ORIGINAL ARTICLE

The neuronal structure of the medial geniculate body in the pig — Nissl and Golgi study

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The studies were carried out on the brains of adult pigs. The preparations were made by means of the Golgi technique as well as the Nissl and Klüver-Barrera methods. Four types of neurons were described in the medial geniculate body (MGB) of the pig: 1. Multipolar neurons (perikarya 30–45 µm) with rounded, oval or quadrangular perikarya from which arise 4–7 dendritic trunks. The dendrites divide dichotomically twice, may send out collaterals and give off ramifications. The dendritic branches possess varicosities and knob-like spines. These neurons predominate in MGB. 2. Pear-shaped neurons (20–35 µm) with one or two dendritic trunks arising from one pole of the cell body. These dendrites have a tufted appearance. 3. Triangular neurons (30–45 µm) possess three thick dendrites which first bifurcate near the soma and then divide profusely into daughter branches. 4. Fusiform neurons (30–50 µm) have usually two dendritic trunks which arise from the opposite poles of the cell body and divide dichotomically twice. The fusiform neurons are the least numerous in MGB. Most MGB neurons have on the secondary tertiary dendrites and on their ramifications have delicate varicose or bead-like appendages and spine-like protrusions. In all types of neurons an axon arises either from the soma or from the initial portion of the dendritic trunk.

key words: medial geniculate body, types of neurons, Golgi and Nissl techniques, pig

INTRODUCTION

The medial geniculate body is the principal thalamic relay nucleus in the thalamic auditory system of all mammals and it projects primarily to the auditory receptive areas of the cerebral cortex. Fibres from the medial geniculate body terminate mainly in the primary as well as in the secondary auditory cortex [5, 7, 10, 12, 15, 18], but there are also at least five additional cytoarchitectonically distinct areas that receive projections from the medial geniculate neurons [15]. Moreover, there are some studies that indicate that MGB neurons give rise to subcortical projections, mostly to the putamen and amygdala [6–8]. Iwata et al. [6] suggest that the neurons within the amygdaloid field innervated by the neurons of the medial geniculate body appear to mediate emotional responses conditioned to acoustic stimuli. The principal inputs to MGB come from the auditory cortex [1, 8, 17, 28, 30], the inferior colliculus [8, 14, 16, 17, 33, 35], the superior colliculus [33], the lateral tegmental system of the midbrain [33], the reticular complex of the thalamus [17], and also from the cerebellum [39]. According to Winer et al. [35] novel and robust projections from the inferior colliculus are GABAergic and they seem to counterbalance the corticothalamic projections and affect the

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thalamic oscilations implicated in shifts in vigilance and attention.

The neuronal structure of the medial geniculate body was investigated in the following mammals: cat [9, 11, 31, 32], rat [4, 27], opossum [34], bat [37], human [25], tree shrew [13]. Moreover, there are some studies describing the topography and cytoarchitecture of MGB [3, 8, 19–21, 23, 24, 36]. Because of the paucity of data concerning the neuronal morphology of the medial geniculate body in domestic animals, the morphological description of the medial geniculate neurons of the pig was done.

MATERIAL AND METHODS

The studies were performed on the brains of seven adult pigs. Preparations were made by means of the Golgi technique and stained according to the Klüver-Barrera and Nissl methods. The sections stained with luxol fast blue and cresyl violet were 50-μm-thick whereas the paraffin blocks with Golgi impregnated tissue were cut into 90 μm sections. The microscopic images of chosen, impregnated cells were digitally recorded by means of a camera that was coupled with a microscope and an image processing system (VIST-Wikom, Warsaw). From 50 to 100 such digital microphotographs 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. First, the neurons were not clarified to show the real microscopic images and then the neuropil was removed to clarify the picture.

RESULTS

On the basis of various criteria (shape and size of perikarya, distribution of the tigroid substance, number and arborisation of dendrites and location of axon) the following types of neurons were distinguished in the medial geniculate body:

