**Some Principles of Organization in the Dorsal
Lateral Geniculate Nucleus; pp. 253–267**

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Key Words

Lateral geniculate nucleus
Retinotopic organization
Vision

Abstract

A comparative survey shows that lamination is a basic feature of the mammalian dorsal lateral geniculate nucleus. *Relay laminae* receive input from the retina, project to the cerebral cortex and represent a complete hemiretina. They are distinguished from incomplete layers or leaflets and from groups of cells for which retinal connections or cortical projections are in question. The separate representations of the visual field in the relay laminae are precisely aligned so that each point in the visual field corresponds to a line passing from margin to margin through the nucleus and at right angles to the layers. Geniculate landmarks that provide clues regarding the organization of the layers are considered, and several experimental methods by which the laminar pattern can be displayed are evaluated.

Introduction

An important generalization about cell groups associated with the visual, auditory, and somatic sensory systems is that they represent their corresponding sensory surfaces in a topological manner. Thus, the primary cell groups in the visual system, such as the dorsal lateral geniculate nucleus, superior colliculus, or striate cortex, all systematically represent the retina and, thereby, the visual field. The purpose of this review is to discuss the manner of the representation of the visual field and to examine the associated issue of the nature of lamination in the

¹ This work was supported by grants 2 P01 HD 03352, 5 P01 NS 06225, 5 T01 NS 05326, and 5 R01 NS 06662 from the USPHS.

dorsal lateral geniculate nucleus.² Several types of observations lead to the conclusions that the manner of the representation of the visual field is similar in the lateral geniculate nucleus of all therian mammals, that the nucleus is subdivided into separate cell groups or layers, and that these layers relate to the visuotopic organization of the nucleus.³

In the following pages, we illustrate principles of lateral geniculate organization with evidence from a number of mammalian species, but primarily from a carnivore, the domestic cat, a primate, the owl monkey (*Aotus trivirgatus*), and a rodent, the grey squirrel (*Sciurus carolinensis*). These principles are also shown, in part, in figure 1

which serves as an aid to subsequent discussion. In brief, in all mammals the contralateral half of the total visual field is represented in each lateral geniculate nucleus, where some layers represent the full half of the visual field via the contralateral eye while other less extensive layers represent the smaller nasal (binocular) portion of the hemifield via the ipsilateral eye. The separate representations are aligned and each point in the visual field corresponds to a line that extends from margin to margin in the lateral geniculate nucleus.

7. The Visuotopic Organization

A. The Representation of Single Points or Areas in the Visual Field: the Lines of Projection, Projection Columns, Projection Units, and Geniculate Segments

Several types of evidence lead to the concept that any point in the visual field corresponds to a line in the lateral geniculate nucleus and, by extension, that a small area corresponds to a columnar volume. This general concept is useful in describing the organization of the lateral geniculate nucleus, although it is a simplification in that the nucleus consists of individual neurons each of which relates to an area of the visual field. BISHOP *et al.* [1962] introduced the term '*lines of projection*' to indicate lines of isorepresentation of points in the visual field and this term has the advantage that it clearly refers to a concept rather than an observation.

² Subsequent mention of the lateral geniculate nucleus refers to the dorsal nucleus only.

³ The homologue of the dorsal lateral geniculate nucleus in monotremes is, as yet, uncertain [CAMPBELL and HAYHOW, 1971; CAMPBELL, 1972] and these mammals are excluded from the present discussion.

Fixation Point

Fig. 1. Schema to show the representation of the visual field on the retina and $\Lambda\Lambda\Lambda$ dorsal lateral geniculate nucleus. A simplified form of the nucleus is shown, with only two layers. The nucleus in any mammalian species is made up of two or more layers that receive contralateral afferents and one or more layers that receive ipsilateral afferents. As shown in the figure, the contralateral layers are always more extensive and also represent a larger portion of the $\Lambda\Lambda\Lambda$ field. The monocular part of the visual field, which is represented in the monocular segment of the nucleus (dots) has also been called the unocular visual field [WALLS, 1942; DUKE ELDER, 1958]. The lines that separate the numbered segments in the lateral geniculate nucleus indicate the orientation of the lines of projection.

