# The neuronal structure of the dorsal lateral geniculate nucleus in the guinea pig: Golgi and Klüver-Barrera studies

Stanisław Szteyn, Krystyna Bogus-Nowakowska, Anna Robak, Janusz Najdzion

Department of Comparative Anatomy, University of Warmia and Mazury, Olsztyn, Poland

[Received 13 February 2001; Revised 6 March 2001; Accepted 6 March 2001]

On the basis of Golgi and Klüver-Barrera preparations we have distinguished four types of neurons in the dorsal lateral geniculate nucleus of the guinea pig: 1. Fusiform neurons with 1–3 thick dendritic trunks arising from each pole of the soma. The dendritic trunks branch twice dichotomically. The branches sometimes show varicosities. 2. Pear-shaped cells. From one pole of the perikaryon one or two thick dendritic trunks arise, from the opposite pole an axon emerges. The ends of the dendritic branches divide in a tuft-like manner (a characteristic feature of the interneurons). 3. Rounded neurons with 4–7 dendritic trunks without cones. The dendritic trunks branch once or twice dichotomically and give finally 2–3 thin ramifications which show a varicose course and knob-like protuberances. 4. Triangular cells with 3 thick, conically arising dendritic trunks. They bifurcate dichotomically. The surface of the dendritic trunks and of their branches is smooth.

key words: lateral geniculate nucleus, types of neurons, guinea pig

# INTRODUCTION

The lateral geniculate nucleus is well known to be the main thalamic centre on the way from the retina to the visual cortex [5,10,14,15,31]. Neurons of this nucleus mainly project to the pretectum and superior colliculus [7]. The lateral geniculate nucleus receives afferents from the following subcortical visual centres: the superior colliculus, pretectum and additional pretectal nuclei, parabigeminal nucleus as well as the lateral terminal nucleus of the accessory optic system [12,16,22]. Moreover, there are "nonvisual" brainstem regions which project to this nucleus: the mesencephalic reticular formation, dorsal raphe nucleus, periaqueductal grey matter, dorsal tegmental nucleus and the locus coeruleus [16,24,25,29]. Villar et al. [29] claim that the serotoninergic dorsal raphe projection may have a coordinating influence on the primary visual centres. Uhlrich et al. [28] assume that neurons of the perigeniculate nucleus have an inhibitory effect on the geniculate cells. A neuronal projection from the lateral geniculate nucleus to the lateral hypothalamus [18] seems to mediate information about the photoperiod influencing the suprachiasmatic nucleus as well as the lateral hypothalamic area. Mikkelsen and Möller [19] noticed that some subregions of the lateral geniculate nucleus might influence the pineal gland. Owing to the fact that the neuronal structure of the lateral geniculate nucleus has been investigated mostly in Primates [2-4,8,9,23], the aim of our studies was to give full morphological characteristics of the geniculate neurons in the guinea pig.

Address for correspondence: Stanisław Szteyn, Department of Comparative Anatomy, University of Warmia and Mazury, ul. Żołnierska 14, 10–561 Olsztyn, Poland, tel: +89 527 60 33, fax: +89 535 20 14, e-mail: odin@matman.uwm.edu.pl

### **MATERIAL AND METHODS**

The studies were carried out on the brains of 6 adult guinea pigs. The material was fixed in formalin, dehydrated in ethyl alcohol, embedded in paraffin and cut into 60 and 15  $\mu$ m scraps. The 60  $\mu$ m scraps were impregnated by means of the different Golgi procedures. The 15  $\mu$ m scraps were stained with cresyl violet and luxol fast blue according to the Klüver-Barrera method. The microscopic images of the chosen impregnated neurons were digitally recorded by means of camera, coupled with microscope and image-processing system. From 50 to 100 such digital microscopic pictures were taken at different focus layers of the section for each neuron, then the computerised reconstructions of cells from microscopic images were done. The neuropil was kept in each sort of the pictures, in order to show the real microscopic images and then was removed to clarify the illustration of neurons.

## RESULTS

On the basis of the features of neurons concerning their soma (size and shape, form and distribution of tigroidal substance), number and arborisation of the



Figure 1. Fusiform neurons. A) Golgi impregnation (non-clarified); B) Golgi impregnation (clarified); C) Klüver-Barrera method; ax — axon. (Scale-Golgi clarified neurons).

dendritic trunks as well as the appearance and location of axon, four different populations of the nerve cells were distinguished in the dorsal lateral geniculate nucleus of the guinea pig.