1. Multipolar neurons (Fig. 1, 2). These cells predominate in the medial geniculate body, both in the ventral and the medial part. The perikarya measure from 30 to 45 μm. Taking into account such features as the shape of the perikarya and the presence of the dendritic cones two kinds of multipolar neurons can be distinguished. The first one (Fig. 1), the majority of the multipolar neurons, contains rounded perikarya and the dendritic trunks without cones and the second one (Fig. 2), the minority of the multipolar neurons, has usually quadrangular or oval perikarya and conically arising dendrites. These multipolar neurons emit in all directions 4–7 dendritic trunks of various thickness. These dendritic trunks
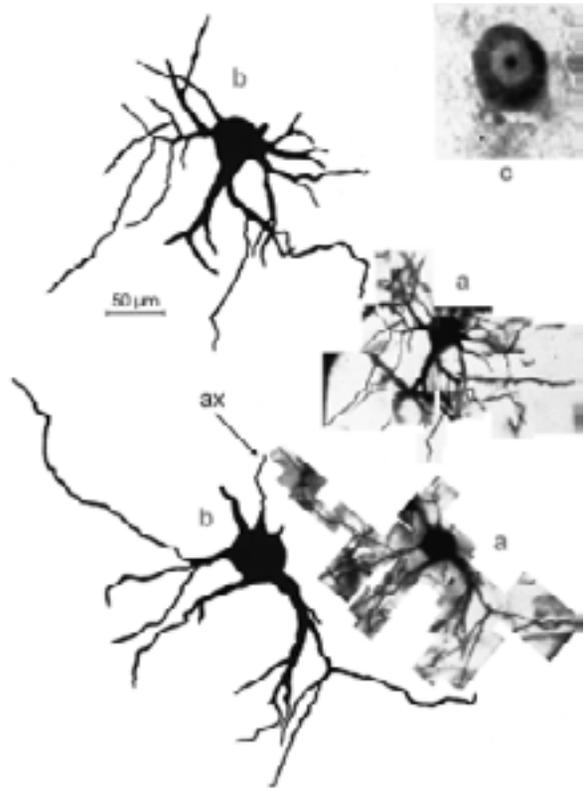
Figure 1. Multipolar neurons (the first kind); a — non-clarified Golgi impregnation, b — clarified Golgi impregnation, ax — axon, c — the Nissl stained soma.
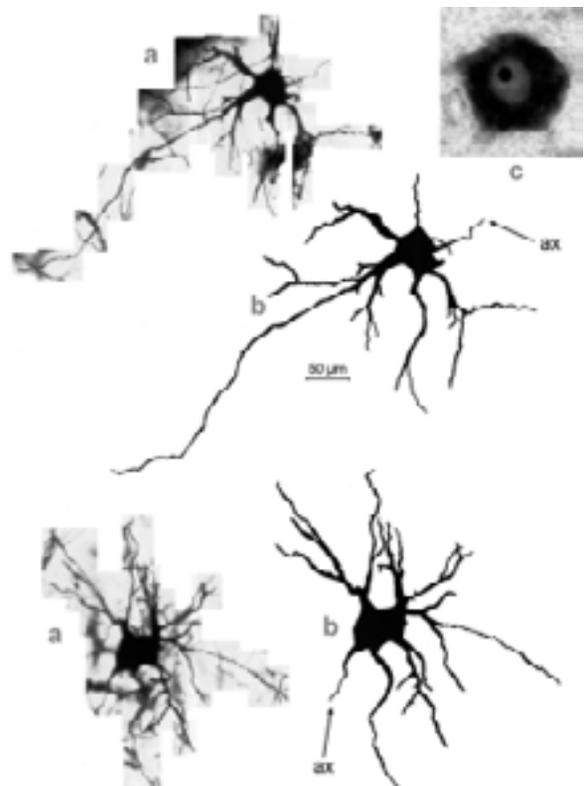
Figure 2. Multipolar neurons (the second kind); a — non-clarified Golgi impregnation, b — clarified Golgi impregnation, ax — axon, c — the Nissl stained soma.

divide dichotomically the first time near the soma (15–30 μm) into secondary dendrites. The secondary dendrites branch at a different distance from the cell body. Sporadically, undivided dendrites are also observed. The length of the primary and secondary dendrites is almost equal but the tertiary branches are usually prominently longer. The dendritic trunks and the daughter branches may send out collaterals and the tertiary dendrites give off thin, final ramifications. The dendritic trunks are smooth and devoid of any protuberances but on the second- and third-order branches and on their ramifications there are moderately distributed delicate varicose appendages and ocasionally spine-like protrusions. The dendritic tree has a spherical or oval shape. An axon arises mostly from the soma and takes a ventral or rarely lateral course. The multipolar neurons have a centrally located, large, spherical nucleus. The neuroplasma contains thick and medium-size granules of the tigroid substance which delicately enter into the initial portions of the dendrites in the second kind (Fig. 2) of the multipolar neurons, whereas in the neurons of the first kind (Fig. 1) it does not penetrate the dendritic trunks.

