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Cytoarchitecture of the dorsal lateral geniculate nucleus in the rabbit

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Summary. The cytoarchitecture and morphometry of the neurons in the α_E sector of the dorsal lateral geniculate nucleus of the rabbit have been studied. The preparation techniques used were those of Golgi-Adams and Klüver-Barrera. Our method was to subdivide the α_E sector into three zones (superior, medial and inferior) and then to cut each zone along the horizontal, transverse and saggital planes in order to obtain precise measurements and descriptions of the neurons whatever their orientation.

Differences exist in both the size and distribution of neurons in the inferior zone of the α_E sector compared to the other two.

Key words: Geniculate nucleus, Cytoarchitecture, Rabbit

Introduction

The dorsal lateral geniculate nucleus (dLGN) of the rabbit, although relatively simple in the structure and similar to that of the rodents, also bears certain resemblances to that of higher mammals whose sense of vision is more acutely developed (Holcombe and Guillery, 1984). In fact, although the nucleus is non-layered and receives optical impulses almost exclusively (90%-95%) from the contralateral eye (Giolli and Guthrie, 1969; Sanderson, 1975), in Nissl preparations it can be subdivided into two sectors (α and B) as demonstrated by Rose (1935) and by Rose and Malis (1965). The α sector can once more be divided into two subsectors (Holcombe and Guillery, 1984); an external one composed of relatively small, tightly packed cells (α_E) and an internal one containing slightly larger, less densely arranged cells (α_I).

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Present-day knowledge of the structural elements of the dLGN allows us to affirm that these cells are similar in all mammals and correspond to two distinct types, with different morphologies and fuctions: neurons, which extend from the geniculate nucleus to the cortex and interneurons, which act exclusively within the nucleus itself, as has been shown by Tello (1904) and later confirmed by O'Leary (1940), Szentágothai (1966), Wong-Riley (1972), Famiglietti and Peters (1972), Grossman et al. (1973), Rafols and Valverde (1973), Ríos et al. (1981), among others. In fact several authors, such as Guillery (1966), working with cats, Krieber (1975), with rats, Caballero et al. (1986), with rabbits, Campos-Ortega et al. (1968) and Wong-Riley (1972), with primates, have identified two subtypes of geniculocortical relay neurons, thus bringing to three the real number of neuron types in the mammal dLGN.

Although on the whole there is agreement about the identification of these three neuron types, there are some researchers who see a still more complicated pattern: Guillery (1966), has created yet a fourth category; Famiglietti (1970) also recognizes a category of isodendritic neurons; Meyer and Albus (1981) and Hitchcock and Hickey (1983) have described five classes of neuron in the C layer of the cat dLGN.

It is this increasing degree of complexity in the neurons in the dLGN, together with a relative absence of data concerning their distribution throughout the various sectors, that has prompted us to carry out this research, the aim of which has been to clarify certain aspects of the cytoarchitecture and morphometry of the neurons in the rabbit dLGN, especially in its α_E sector.

Materials and methods

The rabbits used were hybrid California-New Zealand rabbits, weighing around 3kg. Each animal was anaesthetized with urethane solution and perfusion was carried out via the carotid arteries, first with a saline solution and then with the appropriate fixative. The

brain was removed and the diencephalon was separated from it. This was then cut in half and each half was trimmed down leaving a block containing the dLGN.

Six rabbits were perfused with 10% formaldehyde in saline solution and afterwards with a mixture of alcohol-formaldehyde-acetic acid, in order to prepare the brain for the Klüver and Barrera staining. The blocks containing the dLGN were fixed in Carnoy for 48 hr. They were washed for several hours in a saturated solution of calcium carbonate in absolute alcohol. The blocks were subsequently embedded in paraffin, cut into 15μ sections and stained using Klüver and Barrera's method (1953).

Another six animals were treated according to the Golgi-Adams technique (Adams, 1979). After the fixing and impregnation of the blocks they were coated in paraffin and cut into 60μ sections with a sliding microtome.

Some of the blocks of tissue were cut along the horizontal, others the transverse and the rest the saggital plane. Cutting along these three planes has allowed us to make a detailed analysis of the geniculate nucleus and arrive at precise morphometric definitions of its neurons. As Droogleever Fortuyn pointed out as long ago as 1964, it is impossible to achieve a realistic picture of the whole if the orientation of the cells is not taken into account. This orientation follows «lines of cellular elongation», which, as Rose and Malis (1965) show, correspond to the lines of projection (Bishop et al., 1962; Kaas et al., 1972).

Individual sections of each dLGN were selected at regular intervals (to a total of 25% of the whole) to carry out three-dimensional reconstructions of the nucleus. Sections were traced onto onion paper with the help of a camera lucida and each tracing was divided into three sectors (Figs. 1, 2), α_E, α_I, and β (Holcombe and Guillery, 1984).

To analyze the degree of homogeneity of the α_E sector with regard to its neuronal size, it was subdivided dorso-ventrally into three portions of equal length, referred to as the superior (S), medial (M) and inferior (I) zones (Fig. 3).

