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The neuronal structure of the dorsal nucleus of the lateral geniculate body in the common shrew (Sorex araneus) and the bank vole (Clethrionomys glareolus): Golgi and Nissl studies

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The topography and neuronal structure of the dorsal nucleus of the lateral geniculate body (GLd) of the common shrew and the bank vole are similar. The lateral geniculate body of both the species examined has a homogeneous structure and no observable cytoarchitectonic lamination. On the basis of the shape of the dendritic arbours as well as the pattern of dendritic arborisations the following two types of neurons were distinguished. Type I "bushy" neurons that have multipolar or round perikarya (common shrew perikarya 9–12 µm, bank vole perikarya 10–13 µm), with 4–6 short thick dendritic trunks that subdivide into many bush-like branches. The dendritic trunks are smooth, in contrast to the distal branches, which are covered with numerous spine-like protrusions of different lengths and forms. An axon emerges from the soma, sometimes very close to one of the primary dendrites. The type I neurons are typically projection cells that send their axons to the primary visual cortex. These neurons predominate in the GLd of both species. Type II neurons, which have an elongated soma with primary dendrites arising from opposite poles of the perikaryon (common shrew perikarya 8–10 µm, bank vole perikarya 9–11 µm). The dendritic arbours of these cells are less extensive and their dendrites have fewer spines than those of the type I neurons. Axons were seldom observed. The type II neurons are presumably interneurons and are definitely less numerous than the type I neurons.

Key words: lateral geniculate body, types of neurons, common shrew, bank vole

INTRODUCTION

The dorsal nucleus of the lateral geniculate body (GLd) of mammals is a well developed thalamic area. It is the primary relay nucleus that processes visual information on its way from the retinal ganglion cells to the primary visual cortex. It is believed that at GLd stage form, movement, contrast and colour signals are separated. The lateral geniculate body receives its main input directly from both retinas [7, 13, 20, 21, 42]. It also receives a strong feedback from the visual cortex [16, 35, 36] and other visual regions such as the superior colliculus and pretectal nuclei [5, 9, 11, 15, 27]. The feedback connections from the visual cortex may presumably

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play an important role in modulating visual information that travels along the retina-geniculate--striate pathway [35, 41]. Murphy et al. [18] suggest that neurons of specific cortical areas preferentially target the geniculate cells from which they receive input. In addition, the GLd receives afferent projections from non-visual brainstem centres, namely the dorsal raphe nucleus, periaqueductal grey matter, mesencephalic reticular formation, locus coeruleus and dorsal tegmental nucleus [1, 17, 25, 37, 40]. The lateral geniculate body of mammals sends projections almost exclusively to the striate cortex. Most of the geniculocortical fibres terminate directly within layer IV of cortical area 17 [6, 22, 32, 34].

The aim of our studies was to describe the topography and the neuronal structure of GLd in the bank vole and the common shrew, thus comparing GLd structure of two species that belong to different orders of placental mammals. No description of GLd of these species has so far been published.

MATERIAL AND METHODS

The studies were carried out on 10 brains of adult common shrews and 10 brains of adult bank voles. Preparations were made by means of the Golgi-Bubenaite technique and staining was carried out according to the Nissl method. The brains for the Golgi-Bubenaite impregnation were immersed in 2.5% potassium dichromate for 3–6 days. Next the brains were washed in 2% silver nitrate for one hour, followed by immersion in 3% silver nitrate for 2–5 days. The whole process was conducted in the dark at 34°C. Finally the brains were dehydrated, embedded in paraffin and cut into serial 90 μm and 120 μm sections. The brains for the Nissl method were cut into 50 μm sections. Microscopic images of selected impregnated neurons were digitally recorded by means of a camera coupled with a microscope and an image-processing system. Between 50 and 100 such digital microscopic pictures were taken at different focus layers of the section for each neuron. The computerised reconstructions of microscopic images were made on the basis of these series. The neuropil was kept in all pictures in order to show the real microscopic images and was then removed from each to clarify the neuron illustrations.

