

The neuronal structure of the globus pallidus in the rabbit — Nissl and Golgi studies

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The studies were carried out on the telencephalons of 12 adult rabbits. Two types of neurons were distinguished: 1. Large neurons (perikarya 18–40 µm), which have from 2 to 6 thick, long primary dendrites. Their perikarya have a polygonal, triangular and fusiform shape. The large neurons in the centre of GP have radiated dendritic trees, whereas the dendritic field of the cells along the borders of GP has an elongated shape. The dendritic arbour is not homogeneous. The dendrites may be covered with spindle-shaped dendritic swellings, bead-like processes, not numerous spines or they may be smooth as well. The dendritic branches form thin, beaded dendritic processes, that arise from any part of the dendritic tree, as well as “complex terminal endings”, which have various types of appendages on their terminal portions. An axon emerges from a thick conical elongation either from the cell body or one of the dendritic trunks. These neurons are the most numerous in the investigated material. 2. Small nerve cells have been infrequent in our material. Their cell bodies are rounded or polygonal. From the perikarya there arise 2–4 thin dendritic trunks, which may have irregular swellings and few spines. The dendrites spread out in all directions, making the dendritic field round or oval in shape. Generally most axons of the small cells have not been impregnated. However, a few of them have a thin axon with a conical elongation, which emerges from the cell body and bifurcates into beaded processes.

key words: globus pallidus, types of neurons, rabbit

INTRODUCTION

The globus pallidus (GP) forms the smaller, more medial part of the lentiform nucleus and it lies medially to the putamen throughout most of its extent. It consists of two major segments: the external (or lateral) and the internal (or medial). The external segment of the globus pallidus (Gpe) in primates is homologous to GP in non-primates, whereas their internal segment corresponds to the entopeduncular nucleus in non-primates [11, 12].

The previous studies of GP have been carried out on the Nissl-staining scraps [10, 39, 40]. More de-

tailed research has been conducted with the help of the Golgi technique in the following animals: man [2, 24], monkey [4, 8, 11–14, 44], rat [5, 9, 25, 42], mouse [17], cat [18] and bison bonasus [31].

As a result of the morphological and electrophysiological studies, various types of neurons have been observed in the mammalian GP. In some animals there has been noticed the presence of large and small neuronal populations [8, 11, 25, 31]. Among the large pallidal neurons some authors distinguished only one population of such cells [12], whereas others described two populations, which consist of spin-

dle-shaped and polygonal neurons [5]. Iwahori and Mizuno [17, 18] have observed large and medium-size neurons. The smaller neurons are considered to be short-axon, Golgi type II neurons [11, 12, 44] or interneurons [8, 25, 31]. The intracellular recording studies indicate that two major types of pallidal neurons may be differentiated on the basis of their membrane and firing properties [22, 26, 27].

The GP receives its main afferent input from the neostriatum and the subthalamic nucleus, however its efferent fibres project to various basal ganglia nuclei like the neostriatum, the subthalamic nucleus, the substantia nigra and the pedunculopontine tegmentum [1, 3, 6, 7, 16, 20, 21, 23, 27, 29, 35–38]. There have been observed reciprocal connections between the external and internal segments of GP [19, 41]. The output of the internal segment of GP is more extensive than that from the external segment [41].

The first, short report on the Golgi findings of GP in the rabbit was published in 1911 [30]. The topographic organisation and the extent of the magnocellular nuclei in the basal forebrain in the rabbit were investigated by Schober et al [34]. The aim of our studies was to give detailed morphological characteristics of the pallidal neurons in the rabbit's telencephalon.

MATERIAL AND METHODS

The studies were carried out on the telencephalons of 12 adult rabbits. The preparations were made by means of the Nissl and Golgi methods. The brains were cut into 15 and 50 μm as well as 90 and 120 μm scraps for the Nissl and Golgi methods, respectively. The microscopic images of the selected impregnated cells were digitally recorded by means of a camera that was coupled with a microscope and an image processing system (Corel Photo-Paint). From 40 to 60 such digital microphotographs were taken at the 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 the pictures in order to show the real microscopic images and then was removed from each of them to clarify the picture.

