. On its medial side, the PN is, in turn, bounded by the lateral posterior nucleus (LP) and superomedially by the pulvinar (Pul). Anteriorly and without sharp demarcation, the PN is continuous with the pulvinar. There are significant individual variations in the size and position of the nuclei and in many animals their borders are indistinct. This is particularly true of the borders between the MIN and layer B of the LGNd on the one hand and between the PN and medial thalamus on the other. Fortunately the boundary between the MIN and PN was usually fairly well defined.

Residual eye movements during paralysis

Much of this study is concerned with the region of the visual field close to the visual axis. In man the visual acuity in the center of gaze is a measure of the fineness of the grain of the visual field in the vicinity of the visual axis and projection maps of this region will require a correspondingly fine spacing of the lines of the coordinate grid. An important factor which may limit the accuracy of our projection maps is residual eye movement in relation to the fixed perimeter screen on which the receptive fields were plotted. The details of the organization of the projection may easily be obscured by uncontrolled eye movement especially since we have found it necessary to consider grid lines 1° or less apart. Paralysis of the extraocular muscles by Flaxedil is much less effective under nitrous oxide anaesthesia than it is under barbiturate anaesthesia (Rodieck et al., '67). A marked reduction in residual eye movements can be achieved by bilateral cervical sympathectomy and the use of a mixture of Flaxedil and d-tubocurarine (Rodieck et al., '67).

Partly in an effort to reduce residual eye movements still farther and partly to find a suitable substitute for d-tubocurarine which causes hypotension through histamine release, we tried C-toxiferine-I (toxiferine dichloride). Toxiferine is a natural alkaloid isolated from calabash curare. Though without side effects, it is not used in man because it has such a potent and long-lasting action on the neuromuscular junction (Foldes, Brown, Lunn, Moore and Duncalf, '63). In cats we observed no fall in blood pressure even when 30 to 40 times the normal paralyzing dose was administered. We investigated the effectiveness of toxiferine in respect to residual eye movements by the methods of Rodieck et al. ('67). Light beams were reflected from mirrors firmly attached to the corneas, the eye movements being plotted on

Fig. 1 A and B Artist's impression of the general form and relationship of the three nuclei: dorsal lateral geniculate nucleus (LGNd), medial interlaminar nucleus (MIN) and posterior nucleus of the thalamus (PN). A Left nuclear group viewed from the anterior and medial aspect; B The same viewed from a medial and antero-inferior aspect. C Coronal map of Horsley-Clarke (H-C) anterior 6.0 modified with permission from Jasper and Ajmone-Marsan ('54) to show the relationship of the nuclei to the rest of the diencephalon. Pul, pulvinar; LP, lateral posterior nucleus; GM, medial geniculate nucleus; OT, optic tract; LGNv, ventral lateral geniculate nucleus. D Coronal plane at approximately H-C anterior 5.5 modified with permission from Laties and Sprague ('66). CIN, central interlaminar nucleus (ventral portion); NPG, nucleus perigeniculatus anterior.
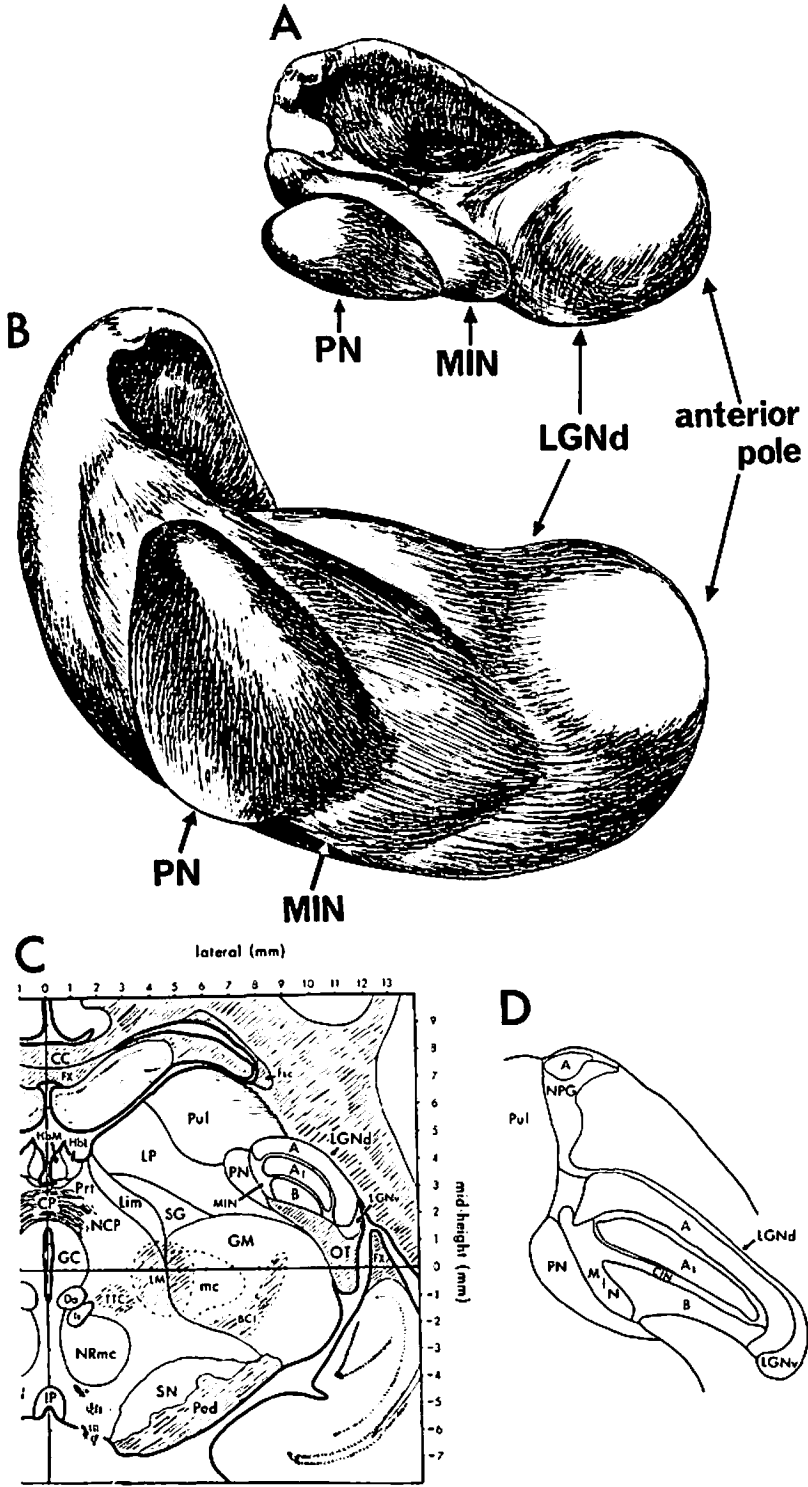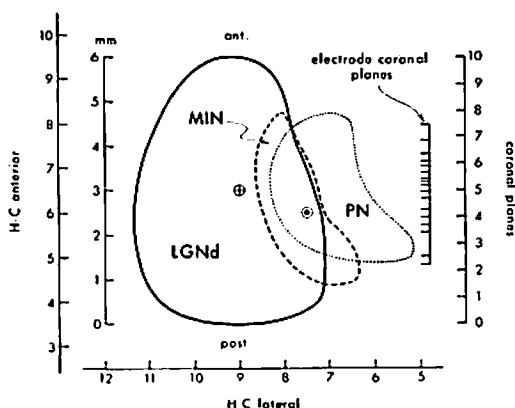
Figure 1

Fig. 2 Semi-diagrammatic plan view of the three nuclei — LGNd, MIN and PN — showing their form and general relation one to another (millimeter and coronal scales) and their position in the brain (Horsley-Clarke anterior and lateral scales). The coronal scale (0–10) arbitrarily subdivides the LGNd into planes to enable comparisons to be made between the nucleus in one animal and that in another. The approximate positions of the coronal planes that were explored are indicated to show the extent of the microelectrode sampling in the series of experiments reported in this paper. ⊕ — The site of the standard initial exploratory electrode track at approximately the midpoint of the LGNd. ⊙ — Approximate position of the projection of the visual axis in the LGNd (H-C Anterior 6.0, Lateral 7.5).

