Some Principles of Organization in the Dorsal Lateral Geniculate Nucleus; pp. 283–299

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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.

magnocellular and parvocellular layers must be regarded as relay laminae.

Ventral to these four well-defined relay laminae, a fifth layer is seen (S in fig. 19). This ventral group of cells has been only briefly mentioned in the owl monkey [JONES, 1966], but a number of investigators have described it, either as a separate layer or simply as a ventral group of cells, in some other primates [GIOLLI and TIGGES, 1970]. It is not clear whether or not layer S is a relay lamina. It has been reported that the layer receives ipsilateral retinal afferents in some primates [TIGGES and TIGGES, 1969, 1970; GIOLLI and TIGGES, 1970]. With the survival periods we have used (6 days) little retinogeniculate fiber degeneration was seen in layer S in the owl monkey. Thus, it is not clear whether or how, the visual field is represented in layer S, nor is it known whether this layer projects to striate cortex. For these reasons, we regard layer S as a potential relay lamina only.

Within the interlaminar zones that lie on either side of the magnocellular laminae, there are some well-defined groups of small cells. These groups correspond to the intercalated laminae described by GUILLEY and COLONNIER [1970] in the macaque monkey, although they are somewhat broader and more continuous in the owl monkey. At present the intercalated layers are not regarded as relay laminae, since there is no evidence that they receive any
retinogeniculate terminations. Their electron microscopic appearance in the macaque monkey suggests that they may receive none [GUILLERY and COLONNIER, 1970]. However, judging from retrograde changes in these laminae in the mandrill (fig. 3), the intercalated layers do project to striate cortex.

If layer S and the intercalated layers are excluded, then four relay laminae are found in the owl monkey and also in a number of other primates. It appears from Nissl preparations that marmosets (Hapale) [LE GROS CLARK, 1941b; CHACKO, 1954b], the titi monkey (Callicebus preus) [personal observation], and the tarsier [CHACKO, 1954c; HASLER, 1966] have four relay laminae. In addition, Nissl preparations and experimental material indicate that the gibbon, Hylobates, has four layers [CHACKO, 1954c; KANAGASUNTHE-ram and WONG, 1968; KANAGASUNTHE-ram and KRISHNAMURTI, 1970].

Six layers are often described as the basic number in the lateral geniculate nucleus of macaque monkeys [LE GROS CLARK and PENMAN, 1934; LE GROS CLARK, 1941b]. However, it has been stressed by CHACKO [1954b] that in one part of the nucleus there are only two parvo-
cellular layers and these split to form four parvocellular layers in another part of the nucleus. Parasagittal sections show clearly that the internal and external parvocellular layers divide as they thicken in the caudal half of the nucleus, and these subdivisions of the parvocellular layers will be called leaflets, because they are not separate layers at all, but are caudal extensions of the full relay laminae. The ventral leaflet of the PE interlaces between the two leaflets of the internal layer, giving the appearance of four parvocellular layers, and thus a total of six geniculate layers. The parvocellular layers may further subdivide near the representation of macular vision so that in a small part of the nucleus there appear to be five or six parvocellular layers and a total of up to eight geniculate layers [LE GROS CLARK and PENMAN, 1934; CHACKO, 1954c]. From our electrophysiological recordings, it is apparent that these subdivisions or leaflets of the parvocellular layers only represent central parts of the visual field and they cannot be considered full relay laminae. LE GROS CLARK and PENMAN [1934] considered the most caudal leaflets only as 'subsidiary laminae' but did not extend this distinction to the larger leaflets of the parvocellular layers, possibly because six layers are compatible with LE GROS CLARK's [1941a] theory of color vision.

Leaflets similar to those of the macaque monkey are found in the parvocellular layers of the lateral geniculate nucleus of a number of other primates including man [CHACKO, 1948]. Thus, it appears that the anthropoid lateral geniculate nucleus consists of four relay laminae which are divided into leaflets in most species. As an interesting variation, the magnocellular rather than the parvocellular layers are reported to form leaflets in the siamang, Symphalangus syndactylus [KANAGASUNTHERAM et al., 1969].