In practice, the process for establishing the three zones in the nucleus depends very much on the plane along which it is cut. Thus, when the cut is along the horizontal plane it is only necessary to divide the number of sections into three equal lots, each of which will correspond to one of the zones: the dorsal lot to the superior zone, the intermediate lot to the medial zone and the ventral lot to the inferior zone. When the cut is along the transverse or saggital plane it is first necessary to make drawings on onion paper of each section of the dLGN selected to study (Fig. 4a). Once the graphic representation of the pile of sections is complete they are projected onto each other and divided into three equal parts by two lines perpendicular to the Y-axis (Fig. 4b). All of the drawings are then divided up in like manner using these lines as reference (Fig. 4c).

The area and maximum diameter of the projection in the plane of the cut of a suitable number of neurons in each zone are measured, following Navascués et al. (1981), with a semiautomatic image analyzer (IMCO-Microm), which receives the images through a video-camera attached to a universal optical microscope with a 40x objective.

As regards selection from the piles of sections of the individual cells to be studied, this is done by a weighted random method. The size of the representative sample of neurons has been established by the Azorín-Poch formula (1972), based of Tchebycheff's unequality. The correction to the overall cell count has been made with the formula provided by Floderus (1944).

With the nuclei processed by the Golgi-Adams method, apart from these parameters (area and maximum diameters of the neuronal profiles), the morphological patterns of the cells have been classified according to the criteria of Caballero et al. (1986) in order to calculate the percentages of each neuron type in each of the three zones.

Results

The parameters that we have used as indicators of the neuron sizes are the area of neuron projection in the section containing the nucleolus (that is to say fairly central sections) and their maximum diameter. Both parameters have been determined with a sufficient number of neuron samples, both in nuclei treated by Klüver and Barrera's method and in those processed by the adapted Golgi-Adams method.

The mean values for these parameters, determined for each region in the α_E (superior, medial and inferior), each direction of cut (horizontal, transverse and seggital) and each method of preparation (Klüver and Barrera and Golgi-Adams) are set out in Tables 1 and 2.

The implications of the results will be analyzed more fully in the «Discussion» but it is worthwhile commenting briefly here on some of the differences to be seen. Firstly, the discrepancies in neuron sizes according to which method was used is quite stricking, although the trend in each region is the same. Thus, whatever the method employed and whichever the direction of the cut, the superior and medial zones show similar characteristics and the values of the parameters are constantly much higher than those of the inferior zone. With the horizontal and transverse cuts the average values are similar and greater than with the saggital ones; this discrepancy can be put down to the fact that the majority of neurons tend to be orientated perpendicularly to the saggital plane in the nucleus.

As well as determining the above parameters, we studied the neurons by the Golgi-Adams method as described each to one of the neuron types already described in the literature, according to the peculiarities of its dendritic processes. These types are comprised of:

Type 1 (t1-).- (Fig. 5a) Thalamus-cortex relay neurons; these are fairly large (maximum diameter ranging from 27μ to 35 μ) with a pyramidal or roughly ellipsoid perikaryon, from which four or five primary smooth dendrites radiate, which then ramify into dendrites with a rougher surface and isolated appendices; the most characteristic appendices are