RESULTS

On the basis of Golgi and Nissl scraps there were distinguished two main types of neurons:

Type I — large neurons (Fig. 1). The perikarya of these cells measure 18–40 μm in their longest dimension. The cell bodies of the large neurons have a polygonal, triangular, fusiform shape, and most of

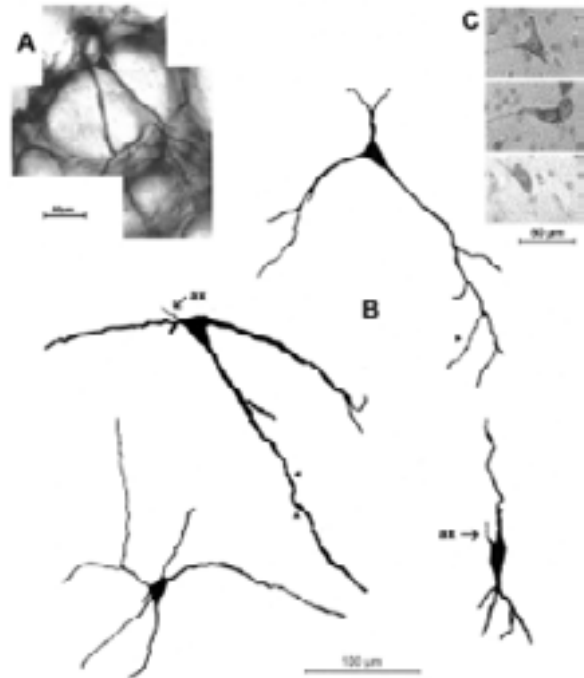


Figure 1. Large neurons: **A.** Non-clarified Golgi impregnation; **B.** Clarified Golgi impregnation; **C.** Klüver-Barrera method; ax — axon.

them are elongated in one direction. The surface of the cell body is devoid of spines and other protrusions. The clear border between the soma and dendrites of the elongated neurons has often been difficult to define. The neurons in the centre of GP have radiated dendritic trees, whereas the dendritic field of the cells along the borders of GP has an elongated shape. The large neurons have 2–6 thick, long primary dendrites, which branch sparsely. They extend very long distances, often exceeding 600 μm . The secondary dendrites and their branches have a wavy route. The dendritic arbour of the large pallidal nerve cells is varied. In a single neuron, the dendrites may be covered with dendritic swellings, not numerous spines or may be completely smooth. In addition, the different portions of the same dendrite may show all of these characteristics. The dendritic swellings are different in size and their density is variable. They are spindle- and bead-shaped (Fig. 2). The highest density of spines has been observed on the terminal portions of the dendrites. An axon emerges from a thick conical elongation, either from the cell body or from one of the dendritic trunks. The axons were seen at a distance of 50–60 μm from the perikarya. The axonal collaterals were not observed in our material. The large cells have a lot of thick and medium-size granules of tigroid matter,

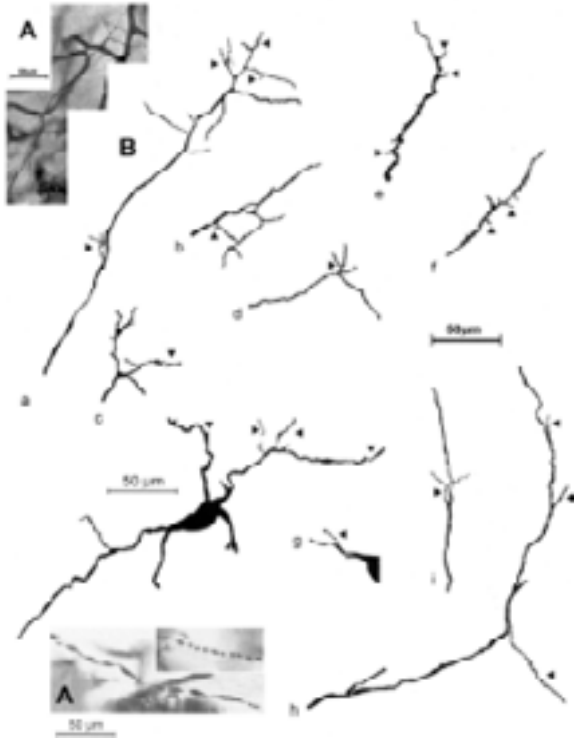


Figure 2. The reconstruction of the whole neuron. The dendritic differentiations of large nerve cells. Spindle and bead-shaped dendritic swellings; **A.** Non-clarified Golgi impregnation; **B.** Clarified Golgi impregnation; a, b, c, d — branched complex terminal endings; e, f — non-branched complex terminal endings; g, h — thin terminal processes; i — branched thin terminal process; ax — axon.

which mostly penetrate into the initial portions of the dendritic trunks. The large neurons are the most numerous in the rabbit's GP.

