A PRELIMINARY STUDY OF THE DISTRIBUTION OF CELL SIZE IN THE LATERAL GENICULATE BODY

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INTRODUCTION

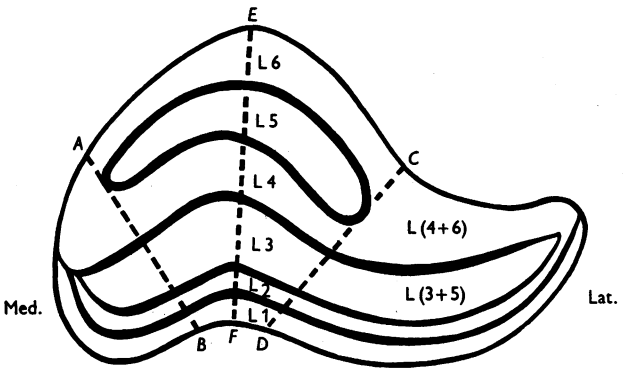
In the course of a comparative study of the laminar organization of the lateral geniculate body (Chacko, 1948*a*), a regular cell-size gradient was observed under the low-power microscope in the six-laminar central vision area as well as in the four-laminar peripheral vision area. It was decided to undertake a preliminary study of the spectrum of cell size, basing it on measurements of the size of the cells in the human geniculate nucleus in the various layers of both the central and peripheral vision projection areas. Supplementary data were obtained in a study of the same nucleus in the macaque monkey.

In studying the morphological details of the lateral geniculate body, it is apparent that the size characteristics of the cells lend themselves readily to quantitative measurements. The larger size and the more deeply staining character of the cells in layers 1 and 2 when compared with the cells in layers 3, 4, 5 and 6 have previously been recognized, and Balado & Franke (1937) have mentioned the approximate cell size in some of the layers. However, no systematic investigation of the mode of distribution of cell sizes has so far been undertaken. As regards the possible significance of such quantitative studies it should be recalled that Malone (1932) advanced the view that the size of a neuron is related to its specific function, to the volume of its activity, and to its tendency to maintain a uniform irritability. Although the central problem of cyto-architecture, namely, its functional significance, is far from solved, additional information along structural lines also may prove to be of value.

MATERIAL AND METHODS

A block of human brain tissue containing the lateral geniculate body was cut in 10 μ sections in a plane at right angles to the course of the optic tract and stained with Borell's methylene blue. The regions of the nucleus chosen for making measurements were selected in terms of the various retinal projection areas. In the central vision area which is, in general, characterized by six laminae, four antero-posterior levels were chosen at regular intervals from the foveal centre towards the periphery (cf. Sections A, B, C and D in Table 1). In the human brain, when these six laminae are traced to the peripheral vision area, layers 1 and 2 are continued as separate and discrete layers, whereas layer 3 fuses with layer 5, and layer 4 with layer 6 to form two 'small-celled' laminae (Text-fig. 1). These two composite layers of the peripheral vision area will be designated in the following as layers (3+5) and (4+6). In the projection area for the lower homonymous quadrants of the peripheral hemiretinae four antero-posterior levels were chosen, and in that for the upper homonymous quadrants three levels were chosen for measurements of the cells of their respective four laminae (cf. Table 1).

As was shown in a previous study (Chacko, 1948*a*), the central vision area has the shape of an inverted pyramid with a flattened apex directed towards the ventral hilum and a convex base directed towards the dorsal crest (Text-fig. 1). In frontal sections this region appears roughly triangular, *EF* representing the axial plane corresponding to the horizontal meridian of the retina. The sample fields in each of the layers of the central vision area were located in a strip extending along the axial plane from the hilum to the dorsal crest. Since layers 1 and 2 (the large-celled elements) are very thin, less dense than the other layers, and limited in extent in this region, only 25–40 cells were found to be available for measurements in the sample fields of these laminae. In the case of layers 3, 4, 5 and 6 (the small-celled elements) 60 cells were measured in each layer of each of the four sections studied so that a total of 240 cells were measured in each layer, amounting to 960 cells in the whole central vision area.



Text-fig. 1. Diagram illustrating the extent of the central and peripheral vision projection areas in a frontal section through the human lateral geniculate body. *AB* indicates boundary between central vision area and the projection area for the upper homonymous quadrants of the peripheral hemi-retinae (medial tubercle). *CD* indicates boundary between central vision area and the projection area for the lower homonymous quadrants of the peripheral hemi-retinae (lateral horn). *EF* represents the axial plane corresponding to the horizontal meridian of the retina. Lat. lateral. Med. medial.