The classification of GLd neurons was principally based on the shape of their dendritic arbours as well as the pattern of dendritic arborisations.

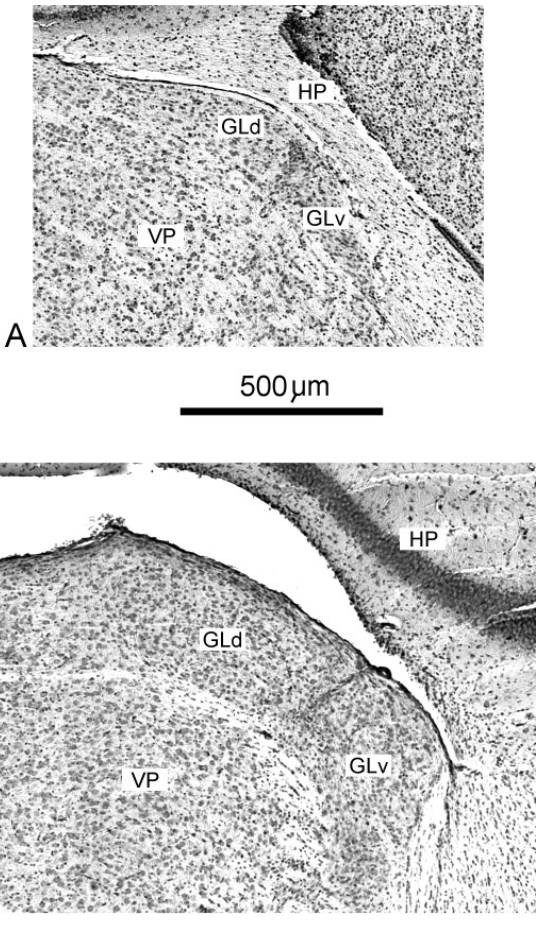

Figure 1. A. The transverse section of the common shrew lateral geniculate body; **B.** The transverse section of the bank vole lateral geniculate body; GLd — the dorsal nucleus of the lateral geniculate body; GLv — ventral nucleus of the lateral geniculate body; VP — nucleus ventralis posterior thalami; HP — hippocampus.

RESULTS

The lateral geniculate body of the common shrew in the Nissl material (Fig. 1)

In transverse sections the rostral pole of GLd appears as a small homogenous group of cells that is located at the lateral edge of the thalamus. The rostral pole has an oval shape and borders ventrally on the ventral nucleus of the lateral geniculate body. On the medial side of GLd lies the nucleus ventralis posterior thalami. Further caudally, GLd increases noticeably and becomes tear-shaped. In the middle part GLd has the largest size and forms a characteristic protuberance on the lateral surface of the thalamus. Toward the posterior end GLd gradually becomes thinner and longer. In this section GLd, along with the ventral lateral geniculate nucleus, takes on a crescent shape. Between these two nuclei there lies a thin layer of cells, which is presumably the intergeniculate

leaflet. The posterior part of GLd is situated laterally to the anterior pole of the medial geniculate body and medially to the thin layer of fibres that form the optic tract. The caudal pole of GLd becomes smaller and disappears. The lateral geniculate body is displaced laterally by the medial geniculate body that becomes larger and forms a knob-like protuberance. The lateral geniculate body of the common shrew has a homogeneous structure and no cytoarchitectonic lamination could be observed. In the Nissl preparations GLd neurons have quite large multipolar or rounded perikarya with a distinctly visible cell nucleus. In the caudal section of GLd fusiform neurons were observed lying along the lateral plane of the thalamus. The lateral geniculate body cells contain numerous thick grains of tigroid matter.

The lateral geniculate body GLd of the common shrew in the Golgi material

Two types of neurons were distinguished in the common shrew GLd.