The fusiform neurons (Fig. 1). The perikarya of these neurons measure from 32 to 40  $\mu$ m (along the long axis). From each pole of the cell body there arise 1-3 thick dendritic trunks, which bifurcate twice dichotomically, the first time close to the perikaryon and the second time after a distance of 40–100  $\mu$ m. The dendritic branches are smooth and only some of them show a varicose course. A thin axon emerges directly from the soma or from dendritic trunks. The fusiform cells contain numerous thick and medium size tigroidal granules, which penetrate into the initial portions of the dendritic trunks. The cell nucleus is pale-stained, and has an oval or spherical form. The fusiform neurons constitute about 4% of the total number of the nerve cells forming the dorsal lateral geniculate nucleus.

The pear-shaped neurons (Fig. 2). These cells have perikarya measuring from 16 to 20  $\mu$ m. From one pole of the soma there arise 1 or 2 thick dendritic



Figure 2. Pear-shaped neurons: A) Golgi impregnation (non-clarified); B) Golgi impregnation (clarified); C) Klüver-Barrera method; ax — axon. (Scale-Golgi clarified neurons).

trunks. The dendritic trunks bifurcate dichotomically close to the cell bodies. These secondary dendritic branches after a distance of 20–30  $\mu$ m divide in a tuft-like manner with many thin ramifications. The ramifications show a varicose course and have on the surface not numerous protuberances. The dendritic trunks and their branches also give off thin collaterals. A short axon emerges conically from the opposite pole of the soma with relation to the dendritic trunks. The cells have many medium size tigroidal granules, which penetrate deeply into the initial portions of the dendritic trunks. The large, palestained cell nucleus has a spherical shape. The pear-shaped neurons are not numerous and constitute only about 1% of all nerve cells in the dorsal lateral geniculate nucleus.

The rounded neurons (Fig. 3). The perikarya of the rounded neurons measure from 15 to 20  $\mu$ m. The cell bodies give off 4–7 dendritic trunks of various thicknesses and without cones. The dendritic trunks bifurcate once or twice into dendritic branches. The distal portions of these dendritic branches give off 2–3 thin ramifications, which show varicose course and have knob-like protuberances. The dendritic trunks and their branches are smooth and give off thin collaterals. A thin axon arises directly from the surface of the cell body. The rounded cells have large, indistinct nucleus. The numerous, small granules of the tigroidal substance make a thin layer around the cell nucleus. The rounded nerve cells are the most numerous in the dorsal lateral geniculate nucleus and constitute about 60 % of the total number of neurons forming this nucleus.

The triangular neurons (Fig. 4). These cells have perikarya measuring from 22 to 30  $\mu$ m. From the soma there arise conically 3 thick dendritic trunks, which bifurcate dichotomically at the distance of 10– -20  $\mu$ m from the cell body. The majority of the secondary dendrites divide once again after 40–60  $\mu$ m of their route. The primary and secondary dendrites are smooth. Only distal, thin portions of the dendritic tree show a varicose course. A thin, long axon emerges directly from the soma, close to one of the dendritic trunks. The cell nucleus is large, distinct



Figure 3. Rounded neurons: A) Golgi impregnation (non-clarified); B) Golgi impregnation (clarified); C) Klüver-Barrera method; ax — axon. (Scale-Golgi clarified neurons).



Figure 4. Triangular neurons: A) Golgi impregnation (non-clarified); B) Golgi impregnation (clarified); C) Klüver-Barrera method; ax — axon. (Scale-Golgi clarified neurons).

and has a spherical shape. The cell bodies contain many thick granules of the tigroidal substance, which penetrate into the initial portions of the dendritic trunks. Neurons of this type constitute about 35% of the neuronal population of the dorsal lateral geniculate nucleus.

## DISCUSSION

In the dorsal lateral geniculate nucleus (GLN) of the guinea pig the dominant types of neurons are the rounded nerve cells with numerous (4-7) dendritic trunks and the triangular neurons. Less frequently there are the fusiform neurons, with diametrically arising dendrites (4%), and sporadically there are observed the pear shaped nerve cells with characteristic features of interneurons (1% of total number of GLN neurons). The investigations concerning the morphology of the neurons in the human and monkey GLN, carried out on the basis of Golgi impregnated preparations, showed the domination of multipolar nerve cells in this nucleus [4,23]. These neurons are comparable to our triangular and rounded neurons (with many dendritic trunks), which in the guinea pig constitute together about 95% of the total number of the GLN neurons. However, in the Primate GLN, there are considerably more bipolar neurons, which are comparable to our fusiform nerve cells. Courten and Garey [4] as well as Saini and Garey [23] have shown that this type of neurons are observed frequently in the GLN of man and monkey. The fusiform nerve cells constitute in the guinea pig only about 4% of the neurons in the investigated nucleus. The pear-shaped neurons, which are distinguished in our studies, have dendrites showing a varicose route and tuft-like final branches. These cells constitute about 1% of the guinea pig GLN neurons and they certainly correspond to the rare nerve cells with beaded dendrites, which were described as interneurons in the human and monkey [4,23].