Relay laminae form complete representations of the visual field and adjacent relay laminae that receive from the same eye commonly differ by architectonically; leaflets do not form complete representations and are cytoarchitectonically similar. Therefore, it is probable that the functional significance of these two types of subdivisions of the nucleus differs. The role of the leaflets may be quite simple. For example, it is possible that cells receiving from one eye interact with cells receiving from the other. This interaction may be limited by the distance that separates the cells and, therefore, by the thickness of the laminae. The parvocellular laminae thicken near the representation of central vision and the formation of leaflets may then prove to be a simple way of maintaining a suitable proximity between the interacting cells. This interpretation is
speculative at present but is of some interest, since there is evidence that primates with leaflets do have dendrites that cross laminar borders [CAMPOS-ORTEGA et al, 1968; WONG-RILEY, 1972] and there is likely to be a limit to the length of such geniculate cell dendrites. Binocular interactions have been most clearly demonstrated in the geniculate layers of the cat [SUZUKI and KATO, 1966; SANDERSON et al, 1969; SINGER, 1970], where there is reason to think that the interactions involve dendrites that cross laminar borders or short axon cells, whose axons cross laminar borders [GUELLERY, 1966; TOMBOL, 1969].

While the lateral geniculate nucleus of anthropoid primates appears to have four basic relay laminae, this is not as certain for prosimians. The tarsier does appear to have only four relay laminae similar to those of the owl monkey, i.e. two parvocellular and two magnocellular layers [HASSLER, 1966; CHACKO, 1954c]. Other prosimians have been described as having six layers: two ventral magnocellular layers, two dorsal parvocellular layers, and two narrow additional layers inserted between the parvocellular layers [HASSLER, 1966]. These additional narrow layers receive projections from the retina [CHACKO, 1954a, TIGGES and TIGGES, 1970; LAEMLE and NOBACK, 1970] and are potential relay laminae. However, tims not certain that they form complete retinal representations, since they are not seen as distinct cell populations in the lateral part of the nucleus [IONESCU and HASSLER, 1968]. In some sections a ventral layer S (or O) is also identifiable [TIGGES and TIGGES, 1970; CAMPOS-ORTEGA and HAYHOW, 1970], but it does not appear possible for this restricted group of cells to form a complete representation of the uncrossed retinal projections in alignment with the representations in the other layers. Therefore, layer S is not presently regarded as a relay lamina.

Tree shrews are often considered the most primitive of living primates, although their relationship to other primates is not close [CAMPBELL, 1966; GOODMAN, 1966; MCKENNA, 1969]. Perhaps HASSLER'S [1966] term, subprimate, is appropriate, but the layers of the lateral geniculate nucleus are not easily homologized with the layers of other primates. The reported laminar pattern in one tree shrew, Tupaia glis, consists of a medial layer of ipsilateral input bordered by three adjacent layers of contralateral input (the middle layer of the three is distinguished by less dense retinal terminations); laterally, a second layer of ipsilateral input occurs which is bordered by a thin, less prominent layer of contralateral input next to the optic tract [GLICKSTEIN, 1967; TIGGES,
All six layers appear to project to the striate cortex in a topographic manner [Diamond et al., 1970; Ward and Masterton, 1970]. Our unpublished results from microelectrode recordings in the lateral geniculate nucleus also indicate an orderly representation of the contralateral visual field. The vertical meridian is represented dorsomedially, where all six layers terminate; the large monocular field is represented in the small ventral segment, which consists of only the layers of contralateral input. Thus, present evidence suggests that all six layers qualify as relay laminae.

In summary, the lateral geniculate nucleus of several New World monkeys consists of four simple relay laminae. In other simians, two of the relay laminae subdivide and form leaflets but the basic number of relay laminae remains the same. Since four simple relay laminae are found in both the New World and Old World simians, it is possible that leaflets were formed independently two or more times in primate evolution. With the exception of the tarsier and excluding tree shrews, pro-simians appear to have six full relay laminae. It is unlikely that the number of layers decreased in evolution and it is probable that a basic primate pattern of four relay laminae did exist at the time of divergence of simians and prosimians. The relation between the laminar pattern in tree shrews and in other primates is presently not clear. At the time both groups diverged, possibly from insectivore (leptictid) ancestors [McKenna, 1969], the laminar pattern of the lateral geniculate may have been as simple as a central pocket of ipsilateral input bordered on both sides by layers of contralateral input such as is seen in the hedge-hog [Campbell et al, 1967; Hall and Ebner, 1970] rabbit [Hughes, 1971; Sanderson, 1972] and rat.

C. Lamination in Rodents
The pattern of lamination has been studied in squirrels and rats but the lamination is easier to demonstrate in the highly developed visual system of the squirrel. In the grey squirrel, sections stained by the Nissl method show that the cells of the lateral geniculate nucleus are grouped into three fairly well-defined layers and these are separated by two relatively cell-free zones (fig. 21) [Kaas et al., 1972b]. The orientation of these three layers in three planes of section is shown in figure 22. The middle layer (layer 2 in figure 21 and 22) does not extend to the lateral part of the nucleus. Instead, in the lateral third, layers 1 and 3 merge. The caudal layer 3 does not have a uniform structure but it cannot be
Fig. 21. A horizontal section of the lateral geniculate nucleus of the grey squirrel showing the interlaminar cell-poor zones (arrows) that separate the three main cell layers (see text). A discontinuity in layer 1 (Disc), which corresponds to the representation of the optic disc, is also shown. VGL = ventral lateral geniculate nucleus. Cresyl violet stain.