2. Pear-shaped neurons (Fig. 3). Their cell bodies measure from 20 to 35 μm. These neurons have one or two dendritic trunks which arise from one pole of the cell body. The primary dendrites divide dichotomically next to the soma into secondary dendrites, which in term after a short distance bifurcate, making the dendrites form tufts. The tufted appearance results from the fact that from the secondary dendrites there arise a few relatively long dendritic branches nearly from the same place. These dendritic branches follow a wavy route and after some distance may divide once again. The primary and secondary dendrites are smooth without any protrusions but the higher order branches possess not numerous bead-like protuberances. The dendrites are oriented dorsally, making the dendritic field fan-shaped. An axon usually arises from the opposite pole of the soma in the relation to the dendritic arbour, or occasionally near the dendritic trunk and takes a dorsal or dorsomedial course. The pear-shaped cells have large, rounded nucleus, which is surrounded by medium-size granules of the tigroid substance, which penetrate the initial portions of the dendrties. The pear-shaped neurons are quite often observed in the ventral part of the MGB, whereas in the medial part they are rarely seen.

3. Triangular neurons (Fig. 4). Their cell bodies measure from 30 to 45 μm. They have three thick, primary
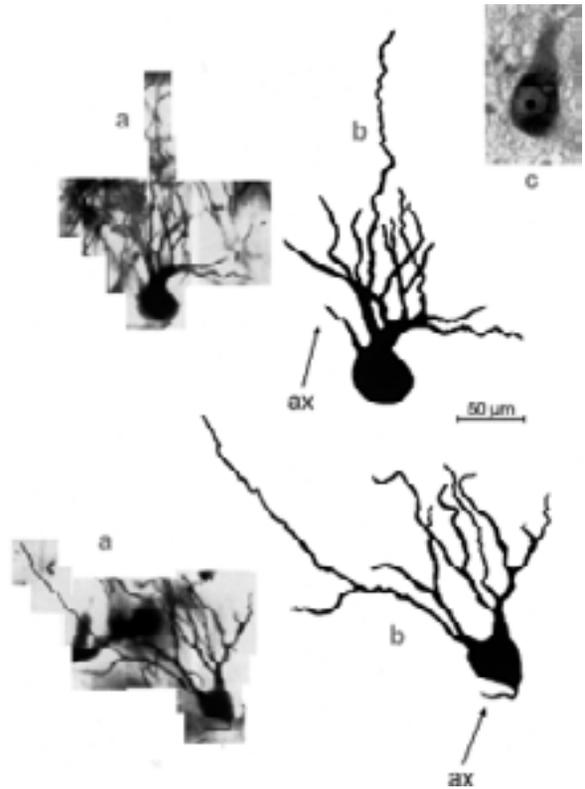
Figure 3. Pear-shaped neurons; a — non-clarified Golgi impregnation, b — clarified Golgi impregnation, ax — axon, c — the Nissl stained soma.
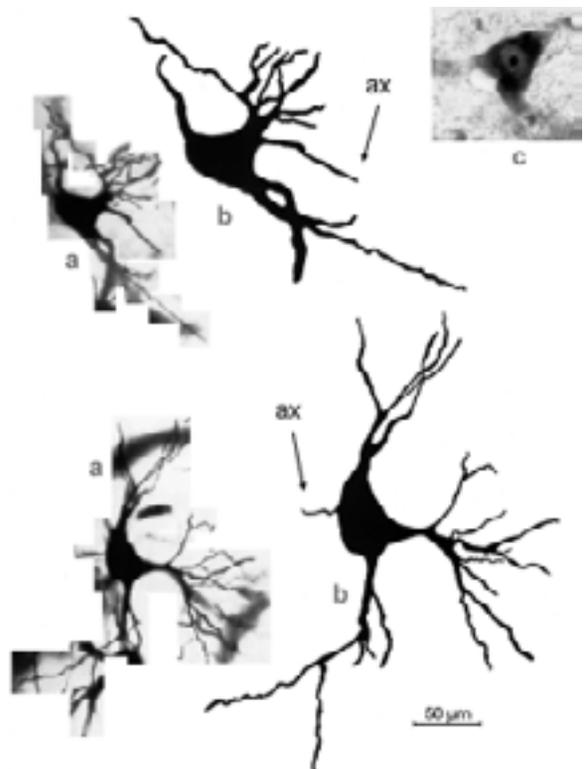
Figure 4. Triangular neurons; a — non-clarified Golgi impregnation, b — clarified Golgi impregnation, ax — axon, c — the Nissl stained soma.

