Some Principles of Organization in the Dorsal Lateral Geniculate Nucleus; pp. 268–282

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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.

Fig. 11. The visual field of the cat as determined by recordings from the geniculostriate system. The projections of the optic disc (DISC) and the line of decussation (LD) are shown.

the lower visual field is provided with a tapetal light reflector, while such a zone is absent in the retina devoted to the upper visual field [WALLS, 1942]. It is thus probable that cat obtains different information from the lower and upper visual fields.

It is obvious from figure 9 that the representation of central vision is greatly expanded in relation to that of peripheral vision. This disproportionate representation of central vision reflects the relatively greater density of retinal ganglion cells in the central part of the retina [STONE, 1965]. In the coronal section of figure 9 it is also possible to see the segments of the lateral geniculate nucleus that deal with binocular and monocular vision. The binocular segment includes the medial two thirds

to three quarters of the nucleus within which layers A1 and C1 are confined, while the monocular segment lies beyond the lateral edges of these layers. Although the segments are unequal in size, each represents about 45° of horizontal visual angle, as can be determined from microelectrode recordings from the lateral edges of layer A1 for the binocular segment, and from layer A for the monocular segment (fig. 10) [GUILLELRY and KAAS, 1971; SANDERSON, 1971a]. The visual field of the cat and its functional subdivisions, as determined from electrophysiological recordings, are shown in figure 11.

The owl monkey and the rhesus monkey. Systematic mapping of the visual field in the lateral geniculate nucleus of the owl and rhesus monkeys has revealed a visuotopic organization in general agreement with that previously demonstrated by anatomical methods [BROUWER and ZEEMAN, 1926; POLYAK, 1932, 1933; LE GROS CLARK and PENMAN, 1934]. Since these results have not been reported elsewhere they are illustrated, in part, here in figures 12 and 14.

It is clear that in the owl monkey the representation of central vision is in the caudal part of the lateral geniculate nucleus (penetration 1, fig. 12); the upper field is represented laterally (penetrations 1-4); the lower field medially (penetrations 7-10) and the temporal periphery of the visual field is represented in a small portion of the rostral extreme of the nucleus (penetrations 5 and 6). While the receptive field for the neuron cluster in penetration 6 of figure 12 extends only a little more than 80° temporal to the vertical meridian, neurons further rostral must correspond to more temporal receptive fields since recordings from striate cortex [ALLMAN and KAAS, 1971] indicate that as much as $90-95^\circ$ of horizontal visual angle are represented in the geniculostriate system. The posterior, medial and lateral margin of the nucleus, where the edges of the layers are aligned, represents the zero vertical meridian. About half of the rostrocaudal extent of the nucleus represents the central 20° of vision and the binocular visual hemifield appears to subtend as much as $70-80^\circ$. The visual field of the owl monkey is illustrated in figure 13.

The organization of the lateral geniculate nucleus of the rhesus monkey is similar to that of the owl monkey (fig. 14). Recording site B in penetration 4 of figure 15 is close to the rostral edge of the external parvocellular layer (PE) and the corresponding receptive field is centered 75° from the zero vertical meridian. Therefore, the rhesus monkey probably has somewhat over 80° of horizontal visual angle represented in the lateral geniculate nucleus of one hemisphere and, judging from the

Fig. 12. Receptive field positions and corresponding microelectrode recording sites in the lateral geniculate nucleus (LG) of the owl monkey (*Aotus trivirgatus*). Left: sagittal sections of the nucleus with ten numbered electrode penetrations and lettered recording sites. Visual responses were noted at recording sites (R) in the pregeniculate nucleus but receptive fields were not determined. The external and internal parvocellular (PE and PI) and magnocellular (ME and MI) layers are shown. Inf. Pul. = inferior pulvinar; MG = medial geniculate nucleus. Lower right: An outline of the dorsal view of the nucleus showing the relative positions of the sections and electrode penetrations. Upper right: The contralateral visual hemifield showing receptive fields that correspond to the recording sites on the left. Receptive fields of the ipsilateral eye are shown as solid black, those of the contralateral eye as open outlines.