The 'lateral horn', which represents the projection area for the lower homonymous quadrants of the hemi-retinae, exhibits a four-laminar pattern throughout its extent. The sample fields in this region were located along a strip midway between the free margin of the 'lateral horn' and its junction with the central vision area. In the projection area for the upper homonymous quadrants, only the medial tubercle shows the typical four-laminar pattern and the measurements were, therefore, limited to the cells of the tubercle. Because this region is relatively limited in extent in any single section, the strips chosen for measurements covered nearly the whole distance between the central vision area and the medial end of the tubercle. In both of the peripheral vision projection areas, the number of cells available for measurements in layers 1 and 2 was somewhat limited, although not to such an extent as in the central vision area. In most of the sections the number of cells measured represented the total number available in each section. The number of cells measured in each of layers 1 and 2 ranged from 18 to 47. In each of the composite layers

(3+5) and (4+6), 40–60 cells were measured. The monocular vision area was not included in the present study.

The central vision area of the geniculate nucleus of the macaque monkey was studied briefly in one typical section (Table 2).

In view of the fact that nerve cells may assume very irregular shapes, it is rather difficult to make precise measurements of their size. The cells of the human geniculate nucleus, as is evident from Pl. 1, appear triangular, polygonal, spindle- or flask-shaped. The method finally adopted for measurements consisted in measuring the long and the short diameters of the cell bodies by means of a screw eyepiece micrometer. The criterion on the basis of which cells were selected for measurements consisted in choosing only cells with intact and well-defined nucleoli. For further statistical studies the mean of the large and small diameters was noted for each cell.

RESULTS

The results of the measurements of the diameters of cells in various projection areas of the human geniculate nucleus are summarized in Table 1. First, the results obtained in measuring the cells of the central vision area will be considered. An inspection of the microphotograph in Pl. 1 shows not only the marked size differences between the cells of laminae 1 and 2 on the one hand and laminae 3–6 on the other, but also seems to indicate a size gradient from lamina 3 to 6. Such an impression is

Table 1. *Means and standard deviations of diameters of cells in μ measured in different laminae of various projection areas in the human lateral geniculate body*

Layer	No. of cells measured	Mean	σ
		Central vision area	
Section A			
1	40	22·0±0·57	3·61±0·40
2	25	24·8±0·65	3·24±0·46
3	60	19·1±0·31	2·41±0·22
4	60	15·6±0·22	1·74±0·16
5	60	15·4±0·25	1·96±0·18
6	60	14·2±0·24	1·89±0·17
Section B			
1	30	23·9±0·38	2·09±0·27
2	28	24·5±0·61	3·25±0·43
3	60	18·9±0·27	2·12±0·19
4	60	17·8±0·31	2·37±0·22
5	60	15·8±0·20	1·54±0·14
6	60	13·8±0·25	1·95±0·18
Section C			
1	30	22·8±0·53	2·89±0·37
2	30	23·0±0·57	3·11±0·40
3	60	18·2±0·34	2·65±0·24
4	60	17·0±0·20	1·56±0·14
5	60	15·5±0·29	2·28±0·21
6	60	14·8±0·21	1·60+0·15
Section D			
1	30	23·6±0·62	3·40±0·44
2	30	23·8±0·58	3·19±0·41
3	60	19·5±0·25	1·96±0·18
4	60	17·9±0·29	2·22±0·20
5	60	16·9±0·31	2·40±0·22
6	60	14·7±0·24	1·87±0·17

Table 1 (*continued*)