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Lines of projection can be demonstrated by several methods, but perhaps the most convenient is to make small lesions in the striate cortex and to study the zone of retrograde degeneration which is produced within the lateral geniculate nucleus [LASHLEY, 1934; POLYAK, 1932, 1933; ROSE and MALIS, 1965; GAREY and POWELL, 1967; GUILLERY, 1967; MONTERO and GUILLERY, 1968; DIAMOND *et al.*, 1970; KAAS *et al.*, 1972a]. Since one half of the visual field is topologically represented in each striate cortex, the zone of retrograde degeneration must always be bounded by a set of projection lines (fig. 1) and, if the lesion is small enough, the zone will be in the form of a narrow column or pencil of cells in the orientation of the projection lines. Such columns of degenerating cells may be called '*projection units*' as suggested by LE GROS CLARK [1941a] but it should be noted that the columns of degeneration are not

'units' in a functional sense since their diameter depends on the size of the cortical lesion.

Large cortical lesions produce large zones of geniculate degeneration and at times it is useful to have a distinct term to describe these regions. GUILLERY and STELZNER [1970] have suggested that '*geniculate segment*' be used to refer to any part of the lateral geniculate nucleus bounded by a set of projection lines. Thus projection units are small segments. Large segments can include much of the nucleus and this term can be used to distinguish the parts of the nucleus that receive from the monocular and binocular portions of the visual field (fig. 1) (see also discussion on pages 265 and 267).

Segments of the nucleus that undergo retrograde degeneration after cortical lesions are shown in figure 2, 3 and 4 (cat, mandrill, squirrel). In each species the borders of the segments and, therefore, the lines of projection, run roughly perpendicular to the geniculate layers and extend from one margin of the nucleus to the other.

The lines of projection are also revealed by other methods. One method is to make small retinal lesions and to study the degeneration that is produced in the lateral geniculate nucleus. Two types of degeneration occur: transneuronal degeneration of geniculate cells and Wallerian degeneration of the retinogeniculate fibers. In some species, for example macaque monkeys, in which there is marked transneuronal degeneration of the geniculate cells, the zones that are innervated by a small retinal patch are clearly shown by the cellular degeneration [LE GROS CLARK and PENMAN, 1934]. Since the changes are seen only in the layers innervated by the damaged eye, the method does not strictly demon-

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Fig. 2. Retrograde degeneration in the lateral geniculate nucleus of a cat, produced by a restricted lesion of the visual cortex. Arrows mark the borders of the column of cellular change, which extends through layers A, A₁, C and C₁. The borders of this column are formed by the lines of projection and

if the fibers pass roughly perpendicular to the plane of the layers. Parasagittal section; rostral is right; cresyl violet stain. Modified from Guillery [1967].

strate segments, but instead shows interrupted parts of whole segments. The Wallerian degeneration that occurs after retinal lesions can also be used for demonstrating the segments [POLYAK, 1957; LATIES and SPRAGUE, 1966; STONE and HANSEN, 1966; GAREY and POWELL, 1968]. Ideally, stains for the terminals of degenerating retinogeniculate fibers should reveal the interrupted parts of the whole segments with the same precision as the method of transneuronal degeneration but, since light microscopical methods do not allow a clear distinction between terminal

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Fig. 5. Retrograde degeneration in the lateral geniculate nucleus of a mandrill (*Mandrillus sphinx*). In this specimen there were several restricted lesions of unknown

origin in the striate cortex. The large column of cellular degeneration corresponds to one of these cortical lesions and the second area of degeneration in the ventral layers (unlabelled arrow) corresponds to a second lesion. Coronal section; medial is left; thionin stain.

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Fig. 4. Retrograde degeneration in the lateral geniculate nucleus of a grey squirrel (*Sciurus carolinensis*) produced by a liHited lesion in the striate cortex. The arrows mark the column of cellular change which, as in figure 2 and 3 passes roughly perpendicular to the layers. The layers are shown more clearly in figures 21–25. Horizontal section; cresyl violet stain. From KAAS *et al.* [1972b].

and nonterminal parts of degenerating axons, there must always be some doubt about the borders of the segments, especially in species in which the course of the retinogeniculate fibers through the lateral geniculate nucleus is not known.