Type I "bushy" neurons (Fig. 2). The perikarya of these cells measure from 9 to 12 μm. The cell bodies are usually multipolar or round and they give off 4–6 short thick dendritic trunks that subdivide into many bush-like branches. The dendritic trunks are smooth, in contrast to the distal branches, which are covered with numerous spine-like protrusions of different lengths and forms. The dendrites do not penetrate adjacent thalamic nuclei. The dendritic arbour is more or less discoidal in shape. There is no regularity in the arrangement of the dendritic spheres and they lie parallel as well as perpendicular to the long axis of GLd. An axon emerges from the soma, sometimes very close to one of the primary dendrites. The type I neurons are typically projection cells that mainly send their axons to the primary visual cortex. These neurons were observed throughout the common shrew GLd, where they predominate over the second type of cells.

Type II neurons (Fig. 3). The cell bodies of these range from 8 to 10 μm. The perikarya are very frequently elongated, usually spindle-shaped. Their dendritic arbour is also fusiform, and its area is smaller than that of the previous type of neuron. They usually have 2 dendritic trunks that originate mostly from both poles of a perikaryon. Generally dendrites are sparsely branched and have occasional appendages. The dendrites do not reach the adjacent nuclei. An axon is rarely observed and, if so, it usually

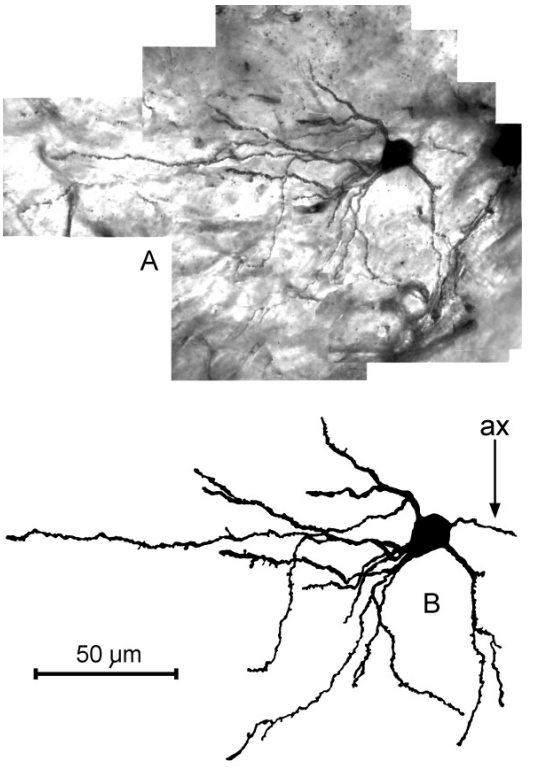

Figure 2. The type I "bushy" neurons of the common shrew dorsal nucleus of the lateral geniculate body; **A.** Non-clarified Golgi impregnation; **B.** Clarified Golgi impregnation, ax — axon.

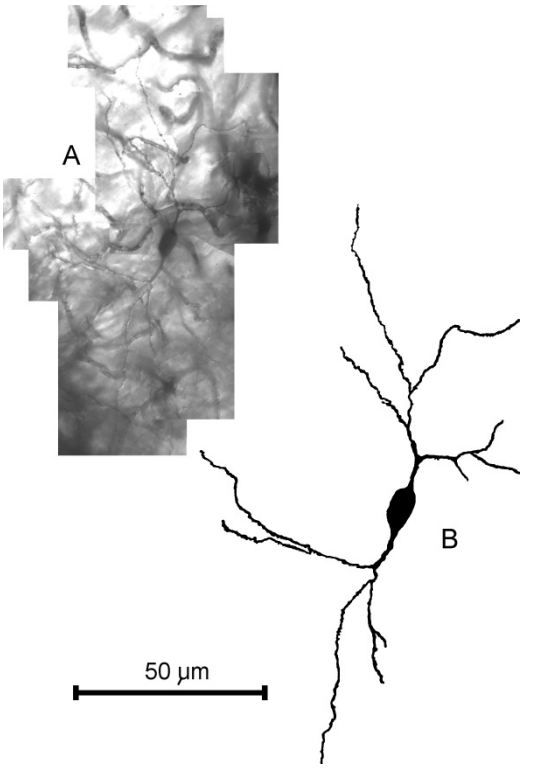

Figure 3. The type II neurons of the common shrew dorsal nucleus of the lateral geniculate body; **A.** Non-clarified Golgi impregnation; **B.** Clarified Golgi impregnation.