Fritschy and Garey [6] reported that small cells of marmoset monkey, which are similar to our rounded neurons, constitute 74% of monkey geniculate neurons. Small nerve cells as well as large neurons, which correspond to our triangular cells, receive the main ipsi and controlateral retinal inputs and project almost exclusively to the area 17 of the cortex [13]. These retinal inputs are segregated in the different layers of the lateral geniculate nucleus, which is the thalamic relay of the primary visual pathway [6,13].

In contrast to our research and studies carried out in the human and monkey GLN [4,6,23], cat neurons with 2–3 main dendritic trunks (interneurons

which correspond to our pear-shaped cells) are claimed to constitute about 20% of all neurons in the GLN [11,30]. Their dendrites are called presynaptic dendrites [27]. The remaining neurons, with a higher number of dendritic trunks (up to 8 in the cat) and with long axon, are described as relay projective neurons [20]. Montero's [20] studies carried out on the Golgi gold-tuning preparates, revealed that GABA-ergic interneurons, with numerous branched tips, support two morphologically and functionally types of inhibitory terminals synapsing the dendrites of relay cells in the cat GLN. It is generally considered that interneurons (Golgi type II nerve cells) play an important role in inhibitory processes [1,17,21,26]. The lateral geniculate nucleus is the primary thalamic relay, through which retinal signals pass to the cortex. Retinal afferent terminals are presynaptic to presynaptic dendrites of GLN interneurons, and these presynaptic dendrites establish synaptic contacts with the relay (projection) neurons [8]. This relay is gated and can be suppressed by activity among local inhibitory interneurons that use GABA as a neurotransmitter [28].

There is a significant difference in the number of interneurons in the lateral geniculate body in various species of mammals. For example, in the human and monkey geniculate tissue, interneurons are rarely observed [4,23]. The results of our studies reveal that there is only about 1% of interneurons in the guinea pig GLN. Studies performed on the structure of the cat GLN [11,30] showed that interneurons in this species constitute from 20 to 22% of nerve cells in this nucleus. It could be supposed that mammals with a more sensitive visual organ (nocturnal life) have more GABA-ergic interneurons forming a local inhibitory system.

### REFERENCES

- Anderson P, Eccles JC, Sears TA (1964) The ventro basal complex of the thalamus: Types of cells, their responses and their functional organisation. J Physiol, 174: 370–399.
- Brauer K, Leuba G, Garey LJ, Winkelmann E (1985) Morphology of axons in the human lateral geniculate nucleus: a Golgi study in prenatal and postnatal material. Brain Res, 1–2: 21–33.
- Conley M, Birecree E, Casagrande VA (1985) Neuronal classes and their relation to functional and laminar organization of the lateral geniculate nucleus: a Golgi study of the prosimian primate, Galago crassicaudatus. J Comp Neurol, 4: 561–583.
- De Courten C, Garey LJ (1982) Morphology of the neurons in the human lateral geniculate nucleus and their normal development. A Golgi study. Exp Brain Res, 2: 159–171.
- 5. Einstein G, Davis TL, Sterling P (1987) Pattern of late-

ral geniculate synapses on neuron somata in layer IV of the cat striate cortex. J Comp Neurol, 260: 76–86.