Fig. 13. The visual field of the owl monkey as determined by recordings from the geniculostriate system. DISC = projection of the optic disc; LD = projection of the line of decussation.

extent of the internal parvocellular layer (PI) as much as 75° of this relates to binocular vision. Recording site A in penetration 2 suggests that about half of the lateral geniculate nucleus is devoted to the central 20° Hfcual field. As in the owl monke>Bhe vertical meridian is represented at the caudal, medial and lateral margin of the nucleus where the edges of the layers are aligned along the lines of projection. The lower field representation is medial and the upper field representation is lateral. It should be emphasized that in both the owl monkey and the rhesus monkey, the monocular crescent of the extreme temporal periphery is represented in the very small rostral tip of the lateral geniculate nucleus.

Fig. 14. Recording sites and corresponding receptive field positions obtained from the lateral geniculate nucleus of a rhesus monkey. Conventions as in figure 6. Receptive fields obtained through the ipsilateral eye are shaded. The section is parasagittal and rostral is to the right.

It has previously been suggested that the representation of this part of the visual field is displaced to the lateral and medial margins of the nucleus in primates [WALLS, 1953; POLYAK, 1957; CHACKO, 1948], but this suggestion is inconsistent with the present evidence.

The grey squirrel and the rat. In comparison with carnivores and primates fewer studies have been reported on the organization of the lateral geniculate nucleus of rodents. However, the visuotopic organization of the lateral geniculate nucleus of the rat and the grey squirrel has been studied, both by electrophysiological mapping [MONTERO *et al.*, 1968] and, indirectly, by the method of retrograde degeneration [LASHLEY, 1934; KAAS *et al.*, 1972b]. Examples of the results of recording in the lateral geniculate nucleus of the grey squirrel are shown in figure 8 and 15. The figures show that the upper visual field is represented in the dorsal and rostral part and the lower visual field in the ventral and caudal part of the nucleus. The zero vertical meridian or line of decussation is represented medially and dorsally while the temporal periphery is represented ventrally and laterally. The eyes of the grey squirrel are more laterally placed than those of cats and monkeys and, therefore, the mon-

Fig. 15. Recording sites and corresponding receptive field positions obtained from the lateral geniculate nucleus of a grey squirrel. The frontal sections were cut at 50 μ m and numbered in a rostrocaudal sequence. The number of each section is shown in the lower left part of its outline. Medial is to the right. Electrode penetrations are numbered and recording sites are lettered. Cell layers, which are described more fully in the text, are numbered 1-3. Recording sites in layer 2 were activated by the ipsilateral eye and the corresponding receptive fields are not shown. The visual field of the contralateral eye is shown below with reference lines as in figure 8. All receptive fields are from the contralateral eye and the different types of shading are used to identify the several electrode penetrations.

Fig. 16. The visual field of the grey squirrel as determined from recordings of the geniculostriate system. The projection of the elongated optic nerve head is indicated DISC. LD = line of decussation.

ocular portion of the visual hemifield is large (fig. 16). However, this large 120° monocular segment of the visual field of the contralateral eye is represented in relatively little tissue in the lateral and ventral segment of the nucleus. The nasal 30° of the contralateral hemifield form the binocular portion [HALL *et al.*, 1971] and this is represented in the large dorsomedial sector which includes all of the geniculate layers (fig. 22, 25). These conclusions on the visuotopic organization of the lateral geniculate nucleus of the grey squirrel are supported by the retrograde de-

generation that has been seen in the nucleus after small lesions of different sectors of striate cortex [KAAS *et al.*, 1972b].

The visuotopic organization of the lateral geniculate nucleus of the rat appears to be very similar to that of the grey squirrel, although the representation of frontal vision may be proportionately smaller. In the experiments reported by MONTERO *et al.* [1968] the nucleus was mapped in detail but the zero vertical meridian or line of decussation was not experimentally defined. The results are more comparable to the squirrel if one assumes that the rat's nose was held unnaturally high in these experiments, as it appears in the illustration, so that the eye was rotated in the vertical plane. If we allow a slight correction for this rotation, then the presumptive vertical meridian is represented dorsomedially in the nucleus and the temporal periphery is represented ventrolaterally, as in the squirrel. The upper visual field representation is dorsal to that of the lower visual field.