Layer	No. of cells measured	Mean	σ
Projection area for the lower homonymous quadrants of the peripheral hemi-retinae			
Section A			
1	30	21·7±0·54	2·98±0·38
2	18	22·8±0·61	2·62±0·44
(3+5)	60	17·5±0·22	1·74±0·16
(4+6)	60	16·8±0·22	1·72±0·16
Section B			
1	47	21·3±0·47	3·26±0·34
2	29	23·5±0·57	3·07±0·40
(3+5)	60	18·3±0·28	2·18±0·20
(4+6)	60	15·8±0·20	1·53±0·14
Section C			
1	44	20·4±0·40	2·65±0·28
2	32	21·2±0·55	3·12±0·39
(3+5)	60	17·8±0·24	1·89±0·17
(4+6)	60	15·4±0·19	1·52±0·14
Section D			
1	22	23·6±0·73	3·43±0·73
2	38	23·5±0·39	2·39±0·27
(3+5)	60	18·9±0·28	2·17±0·20
(4+6)	60	16·2±0·24	1·88±0·17
Projection area for the upper homonymous quadrants of the peripheral hemi-retinae			
Section A			
1	20	23·6±0·42	1·92±0·30
2	20	21·4±0·51	2·27±0·36
(3+5)	40	16·7±0·32	2·01±0·22
(4+6)	60	15·5±0·22	1·67±0·15
Section B			
1	47	23·4±0·47	2·99±0·33
2	29	23·7±0·54	2·43±0·38
(3+5)	60	17·9±0·28	2·15±0·20
(4+6)	60	16·1±0·25	1·92±0·17
Section C			
1	40	23·0±0·41	2·60±0·29
2	20	25·8±0·37	1·64±0·26
(3+5)	60	17·0±0·21	1·62±0·15
(4+6)	60	16·8±0·29	2·27±0·21

confirmed by the data presented in Table 1. It is seen that there is a decrease in the mean diameters of the cells in the ventro-dorsal direction from lamina 3 to 6 in all the sections studied. Further analysis indicates that the differences between the means of the cell diameters in the small-celled laminae 3–6 are, in practically all instances, statistically significant. The fact that the cells decrease significantly in size in the ventro-dorsal direction is also evident from the histograms of laminae 3–6 in Text-fig. 2 and from the smoothed frequency polygons in Text-fig. 4.

As regards the results obtained in measuring the cells of the projection areas for the lower and upper homonymous quadrants of the peripheral hemi-retinae, the findings are similar to those in the central vision area in that there exists a size gradient in the small-celled layers (3+5) and (4+6). There is a decrease in the mean diameters of the cells in the ventro-dorsal direction from one lamina to the other (Table 1). The mean diameter of the cells in lamina (4+6) is significantly smaller than that of the cells in lamina (3+5) in six out of the seven sections studied. The histograms in Text-fig. 3 and the smoothed frequency polygons in Text-fig. 5 illustrate this decrease in size with reference to the projection area for the lower homonymous quadrants of the peripheral hemi-retinae.

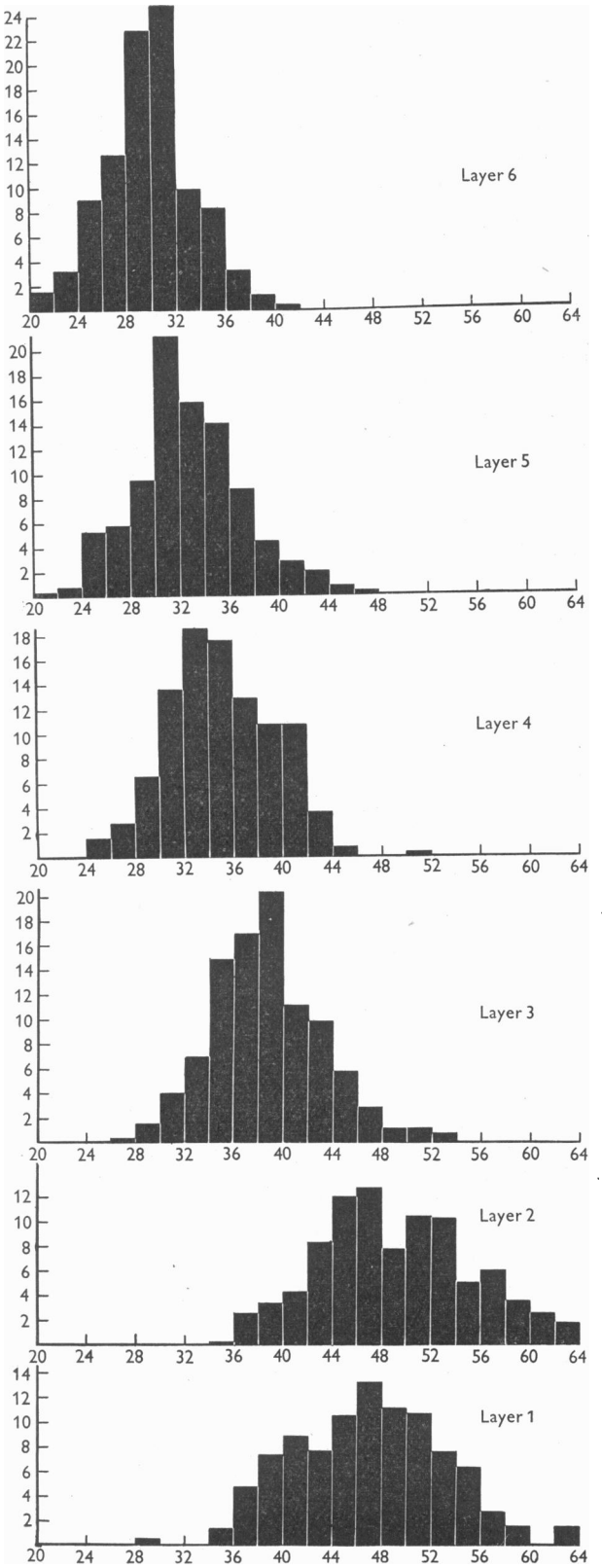
An analysis of the measurements in the sample fields of the large-celled laminae 1 and 2 does not reveal a size gradient as definite as that found in the small-celled laminae. As regards the central vision area, the mean diameter of the cells in lamina 2 is larger than that of the cells in lamina 1, but only in one of the four sections studied is the difference between the means statistically significant (Table 1; cf. also Text-figs. 2 and 4). In considering the measurements in the projection area for the lower homonymous quadrants of the peripheral hemi-retinae it is evident from Table 1 that the mean diameter of the cells in lamina 2 is larger than that of the cells in lamina 1 in three of the four sections studied. This difference is found to be at least tolerably significant (cf. also Text-figs. 3 and 5). In the projection area for the upper homonymous quadrants of the peripheral hemi-retinae the mean diameter of the cells in lamina 2 is found to be larger than that of the cells in lamina 1 in two of the three sections studied, but in only one is the difference statistically significant. It must be remembered that the laminar organization of this region is not as uniform as in the projection area for the lower homonymous quadrants, and that the medial tubercle presents a limited and rather unsatisfactory area for making measurements. If the data on cell diameters in the large-celled laminae of the central and peripheral vision areas are viewed as a whole, it becomes apparent that they have failed to establish any clear-cut size gradient.