- Fritschy JM, Garey LJ (1986) Postnatal development of quantitative morphological parameters in the lateral geniculate nucleus of the Marmoset Monkey. Develop Brain Res, 30: 157–168.
- Hada J, Yamagata Y, Hayashi Y (1985) Visual response properties of ventral lateral geniculate nucleus cells projecting to the pretectum and superior colliculus in the rat. Brain Res, 363: 165–169.
- Hajdu F, Hassler R, Somogyi Gy (1982) Neuronal and synaptic organization of the lateral geniculate nucleus of the tree shrew, Tupaia glis. Cell Tissue Res, 224: 207–223.
- Hajdu F, Hassler R, Somogyi Gy, Wagner A (1983) Neuronal and synaptic arrangements of the lateral geniculate nucleus in night-active primates. Anat Embryol, 168: 341–348.
- Hajdu F, Hassler R, Wagner A (1982) The distribution of crossed and uncrossed optic fibers in the different layers of the lateral geniculate nucleus in the tree shrew (Tupaia glis). Anat Embryol, 164: 1–8.
- Hamori J, Silakov VL (1980) Plasticity of relay neurons in dorsal lateral geniculate nucleus of the adult cat: morphological evidence. Neuroscience, 5: 2073–2077.
- Harting JK, Huerta MF, Hashikawa T, van Lieshout DP (1991) Projection of the mammalian superior colliculus upon the dorsal lateral geniculate nucleus: organization of tectogeniculate pathways in nineteen species. J Comp Neurol, 2: 275–306.
- Hendrickson AE, Wilson JR, Ogreen MP (1978) The neuroanatomical organisation of pathways between the dorsal lateral nucleus and visual cortex in Old World and New World primates. J Comp Neurol, 182: 123–136.
- Jeffery G (1988) Shifting retinal maps in the development of the lateral geniculate nucleus. Dev Brain Res, 46: 187–196.
- Kennedy H, Bullier J, Dehay C (1985) Cytochrome oxidase activity in the striate cortex and lateral geniculate nucleus of the newborn and adult macaque monkey. Exp Brain Res, 61: 204–209.
- Mackay-Sim A, Sefton J, Martin PR (1983) Subcortical projections to lateral geniculate and thalamic reticular nuclei in the hooded rat. J Comp Neurol, 213: 24–35.
- McIlwain JT, Creutzfeldt OD (1967) A microelectrode study of synaptic excitation and inhibition in the lateral geniculate nucleus of the cat. J Neurophysiol, 30: 1–21.
- Mikkelsen JD (1990) A neuronal projection from the lateral geniculate nucleus to the lateral hypothalamus

of the rat demonstrated with Phaseolus vulgaris leucoagglutinin tracing. Neurosci Lett, 1–2: 58–63.

- Mikkelsen JD, Möller M (1990) A direct neural projection from the intergeniculate leaflet of the lateral geniculate nucleus to the deep pineal gland of the rat, demonstrated with Phaseolus vulgaris leucoagglutinin. Brain Res, 1–2: 342–346.
- Montero VM (1987) Ultrastructural identification of synaptic terminals from the axon of type 3 interneurons in the cat geniculate nucleus. J Comp Neurol, 264: 268–283.
- Pasik P, Pasik T, Hamori J, Szentagothai J (1973) Golgi type II interneurons in the neuronal circuit of the monkey lateral geniculate nucleus. Exp Brain Res, 17: 18–34.
- Reese BE (1984) The projection from the superior colliculus to the dorsal lateral geniculate nucleus in the rat. Brain Res, 305: 162–168.
- Saini KD, Garey LJ (1981) Morphology of neurons in the lateral geniculate nucleus of the monkey. A Golgi study. Exp Brain Res, 42: 235–248.
- Saki K, Jouvet M (1980) Brain stem PGO-on cells projecting directly to the cat dorsal lateral geniculate nucleus. Brain Res, 194: 500–505.
- Sefton AJ, Martin PR (1984) Relation of the parabigeminal nucleus to the superior colliculus and dorsal lateral geniculate nucleus in the hooded rat. Exp Brain Res, 56: 144–148.
- Singer W, Poppel E, Creutzfeldt OD (1972) Inhibitory interaction in the cat's lateral geniculate nucleus. Exp Brain Res, 14: 210–226.
- Szentagothai J (1967) Models in specific neuron arrays in thalamic relay nuclei. Acta Morph Acad Sci Hung, 15: 113–124.
- Uhlrich DJ, Cucchiaro JB, Humprey AL, Sherman SM (1991) Morphology and axonal projection patterns of individual neurons in the cat perigeniculate nucleus. J Neurophysiol, 6: 1528–1541.
- Villar MJ, Vitale ML, Hökfelt T, Verhofstad AAJ (1988) Dorsal raphe serotoninergic branching neurons projecting both to the lateral geniculate body and superior colliculus: a combined retrograde tracing-immunohistochemical study in the rat. J Comp Neurol, 277: 126–140.
- Weber AJ, Kalil RE, Hickey TL (1986) Genesis of interneurons in the dorsal lateral geniculate nucleus of the cat. J Comp Neurol, 252: 385–391.
- Weber JT, Huerta MF, Kaas JH, Harting JK (1983) The projections of the lateral geniculate nucleus of the squirrel monkey: studies of the interlaminar zones and the S layers. J Comp Neurol, 213: 135–145.