a screen at four meters in front of the animal. Toxiferine is clearly preferable to d-tubocurarine not only because of its greater potency but also because of the absence of side effects. Used in conjunction with Flaxedil and bilateral cervical sympathectomy (see Methods) we found that, over a three hour period, the total range of eye movements was less than ten minute arc. The effectiveness of the toxiferine mixture over longer periods has been studied by Nikara, Bishop and Pettigrew ('68). They showed that the distribution of the scatter of residual movements in the one eye about a mean position has a standard deviation of about 0.2° for periods of paralysis of up to 30 hours or more with no significant difference between the vertical and horizontal directions. These observations have been confirmed by later studies (D. E. Joshua and P. O. Bishop — unpublished observations) atlhough an hour or more of paralysis is necessary before the eye settles to its final relatively

stable position. The use of toxiferine as the sole paralyzing agent did not give good results. We also tested diallynortoxiferine (Alloferin-Roche) which is more suitable for use in man than toxiferine (Foldes et al., '63). Our experiments show that Alloferin is comparable to d-tubocurarine in eliminating residual eye movements and is without the hypotensive effect of the latter drug.

Effects of anaesthesia

The first experiments were carried out under barbiturate anaesthesia. However visual field projections to regions of the thalamus medially adjacent to the LGNd almost certainly involve synaptic relays beyond the primary optic afferents and it was essential to consider whether these synapses might be especially susceptible to barbiturate anaesthesia. Since investigators searching for extralemniscal pathways to the thalamus have favoured chloralose anaesthesia (e.g. Buser and Borenstein, '59) a series of experiments was carried out using chloralose. The majority of the experiments were however carried out under nitrous oxide which was found to be less depressant than either sodium pentobarbitone or chloralose. While we observed characteristic differences between the neural discharges with the various anaesthetic procedures we did not attempt a systematic analysis of these differences. The nature of the visual field projections on the various nuclei however seemed independent of the particular anaesthetic agent.

Outline of typical experiment

The cat having been aligned in the stereotaxic apparatus in front of the one meter tangent screen and due time allowed for the paralyzed eyes to settle, the optic discs were projected to blind spots on the screen. Using data from previous studies (Bishop, Kozak and Vakkur, '62; Vakkur, Bishop and Kozak, '63), the direction of the visual axis for each eye was then estimated from the position of the respective blind spot. The blind spots were plotted several times during the course of the experiments so that due allowance could be made for any movements that might occur. Towards the end of the series of ex-

periments, the data of Leicester ('68) and Nikara et al. ('68) became available to provide a more accurate estimate of the location of the zero (vertical) meridian. On a one meter tangent screen with the visual axis in a H-C horizontal plane, they showed that the mean value of the horizontal distance of the zero meridian from the blind spot was 28.2 cm (15.8°). The vertical distance from the zero horizontal to the line joining the blind spot centers was taken to be 13 cm (7.4°). The visual axis of the paralyzed eye diverges from the straight ahead by a mean angle of 2° but as this value is very variable (Nikara et al., '68) we have always estimated the direction of the visual axis from the position of the blind spot. The earlier data in the present series of experiments were then recalculated to take account of these new measurements. After the blind spots had been plotted the perimeter was swung into place in front of the cat and the arm adjusted so that the zeros of the azimuth and elevation scales coincided with the estimated direction of the visual axis. Separate adjustments had to be made for each eye but these were readily made during the course of the experiment as the laterality of the receptive field required.

The aim of these experiments was to explore the medial 1–2 mm of the LGNd proper together with the immediately adjacent thalamic nuclei likely to have a fairly direct visual input. Since the MIN and PN are both very small nuclei each having a medio-lateral extent of about 1 mm, it was essential that the electrode tracks be carefully planned and optimally located. It was decided to space the electrode tracks a minimum of 0.3 mm apart after earlier experiments had shown that closer spacing led to difficulties in histological identification and increased the likelihood of damage from one electrode track affecting the responses from the next adjacent to it. This meant that in the one coronal plane, only two or possibly three electrode tracks could penetrate each nucleus. In general only one coronal plane was examined in each experiment. In these experiments, systematic study has been restricted to coronal planes that lay between the anterior and posterior extremities of the MIN, figure 2 indicating

the relative positions of all the coronal planes that were sampled by our electrodes. Except for their posterior extremities, both the MIN and PN have been well covered.

After the microelectrode tip had been adjusted to a known set of H-C coordinates, an exploratory track was directed at approximately the mid point of the LGNd (H-C anterior, 6.5; lateral, 9.0). As the electrode was moved through the brain a diffuse flashing light produced a characteristic geniculate "swish" over the loudspeaker at a H-C basi-height of about 15 mm. The electrode was correctly placed if, within the next 2 mm, the electrode recorded units whose receptive fields had azimuths of about + 5° to + 10° and elevations of about 0 to − 5°. Depending upon the evidence provided by this exploratory probe, a coronal plane was selected and recording begun along a track located about 1.5 mm lateral to the medial edge of the LGNd proper. A further twelve or more tracks were then made progressively more medial, usually in steps of 0.3 mm, until two in succession failed to yield significant visual activity. Typically about 70 single units were examined in each experiment. The type of electrode used meant that the background or "swish" response to a flashing light came from a relatively small number of units. However the swish response was of value in marking the transition from nonvisual to visual areas and in helping to define, in the case of the LGNd, the A/A_1 and B/OT transitions. There was however little indication of the transitions from LGNd to MIN to PN. Departure inferiorly from both the MIN and PN was usually evident but the medial edge of PN was poorly defined both electrophysiologically and histologically. Tracks in the pulvinar and lateral posterior nucleus did not produce a swish response. Since the electrode tracks were contained within a few consecutive histological sections it was easy to include them in a composite outline drawing of the relevant nuclei using a microprojector. Before the electrophysiological data could be added to the histological maps it was necessary to determine the levels of the nuclear outlines along the electrode tracks. Particular use was made

of the data obtained from the medial third of the LGNd where the general organization was already known (Bishop, Kozak, Levick, Vakkur, '62; Bishop, '65) and the landmarks (e.g., laminae) are fairly clear-cut. While preserving the relative levels of the units along their respective electrode tracks, their positions were superimposed on the outline of the LGNd on the basis of the "swish" response to a flashing light and with the contralateral and ipsilateral units falling on their respective laminae. Isoazimuth and isoelevation lines were drawn on the maps by joining units with the same azimuths and elevations respectively. Such a line was, however, drawn only when no unit had values which contradicted it. In some cases extrapolations were made such as passing a 3° line between units with values of 2° and 4°. The location of the coronal plane with respect to the anterior and posterior poles of the LGNd were determined by counting the histological sections. It is important to appreciate that, in the various figures illustrating this paper, the values for the coronal planes refer to the posterior pole of the LGNd along a 0–10 scale and are *not* H-C coronal values.

Some general observations

Eye laterality. The distribution of contralateral and ipsilateral units within each of the three nuclei, LGNd, MIN and PN, was approximately the same, about 75% of the units being activated by the contralateral eye (fig. 6). Within the MIN the contralateral and ipsilateral units tended to occur in separate groups but the groups themselves seemed to be randomly distributed throughout the nucleus. We found no evidence for the trilaminar pattern in the MIN as suggested by Hayhow ('58) and supported by later anatomical studies (Stone and Hansen, '66; Laties and Sprague, '66; Garey and Powell, '68).