dendrites that arise conically from the perikaryon. Most of them bifurcate in the vicinity of the soma (10–20 μm) into secondary dendrites, and these branch profusely almost from the same place (close to the cell body) into daughter branches in a manner that resembles a tuft. Thus the dendritic arborisation is similar to that described in the pear-shaped neurons. The daughter branches are much thinner and much longer than the primary and secondary dendrites and they show a varicose course. The dendrites run in the dorsal, ventral and lateral directions causing the dendritic field has an ovoid, or even an elongated shape. An axon emerges directly from the soma or from the initial portion of the dendritic trunks and directs ventrally or seldom medially. The triangular neurons contain a large, round or oval nucleus. The tigroid substance in the form of thick granules surrounds the nucleus and penetrates initial portions of the dendritic trunks. These neurons occur in the medial and ventral part of the MGB in similar number.

4. Fusiform neurons (Fig. 5). The fusiform cells measure from 30 to 50 μm along the long axis. These neurons possess two dendritic trunks which arise from the opposite poles of the cell body. Sometimes three or four dendritic trunks are obseved, in that case one or two dendrites arise from one pole of the cell body and the remaining two dendrites emerge from the second pole of the fusiform perikarya. Most of the primary dendrites divide dichotomically after 20–50 μm of their route and quite often branch once again after 20–30 μm from the frst bifurcation. The secondary and tertiary dendrites may give off two or three thin ramifications. The dendritic arborisation in some places may resemble the tufted dendrites described above in the pear-shaped and triangular neurons, but generally these dendrites are weakly tufted. Delicate bead-like appendages are sporadically observed on the second- and higher-order dendritic branches. The dendrites are arranged from the dorsomedial to the ventrolateral direction and the dendritic field has a stream-like form. An axon emerges conically from the soma and directs ventrally. The fusiform cells have the large, spherical nucleus with the dark stained nucleolus. The tigroid substance in the form of coarse granules is concentrated at the poles of the cell body and enters into the initial portions of the dendritic trunks. The fusiform cells are the least numerous neurons in the medial geniculate body; however, in the medial part they are more numerous than in the ventral.

DISCUSSION

The medial geniculate body of mammals is a very intricate structure and most authors divide MGB into two, three or four divisions. On the basis of the neuronal organisation, cytoarchitecture, fibre architecture, thalamocotrical and corticothalamic connections, the rat MGB is found to be a tripartite structure composed of: ventral, dorsal and medial division [3, 4, 8, 28]. Three divisions of MGB were also described in the human [25], tree shrew [13], bat [36] and cat [26]. Four chemoarchitectonic subdivisions were detected in the rabbit MGB: ventral, dorsal, internal and mediorostral [2] but only two parts were repotred in the Tarsioidea: ventrolateral — parvocellular and dorsomedial — magnocellular [19], and in the pig: ventral and lateral [24]. The area that is called the dorsal division of MGB was not taken into consideration in our study. According to Winer [26] the dorsal division of the cat MGB should be regarded as a part of the pulvinar-lateralis posterior complex, both structurally and functionally.

In the medial geniculate body of the pig four described neurons are present in the medial and in the ventral part. The multipolar neurons are the most common cells in the two parts whereas the remaining types appear in a different number. The ventral
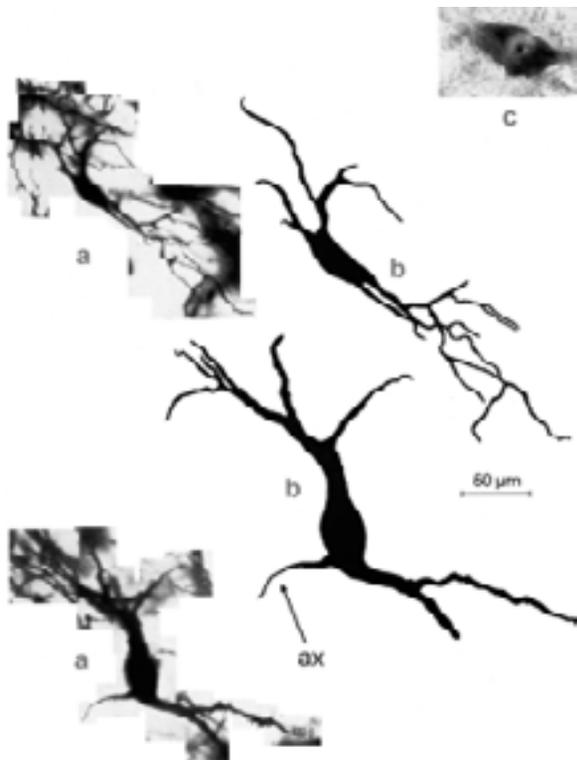
Figure 5. Fusiform neurons; a — non-clarified Golgi impregnation, b — clarified Golgi impregnation, ax — axon, c — the Nissl stained soma.