emerges directly from the soma. The type II neurons are presumably interneurons. Although they were observed throughout GLd, they are definitely less numerous than the type I neurons.

The lateral geniculate body of the bank vole in the Nissl material (Fig. 1)

The rostral pole of the bank vole GLd is represented by a group of cells that make up a portion of the dorsal edge of the thalamus. In transverse sections the rostral pole has the shape of a thin wedge. Its sharpened tip is turned towards the medial part of the thalamus. At this level GLd borders the ventral nucleus of the lateral geniculate body and the nucleus ventralis posterior thalami. As GLd extends more posteriorly, it rotates ventrally to occupy a dorsolateral position. Further posteriorly, GLd lies laterally and forms the lateral wall of the thalamus. At this level GLd, together with the ventral lateral geniculate nucleus, has a crescent shape. A thin layer of cells, presumably the intergeniculate leaflet, lies intercalated between GLd and the ventral lateral geniculate nucleus. All these nuclei form a bulbous protuberance on the lateral wall of the medial diencephalon. The appearance of these nuclei in both examined species is similar, although in the bank vole they are noticeably thicker. The caudal poles of both lateral geniculate nuclei are bordered by the anterior pole of the medial geniculate body. Further caudally GLd becomes thinner and smaller and vanishes, leaving the well-shaped medial geniculate body in its place. The bank vole GLd does not show any lamination or subdivision into different cell regions. In the Nissl preparations the rostral portion of the bank vole GLd consists of large fusiform and oval perikarya that contain well impregnated grains of tigroid matter. Further posteriorly the number of fusiform neurons is low, and the round and multipolar cells prevail.

The lateral geniculate body of the bank vole in the Golgi material

Two types of neurons were distinguished in the bank vole GLd.

Type I "bushy" (Fig. 4). Their perikarya are usually multipolar or round in shape and measure from 10 to 13 μm. The neurons have 4–6 primary dendrites that branch into numerous distal dendritic branches. In general, the dendrites have the typically bushy pattern of their dendritic arborisations and bear a considerable number of diverse appendages. The dendritic arbour is extensive and is usually round