Further subdivided on the basis of the normal appearance of the nucleus. From the orientation of these cell groups, several preliminary statements about the organization of the lateral geniculate nucleus are possible. Since relay laminae with ipsilateral input are less extensive, one would suppose that layer 2 receives projections from the ipsilateral eye while layers 1 and 3 receive from the contralateral eye. Further, the segment in which layers 1 and 3 merge would correspond to the monocular vi-
Fig. 22. The extent of the three main cell layers in the lateral geniculate nucleus of the squirrel. These layers are shown in three intersecting planes: Dorsal (D), ventral (V), medial (M), lateral (L), rostral (R) and caudal (C) are indicated.

Sual field and the margin of all three layers on the dorsomedial edge would correspond to the zero vertical meridian. We have seen from the previous section (visuotopic organization) that these deductions about the representation of the visual field are correct. However, experimental methods indicate that the laminar pattern is more complex than shown in normal Nissl sections.

After eye removal, very little transneuronal degeneration occurs in the lateral geniculate nucleus of the adult squirrel [Tigges, 1970]. However, in one case of accidental eye loss in infancy, transneuronal degeneration was obvious in the adult. Contralateral to the eye loss, degeneration was seen in layers 1 and 3 (fig. 23); but layer 3 was not uniformly
Fig. 23. Transneuronal degeneration in the lateral geniculate nucleus of a grey squirrel that had ISSJttfe contralateral eye (see text). The cells in layers 1 and 3 are shrunken (deg). Coronal section, thionin stain. VGL = ventral lateral geniculate nucleus.
Fig. 24. Degenerating retinogeniculate fibers in the lateral geniculate nucleus of a grey squirrel that survived 6 days after removal of the ipsilateral eye. Dense pericellular degeneration is seen in layer 2, the middle portion of layer 3 and along the inner margin of the optic tract (OT). Horizontal section, Fluorescin stain and cresyl violet.

degenerated and this suggested that layer 3 was not a single relay lamina. Ipsilaterally, transneuronal degeneration was seen in layer 2.

The pattern of fiber degeneration that occurs following removal of one eye (fig. 24) provides additional evidence that the input to layer 2 is, indeed, ipsilateral, while that to layer 1 is contralateral. The third cell group, however, shows further subdivisions in terms of the degenerating retinogeniculate axons. Three subdivisions are recognizable and each appears to be a full relay lamina. The rostral and caudal of these (3a and 3c) receive contralateral input and the middle one (3b), ipsilateral. All three contralateral relay laminae merge with each other and continue into the ventrolateral part of the nucleus while the ipsilateral two laminae do not. This same five-layered pattern of degeneration after eye re-
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Moval has been observed in the squirrel by ROBSON and HALL [personal commun.].

Microelectrode recordings obtained from the lateral geniculate nucleus also show that layer 3 (fig. 8, 15) receives afferents from the contralateral eye, but the thin middle layer of ipsilateral representation which can be seen in Nauta and Fink-Heimer sections, does not appear clearly in terms of the microelectrode recordings. Contralateral input to layer 1 and ipsilateral input to layer 2 is clearly shown in these figures.

A summary of the lamination of the lateral geniculate nucleus of the grey squirrel is shown in figure 25. As a relay lamina with contralateral BMc; layer 1 has a discontinuity that may correspond to the optic disc [KAAS et al., 1972] but similar discontinuities were not apparent in layers 3a and 3c. The grey squirrel resembles the cat in having unevenly matched sets of laminae. One must expect cortical activity to reflect this uneven balance between the two inputs but the details regarding binocular interaction in the squirrel's cortex remain to be determined.

The pattern of lamination in the grey squirrel differs from that described by TIGGES [1970] in flying squirrels and ground squirrels, but the pattern reported for these squirrels indicates that the ventrolateral disposition of the monocular sector and the dorsomedial disposition of the binocular sector are similar to that in the grey squirrel.

WhiSme visual system of the squirrel is well developed in comparison to that of the rat, and in many ways is easier to study, rats have been used extensively in experimental investigations of central visual pathways. A recent report [GUILLERY et al., 1971] provides evidence that the rat has three relay laminae in almost the same orientation as the layers in the squirrel. The middle less extensive layer receives input from the ipsilateral eye and is bordered rostrally and caudally by layers receiving input from the contralateral eye.