In considering the transition from the large-celled to the small-celled layers, that is, the difference between laminae 2 and 3 in the central vision area and that between 2 and (3+5) in the peripheral vision areas, it is evident that the mean diameter of the cells in lamina 2 tends to be markedly larger in all the sections studied (Table 1). In all instances the differences between the means of laminae 2 and 3 or between 2 and (3+5) are statistically significant.

An inspection of the histograms in Text-figs. 2 and 3 and of the smoothed frequency polygons in Text-figs. 4 and 5 clearly indicates that the several laminae differ in variability or dispersion of measurements. The range of cell diameters measured in the dorsal laminae is definitely smaller than that in the ventral laminae.

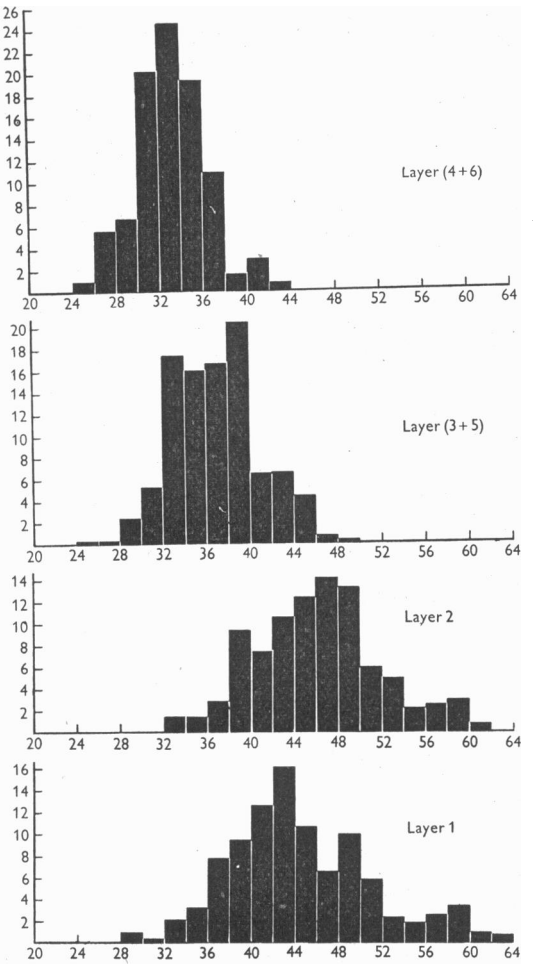
An analysis of the results with reference to crossed and uncrossed laminae readily shows the significant differences which exist in the central vision area between the mean diameters of the cells in layers 1 and 4 and layers 4 and 6 as well as between the mean diameters of the cells in layers 2 and 3 and layers 3 and 5. Similarly, significant differences exist between the means of the crossed and uncrossed layers of the peripheral vision area, that is, between layers 1 and (4+6) as well as between layers 2 and (3+5). Since in Text-figs. 4 and 5 the frequency distribution curves for the crossed laminae have been indicated by solid lines in contrast to the dotted lines for the uncrossed laminae, it can be seen at a glance that the curves for the crossed laminae are displaced towards the shorter diameters. This displacement is found in both central and peripheral vision areas and is especially marked in the small-celled layers. In Text-fig. 4, although there is an overlapping of the curves, L6 is located more to the left than L5, L4 more to the left than L3, and L1 more to the left than L2. In Text-fig. 5, L(4+6) is located more to the left than L(3+5), and L1 more to the left than L2.