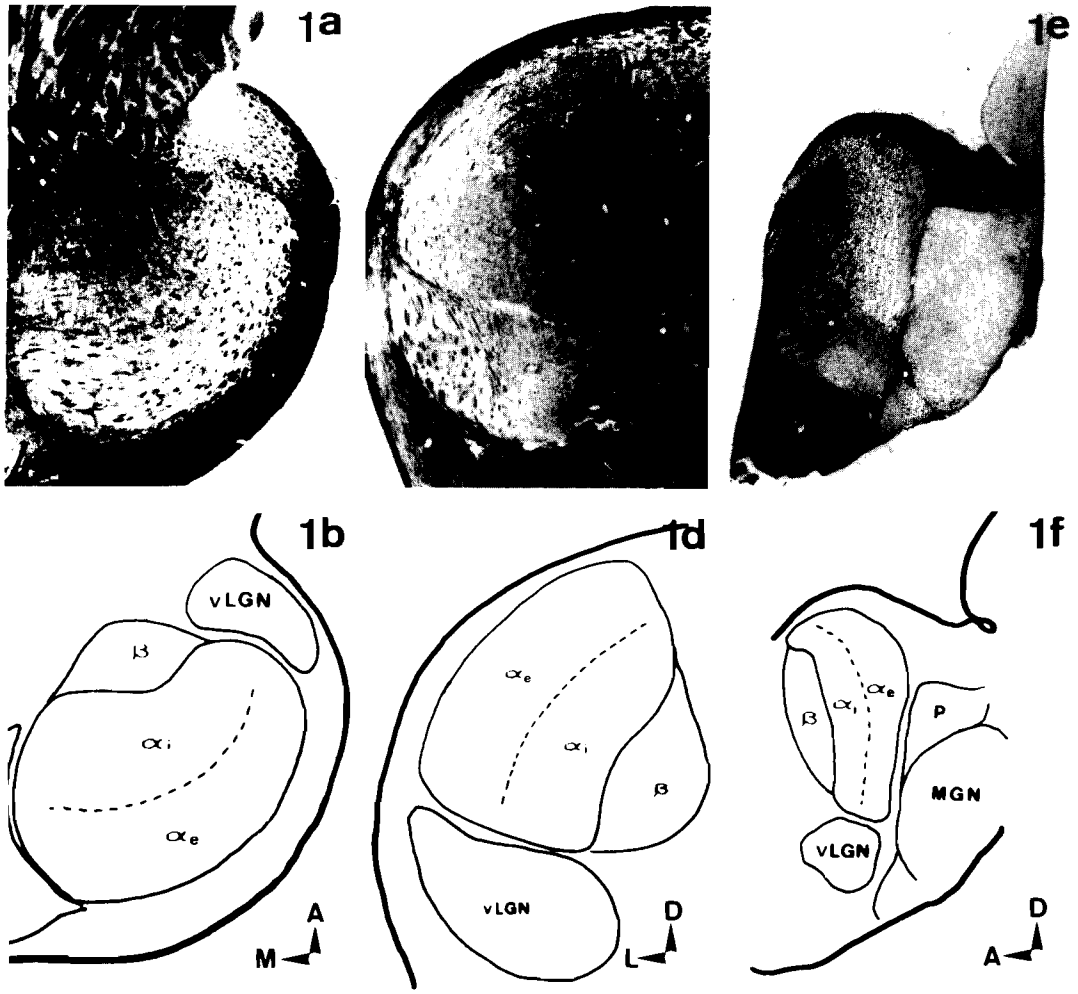


Fig. 1. Histological images and drawings corresponding to a horizontal (a-b), transverse (c-d) and saggital (e-f) section of rabbit dLGN (α_E, α_i and ß sectors) prepared by the Klüver and Barrera method. vLGN: ventral lateral geniculate nucleus; P: pulvinar nucleus; MGN: medial geniculate nucleus; A: anterior; D: dorsal; L: lateral; M: medial. a, x 20; c, x 15; e x 8

Table 1. Mean values in μ^2 of the areas of the neuron profiles for each of the zones (superior, medial and inferior) in the α_E sector of the rabbit dLGN, each direction of cut (horizontal, transversal and saggital) and each method used (Klüver and Barrera and Golgi-Adams).

	Plane of section					
	Horizontal		Transverse		Saggital	
	Golgi	K&B	Golgi	K&B	Golgi	K&B
Superior Zone	292 ± 5	207 ± 3	302 ± 5	207 ± 3	261 ± 4	189 ± 2
Medial Zone	297 ± 5	209 ± 3	300 ± 5	211 ± 4	246 ± 4	194 ± 2
Inferior Zone	277 ± 5	175 ± 2	270 ± 5	187 ± 3	228 ± 4	168 ± 2

Table 2. Mean values, in μ, of the greatest diameters of the neuron profiles for each of the zones (superior, medial and inferior) in the α_E. sector of the rabbit dLGN, each direction of cut (horizontal, transversal and saggital) and each method used (Klüver and Barrera and Golgi-Adams).

	Plane of section					
	Horizontal		Transverse		Saggital	
	Golgi	K&B	Golgi	K&B	Golgi	K&B
Superior Zone	23.9 ± .2	20.8 ± .2	24.3 ± .2	19.7 ± .2	23.9 ± .2	19.7 ± .2
Medial Zone	24.0 ± .2	21.3 ± .2	24.5 ± .2	19.7 ± .2	24.3 ± .2	20.1 ± .2
Inferior Zone	22.5 ± .2	18.8 ± .2	22.9 ± .2	18.3 ± .2	23.0 ± .2	18.3 ± .2

Table 3. Mean values in μ, of each of the neuron types (t1, t2, t3 and dubious classification) identified by the Golgi-Adams method, for each of the zones in the α_E sector (superior, medial and inferior) of the rabbit dLGN.

Zone	t1 (relay)	t2 (relay)	t3 (interneurons)	?
Superior	29.03 ± .20	23.38 ± .07	18.86 ± .14	26.10 ± .22
Medial	29.16 ± .20	23.15 ± .08	18.90 ± .13	25.97 ± .23
Inferior	27.87 ± .23	22.25 ± .09	18.66 ± .11	25.23 ± .23

Table 4. Percentages of each of the neuron types (t1, t2, t3 and dubious classification) identified using the Golgi-Adams method, for the whole of the α_E sector of the rabbit dLGN, and for each of the individual regions (superior, medial and inferior).

Zone	t1 (relay)	t2 (relay)	t3 (interneurons)	?
Superior	13.5%	55.3%	9.1%	22.1%
Medial	16.8%	53.0%	9.4%	20.8%
Inferior	9.7%	48.9%	23.0%	18.4%
Total α_E sector	14.5%	52.9%	11.8%	20.8%