Binocular units. Under 2% (5 in 352) of the units in the medial third of the LGNd could be activated from either eye and all but one of these units lay in the CIN. The locations of the binocular receptive fields were in keeping with those of adjacent monocular fields so that the

visual field co-ordinate grid passes across the interlaminar zone without distortion. Except for one experiment (fig. 9), about 2% (4 in 196) of the units in the MIN and PN taken together were binocular. At least 25% of the units in the Pul and LP showed evidence of binocular activity and many of these were clearly directionally-selective in their response to moving stimuli. The preparation illustrated in figure 9 was quite unusual in that 14 binocular units were recorded in two tracks that passed through Pul, PN and LP. The receptive fields were however difficult to localize accurately and the stimulus requirements were more specialized than was the case with units in the LGNd. The explanation for these findings may be related to the chloralose anesthesia.

Receptive field properties. No systematic attempt was made to study the properties of the receptive fields and they were only rarely examined in any detail. No obvious difference was found between the properties of MIN units and those in the LGNd proper so that the properties provided no clue to the location of the units. Passing medially into PN and LP and Pul it became progressively more difficult to activate the units and to define a receptive field.

Units in the lateral part of the LGNd have peripherally located receptive fields which tend to be larger than those in the center. We concentrated on the medial third of the LGNd and here we found that the units had small receptive fields (2° or less across) exect in lamina B where a few units had fields larger than 3°. In general the receptive fields got larger as we passed through the laminae: commonly less than 0.5° in lamina A, about 0.5° for lamina A_1 and commonly 1 to 2° for layer B. A majority of the units in the MIN and PN had receptive fields of 2° or more, an observation to be associated with the fact that a large number of these fields lie much more peripherally than is the case with units in the medial third of the LGNd. Centrally-located receptive fields of MIN units had small receptive fields similar to those in the adjacent LGNd.

The projection of the visual field on the LGNd

The present study confirms and extends the earlier observations of Seneviratne and Whitteridge ('62), Bishop, Kozak, Levick and Vakkur ('62) and Bishop ('65). The vertical midline in the visual field (zero isoazimuth) is projected onto a roughly parasagittal plane or thin section along the medial border of the LGNd where it abuts the medial interlaminar nucleus. The more lateral parts of the visual field, having increasing azimuth values, are represented successively more and more laterally in the nucleus. The fixation plane or zero horizontal in the visual field (zero isoelevation) projects across the full width of the LGNd proper onto a thin "coronal" section centered about the junction of the posterior two-fifths and anterior three-fifths of the nucleus, the thin section passing downwards and backwards across, and roughly at right angles to, the cellular laminae. The upper parts of the visual field (positive elevations) project posteriorly in the nucleus and the lower parts (negative elevations) project anteriorly. Thus the lower part of the visual field, to which the tapetum is largely confined, has a somewhat larger representation in the nucleus than the upper field which occupies only the posterior two-fifths of the nucleus. To a rough approximation isoazimuth lines (vertical parallels) project onto parasagittal planes in the nucleus and isoelevation lines (approximately horizontal parallels) project onto coronal planes. The central visual field, corresponding to the area centralis in the retina, has proportionately a much greater representation in the nucleus than do the peripheral parts of the visual field (Bishop, Kozak, Levick and Vakkur, '62). Taking the area centralis as extending out to about 5° from the center of vision, its representation in the LGNd occupies the medial half of the nucleus and about one-third of its anteroposterior extent.

Central vision: azimuths. We paid particular attention to the region in the vicinity of the projection of the visual axis, the latter having the Horsley-Clarke coordinates centered on anterior 6.0 and lateral 7.5 (fig. 2). Figure 3 is an example of a coronal plane close to the projection of the visual axis within the LGNd. Because of the greatly expanded representation devoted to central vision, it was possible to draw isoazimuth lines separated by only only one degree or less. The locations of the units in the nucleus are indicated in figure 3 by the filled and open circles, the convention throughout this paper being that filled symbols denote contralaterally-activated units and open symbols ipsilateral ones. In most of the experiments the isoazimuth lines in the projection maps of the LGNd were approximately vertical (fig. 3), the ipsilateral units in layer A_1 having azimuth values closely similar to those of the contralateral units recorded from the immediately adjacent part of layer A above. The shape of the isoazimuth lines as they cross from lamina A to A_1 is largely dependent upon the degree to which the assumed location of the zero meridian (28.2 cm from the blind spot meridian) departs from that in the cat under consideration (cf. Nikara et al., '68). There seems to be a somewhat greater variability in the location of the receptive fields of units in layer B. While the zero meridian (vertical midline) is represented close to the medial edge of the LGNd, it is difficult to be equally precise with respect to the zero horizontal. In the first place the latter is difficult to define in relation to either the retina or the visual field (Nikara et al., '68). Furthermore electrode samplings along coronal planes are not well suited to defining anteroposterior organization particularly since, in our experiments, only one or perhaps two coronal planes were sampled in each experiment.

Central vision: elevations. The planes of isoelevation in the LGNd pass downwards and backwards across the nucleus, so that a vertically-oriented electrode in its downward path, crosses successive planes corresponding to lower and lower horizontal parallels in the visual field. This is particularly the case in the anterior part of the nucleus not only because the isoelevation planes, by conforming to the curve of the cellular laminae, tend to become more horizontal but also because of the relatively rapid changes in elevation values that occur in this region. However in the central part of the nucleus the iso-
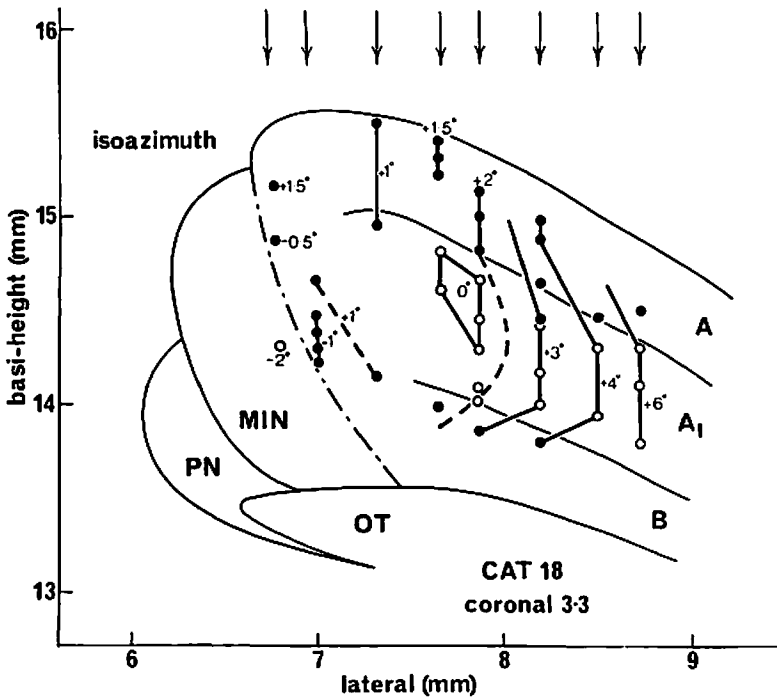
Fig. 3 Pattern of isoazimuth lines for the medial part of the LGNd in the one experiment (Cat 18) based on plots of the receptive fields of units whose locations in the nucleus are indicated by the filled (contralateral) and open (ipsilateral) circles. The portion of the LGNd shown is virtually a plane of isoelevation at + 1.5°. The vertical arrows indicate the relative positions of the electrode tracks as revealed in histological sections. The coronal plane (3.3) as specified in this and other figures refers to an arbitrary 0–10 scale. (For details see text.)

elevation planes approximate more nearly to the vertical and, in addition, only small changes in elevation values are found in successive coronal planes. Thus a much larger range of elevations are represented in anteriorly-placed coronal planes than those in the center and in the region of the projection of the area centralis each coronal plane approximates an isoelevation plane. Nearly all the elevation values of the units in the LGNd in figure 3 were within 0.5° of elevation + 1.5° so that the whole section was virtually an isoelevation plane.