If the means of the cell diameters of the various laminae of the central and peripheral vision areas are compared (Table 1), it is found that the laminae with the



Text-fig. 2. Frequency of diameters of cells in laminae 1–6 in central vision area. Abscissa: diameter in μ ($\times 2$). Ordinate: percentage frequency.

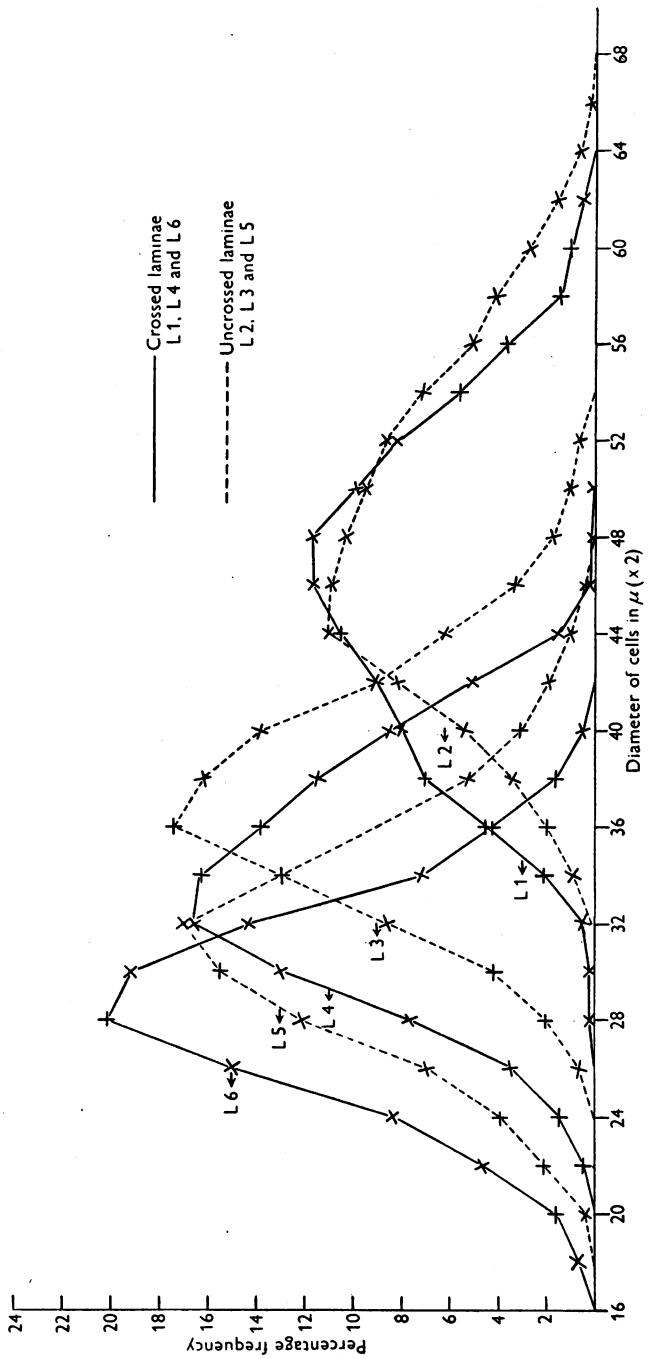
smallest mean cell diameters are located in the central vision area. There is a greater range of cell diameters in the central than in the peripheral vision area. This greater range is brought about by the occurrence of smaller cell diameters. Further, if the composite laminae of the peripheral vision area and their daughter laminae in the central vision area into which the former split, are compared, the laminae of the