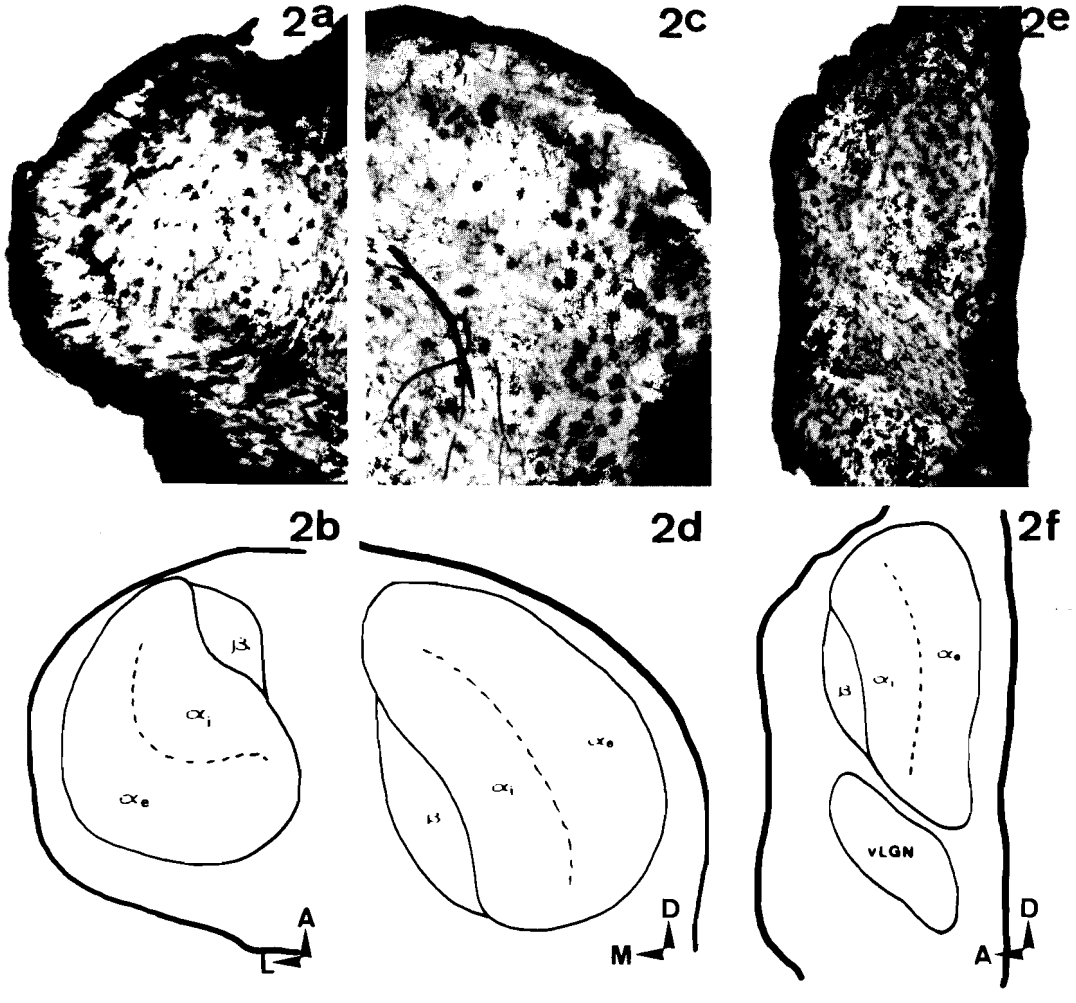


Fig. 2. Histological images and drawings corresponding to a horizontal (a-b) transverse (c-d) and saggital (e-f) section of rabbit dLGN (α_E, α_I and ß sectors) prepared by the Golgi-Adams method. vLGN: ventral lateral geniculate nucleus; P: pulvinar nucleus; MGN: medial geniculate nucleus; A: anterior; D: dorsal; L: lateral; M: medial. a, x 16; c, x 20; e, x12

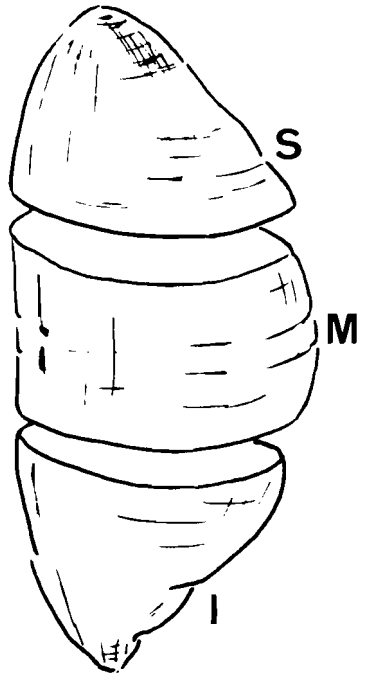


Fig. 3. Diagram showing the spatial criteria used to delimit the zones in the α_E sector. S: superior zone; M: medial zones; I: inferior zone.

conical and are most numerous on the distal dendrites.

Type 2 (t2-).– (Fig. 5b) Thalamus-cortex relay neurons with an ellipsoidal or roundish perikaryon of some 22μ, from which four or five smooth dendrites radiate. The most characteristic feature of this type of neuron is the clusters of appendices close to the point where the dendrites ramify.

Type 3 (t3-).– (Fig. 5c) These are probably intrinsic to the nucleus (interneurons) and effect some sort of internal control. The perikaryon is spherical and about 18μ in diameter; from six to eight smooth dendrites radiate from it in all directions, some ramifying extensively very close to the perikaryon. The secondary and tertiary dendrites have large numbers of isolated appendices of varied morphology (filiform, conical, uni- or multilobulate).

For more detailed information about these three types of neurons see: Guillery, 1966; Campos-Ortega, 1968; Wong-Riley, 1972; Kriebel, 1973; 1975; Caballero et al., 1986.

As far as the neurons of dubious classification are concerned, we have chosen to put them all together in a single category (?) and as such we have taken into account their dimensions and frequency.