A third method of revealing lines of projection, which we have recently discovered [GUILLERY and KAAS, 1971; KAAS *et al.*, 1972a], depends on the fact that there is a small area of the retina naturally devoid

Fig. 5. The cellMx discontinuity in layer A of the lateral geniculate ^Kleus of a cat is shown (DISC). The single arrow shows an electrode track (ET). Receptive fields of neurons along this track were adjacent to the KB8I spot of the contralateral eye. Coronal section; cresyl violet stain.

of receptors, i.e. the optic disc or nerve head. The optic disc is in the portion of the retina that projecMto layers in the contralateral lateral geniculate nucleus and a cell-free column, which corresponds to the optic disc, is apparent in at least some of these layers. This column reveals interrupted parts of a geniculate segment and the orientation of a line of projection. We have termed these cell-free columns cellular *discontinuities* [GUILLERY and KAAS, 1971; KAAS *et al.*, 1972a] and the one that lies in layer A of the cat is shown in figure 5 (DISC). Such discontinui-

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Fig. 6. Receptive field positions for recording sites in the lateral geniculate nucleus of a cat. Above: A coronal section with five numbered electrode penetrations shown as vertical lines and recording sites shown as lettered horizontal bars. Below: Part of the contralateral half of the visual field in which receptive fields are labelled to correspond to the geniculate recording sites. Note that adjacent portions of the several geniculate layers represent the same region of the visual field (penetrations 2–5). Penetration 1 is oblique to layer A and successively deeper recording sites correspond to successively more temporal receptive fields. Receptive fields of the ipsilateral eye are outlined by dots and those of the contralateral eye by a continuous line. The vertical line shows the zero vertical meridian and the horizontal line shows the zero horizontal meridian. The visual field is marked in 10° divisions. OD, blind spot; A, AI, C, and CI indicate geniculate layers. From GUHXERY and KAAS [1971].

ties have been found in other carnivores such as the lion and weasel, in primates including the owl monkey, slow loris and galago and in a rodent, the grey squirrel/ [KAAS *et al.*, 1972a]. It is probable that similar discoaSoities also exist in some layers of the lateral geniculate nucleus of other mammals.

A fourth method of revealing lines of projection in the lateral geniculate nucleus is to record the acfnty of geniculate cells with microelec-trodes and relate receptive field locations to recording sites. With a large number of recordings it is possible to determine the orientation of projectifiSL lines throughout much of the lateral geniculate nucleus in a single animal [HUBEJWL960; BISHOP *et al.*, 1962; MONTERO *et al.*, 1968; GUHXERY and KAAS, 1971; SANDERSON, 1971a]. Examples of microelec-

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Fig. 7. Receptive field positions and recording sites in the lateral geniculate nucleus of an owl monkey (*Aotus trivirgatus*). Right: Sagittal sections of the nucleus with three numbered electrode penetrations shown as vertical lines and recording sites shown as lettered horizontal bars. The external and internal parvocellular

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trode penetrations through the dorsal lateral geniculate nucleus of a cat, owl monkey, and squirrel are shown in figure 6, 7 and 8, respectively. Microelectrode penetrations that are roughly perpendicular to the layers show very little change in receptive field position with successive recording sites and, therefore, these penetrations must pass nearly parallel to the lines or projections. However, the eye through which the nerve cells are excited does change as the recording site shifts from one layer to another (fig. 6-8); and a correction is necessary for the misalignment of the eyes that may occur in experimental situations [SANDERSON and SHERMAN, 1971]. When electrode punctures pass more obliquely to the layers as in penetration 3 in figure 7 and penetrations 2 and 3 in figure 8, they also pass obliquely to the lines of projection and, therefore, one

sees systematic shifts in receptive field locations for successive recording sites. The shifts are always in one direction within a single penetration and form a continuous series even where laminar borders are crossed.

Results such as these show clearly that neurons with receptive fields of similar locations are grouped along lines extending from margin to margin in the lateral geniculate nucleus. The volume of space in the nucleus that contains 90% of all the cells with receptive fields centered at the same point in the visual field or with the same 'visual direction' has been called a '*projection column*' by SANDERSON [1971b]. The term is useful in describing the visuotopic organization of the nucleus but should not be mistaken for a functional unit comparable to the columns that have been described in the visual cortex [HUBEL and WISEL, 1963].

In summary, each of the research methods that has been used shows that, in all of the mammals that have been studied, the lines of projection are roughly perpendicular to the geniculate layers. It is reasonable to conclude that this principle of organization applies to all therian mammals. It will be shown that the principle is basic to evaluating the significance of the geniculate layers, to understanding the way in which the visual fields are represented in the lateral geniculate nucleus and

(PE and PI) and magnocellular (ME and MI) layers are shown. Upper left: A portion of the contralateral visual field with the zero horizontal and vertical meridians marked in 10° segments. Receptive fields are labelled to correspond to the recording sites on the right. Receptive fields of the ipsilateral eye are shaded, those of the contralateral eye are unshaded. Lower left: An outline of the dorsal aspect of the nucleus in which the planes of the three sections and the positions of the three electrode penetrations are shown.