D. Congenitally Abnormal Laminae

Studies of Siamese cats, albino rats and albino ferrets have implicated that interpretations based only on the normal cytoarchitectonic structure and on the distribution of retinogeniculate axons may lead to incorrect views of the laminar pattern in the lateral geniculate nucleus [GUILLERY, 1969, 1971; GUILLERY and KAAS, 1971; GUILLERY et al., 1971]. Our investigations of Siamese cats have shown that layers Al and Cl, which normally receive only an ipsilateral input, are broken up into four segments in these cats. Two segments receive an input from the ipsilateral
eye and appear normal. The other two segments receive their input from the contralateral eye, but from the part of the retina that normally projects ipsilaterally. These abnormal segments are separated from the normal segments by narrow interlaminar zones that resemble the interlaminar zones. Further, the abnormal segments tend to fuse with the adjacent relay laminae that receive from the contralateral eye, so that cell groups
receiving from the same eye are continuous. Thus, the Nissl appearance and the pattern of the retinogeniculate terminations both give a false impression of the laminar structure [KALIL et al., 1971; HUBEL and WRIESEL, 1971].

The analysis of the nucleus in the Siamese cat was based upon a thorough knowledge of the anatomy of the normal cat's nucleus and on serial microelectrode punctures through the nucleus in normal and Siamese cats. In rats the situation was more complex because, for some time, the nucleus of the albino rat was regarded as a model for the normal. The patches of ipsilateral degeneration that were seen in albino rats [HAYHOW et al., 1962] were interpreted as ipsilateral laminae. However, these 'laminae' were oriented parallel to the lines of projection, which could be defined by studies of retrograde cell degeneration [LASHEY, 1934; MONTERO and GUILLERY, 1968] and by microelectrode studies [MONTERO et al., 1968]. Thus, it became necessary to reevaluate the laminae of the rat. It now appears that the albino rat is exactly comparable to the Siamese cat. In a pigmented rat one sees a single continuous ipsilateral lamina that lies perpendicular to the lines of projection, and in an albino rat this single lamina is broken up into discontinuous patches.

Siamese cats are homozygous for a gene of the albino series. Albino rats, albino ferrets and Siamese cats all show the same type of abnormality of the visual pathways and from information available at present, it appears that albino rabbits and mink do too [SANDERSON, 1972]. It is necessary to conclude that genes of the albino series can produce a very specific misrouting of some retinogeniculate axons. It remains to be determined whether there are other genes that have similar effects and that can also produce an aberrant and, to the anatomist, confusing pattern of lamination in the lateral geniculate nucleus.

Summary and Conclusions

The basic subdivision of the mammalian lateral geniculate nucleus is the relay lamina. Each serves a complete and orderly representation of a hemiretina and the several retinal representations are organized so that a single point in the visual field can be represented as a line, the line of projection, passing through the nucleus from one margin to another, through all the layers and more or less perpendicular to them.

This account demonstrates that it is possible to determine much of the basic organization of the dorsal lateral geniculate nucleus of any particular species from a study of normal brains and from a few relatively simple experiments. When the
central visual pathways are to be studied in a mammalian species about which relatively little is known this approach may prove of especial value.

Study of a normal Nissl series will often show how the layers are oriented and, therefore, how the lines of projection are organized. If one can see where one set of layers extends beyond the borders of another, it may be possible to define the monocular segment and thus to determine where the temporal parts of the visual field are represented. Further, one can conclude that the layers which extend into the monocular segment must receive their input from the contralateral eye. The representation of the zero vertical meridian will lie in the nucleus opposite to that of the monocular crescent and the borders of all the layers will lie more or less in line along the lines of projection that correspond to the vertical meridian.

In many species there will be a cellular discontinuity that represents the blind spot. The layers which show this discontinuity will receive thalamic innervation from the nasal retina of the opposite eye and, further, identification of this discontinuity can help in determining the orientation of the lines of projection.

If the lamination of the nucleus is not clear, or if there is doubt about the identification of some layers, an important first step is to determine how the lines of projection are organized by looking at retrograde degeneration after small lesions in the visual cortex. Subsequently, the lamination and the visuotopic organization can be studied in terms of the retinogeniculate fiber degeneration and by serial microelectrode punctures.

When these several points have been determined, it may be possible to define specific problems concerning the organization of the lateral geniculate nucleus. Thus, where the ipsilateral and contralateral layers are not evenly matched one can enquire about the nonmatched parts of the geniculocortical systems. If individual layers do not contain complete representations of a hemiretina, the significance of this partial representation merits investigation. The interlaminar regions may prove of particular interest. Whether these consist primarily of a fiber plexus, as they do in some species, or whether they form a more or less distinct cell group, as they do in others, their innervation and their relationship to adjacent laminae may provide important clues to geniculate function.

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