In Table 3 we have set out the results of a comparison of the four categories of neurons with the diameter of neurons with the diameter of each neuron, measured using Golgi's method, for each of the three zones in the α_E sector. It can be seen that the t1 neurons in the superior and medial zones are significantly larger than those in the inferior zone. Finally, in Table 4, we show the percentages of each category of neurons both for the whole α_E sector and for each of its zones. The percentages for the three zones are represented graphically in Figure 6. These percentages reveal that the t3 neurons are much more numerous in the inferior zone and that there are slightly fewer t1 and t2 neurons in this zone compared to the two higher ones.

Discussion

In this work we have determined certain morphometric parameters in the neurons of the rabbit dorsal lateral geniculate nucleus which have enabled us to reach some fairly reliable conclusions about their differences and relative distribution. Our methodology has included most importantly the sectioning of the nucleus in three different directions, horizontal, transverse and saggital, a technique which is frequently and wrongly ignored, as the cells and fibres tend to be aligned along definite planes, just as they are in other areas of the central nervous system (Droogleever Fortuyn, 1964).

The first point worth noting is that the areas and diameters of the neurons were larger when measured after the Golgi-Adams preparation than with that of Klüver and Barrera (Tables 1, 2). This can be put down to the difference in thickness between the sections (60 μ with the former and only 15 μ with the latter). This will obviously influence the final average values as the thicker the sections examined, the greater will be the number of neurons left intact and thus the higher the possibility of gauging their complete size. As far as Klüver and Barrera's method is concerned, in spite of the fact that only neurons containing nucleoli are measured, because the sections are only 15 μ thick the corresponding projections of the transverse sections will only be partial images of the whole (Fig. 7).

Apart from this we found that whichever the method used both the diameters and areas of the neurons in the lowest third of the α_E sector were considerably smaller than those in the medial and superior ones. The fact that both methods produced the same results lends credence to this conclusion. Nevertheless, there remains the doubt when asserting this fact that in many areas of the central nervous system the cells are orientated in certain preferred directions. This makes it essential in cytomorphometric studies to make cuts along several planes to avoid the error of attributing illusory differences to the various sectors. Droogleever Fortuyn (1964), for example, made it clear that for a cytomorphometric study to be in any way reliable cuts along at least three planes had to be made. Furthermore, cutting sections at several angles has the added advantage of giving guidance for the most favourable plane for later physiological or electronic microscopic studies.

In our study we have found that, whichever method used, the neurons appear to be smaller in the inferior third of the α_E sector in all three planes of section (Tables 1, 2).

If we accept the considerable evidence that the neurons in the lower third of the α_E sector of the rabbit dLGN are smaller than those in the higher two sectors we

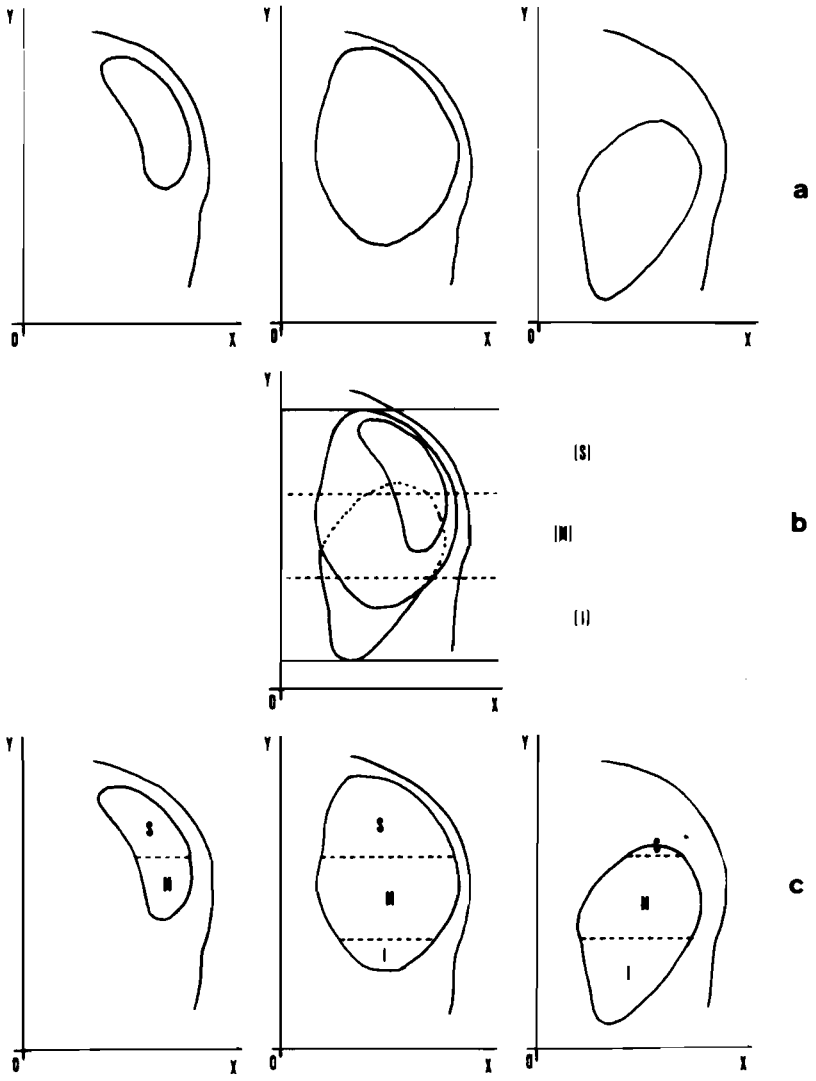


Fig. 4. Graphic plan of the procedure followed for establishing the zones in the α_E sector when cut along the transverse and saggital planes: a) drawings of individual sections; b) superimposition of all the drawings one upon the other and the division of the whole into three equal zones; c) final result on three example sections. S: superior zone; M: medial zones; I: inferior zones.

must then ask why this might be so.