Naso-temporal overlap. Figure 4 shows the location of the receptive fields of all the units in our experiments that were recorded in the medial third of the LGNd. As expected most have azimuth values within 5° of the visual axis and very few are located further out than 10°. Similarly the receptive fields have elevations that are

nearly all within 10° of the zero horizontal. It was a consistent finding that many of the receptive fields were located across the zero azimuth and up to 2° or more into the ipsilateral hemifield. This finding closely parallels a similar observation that has been made on the receptive fields of units in the striate cortex (Nikara et al., '68). It is now clear that there is a naso-temporal overlap in the retina such that the ganglion cells in a vertical strip on either side of the midline issue fibers to both optic tracts (Stone, '66) and that this strip, 1–2° across, projects to both occipital cortices independently of the corpus callosum (Leicester, '68). Our data provide an obvious link between the observations on the retina and those on the cerebral cortex. It is most unlikely that this overlap at the thalamic level results from a direct projection from the optic tract of the other side via diencephalic commis-
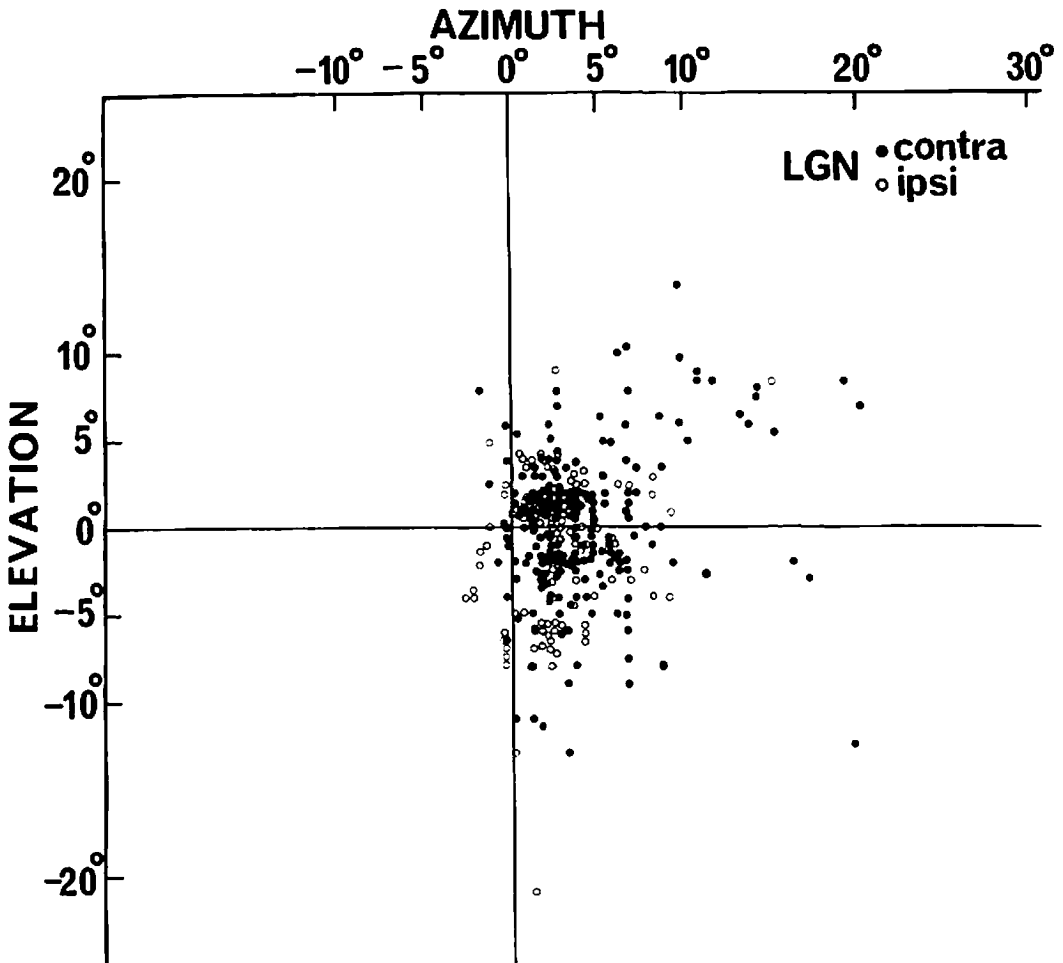
Fig. 4   Distribution in the visual field of the positions of the receptive fields of all the units recorded in this series of experiments in the medial part of the LGNd. Note the naso-temporal overlap involving contralateral and ipsilateral units about equally over the midline.

sures (Laties and Sprague, '66; Garey and Powell, '68). Since our recordings were restricted to the left LGNd the receptive fields were located in the right hemifield with a small overlap into the left hemifield. Direct evidence (Stone, '66) indicates that the strip of overlap is symmetrically located about the vertical midline (zero azimuth). Provided the sample of receptive fields is adequate, it is therefore only when the zero meridian has been correctly estimated that the receptive fields of the two eyes will be disposed equally over the midline. It can be seen from figure 4 that the medial edges of the two distributions,

ipsilateral and contralateral, are virtually coincident and both are located about the same small distance over the midline.

The medial interlaminar nucleus

The MIN is placed obliquely across the medial aspect of the LGNd (fig. 1). Towards the posterior end of the LGNd, it rises above and medial to the main laminae, A and A₁; in the central region it lies along the medial aspect of these laminae (fig. 3) and further anteriorly it passes downwards and laterally so as to lie below the medial portion of the laminae (fig. 5).
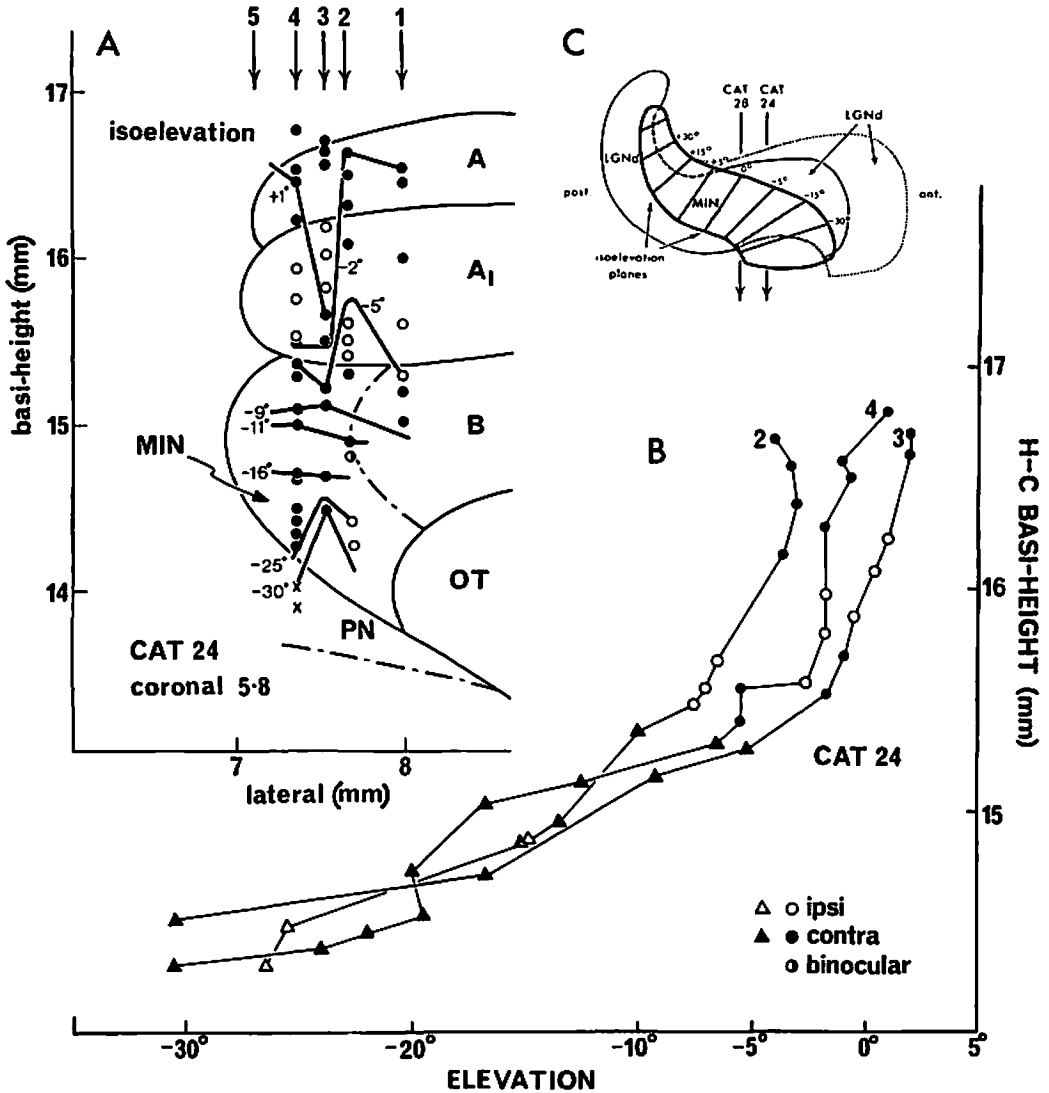
Fig. 5 A Pattern of isoelevation lines, both for the medial part of the LGNd and the MIN below it, based on plots of the receptive fields of units whose locations in the nuclei are indicated. The corresponding isoazimuth pattern is shown in figure 8A. Note the one binocular unit (half-filled circle) situated on the boundary between the MIN and layer B. X, visually active units but with indefinite receptive fields. Other symbols as for figure 3. B Elevations of receptive fields plotted against the vertical locations of their units along the electrode tracks (2, 3 or 4) in which they were recorded, showing the much greater range and rate of change of elevations for units in the MIN in comparison to those in the LGNd. C Diagram of the medial aspect of the MIN in relation to that of the LGNd, showing how the electrode tracks in Cats 28 and 24 cut successive iso-elevation planes in the MIN to give the plots of figure 5B and the patterns of figures 5A and 7.