Complex terminal endings (Fig. 2). The pallidal distal dendrites taper progressively and they may form many types of appendages on their terminal portions that are called "complex terminal endings". Some terminal differentiations are branched (Fig. 2a–d). The lateral branches of the complex may connect with each other, creating a polygonal figure or they arise from the distal dendrites and form broom-like shapes. Most of the terminal portions have a shaggy appearance with different types of appendages such as: thin processes, bulges or knobs and thorns. The terminal complexes may have pediculated and beaded processes, which look like axonal endings. The unbranched complex terminal endings (Fig. 2e, f) have dendritic protrusions, which are differentiated in shape and size. These protrusions have the form of mushroom-, knob-, filiform- or hook-shaped spines and they bend at different angles to the mother branch. The unbranched terminal portions appear more often than the branched ones. The unbranched, but rich in various processes, final parts of dendrites

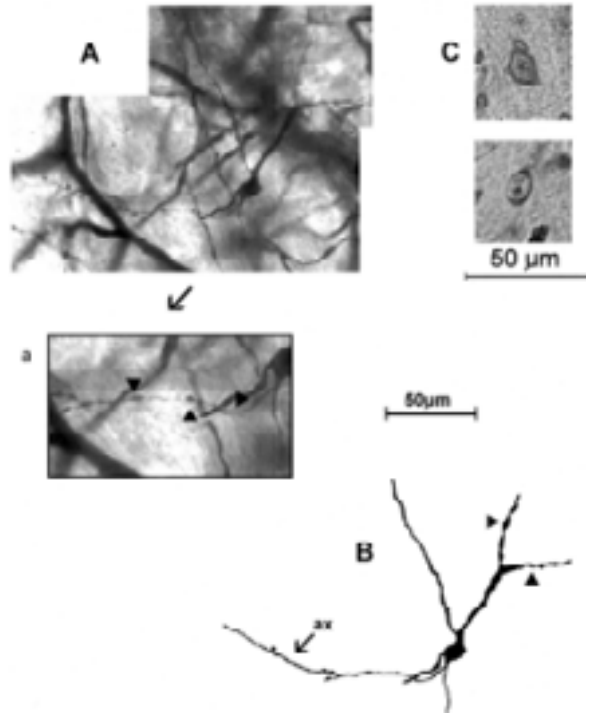


Figure 3. Small neurons: **A.** Non-clarified Golgi impregnation; **B.** Clarified Golgi impregnation; **C.** Klüver-Barrera method; ax — axon.

are always preceded by the smooth dendritic surface. Having compared both kinds of complex terminal endings, we came to the conclusion that the more branched the complex is the fewer processes and spines it has. The distribution of the complex endings is irregular on the dendrites of the large neurons. The presence of these complexes in GP is sparse. The terminal complexes are observed to contact with the dendrites of other large neurons and rarely with their soma.

Other types of morphological differentiations are thin processes (Fig. 2). They arise from any part of the dendritic tree, from small, triangular bulges. These processes are beaded and have very thin, filiform portions. Their swellings have a distinctly irregular shape and size. The lengths of the portions between them are also varied. The thin processes are usually unbranched (Fig. 2g, h), but sometimes the branched ones were observed (Fig. 2i). Many pallidal neurons do not have thin processes, while others have lots of them on the dendritic trees. The thin processes have been seen more often than the complex terminal endings. They contact either with the soma or the dendrites.

Type II — small neurons (Fig. 3). The dimensions of their perikarya are from 12 to 15 μm . Their cell bodies are rounded or polygonal. From the perikarya there arise 2–4 thin dendritic trunks, which may have

irregular swellings and few spines. The dendrites spread out, making the dendritic field round or oval in shape. The dendritic trees have a radius of about 160 μm . Axons of most of the small cells were not impregnated. However, there are some neurons that have a thin, conically elongated axon, which emerges from the cell body and bifurcates into beaded processes (Fig. 3a). Thin and medium-size granules form the tigroid substance. In the Golgi material the small neurons are sparsely distributed, but the Nissl-staining tissue suggests that relatively greater proportions of such cells exist in GP than the Golgi preparations would indicate.