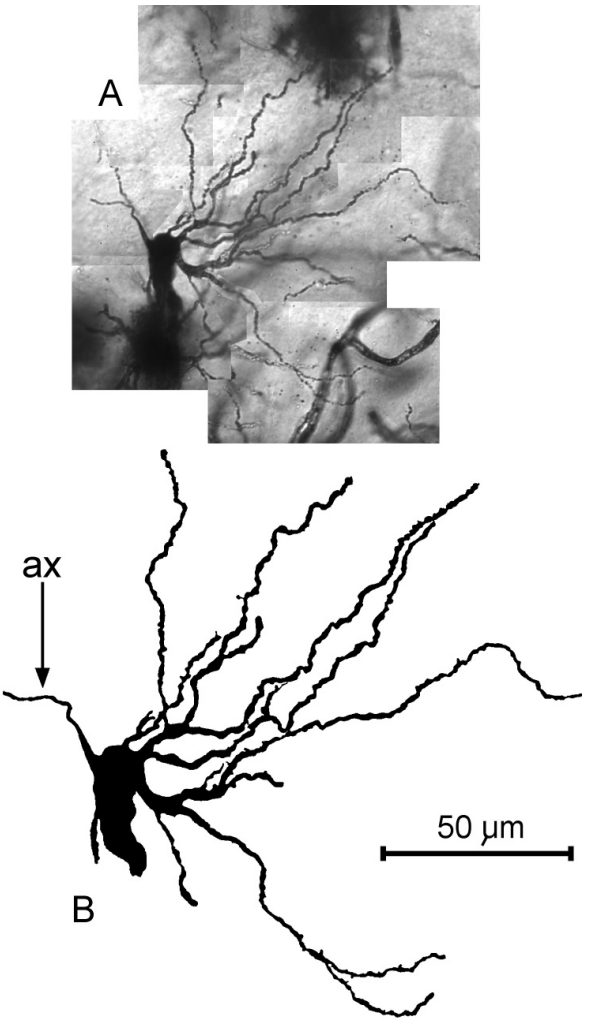

Figure 4. The type I "bushy" neurons of the bank vole dorsal nucleus of the lateral geniculate body; **A.** Non-clarified Golgi impregnation; **B.** Clarified Golgi impregnation, ax — axon.

in shape. The dendrites do not extend beyond the limits of GLd and branch locally. An axon more often than not emerges directly from the soma. Since the type I neurons are geniculocortical relay cells, they are common throughout the bank vole GLd, where they constitute the main neuronal type.

Type II neurons (Fig. 5). Their cell bodies range from 9 to 11 μm. The majority of type II neurons have an elongated soma with primary dendrites arising from opposite poles of the perikaryon. The primary dendrites bifurcate into thinner secondary branches. Tertiary branches were seldom observed. The dendritic arbours of these cells are less extensive than those of the type I neurons. Generally, the surface of the dendrites is smooth and spines are rare on these neurons. The dendrites do not penetrate adjacent thalamic nuclei. An axon is not often observed and, when it is, it arises mostly from the

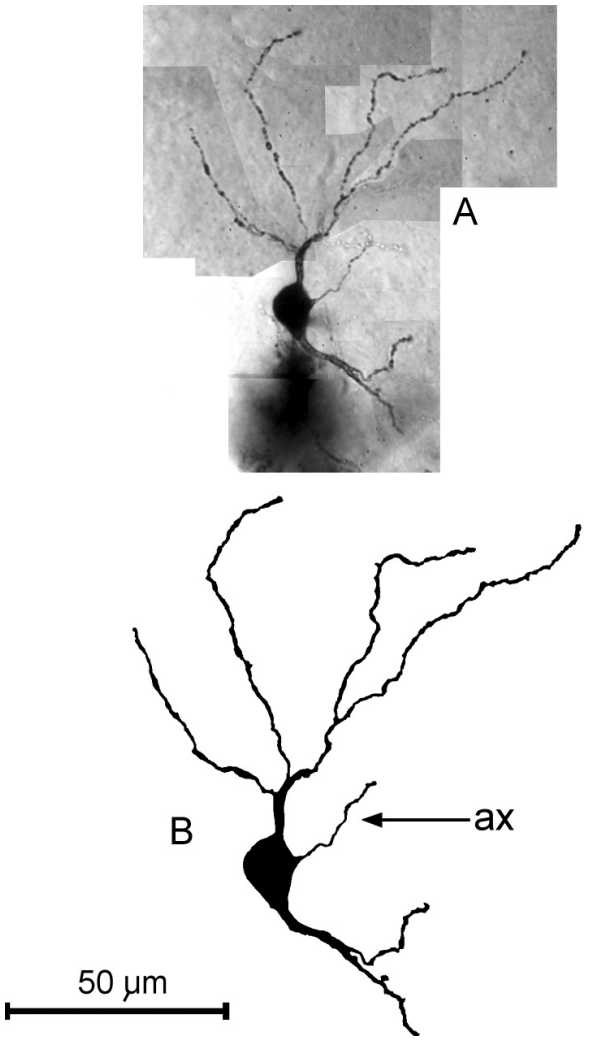

Figure 5. The type II neurons of the bank vole dorsal nucleus of the lateral geniculate body; **A.** Non-clarified Golgi impregnation; **B.** Clarified Golgi impregnation, ax — axon.

soma. The type II neurons are quite common in the bank vole GLd, although far fewer in number than the type I cells.