part (in decreasing number of frequency) consists of: the multipolar, pear-shaped, triangular and single fusiform neurons whereas in the medial division (in the same order of frequency) the multipolar, fusiform, triangular and pear-shaped neurons are observed. On the basis of the cytoarchitectonic data the round, spindle-shaped, triangular and multipolar cells were observed in different mammals [3, 20, 21, 23] whereas the pear-shaped cells described in the pig were not reported in the studies. According to various methods and criteria used by investigators, different numbers of neurons (even in the same animal) were described in the examined mammals, for example: 2 [4, 26] or 4 [8] categories in rat, 2 [11, 26] or 3 [31] in cat, 2 types in opossum [34] and human [25] and only the medial division of the bat MGB has at least 6 types of cells [37]. In the rat, Clerici et al. [4] identified bushy and stellate cells, but LeDoux et al. [8] described spherical, triangular, elongated and multiangular cells. In the cat, medium-sized, small and large neurons were reported by Winer and Morest [31] whereas principal neurons (from spherical to elongate) and Golgi type II neurons were described by Morest [11]. The medial division of MGB of the bat [37] consists of the magnocellular, bushy tufted, disc-shaped, medium-sized multipolar, elongated and small stellate neurons. Despite the great diversity concerning the number and nomenclature of MGB neurons, they have some features of their structure in common. The multipolar neurons of the pig seem to be similar to the bushy and stellate cells [4], spherical [8] of the cat, as well as to the medium-sized neurons of the cat [31] and also to the bushy-tufted and medium-sized multipolar of the bat [37]. The triangular cells (present study) resemble most probably the triangular neurons of the rat [8]. These multipolar and triangular neurons have a very characteristic tufted, bushy dendritic tree, the similar shape of cell bodies, and the orientation of the dendrites. The fusiform neurons, the largest neurons of the pig MGB with weakly tufted dendrites, may be comparable to the elongated neurons of the cat [26] and bat [37] as well as with the magnocellular neurons of the rat [3]. The proximal dendrites of the rat MGB neurons are devoid of spines and other irregularities but the intermediate branches possess the heaviest concentration of dendritic spines including knob-like bumps, crenations and a few needle-like spines [4]. In our study the dendritic trunks are smooth, but the second- and third-order branches have delicate varicose appendages, bead-like protuberances and not numerous spine-like protrusions.

On the intermediate and distal dendrites there end mainly the colliculogeniculate axons whereas the corticogeniculate ones occur on the cell body and on the proximal and intermediate dendrites [11]. The pear-shaped neurons, the smallest cells of the pig MGB that have similar arborisation of the dendrites to the multipolar and triangular neurons were not reported in MGB of other mammals. Small neurons were described as Golgi type II neurons in the cat [9, 11, 31], rat [27], and in the opossum [34]. The Golgi type II neurons form dendro-dendritic synapses with the principal neurons in terminal aggregates called synaptic nests [11]. The Golgi type II cells receive endings from afferent axons and send presynaptic processes to principal cells that receive the same afferent axons [11]. Some authors [9, 11, 38] suggest that the Golgi type II cells might be either inhibitory or excitatory interneurons or both. In rat [29] the GABAergic neurons represent only a fraction, perhaps less than 1% of neurons, however their influence may be much larger than the number suggests. Winer and Morest [32] suppose that certain types of neurons are consistently observed in the sensory nuclei of the thalamus. Bushy principal neurons with tufted dendritic fields are common in the main sensory nuclei — ventral nucleus of MGB, ventrobasal complex and the dorsal nucleus of the lateral geniculate body [32]. According to Winer [22] the multipolar, pear-shaped, triangular and fusiform cells of the pig correspond to the rounded, pear-shaped, triangular and fusiform neurons described in the dorsal lateral geniculate nucleus (GLN) of the guinea pig, respectively. These cells show similar shapes of cell bodies, have similar arborisation of the dendrites, however there exists a discrepancy between the number of the guinea pig GLN cells and the pig MGB cells.

The neurons of the pig MGB resemble in some respects those in rodent or carnivore auditory thalamic nuclei. In spite of the morphological similarities, functional differences, such as the evolution of combination sensitivity, suggest that structurally comparable auditory thalamic neurons may subserve diverse physiological representations [37].

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