II. The Lamination of the Nucleus

Studies of the lateral geniculate nucleus of a wide range of mammals including such primitive members as the hedgehog [HALL and EBNER, 1970; CAMPBELL *et al.*, 1967] and the opossum [BENEVENTO and EBNER, 1970] indicate that ipsilateral retinogeniculate terminations are segregated from the contralateral ones.⁴ These separate zones of termination must be considered separate layers. In some species the normal appearance of the nucleus does not indicate the lamination which is then regarded as a concealed lamination [HAYHOW *et al.*, 1962]. In many species, including all primates and carnivores, the lateral geniculate nucleus is grossly subdivided into sheet-like aggregates of cells or layers that are separated from each other by narrow zones almost devoid of cells. In some mammals, such as the squirrel monkey [CAMPOS-ORTEGA and GLEES, 1967; DOTY *et al.*, 1966; TIGGES and TIGGES, 1969] both manifest and concealed layers occur.

Not all subdivisions of the lateral geniculate nucleus that have been called layers are functionally equivalent. Several different types of lamination will be defined and are discussed on the following pages. Most layers include complete representations of the contralateral hemifield or

⁴ Whether the segregation is complete or not remains an issue to be resolved by more precise methods, including electron microscopical studies.

of its binocular portion and project to striate cortex. We regard these subdivisions of the lateral geniculate nucleus as having primary functional significance and define them as *relay laminae*. For individual *relay laminae* to be recognized they must meet the following criteria: (1) They must be distinct in their appearance, or they must be innervated by different eyes, or they must be clearly separated by an interlaminar zone. Often adjacent relay laminae are distinguishable on the basis of at least two of these three features, although any one would be sufficient for a distinction. (2) *Relay laminae* must lie in a plane that is approximately perpendicular to the *lines of projection* (fig. 1). Cell groups that do not appear to lie perpendicular to the lines of projection may be segments of full layers which are either infolded or abnormally connected to the retina. They may also be part of another nucleus. Thus, the observation that the layers of the medial interlaminar nucleus of the cat lie in a plane that is roughly parallel to the lines of projection in the adjacent dorsal lateral geniculate nucleus is part of the evidence that this medial group of cells is a separate nucleus. (3) Each *relay lamina* must carry a complete representation of either the full contralateral hemifield via the contralateral eye or of the smaller binocular segment of this hemifield via the ipsilateral eye (fig. 1). Since the full contralateral projection is always larger than the ipsilateral projection, the relay laminae receiving from the contralateral eye are more extensive than those receiving from the ipsilateral eye. (4) *Relay laminae* must project to striate cortex.

Examples of relay laminae are illustrated and discussed in the following pages. Other types of lamination are also noted and defined.

A. Lamination in the Cat and Other Carnivores

In the lateral geniculate nucleus of the cat it is possible to distinguish four relay laminae and these have been called layers A, A1, C and CI [GUILLERY, 1970b] (fig. 2, 9). A fifth layer, labelled C2 in figure 9, which lies next to the optic tract, cannot at present be regarded as a relay lamina. It is not known whether layer C2 receives afferents from the retina [GUILLERY, 1970b; GUILLERY and SCOTT, 1971], nor is it certain that retrograde degeneration occurs in this layer after corneal lesions. Some afferent fibers from the superior colliculus to layer C2 have been noted [GRAYBIEL and NAUTA, 1971], but nothing further is known of its connections.