Elevations. Figure 5 is typical of the results obtained from the anterior part of the MIN. In cat 24 (fig. 5A) three electrode penetrations were made through the MIN, the electrode in each case first traversing the laminae, A and A₁, of the LGNd. Isoelevation lines for these units have been superimposed on the map and the corresponding isoazimuth lines are shown in figure 8A. Figure 5B plots the

vertical positions along the three electrode tracks (2, 3, 4) of all the units that were recorded against the elevations of their receptive fields. It can be seen that the elevations of units in the LGNd change only very slowly in a downward direction, over a range of about 5°, as the electrode moves through the layers. On entering the MIN the elevations continue falling without any duplication of the values along any one track, but the rate of change increases markedly so that a much greater range of elevations is encompassed and hence a much greater section of the visual field is represented than in the adjacent parts of the LGNd (fig. 6). Thus in the anterior region of the MIN, the upper limit of the elevations of the units is set by elevations of the receptive fields of the lowest units in lamina A_1 close to the A_1, MIN border. In the central part of the anteroposterior extent of the MIN, where it lies medial to and on a level with the laminae of the LGNd, the upper isoelevation lines on the map are continuous horizontally straight across from the one nucleus to the other rather similar to those between the MIN and PN in figure 7. However, it is still the case that, in the lower part of the MIN where it is adjacent to layer B, the elevations fall rather more rapidly than they do in the LGNd. In the posterior part of the MIN the relationship between the two nuclei is the reverse of that which obtains anteriorly. As the electrode enters the MIN the elevations are high in the visual field but again fall with downward advance of the electrode. At first elevations fall quite rapidly but progressively more and more slowly until the electrode is on a level with the main laminae of the LGNd when they again correspond to and fall with the elevations of units in the latter nucleus. Thus the anteroposterior organization of the MIN resembles that in the LGNd except that there is greater upward and downward curling and compression of the two ends anteriorly and posteriorly respectively.

Figure 5C is a diagrammatic representation of the MIN and LGNd viewed from the medial aspect showing the oblique relationship of the MIN to its lateral neighbour. Two outlines of the LGNd are shown, the dotted outline indicating the anterior expansion of the nucleus at a more lateral parasagittal level. The change of elevations along the electrode tracks for cat 24 (fig. 5) and cat 28 (fig. 7) are indicated by the arrows and it can be seen why the pattern of change of elevations for posteriorly placed electrodes is the reverse of that for electrode penetrations in the anterior part. As in the LGNd the elevations in the MIN rise as one moves posteriorly. However, so long as the MIN is close to the medial side of the upper two laminae of the LGNd the change in elevation is small like that in the LGNd itself and rapid changes of elevation only occur anteriorly and posteriorly as the MIN moves away from these laminae.

Azimuths. A large range of azimuth values from about + 60° to − 13°, are represented in the MIN. As with the LGNd, central vision has the largest representation and relatively few units were found with receptive fields beyond about + 30° from the zero meridian. Changes in azimuth values take place predominantly in a medial direction with a progression which is the reverse of that in the LGNd, the most positive azimuths being usually the most medial. There was no evidence of an antero-posterior organization with respect to azimuth values except that in the posterior portion (positive elevations) there were no units whose receptive fields had azimuth values greater than + 20°. This is clearly evident from figure 10 which suggests that the upper visual field has a restricted representation in the MIN. While this absence, in the posterior portion of the nucleus, of units with azimuth values beyond + 20° is probably largely the result of inadequate sampling, it is nevertheless the case that the upper visual field has a relatively small representation in the MIN. In the PN the representation of the upper visual field appears to be even more restricted (fig. 10).

The fact that the whole range of azimuth values (+ 60° to − 13°; fig. 10) is projected onto the MIN over a mediolateral extent of a millimeter or even less, makes it very difficult to arrive at a clear understanding of the details of this representation. It was usually only possible to place two electrode tracks through the nucleus and these, being vertically orien-

tated, were not well suited to reveal an organization predominantly at right angles to them. Except in one or two experiments, it was generally not possible to draw a satisfactory pattern of isoazimuth lines but the general arrangement of the representation could be made out over the series of experiments. This arrangement was however clearly revealed in the experiment illustrated in figure 8B.

It can be seen that the zero isoazimuth was represented at or close to the MIN/LGNd border and that it was possible to draw successive isoazimuth lines, progressing inferomedially in the nucleus, up to an azimuth value of + 60° near the MIN/PN border. As one moves into the part of the MIN that lies below the A and A₁ laminae there is a general tendency, suggested in figure 8B and more evident in figure 8A, for the pattern of isoazimuth lines to change from the predominantly vertical arrangement characteristic of the LGNd to one that is more horizontal. Further work will be needed to make clear the details of this change as well as the pattern of azimuth values in the posterior part of the nucleus. In summary therefore low values of azimuth are found superiorly and along the lateral border of the MIN, the higher positive values being located medially and inferiorly.

Naso-temporal overlap. A striking feature of the plot of the spatial distribution of all the receptive fields of MIN units recorded in this series (fig. 10) is that many are to be found well into the ipsilateral hemifield. However, with the exception of the two units at about azimuth — 12°, all the MIN units in the ipsilateral hemifield are within about 6° of the midline, the overlap being apparently independent of the elevation. Stone ('66) found scattered ganglion cells well into the temporal retina of the left eye that survived section of the optic tract of the same side indicating that their axons crossed to the opposite optic tract. No comparable surviving cells were found in the nasal retina of the right eye. A direct correlation between our results and those of Stone is however difficult because we found a scattered population of both ipsilateral and contralateral units with receptive fields in the ipsilateral hemifield.

Posterior nucleus

With the exception of the reversal of the progression of azimuth values the general nature of the representation of the visual field in the PN is similar to that found in the MIN.