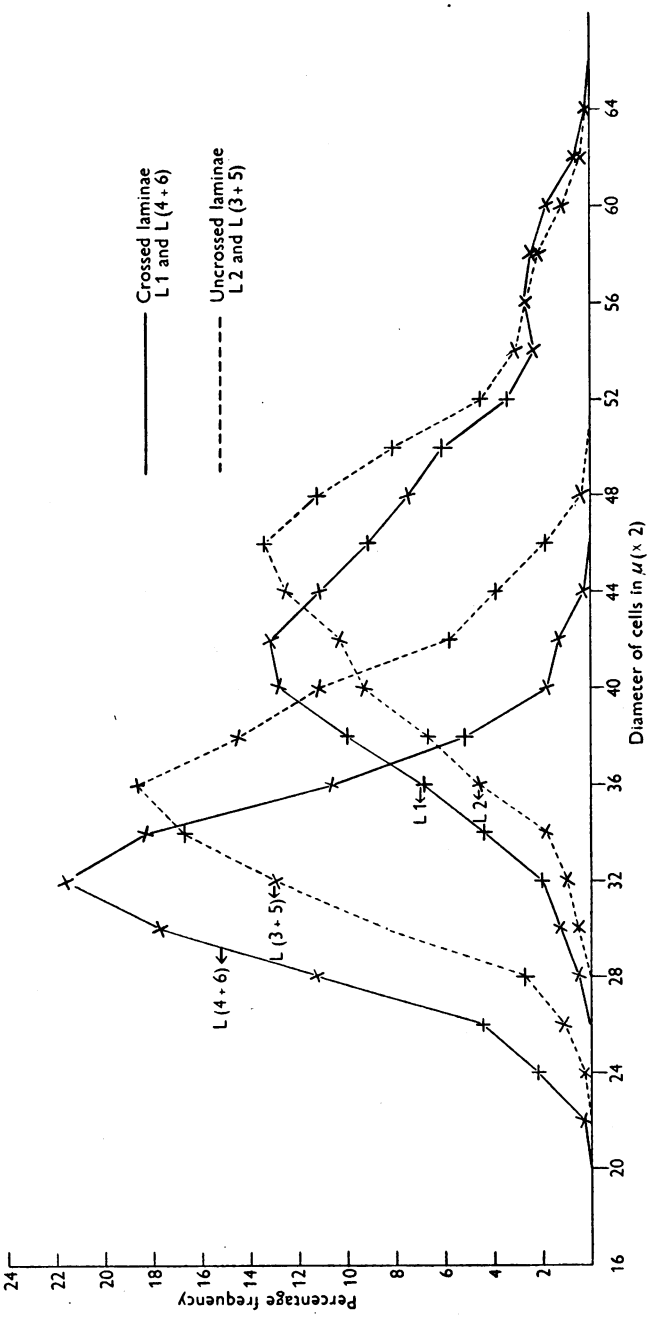
Text-fig. 3. Frequency of diameters of cells in laminae 1, 2, (3+5) and (4+6) in the projection area for the lower homonymous quadrants of the peripheral hemi-retinae. Abscissa: diameter in μ ($\times 2$). Ordinate: percentage frequency.

central vision area are found to have a greater range of cell diameters. The mean of the distribution of all cell diameters measured in each of the parent laminae of both the peripheral vision areas lies between the means of the two daughter laminae. Similarly, the median of the distribution of the cell diameters of each parent lamina lies between the medians of the distributions of the corresponding daughter laminae.

From a comparative point of view it is of special interest that a cell-size gradient



Text-fig. 4. Frequency of diameters of cells in different laminae of the central vision area.



Text-fig. 5. Frequency of diameters of cells in the different laminae of the projection area for the lower homonymous quadrants of the peripheral hemi-retinae.

similar to that in the human geniculate nucleus is also present in the lateral geniculate body of the rhesus monkey (Pl. 2 and Table 2).