GREY SQUIRREL

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Sagittal Sections

Fig. 8. Receptive field positions and recording sites in the lateral geniculate nucleus of a grey squirrel (*Sciurus carolinensis*). Upper left: A horizontal section of the nucleus showing the planes of the three sagittal sections in the upper right part of the figure. These three sections show three numbered electrode penetrations and lettered recording sites. Below: A portion of the visual field of the contralateral eye is represented by a hemisphere divided by meridians and horizontals at 15° intervals; the zero meridian corresponds to the line of decussation of the retina and receptive fields are labelled to correspond to the recording sites above. The single receptive field which was obtained from the ipsilateral eye in penetration 1 is not shown.

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to interpreting experiments in which the parts of the visual field representation are affected differentially.

B. The Representation of the Visual Field

The representation of the visual field in the lateral geniculate nucleus is topological, i.e. adjacent points in the visual field correspond to adjacent lines of projection in the nucleus. The basic pattern of the representation appears to be similar in all mammals for which extensive data are available. The region of the visual field that corresponds to the *line of decussation* of each retina, is represented along the margin of the lateral geniculate nucleus where a full complement of relay laminae abut (fig. 1 and part II). The temporal periphery of the contralateral visual field is represented along the margin of the nucleus where the layers of contralateral input extend beyond the layers of ipsilateral input (fig. 1). The rest of the contralateral hemifield is represented topologically between these margins. The nucleus can be divided into a

segment representing the binocular field and a smaller segment representing the monocular field.

It is possible to reveal the visuotopic organization of the lateral geniculate nucleus in several ways. If, for example, the visuotopic organization of striate cortex is known, then the organization of the lateral geniculate nucleus can be determined indirectly, by relating the locus of retrograde lateral geniculate degeneration to the site of a small lesion in the striate cortex in a number of cases with differing lesions. It is also possible to obtain a general view of the visuotopic organization of the lateral geniculate nucleus by comparing the sites of degeneration after restricted retinal lesions in a number of cases. However, the most complete and accurate information has been obtained by electrophysiological experiments in which the representation of the visual field was studied by serial microelectrode punctures. These studies have shown how the parts of the visual field are represented in the segments of the lateral geniculate nucleus and have also indicated the proportionate amounts of geniculate tissue devoted to different parts of the visual field, so that the relative importance of central or peripheral, and monocular or binocular vision in geniculocortical mechanisms could be assessed for each of several species. The results of electrophysiological mapping studies in several mammals are discussed below.

The domestic cat. Electrophysiological mapping studies have been reported in detail by BISHOP *et al.* [1962], KINSTON *et al.* [1969], GUJX-

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Fig. 9.

Schematic representation of the visuotopic organization in the lateral geniculate nucleus of the cat. Above; A sagittal section (rostral to the right) with lines of projection corresponding to indicated degrees above and below the hori-

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Fig. 10. Records obtained from two microelectrode punctures through the lateral geniculate nucleus of a cat. Conventions as in figure 6. The recording sites at the lateral edge of layer A1 show that about 45° of visual angle are represented in the binocular part of the geniculostriate system on each side. From GUILLERY and KAAS [1971].

GUILLERY and KAAS [1971] and SANDERSON [1971a]. Figures 6 and 10 illustrate the type of information that is obtained. Such studies indicate that the reference or zero vertical meridian of the visual field, which corresponds to the *line of decussation* of the retina, is represented medially in the lateral geniculate nucleus. The temporal periphery of the contralateral hemifield is represented laterally, the upper visual field dorsocaudally and the lower visual field rostroventrally. These conclusions are summarized in figure 9, which also shows that in the dorsocaudal parts of the nucleus the layers are relatively slender while in the rostroventral parts of the nucleus they are markedly thicker. Thus, the geniculate tissue that deals with information from the lower visual field is expanded

relative to the tissue related to the upper visual field. The difference between these two parts, in terms of the geniculate connectivity patterns involved, are not known. However, it should be noted that much of the retina devoted to z. meridian. zontal meridian. From Guillery and Kaas [1971]. Below: A coronal section (medial to the right) with lines of projection marked in degrees temporal to the zero vertical meridian. The position of the cellular discontinuity (DISC) that corresponds to the blind spot is shown. The values of the displacement of the blind spot from the vertical and the horizontal meridians are based on the reports of Kinston et al. [1969] and Sanderson and Sherman [1971].