Layers A and A1 form a matched pair of layers, A receiving its afferents from the contralateral and A1 from the ipsilateral eye, respec-

lively. They both have basically the same structure and are made up of mixed large, medium and small neurons. Layers C and CI receive their retinal afferents from the contralateral and ipsilateral eye, respectively. However, these layers do not form a matched pair as do A and AI. Layer C is characterized by a concentration of large cells and receives a relatively coarse-fibered retinogeniculate input, while layer CI consists of small cells that receive a fine-fibered input. Thus, it appears that the geniculate relay for axons from the temporal retina is not morphologically identical to that from the nasal retina. The ipsilateral pathway from the temporal retina has smaller cells and finer axons and it is possible that this may be related to the report that cortical neurons of this pathway have less accurately aligned receptive fields [BLAKEMORE and PETTIGREW, 1970].

The four relay laminae are separated from each other by relatively cell-free zones. Between layers A and AI there is a well-defined inter-laminar plexus which contains a few scattered large cells. Since these cells do not differ from large cells in the adjacent layers, there is no justification for regarding this interlaminar zone as another 'nucleus' [THU-MA, 1928; HAYHOW, 1958]. The interlaminar zones on either side of layer C are narrower and harder to see, especially in sections that cut the zones somewhat obliquely [LATIES and SPRAGUE, 1966; GUILLERY, 1970tp||

The four relay laminae are not always easy to recognize in the cat. They are more easily distinguished in the dog [RIOCH, 1929] and in some other carnivores. Figure 17 shows that in the red fox the four relay laminae are well defined and easily demonstrated.

The evidence that layers A and C receive projections from the contralateral eye is of several types. First, some deductions can be made from the normal histology, and it is interesting to do so, if only to illustrate how similar conclusions may be drawn from the normal histology of other species in which experimental investigations are not possible. Layer A is clearly extended further laterally than AI and layer A has a conspicuous discontinuity. As noted previously these factors indicate that layer A receives projections from the contralateral eye while layer AI receives projections from the ipsilateral eye. The separation of layer C from layer CI is too indistinct in normal material to serve as a basis for similar conclusions.

The most direct evidence about the connections of the layers comes from studies of degenerating retinogeniculate axons stained by the meth-

Fig. 17. A sagittal section through the lateral geniculate nucleus of a red fox (*Vulpes fulva*). Rostral is to the upper left. The four relay laminae, A, AI, C and CI are clearly shown. The small scattered cells that lie amongst the fibers of the optic tract form layer CI. Thionin stain.

ods of NAUTA and GYGAX [1954] or FINK and HEDVCER [1967] 6-12 days after removal of one eye. The pattern of the degenerating axons is illustrated in figure 18. ContralateralUfo the lesion there is dense degeneration in layers A and C. The-small amount of degeneration in layers AI and CI probably represents axons on their way from the optic tract to layers A and C and should not be regarded as terminal degeneration. It is important to note, however, that one is justified in accepting this conclusion only because it is supported by other lines of evidence. The silver-stained sections do not show the difference between terminal degeneration and fibers of passage, and they do not, by themselves, show that layers AI and CI receive no contralateral input [GUILLERY, 1970a]. Ips-ilaterally there is dense degeneration in layers AI and CI. The sparser degeneration in layer C is again regarded as fibers of passage, but on this side the sections show quite clearly that there is no retinal input to layer A orftpHhe interlaminar zone between layers A and AI.

Fig. 18. Coronal sections through the lateral geniculate nucleus of a cat ipsilateral (left) and contralateral (right) to a unilateral eye removal 12 days before death. Dots show the density, distribution and orientation of degenerating fibers stained by the Nauta method. Layers A and C receive afferents from the contralateral eye while layers A1 and C1 receive from the ipsilateral eye. OT = optic tract; MIN = medial interlaminar nucleus. Scale = 500 μ m. Modified from GUILLEMY [1970].

A third type of evidence depends on the observation that geniculate cells undergo transneuronal degeneration after removal of one eye. Thus, the cells in layers A and C become pale and shrunken after a contralateral removal, while the cells in layer A1 atrophy after an ipsilateral removal. There is some evidence that the cells in layer C1 also show some changes [GAREY and POWELL, 1968], although these small cells undergo only minor changes that are difficult to interpret [GUILLEMY, 1970b, 1972].