Elevations. Figure 6 shows the different ranges of elevation values encompassed within the same coronal planes for the three nuclei, LGNd, MIN and PN respectively. In the PN the elevations ranged over the lower hemifield but penetrated only 5° to 10° into the upper hemifield (fig. 10). Within this range the general organization was similar to that found in the MIN. Thus when an electrode track passes down through the MIN and into the PN, the elevation values continue falling. However with more medially-placed electrode tracks that enter the PN directly without prior passage through the MIN, the
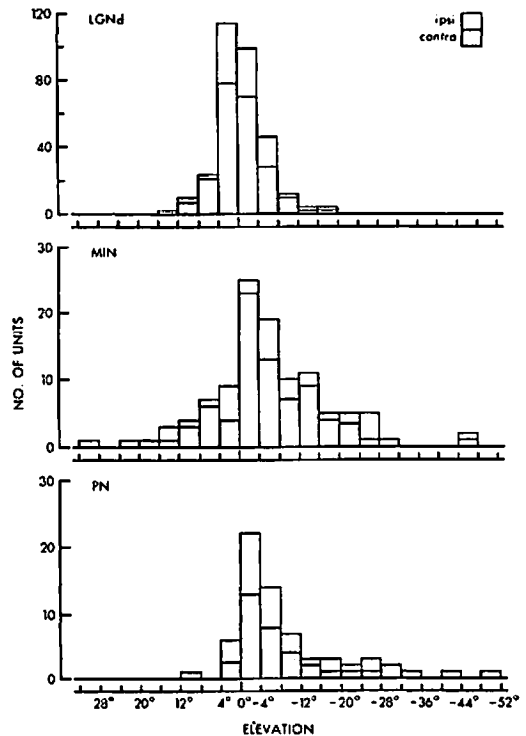

Fig. 6 Distributions of the elevations of the receptive fields of units in the three nuclei, LGNd, MIN and PN respectively, showing the relative numbers in each nucleus activated by the ipsilateral or the contralateral eye.

elevations usually begin at a level comparable to that found in the adjacent part of the MIN and then fall, in most cases fairly rapidly. Thus it is possible to draw isoelevation lines across the MIN and PN (fig. 7) joining the positions of units in the two nuclei and occasionally, when sufficient units were recorded, these isoelevation lines could be continued on more or less horizontally, into the LGNd. Cat 28 (figs. 7, 8B) was a favourable experiment in that it was possible to draw the full coordinate grid for both the PN and the MIN. There was little indication in the PN of any anteroposterior organization of elevation values. There was a singular lack of positive elevations (i.e., upper hemifield — figs. 7, 10). While this may be partly explained by deficient sampling (fig. 2) it is probably also a consequence of the relatively limited posterior extension of the PN in relation to the MIN and LGNd. Most of the upper visual field is represented posteriorly in the latter nuclei in the upward recurved portions that have no
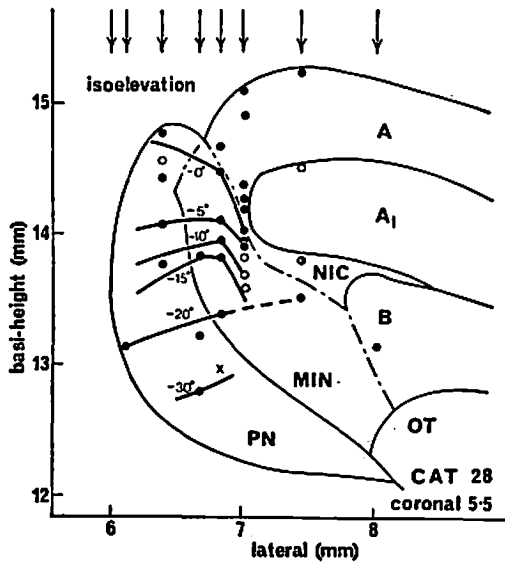
counterpart in the PN. The isoelevation lines in the PN are continuous with those in the MIN and LGNd and, over the posterior portion of the PN, there is relatively little change anteroposteriorly in the elevation values in the adjacent LGNd.

Azimuths. A large range of azimuth values is represented in the PN, taking in most of the contralateral hemifield and, across the midline, up to about 13° into the ipsilateral hemifield. For reasons already discussed in relation to the MIN, in most experiments it was not possible to draw a satisfactory pattern of isoazimuth lines. However, in two experiments (figs. 8B, 9) isoazimuth lines could be drawn with confidence. The isoazimuth lines lie parallel to the border between the PN and MIN and progressing medially across the PN the azimuth lines change from having peripheral to central values. In most experiments, along any one track passing down through the PN, there was a general tendency for negative and central azimuth values to occur before the larger positive values. The azimuth pattern in the PN therefore resembles that in the LGNd with the lateral periphery of the visual field represented in the lateral part of the nucleus and central vision represented medially. Thus there is an orderly progression of azimuth values from lateral to medial across the three nuclei as a group — peripheral to central, central to peripheral and finally peripheral to central, a progression remarkably like a mirror image of that found in the three visual areas of the cerebral cortex. Like the MIN there was no evidence of an anteroposterior organization of the azimuth values in the PN.

Naso-temporal overlap. The spatial distribution of receptive fields of PN units in the ipsilateral hemifield was similar to that of units in the MIN.

Pulvinar and lateral posterior nucleus

There was no indication from the relatively small number of receptive fields we have plotted that the visual field has a topographical representation in these nuclei. It is interesting that once again we did not plot any receptive fields in the upper peripheral field of the contralateral side. The distribution over the midline into the ipsilateral hemifield is perhaps

Fig. 7 Pattern of isoazimuth lines for the MIN and PN in the one experiment (Cat 28) based on plots of receptive fields of units whose locations in the nuclei are indicated by the filled (contralateral) and open (ipsilateral) circles. The vertical arrows indicate the relative positions of the electrode tracks. ◐ binocular unit. X, visually active unit but with indefinite receptive field.
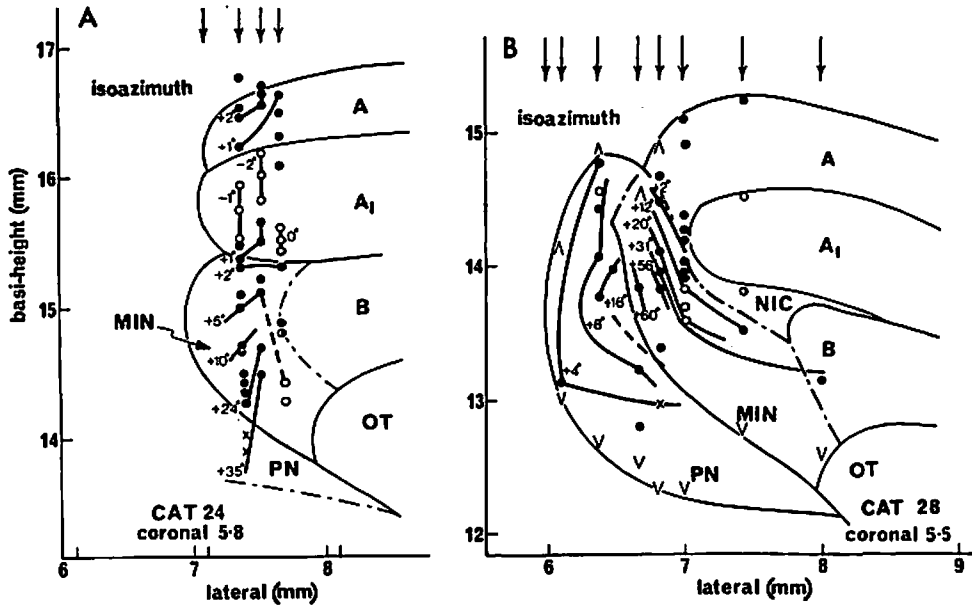
Fig. 8 A Pattern of isoazimuth lines for the medial tip of the LGNd and MIN in the one experiment (Cat 24) based on plots of receptive fields of units whose locations in the nuclei are indicated by the filled (contralateral) and open (ipsilateral) circles. The corresponding isoelevation pattern is shown in figure 5A. The vertical arrows indicate the relative positions of the electrode tracks. ◑ binocular unit; X, visually active unit but with indefinite receptive field. B · Pattern of isoazimuth lines for the MIN and PN in the one experiment (Cat 28). The corresponding isoelevation pattern is shown in figure 7. V, end of "swish" response along the respective electrode tracks. Other symbols as for figure 8A.

even more extreme than is the case with units in the more lateral nuclei. As noted earlier many of the units are binocularly activated and show directional selectivity in their response to moving targets.