DISCUSSION

Comparison of GLd in the mammalian orders that have been examined so far shows that two types of GLd can be distinguished. The first type, the cytoarchitectonically uniform GLd, cannot be anatomically subdivided and is considered to be a basic and more "primitive" type. The second type of GLd is characterised by a multilayer laminated structure. The number of layers and their three-dimensional pattern appear to be species-specific. The lateral geniculate body of the common shrew, as well as that of the bank vole, has clear boundaries and does not exhibit lamination. The lateral geniculate body of both species is surrounded by several areas: the ventral nucleus of the lateral geniculate body, the nucleus ventralis posterior thalami, the medial geniculate body and the optic tract. To a large extent, the general structure and appearance of GLd are alike in the two mammals examined. Descriptions of the cytoarchitecturally uniform GLd have been published for the coypu, European beaver, porpoise and rat [23, 24, 28, 30]. The lateral geniculate body of carnivores, primates and some rodents is made up of several characteristic laminae [2, 4, 12, 31]. For example, in the tree shrew, which bears some anatomical resemblance to both insectivores and primates, the cytoarchitectonic pattern of GLd comprises six cellular layers divided by neuropilar interlaminar zones [10, 14]. Generally, the lamination of GLd can be observed in mammals with a highly developed visual system and a proportionally large number of ipsilaterally projecting retinogeniculate fibres. The number and sequence of ipsilaterally and contralaterally innervated laminae vary between species of different taxonomical categories [2].

Neurons in GLd of the common shrew and the bank vole can be divided into two distinct types on the basis of dendritic morphology. The lateral geniculate body of the mammals examined consists mainly of the type I neurons, which are relay nerve cells projecting to the visual cortex. The relay neurons are large or medium-sized and have between 4 and 6 mainly short primary dendrites that give off many bushy branches covered with numerous diverse appendages. The type II cells are smaller local interneurons that are less numerous than the relay cells. The type II neurons usually have two dendritic trunks that branch into less developed and almost smooth dendrites.

A comparison of our results reveals similarities with published material on the neuronal structure of GLd in other mammals. In the cat GLd Tömböl et al. [33] distinguished two main neuronal types: the thalamocortical relay neurons and the interneurons. Both types were further subdivided. The thalamocortical relay cells were divided into the large class I neurons and the medium-sized class II (principal) neurons. The interneurons were also divided into two subgroups: the Golgi IIa and the Golgi IIb cells. The division of interneurons was based primarily on the size of the axonal arborisation fields. The presence of two main types of GLd neurons has also been reported in the rat, common tree shrew, porpoise and guinea pig [3, 24, 38, 39]. On the basis of the shape of the perikarya, four types of nerve cell were

distinguished in the guinea pig GLd: fusiform, pear-shaped, rounded and triangular neurons [29]. A comparative analysis of the dendrites of these neurons shows that the fusiform cells correspond to interneurons, whereas the remaining three types are similar in appearance and morphological features to the relay neurons of other mammals.

The relative proportions of relay cells and interneurons in various mammals appear to differ. Most estimates of the percentage of interneurons in GLd of the cat range from 25–57%, depending on the method used to define both types of cell [19]. Gabbott et al. [8] estimated that approximately 22% of rat cells are interneurons. In primates interneurons have been estimated to account for fewer than 15% of the neurons of GLd [19]. Norden and Kaas [19] indicate that nearly all the neurons of the main relay layers of GLd in the owl monkey and rhesus are relay cells. They suggest that the organisation of GLd in primates may differ significantly from that of other mammals with respect to the percentage of interneurons. It is believed that GABA is the transmitter for small interneurons which appear to mediate, by means of local circuits, a feed-forward inhibition onto the relay cells [26].

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