Table 2. *Means and standard deviations of diameters of cells in μ measured in different laminae of the central vision area in the lateral geniculate body of the rhesus monkey*

Layer	No. of cells measured	Mean	σ
1	28	23·5±0·47	2·47±0·33
2	28	24·5±0·65	3·20±0·43
3	28	17·6±0·40	2·12±0·28
4	28	15·3±0·36	1·90±0·25
5	28	14·9±0·30	1·57±0·21
6	28	14·5±0·37	1·97±0·26

DISCUSSION

It has been suggested by several investigators, but principally by Malone (1932), that the functional specificity of nerve cells is related to their internal structure, their shape, and their size. Malone has made an extensive study of the fundamental types of nerve cell structure. He emphasizes the point that the cell bodies and dendrites have a higher metabolic rate and exhibit a greater variation in histological character than axons, and assumes that these features are associated with a wide range of local activity radically different from that of the axons. According to him, the size of the cell body and dendrites is dependent on the activity of the neuron and the extent to which it receives stimuli. He points out, for instance, that typical correlating neurons have small cell bodies with extensively branched axons and poorly developed dendrites and, furthermore, that they are numerous and lie close together in centres in which impulses diffuse widely and do not enter into definite common paths in contrast to co-ordinating centres containing relatively few neurons with large cell bodies and well-developed dendrites. In his opinion, the resistance to fatigue varies with the size of the cell body, the small cell bodies of typical correlating centres fatiguing more easily than large cell bodies.

The present study has established the existence of a size gradient in the central and peripheral vision areas of the lateral geniculate body. The measurements indicate that the range of cell diameters is smaller in the peripheral than in the central vision area. It has also been found that each of the layers (3+5) and (4+6), when traced to the central vision area, splits into two laminae and that the means (as well as the medians) of the frequency distributions of the two daughter laminae are larger or smaller than the mean (or median) of the parent lamina.

In speculating on the possible significance of these findings, the attempt may be made to interpret the activity of the laminae as follows: a lamina possesses a number of neurons comprising a certain range of sizes and yielding a typical frequency distribution. These elements acting as a whole are capable of producing a certain type of total activity. The resultant activity of any particular lamina will be chiefly determined by the activity of its middle range elements, but such activity will probably be modulated by the elements at the two extremes of the distribution. The splitting of a particular lamina into two discrete laminae will widen the range

of activity within which each daughter lamina may then be assumed to establish its own specific maximum activity, and the latter is directly determined by its middle-range elements. Various findings in sensory physiology and psychology clearly indicate that there exist numerous visual functions with respect to which the discriminative capacities of the central retina are superior to those of the peripheral retina.

It has been previously pointed out in Text-figs. 4 and 5 that the distribution curves for the crossed laminae L1, L4 and L6 are displaced towards the shorter diameters when compared with the distribution curves for the uncrossed laminae L2, L3 and L5. Differently expressed, the cells of the uncrossed laminae are on the whole relatively larger than those of the crossed laminae. The laminae related to the corresponding halves of the two eyes are identical in number, but they are not necessarily duplicate mechanisms in functional respects since they are not identical morphologically. It appears likely, therefore, that the neural elements related to one eye respond to a certain extent differently from those related to the other eye whenever corresponding points of the retinae are simultaneously stimulated. The impulses from the two corresponding points are relayed to the same 'unit' in the geniculate body although it must be remembered that the crossed laminae of such a 'unit' are, as enucleation experiments indicate, morphologically independent of the uncrossed laminae. Anatomical considerations of this nature thus lead to the assumption of certain functional differences between temporal and nasal halves of the retina, but they do not suggest that such differences are very pronounced. It is to be expected that the functional efficiency of either the temporal or nasal half of one retina is less than that of two homonymous hemi-retinae and that the impulses arriving from the contralateral eye lead quantitatively and qualitatively to a widening of the response activity. The functional superiority of the nasal retina in visual acuity, colour sensitivity, etc., has been commented on by various investigators (Köllner, 1920; Best, 1917; Gelb & Goldstein, 1925; Klüver, 1927). It is Köllner's thesis that there exists an inequality of 'corresponding impressions' and a superiority of the nasal retina. The data of the present investigation do not suggest a functional superiority of either the nasal or temporal half of the retina, but they do seem to provide an anatomical basis for an inequality of 'corresponding impressions'. Since the nasal as well as the temporal retina, each in its own specific way, contributes to binocular vision, the conducting units of fibres from both eyes and the total number of laminae in each projection area will have to be taken into consideration in analysing 'units' in the visual system.