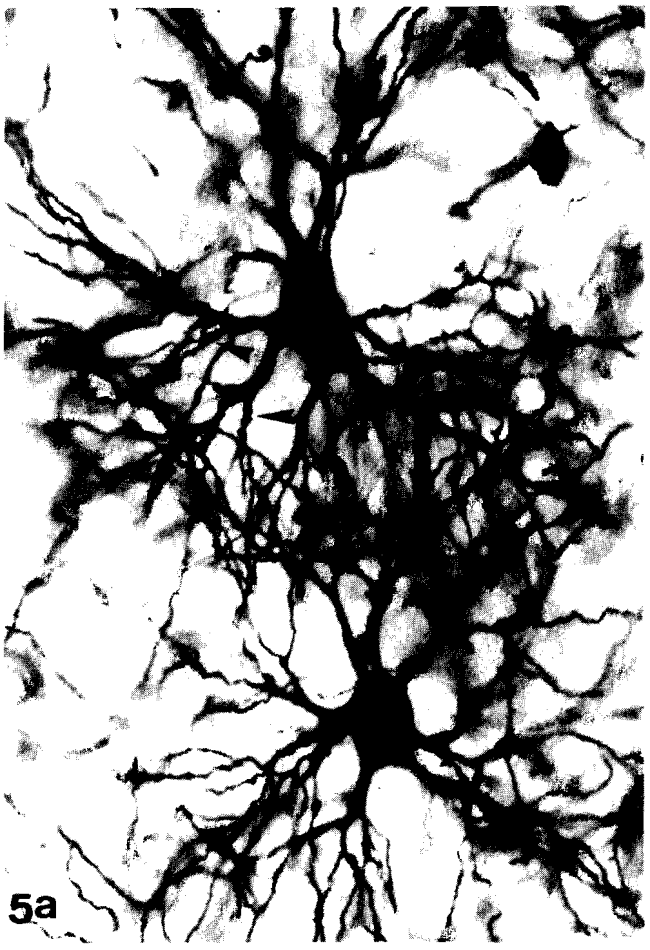
First of all we categorised the neurons according to the descriptions in the literature, taking into account the nature of the dendrites and other general somatic characteristics, using the Golgi-Adams method. The results appear in Tables 3 and 4 and in Figure 6, where the reasons for the differences in the cells of the inferior region are clearly revealed: firstly in this zone there is a far greater number of t3 neurons, the smallest type identified, there are far fewer of the larger t1 cells, and where these do occur they are somewhat smaller than their counterparts in the higher regions (27.9μ on an average as opposed to 29μ).

With regards to our methodology we should like to stress once more that the differences we have found within the apparently homogeneous structure of the α_E sector of the dLGN would have passed unobserved if we had avoided cutting it into distinct zones.

As well as differences in the size of the neurons in the inferior third of the α_E sector we have also noted differences in their relative distribution and a significant decrease in their density (Carmona et al., 1987), all of which points to a special function for this region, the more so if we take into account that the t3 neurons are morphologically similar to Golgi's type II, based on the descriptions of other thalamic nuclei made by Morest (1964, 1971), Guillery (1966), Tömböl (1967), Ralston (1971) or Famiglietti and Peters (1972). They also correspond to those reported by Kriebel (1975) in the dLGN of rats. It is interesting to note here that Gonzalo et al. (1985), using the technique of anterograde staining with horseradish peroxidase, have found that there are far fewer contralateral terminals deriving from the retina in the ventrolateral region of their α sector of the rabbit dLGN, which corresponds to the lower third of our α_E sector, than in the rest of the α sector.

If, as we believe, our t3 neurons are interneurons we must point out certain discrepancies in the overall percentages of these cells compared to those reported by other authors in other orders of mammals. The number of t3 neurons according to our calculations represents something like 12% of the total in the α_E sector (Table 4), which does not agree with the findings of Werner and Wilke (1985), who, using Nissl's procedure, give a figure as high as 36% for interneurons in the α sector of dLGN in rodents. Some of this discrepancy may well be due to the fact that we have confined ourselves to a study of the α_E sector, which accounts for only 60% of the whole (Carmona et al., 1987). Lin et al. (1977) have estimated that in the cat dLGN interneurons account for 10% of the total, Le Vay and Ferster (1979) say 25% and Geisert (1980) asserts 20%. Weber and Kalil (1983) working with the cat A layer of the dLGN, which is comparable to our α_E sector, have estimated that interneurons make up 22% of the total, while Fitzpatrick et al. (1982) report values ranging between 19% and 26%. These discrepancies are easily understood if we bear in mind that the t3 interneurons represent a considerably lesser proportion of the total (9%) in the upper regions than in the lower one (23%) and thus a final estimation of the total percentage of interneurons will depend not only on the variety of cuts made but also on the regions studied within the sector as a whole.