DISCUSSION

Our observations regarding the projection of the visual field on the LGNd and MIN are in good agreement with both the earlier anatomical and electrophysiological studies (see Introduction). The one major point of difference is our failure to find evidence of a trilaminar organization in the MIN analogous to that in the LGNd whereby there is a segregation in the nucleus of contralateral and ipsilateral optic tract terminals. Hayhow ('58) first suggested such a segregation and subsequent anatomical studies (Stone and Hansen, '66; Laties and Spraque, '66; Garey and Powell, '68) have been in agreement that there is a mediolateral lamination with the contralateral fibers terminating along the me-

dial and lateral edges of the nucleus and the ipsilateral fibers ending in the middle of the nucleus. The term "concealed lamination" (Hayhow, '58) may be applied to it since the layering cannot be seen in normal Nissl-stained sections. The anatomical studies suggest extensive overlapping of these layers so that the laminar arrangement would be difficult to detect by our vertically-orientated electrodes and the limited sampling permitted by the small size of the nucleus. However it is not easy to imagine how the lamination described above would fit in with the coordinate grid implied by our studies. The latter suggest a lamination which is the mirror-image of that in the LGNd but sloping more acutely downwards and medially. The complex folding of the laminar planes in the LGNd also suggests that an analogous pattern in the MIN would be at least as complex. The extensive bilateral intermingling of the cellular layers in the MIN suggested to Hayhow ('58) that many of the neurons
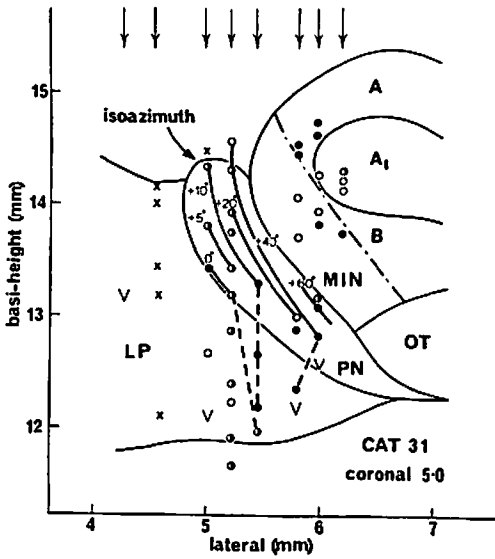
Fig. 9 Pattern of isoazimuth lines in the posterior nucleus (PN) showing an orderly mediolateral progression with central vision (0°) projecting to the medial border of the nucleus and the far periphery of the contralateral hemifield projecting in the vicinity of the PN/MIN border. Symbols as for figure 8A,B.

would be supplied with afferents from both eyes. However the relatively small number of binocularly-activated cells that we found in the MIN argues against this suggestion. The coordinate maps that we have prepared suggest that the concept of functional lines of projection as proposed for the LGNd (Bishop, Kozak, Levick and Vakkur, '62) applies to the MIN as well. In order to decide this point it would be desirable to study a number of closely-spaced parasagittal planes in the one animal. Much further work is clearly needed to reveal the details of the functional architecture of the MIN.

Our estimate of the site of projection of the visual axis in the LGNd is in good agreement with that of Stone and Hansen ('66). However the latter authors failed to find any corresponding projection in the MIN which suggested to them that the MIN does not take part in the pathways directly involved in visual perception. We have found that the projection for central vision in the MIN is immediately adjacent to the corresponding LGNd projection and continuous with it over the MIN/LGNd

border. This particular border of the MIN is however difficult to define.

To date homologues of the MIN have yet to be described in mammals other than the carnivora. However Choudhury and Whitteridge ('65) have described a second mirror-image projection for a sector of the inferior visual field in the posteromedial part of the dorsal lateral geniculate nucleus in the rabbit. A possible extrageniculate visual relay nucleus at the anteromedial margin of the LGNd has also been described by Montero, Brugge and Beitel ('68) in the rat.

Our finding of a topographical projection of the visual field onto the PN is new. There is no doubt that we have plotted three separate but related representations of the visual field and that the most medial representation is in a region immediately adjacent to, but distinct from, the LGNd and MIN. While most of the boundaries of the PN are somewhat vague, the lateral boundary with the MIN can usually be defined, particularly when a fiber plexus is present between the nuclei. It is our conclusion therefore that the most medial representation of the visual field is in an area similar to, if not identical with, the PN of Rioch ('29). We have described three separate representations of the visual field in the thalamus (LGNd, MIN and PN) but the projection onto the central interlaminar nucleus (CIN) is sometimes also regarded as a separate localization (Garey and Powell, '68). While morphological grounds establish the CIN as a separate subdivision of the LGNd, it seems hardly profitable at this stage to distinguish as separate the respective representations of the visual field in the two subdivisions, particularly in view of their very close interrelations and the absence of any clear functional distinction between them. However if we do regard the CIN projection as separate, there is the possibility of yet another (fifth) projection, the latter being onto the ventral lateral geniculate nucleus (LGNv). Montero et al. ('68) have found electrophysiological evidence of a separate retinotopic organization in the LGNv. However since primary optic axons are only a minor source of LGNv innervation (Hayhow, '58; Laties and Sprague, '66; Garey and Powell, '68), the nucleus is probably

mainly a secondary visual center like the PN.

While the LGNd, the MIN and the PN have been generally recognised as nuclei for many years, it is only very recently that their identities have been preserved when considering their interconnections and projections, so that most of the literature is not particularly helpful in these respects. The MIN has generally been included with the LGNd and the PN has been included either with the LP as a lateral posterior group or with the pulvinar. Although the connections of the MIN are now becoming much clearer, the position regarding the PN is still rather unsatisfactory. The major input to the MIN is from optic tract terminals but to what extent it is interconnected with other thalamic nuclei and mesencephalic centers is far from clear. The PN, on the other hand, is not a primary optic center (see Introduction) and appears to have its main input from the dorsal lateral geniculate body, but the evidence that is available on this point fails to distinguish between the LGNd and MIN as the source of the projection. Rioch ('31) and, more recently by the Nauta method, Van Straaten ('62) and Altman ('62) have described a projection from the dorsal lateral geniculate nucleus onto the PN. Physiological evidence for a similar pathway has been provided by Buser and Borenstein ('59), Vastola ('61) and Bruner ('65). The PN also receives a major input from the cerebral cortex particularly from those areas to which the PN itself projects (see below) and there is probably a direct projection from the superior colliculus (Altman and Carpenter, '61). The recording by Bruner ('65) of single units in the PN that were activated by both visual and auditory stimuli is in keeping with an earlier observation of Rioch ('31) that the PN has connections with the medial geniculate body. Such a pathway to the cerebral cortex and the topographical organization in the PN suggests a way in which sounds may be localized in visual space by the appropriate conjunction of auditory (Rose, Gross, Geisler and Hind, '66) and visual receptive fields.