The existence of a size gradient in the central and peripheral vision areas of the lateral geniculate body is of particular interest in view of the existence of various morphological gradients in other parts of the visual system. In the receptor layer of the retina, the rods slowly and gradually increase in thickness and decrease in length from the central area to the periphery. Similarly, the cones change from short and thick to long and fine structures, thus exhibiting a gradient in regard to both size and shape. An investigation of the different varieties of bipolar and ganglion cells likewise yields size gradients. It has been observed that the axons and telodendria of the larger retinal neurons are thicker than those of the smaller neurons (Polyak, 1941). A study of the optic nerve reveals a continuous fibre

spectrum (Chacko, 1948*b*). As regards the optic radiation, Polyak mentions that the calibre of the fibres varies from fine to medium and coarse fibres.

If the assumption is made that cell size is one of the morphological characteristics related to functional specificity, cell-size gradients, such as exist in the geniculate body as well as in various layers of the retina, may be thought to have some relation to functional gradients of various kinds. Gasser and his collaborators have, for instance, established an approximately linear relationship between the velocity of conduction and the diameter of nerve axons (Gasser, 1941). As regards the visual system, it mediates responses to differences in radiation varying in luminous intensity or in wave-length. The responses made are frequently responses to stimuli of a graded character. The organism must be able to fall back on mechanisms capable of dealing with stimuli lying in the same 'dimension', such as neutral colours constituting a brightness series or the variations in hue in certain portions of the spectrum. The question may be raised whether cell size gradients or fibre gradients are related to or suggestive of mechanisms which cope with variations in the 'quantity' or 'quality' of light. The problem also arises whether mechanisms, such as Granit's modulators (1947) yielding narrow sensitivity curves in different regions of the spectrum, have some counterpart in the anatomical organization of the lateral geniculate body. Neither the histological nor the electrophysiological analysis has reached the point at which profitable hypotheses can be offered. In the meantime, Hartridge (1948) is undoubtedly right in pointing out that Granit's modulators form 'what amounts to a polychromatic series'. Further research will be necessary to determine whether the serial character of the modulators is in some way related to size gradients or other morphological gradients in the visual sector of the central nervous system.

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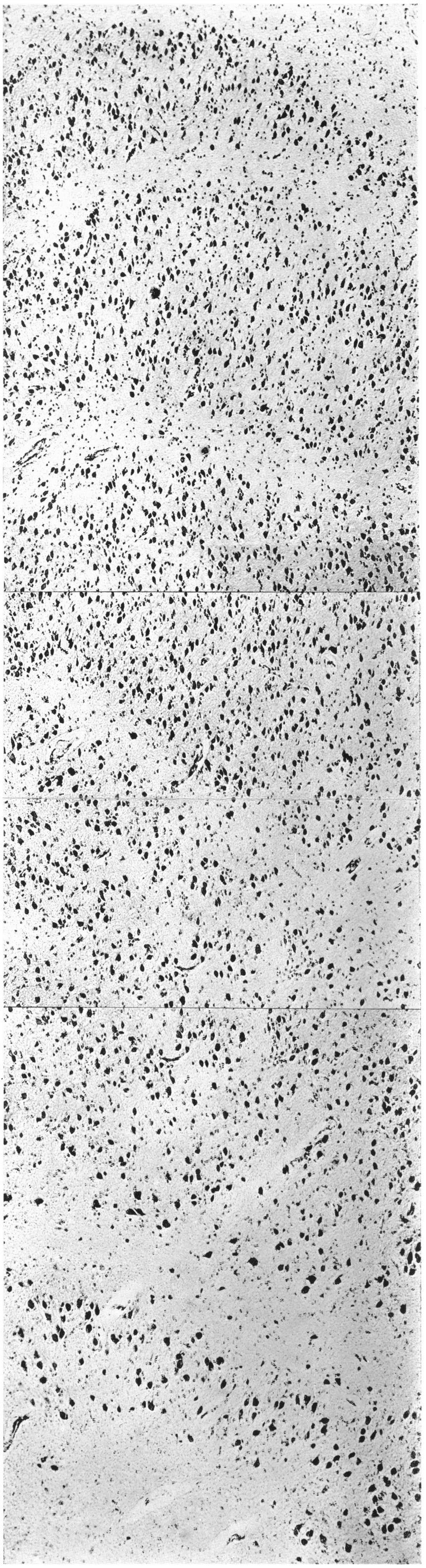
EXPLANATION OF PLATES

PLATE 1

Microphotograph of a section through the central vision area of the human lateral geniculate body. ×80.

PLATE 2

Microphotograph of a section through the small-celled laminae of the central vision area in the lateral geniculate body of the rhesus monkey. ×80.



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