Lastly, as far as the «dubious» neurons are concerned,



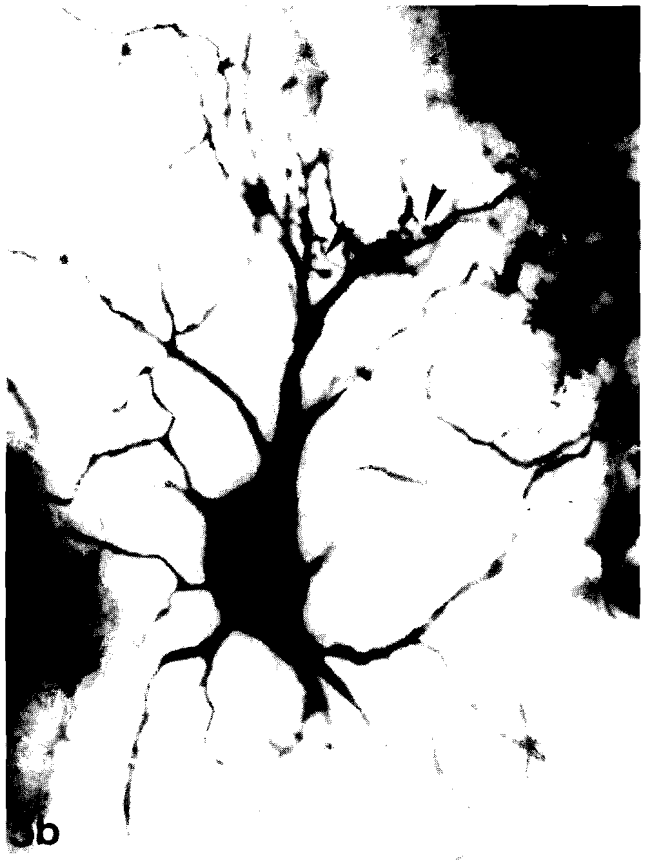
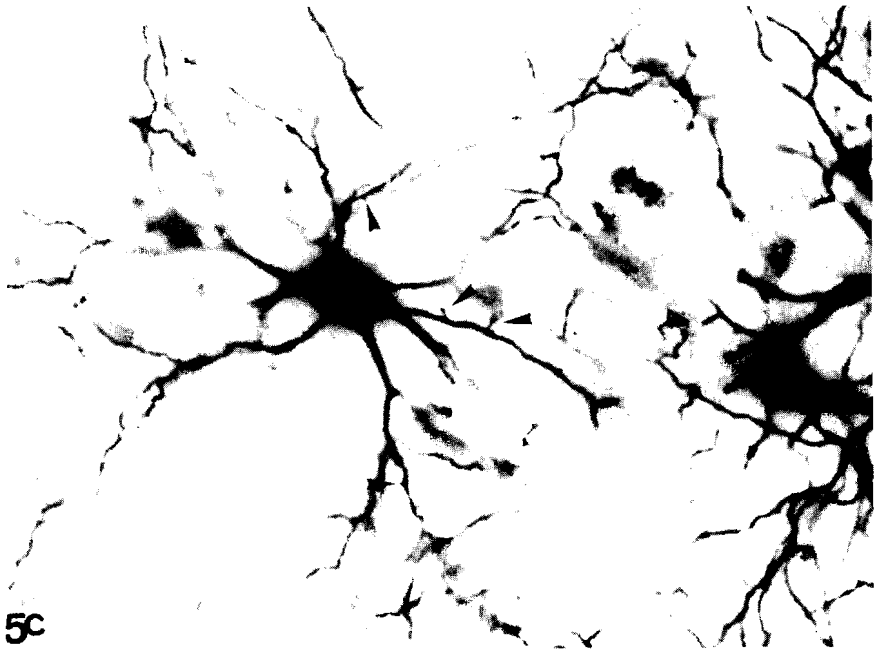


Fig. 5. a) t1 neuron type. Note the characteristic rough surface of the dendrites after first ramification (arrows). **b)** t2 neuron type. Note the clusters of appendices close to the ramification points of the dendrites, characteristic of this neuron type (arrows). **c)** t3 neuron type whose secondary and tertiary dendrites show isolated appendices (arrows). a, x 450; b, x 685; c, x 480



although it is possible that some of them do in fact fall into the three principal categories but are unrecognisable due to incomplete staining, the majority of them appear to be cells with their own proper characteristics. Thus we believe that there may well be other cells types and/on subtypes in the dLGN apart from those clearly identified. We agree with many other authors in that the situation is fairly complex. Guillery (1966), for example, dealing with the cat dLGN, makes the comment that only 60% of the neurons fit into the three accepted categories and that the rest show intermediate characteristics. Similar conclusions have been arrived at by Famiglietti (1970), Grossman et al. (1973), Meyer and Albus (1981) and Hitchcock and Hickey (1983), for which reason we consider it necessary to carry out further, even more detailed experiments, in order to clarify the true nature and function of these cells.