The segregation of ipsilateral from contralateral terminations in separate layers can also be demonstrated by electrophysiological techniques. Experiments in which recordings were obtained with micro electrodes from neurons in all four relay laminae in the cat [GUILLEMY and KAAS, 1971; SANDERSON, 1971a; DAW and PEARLMAN, 1970] (fig. 6) completely support the anatomical evidence summarized above. Figure 6 shows that as an electrode is advanced through the nucleus it encounters, in order, cells activated by the contralateral, then the ipsilateral, then the contralateral and finally the ipsilateral eye. Recordings from these last ipsilateral cells in layer C1 are more difficult to obtain because the cells are

small and the layer is narrow. Since layer CI shows little transneuronal degeneration and since the fibers ending in it are very fine, the lateral geniculate nucleus of the cat was for many years wrongly regarded as a trilaminar structure.

The evidence regarding the layers in the cat has been described fully because it illustrates the difficulties that can arise when one tries to determine how many layers there are in a particular species. None of the four methods that have been used for studying laminae is entirely reliable. Some of the layers may not be readily apparent in normal material. Transneuronal degeneration may be relatively mild in some species and its absence in a lamina cannot be taken as a demonstration that there is no neural connection. The silver methods often give a useful picture but rarely allow a certain distinction between fibers of passage and terminals. The electrophysiological evidence is most convincing where it demonstrates a laminar structure*-that matches the anatomical evidence. However, thin layers of small cells are easily missed.

B. Lamination in Primates

The primate lateral geniculate nucleus is generally regarded as consisting of six layers, although some exceptions have been noted [GIOLLI and TIGGES, 1970; HASSLER, 1966]. The lateral geniculate nucleus of the owl monkey, *Aotus trivirgatus*, has been described as one of these exceptions. It has four relay laminae and for reasons given below we regard this as the basic primate pattern. Therefore, this species will be considered in detail first.

The laminar structure of the lateral geniculate nucleus of the owl monkey is shown in figure 19. Dorsally, there are two adjacent parvocellular layers which are separated from each other over much of the nucleus by a narrow cell-free zone; ventrally, a pair of magnocellular layers are separated from each other and from the parvocellular layers by broad interlaminar zones. These four layers have been described previously by LE GROS CLARK [1941b], CHACKO [1954b], HASSLER [1966] and JONES [1966].

The external parvocellular layer (PE) and the external magnocellular layer (ME) receive projections from the contralateral eye while the internal layers (PI and MI) receive from the ipsilateral eye. This pattern of retinal input is suggested by the appearance of normal Nissl preparations, which show that the external layers (PE and ME) extend beyond the borders of the internal laminae in the rostral parts of the nucleus,

Fig. 19. A sagittal section of the lateral geniculate nucleus of the owl monkey. Rostral is right. The internal (PI) and external (PE) parvocellular and the internal (MI) and external (ME) magnocellular layers are labelled. A fifth superficial layer (S) lies ventral to ME (see text). From KAAS *et al.* [1972a].

where the temporal visual field is represented (fig. 19). In addition, a discontinuity corresponding to the optic disc is seen in the two external layers [KAAS *et al.*, 1972b] so that these must receive afferents from the contralateral eye.

The conclusion that the external layers receive contralateral projections, while the internal layers are innervated via the ipsilateral eye, is also supported by experimental evidence. After eye removal, transneuronal degeneration is seen contralaterally in the external and ipsilaterally in the internal layers [MUNOZ, 1966]. The fiber degeneration that occurs after removal of one eye confirms this pattern (fig. 20) as does electrophysiological evidence, some of which is illustrated in figure 12.

In part I, we showed that the parvocellular and magnocellular layers form complete retinal representations and, since our retrograde degeneration studies indicate that these layers also project to striate cortex, the

Fzg. 20. Degenerating retinogeniculate fibers in the dorsal lateral geniculate nucleus of an owl monkey that survived 6 days following the removal of one eye. The small triangles mark the dorsal and ventral borders of the layers. Ipsilaterally (left) there is degeneration in the internal layers (PI and MI) and contralaterally (right) there is degeneration in the external layers (PE and ME). Fink-Heimer stain and cresyl violet.