DISCUSSION

The analysis of our material shows the presence of two main types of neurons in the rabbit's GP: large and small. The first one is represented by large polygonal, triangular and fusiform neurons with thick, long, usually infrequently branched, dendrites. The second one consists of small, mostly rounded cells with a beaded axon.

Salter [33], using thionine-stained scraps, distinguished the typical large, heavily stained multipolar cells with smaller neurons mixed in. In the ventral portion, the large cells were predominant, whereas in the dorsal portion the smaller cells prevailed. Both distinguished subpopulations of neurons are similar to the neurons in the present study. Sztejn [39] observed the large and larger neurons in the sheep, goat and cattle, which seem to correspond to the type I neurons in the rabbit.

Golgi analysis of GP has been performed mainly in the monkey and rat. Most authors distinguished two types of neurons: large and small in the monkey [8, 11], bison bonasus [31] and rat [25]. Totterdell et al. [42], by using a combination of Golgi impregnation and retrograde transport of horseradish peroxidase methods in the rat, observed neurons, whose perikarya ranged from 15 to 30 μm in diameter. Danner and Pfister [5] described the cellular population of the rat's GP, which is composed of 4 morphologically different neuronal types. The large spindle-shaped neurons and the large polygonal neurons were considered to be efferent pallidal neurons. The small spindle-shaped neurons and the small spiny neurons were suggested to be pallidal interneurons. Having compared our results with these observations, we came to the conclusion that almost all types of neurons that were distinguished in the rat are very similar to the rabbit's nerve cells. However, the small spiny neurons were not found in our material.

The studies of the synaptic organisation of GP in the rat, which were carried out by Difiglia and Rafols [9], indicated that GP contained principal efferent neurons with smooth or spiny dendrites and simple or complex terminal dendritic arborisations, which received convergent inputs from intrinsic and extrinsic sources and used gamma-aminobutyric acid as a transmitter. A smaller and separate population of pallidal projection neurons contained acetylcholine. Two other less frequent neuronal types were small and medium-sized.

Park et al. [28], during an intracellular HRP study in the rat, recognised two subtypes of the large pallidal neurons. The large cells located medially in the nucleus had dendritic fields with large dorsoventral extent and they did not emit any axon collaterals. Large neurons located laterally in the nucleus had disk-like dendritic fields with both dorsoventral and rostrocaudal dimensions. The axons of these neurons possessed collaterals. The similar forms of the dendritic trees of the large neurons were also defined by Millhouse [25]. In the present study we observed only large neurons with axons that were impregnated only in their initial portions. They might become myelinated beyond this point. The axonal collaterals were not observed in the rabbit.

According to Fox et al. [11] the cytoarchitecture of the lateral segment of GP in the monkey was essentially the same as the medial segment. Similar results were observed in the mouse, where neurons of the entopeduncular nucleus were similar to those of GP [17]. Both types of neurons distinguished in the mouse (large and medium-size) appear to correspond to the rabbit's large neurons in the previous study and to the large cells described in the monkey by Fox et al. [11].

The small neurons that were found in the rabbit's GP correspond to the small cells in the monkey [8], bison bonasus [31] and rat [25], but the axons of the rat's small neurons were not seen. According to van der Kooy and Kolb [43] small cells in GP may project to the cerebral cortex.

The large pallidal neurons of the rabbit form "complex terminal endings" that consist of various types of appendages, which are located on the dendritic terminal portions. Similar structures were observed by several authors [8, 11, 14, 31]. The terminal differentiations of the rabbit's GP are branched or unbranched and they seem to be similar to the type of synaptic endings distinguished by François et al. [14]. Difiglia et al. [8] suggested that "complex terminal endings" did not characterise a particular

neuronal type, but they were merely a property of large pallidal neurons on which they were irregularly distributed.

The electron microscopic study [8] showed that “complex endings” could be postsynaptic to striatal axons, and also presynaptic to the neuronal elements, like soma, dendrites and “complex endings” of other large pallidal neurons. In the present study there has been observed the contact with other large neurons, their dendrites and soma.

The thin processes have been previously observed in monkey [14], bison *bonasus* [31] and rat [28]. They were also seen in the substantia nigra [15] and described as “axonlike dendritic processes” in the lateral geniculate nucleus [32]. The thin branched processes were seen in the monkey [14], which corresponds to the present observation. Francois [14] claimed that they could be of “axonal nature”, even though their origin is dendritic.

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