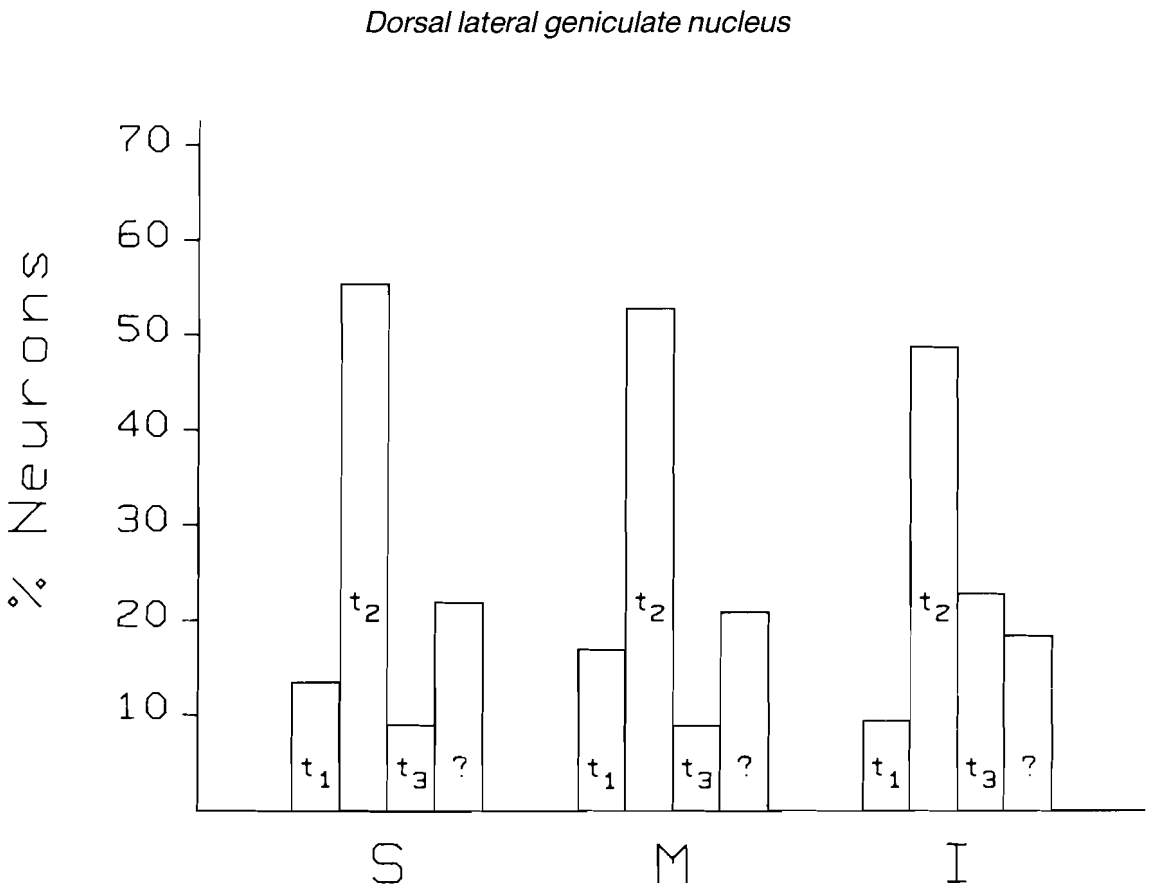


Fig. 6. Graphic representation of the percentages of each neuron type t1, t2, t3 and (?) in each of the α_E zones. S: superior zone; M: medial zones; I: inferior zone.

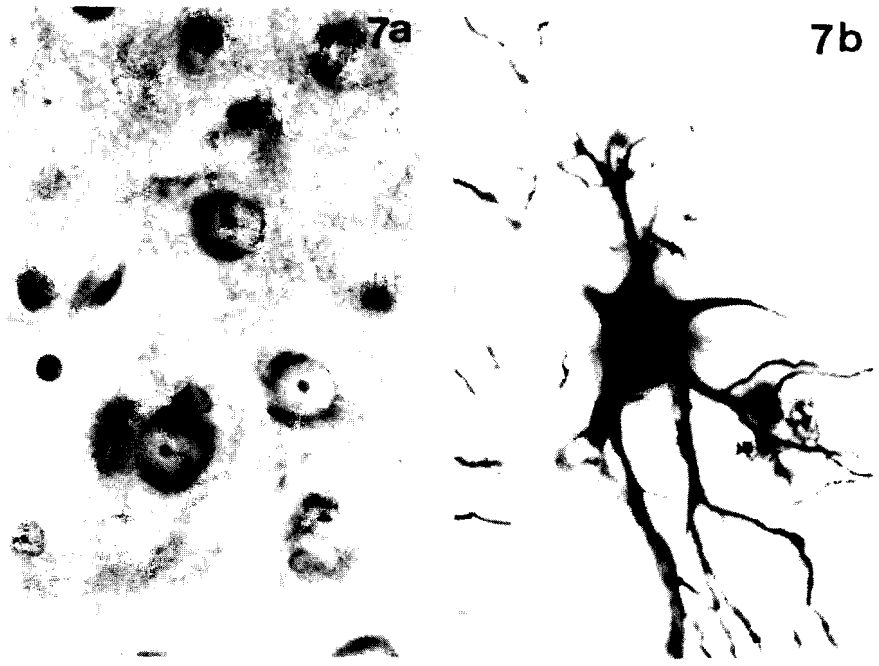


Fig. 7. Neurons of similar size in the medial zone, stained using Klüver and Barrera's method (a) and the Golgi-Adams technique (b). Magnification is the same in both; note however that the neurons prepared with the Golgi-Adams method appear larger, due to the greater thickness of the sections. x 450

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