The topographical organization of the projection of the central (0°) and peripheral (e.g., 90°) parts of the visual field on the three nuclei (LGNd, MIN and PN) is arranged from lateral to medial across the group such that azimuth values progress in the following order: peripheral-central; central-peripheral; peripheral-central. The relevant observations for the PN however need further confirmation (see Results). The corresponding topographical organization in the visual areas of the cortex is a mirror-image of that in the thalamic nuclei (fig. 11). The three cytoarchitectonic areas of Otsuka and Hassler ('62; Areas 17, 18, 19) have been shown to be functionally different and to have three separate representations of the visual field such that the central region projects to the 17/18 boundary and again to the lateral margin of Area 19 (Hubel and Wiesel, '65; cf. also Bilge, Bingle, Seneviratne and Whitteridge, '67). All three thalamic nuclei are known to project to the cerebral cortex and it is of obvious interest to consider to what extent the topographical organization in the visual cortex results from a reverse one-to-one projection from the thalamic nuclei. The cortical projections of the thalamic visual centers were recently studied or are currently under investigation in a number of laboratories either by observing terminal fiber degeneration in the cortex following focal electrolytic lesions in the thalamus (Glickstein, King, Miller and Berkley, '67; Wilson and Cragg, '67; W. R. Hayhow and Gwenneth R. Burrows — personal communication) or by retrograde cell degeneration in the thalamus following focal cerebral lesions (Garey and Powell, '67; K. Niimi and J. M. Sprague — personal communication). While the results differ somewhat, figure 11 summarizes the main observations in diagrammatic form. It can be seen that the organization of the projections departs somewhat from the simple one-to-one arrangement suggested above. In addition it should be noted that all three thalamic nuclei project to the lateral part of the suprasylvian gyrus. The projections of the visual areas of the cor-

Fig. 10 Distribution in the visual field of the positions of the receptive fields of all the units in this series of experiments recorded in the MIN, PN, LP and Pul. Note the marked nasotemporal overlap involving both eyes and also units in all four nuclei. Note also the absence of receptive fields in the upper peripheral region of the contralateral hemifield.
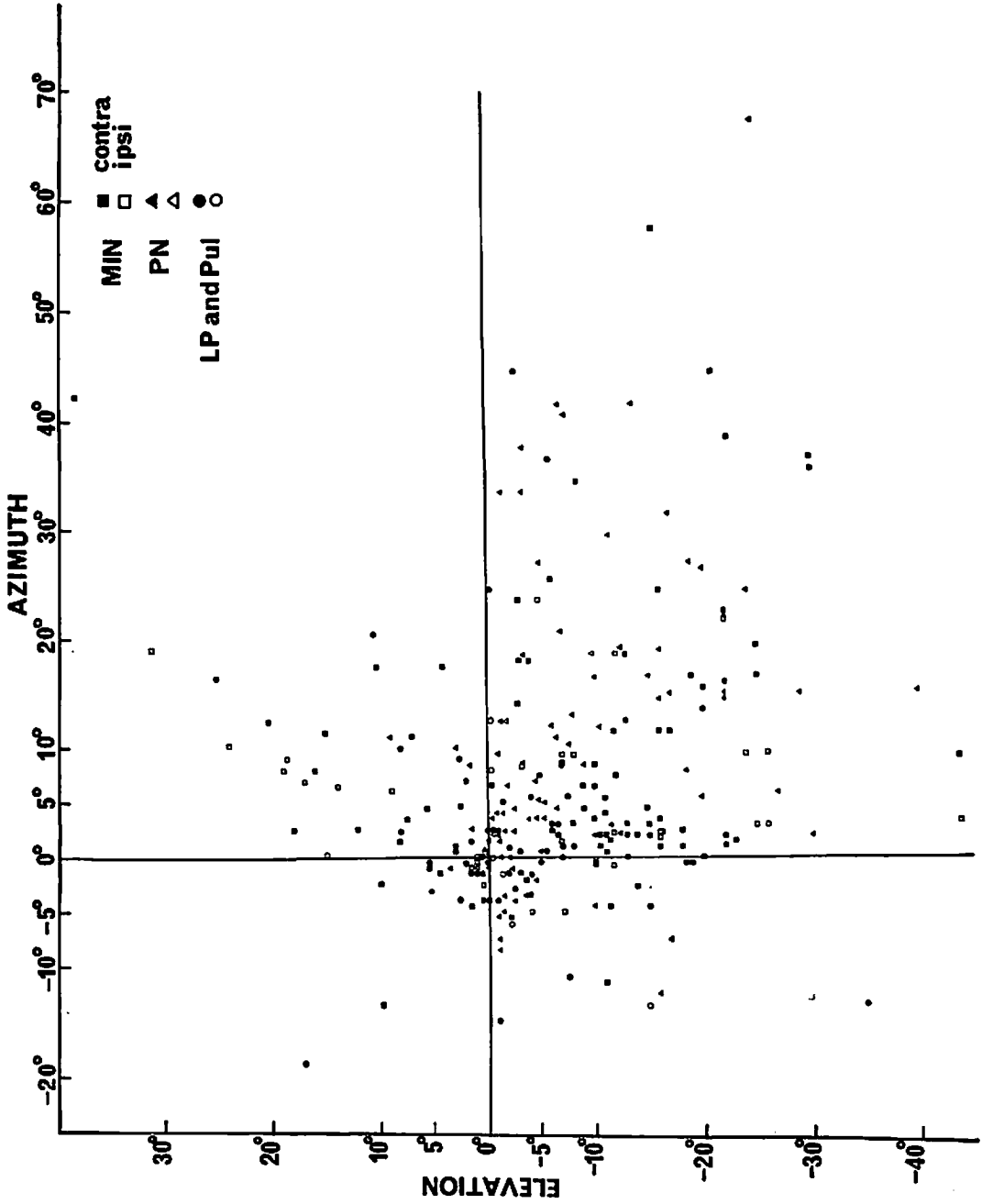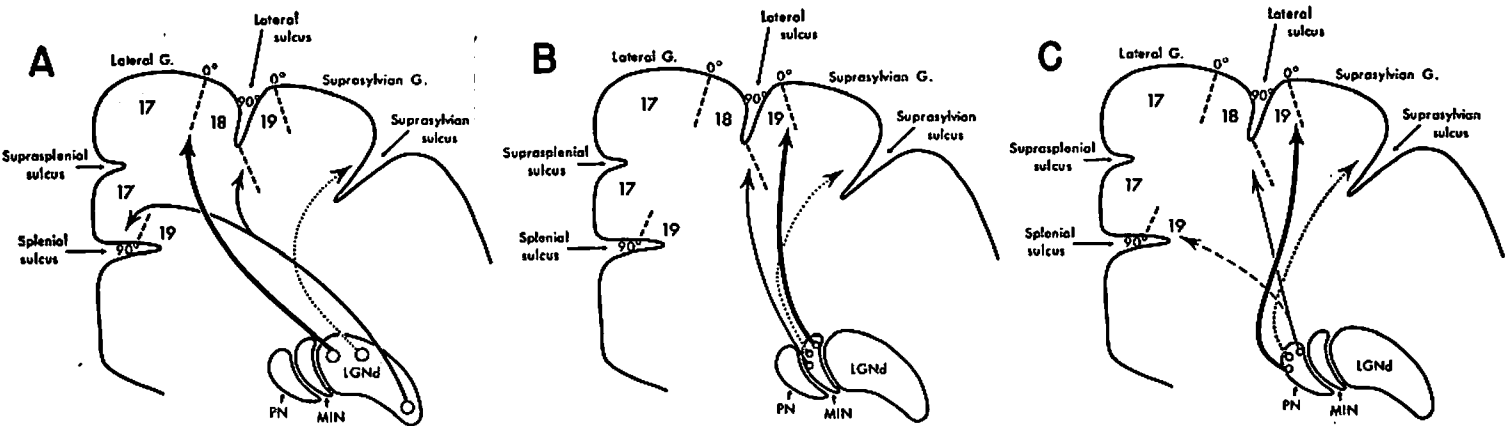
Figure 10

Fig. 11 Diagram summarizing current undersnd PN (C). For details see text. tions of the three nuclei, LGNd (A), MIN (B) atanding of the principal thalamo-cortical projec-

tex back onto the thalamic nuclei have been studied by Beresford ('61) and Garey, Jones and Powell ('68). In general the thalamic nuclei receive cortical projections from those areas of the cortex to which they themselves project and the cortico-thalamic projections are topographically organized in the same manner as are those from the thalamus to the cortex.

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