

# The neuronal structure of the substantia nigra in the guinea pig: Nissl and Golgi study

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*The studies were carried out on the mesencephalons of adult guinea 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 distinguished in the substantia nigra (SN) of the guinea pig:*

1. *Bipolar neurons of two kinds: the neurons of the first kind have elongated, fusiform perikarya (25–40 µm), whereas the cells of the second kind have rounded and oval perikarya (15–22 µm). These neurons possess two dendritic trunks which arise from the opposite poles of the cell body and run for a relatively long distance. The bipolar neurons are the most numerous in the pars compacta of SN.*
2. *Triangular neurons with three primary dendrites arising conically from a perikaryon (20–35 µm). They are the most often observed type of neurons in the pars reticulata of SN.*
3. *Multipolar neurons with quadrangular or oval perikarya (22–35 µm) and 4–5 dendritic trunks which spread out in all directions.*
4. *Pear-shaped neurons (perikarya 15–25 µm), which have one or two primary dendritic trunks arising from one pole of the cell body. In all the types of neurons an axon originates either from the dendritic trunk or from the soma and is observed only in its initial segment.*

**key words:** substantia nigra, types of neurons, Golgi and Nissl pictures

## INTRODUCTION

The substantia nigra is one of the major output structures to the basal ganglia. Numerous anatomical and physiological studies have given evidence that substantia nigra creates dopaminergic projections to the striatum [3,9,10,12,16,20,22,39,42] and non-dopaminergic projections to the tectum [5,11,12,16,17,25,27,49], which use GABA as a neurotransmitter [11]. Substantia nigra is also known to give rise to projections via the neurons of the pars reticulata of SN to the thalamus [3,5,8,16,24,25,31] and to the tegmentum [5,16]; some of them display GABA immunoreactivity [5,25]. In addition, more substantial

or discrete efferent connections with other centres in the brain have been described [16,17]. On the other hand major sources of afferent fibres of the SN are the striatum and the globus pallidus [1,4,16,18,26,32,36–39,41,42,45,48]. The striatonigral and pallidonigral projection neurons have been demonstrated to contain GABA [18,19,26,36,37,45] and substance P [4,15,40] and they exert a very powerful control over the output neurons of the substantia nigra [15,37]. Moreover, SN receives fibres from the anterior and the postero-lateral hypothalamic area, the nuclei of amygdala, parafascicular thalamic nucleus [16], tegmental cholinergic neu-

rons [2,16], subthalamic nucleus [16,29,47], the motor and premotor cortex [30] and from the serotonergic neurons of the dorsal raphe nucleus [18,28,46].

The neuronal morphology of the substantia nigra was described in a few mammals: rat [7,23], bison [43], and primates [13,34,35,50]. Some authors observed also the cytoarchitecture and ultrastructure of SN in mammals, for example: in kitten [33], rats [18,21], opossum [27] and insectivorous species [14]. The aim of our study was to describe types of neurons in the substantia nigra in the guinea pig.

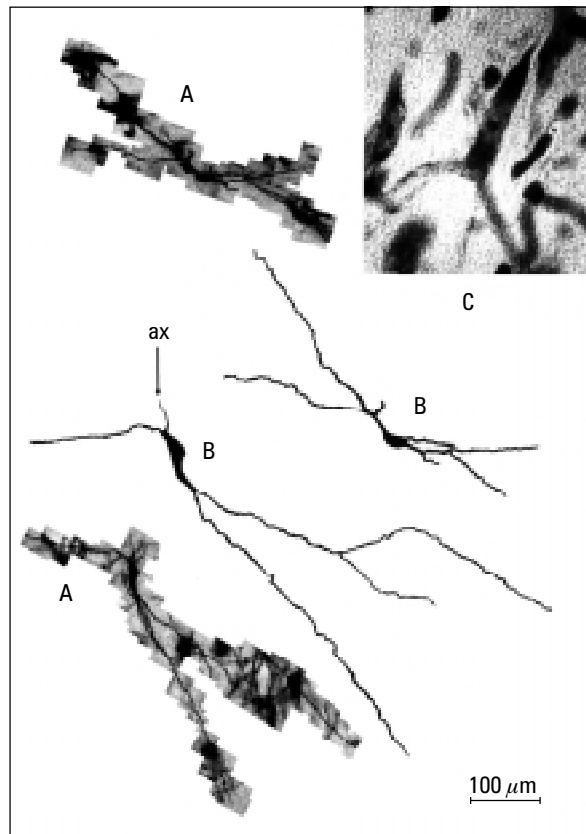
### MATERIAL AND METHODS

The studies were carried out on the mesencephalons of six adult guinea pigs. Preparations were made according to the Bagiński and Golgi-Kopsch techniques and stained by means of the Nissl or Klüver-Barrera methods. The brains were cut into 60  $\mu\text{m}$  and 10  $\mu\text{m}$  sections for the Golgi and Nissl methods respectively (in frontal and sagittal planes). The microscopic images of selected, impregnated cells were digitally recorded by means of camera that was coupled with microscope and 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

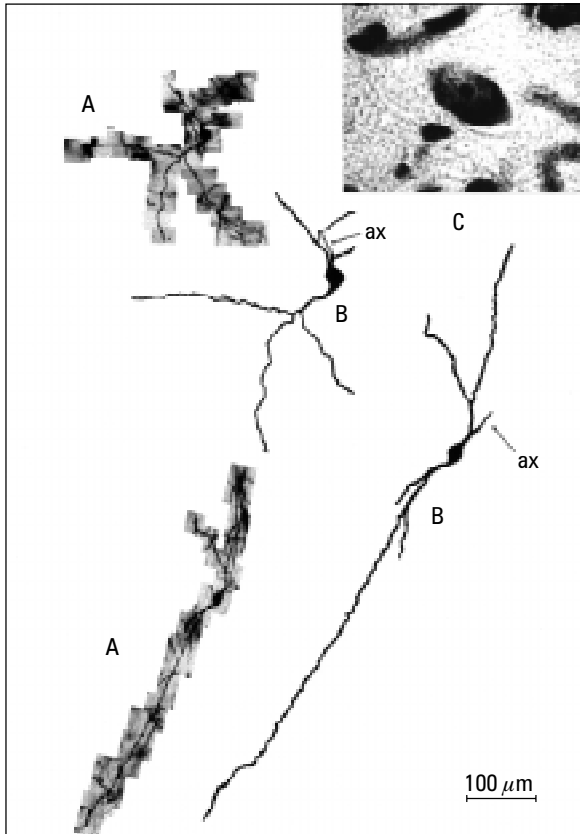
The following morphological criteria were taken into account to categorise the neurons: the shape and size of soma, distribution of tigroid substance, number and arborisation of dendrites and location of axon. On the basis of these criteria the following types of neurons were distinguished in the substantia nigra:

Bipolar neurons (Fig. 1,2). They are the most often observed type of neurons in the pars compacta of SN. As regards the shape and the size of the perikarya, two kinds of bipolar neurons can be distinguished. The first one (Fig. 1) contains elongated, fusiform perikarya which measure from 25 to 40  $\mu\text{m}$  along the long axis whereas the second one (Fig. 2) has rounded or oval perikarya measuring from 15 to 22  $\mu\text{m}$ . Generally, these neurons possess two dendritic trunks which emerge from the opposite poles of the cell body (the third is sometimes observed to arise directly from the soma). These dendrites have

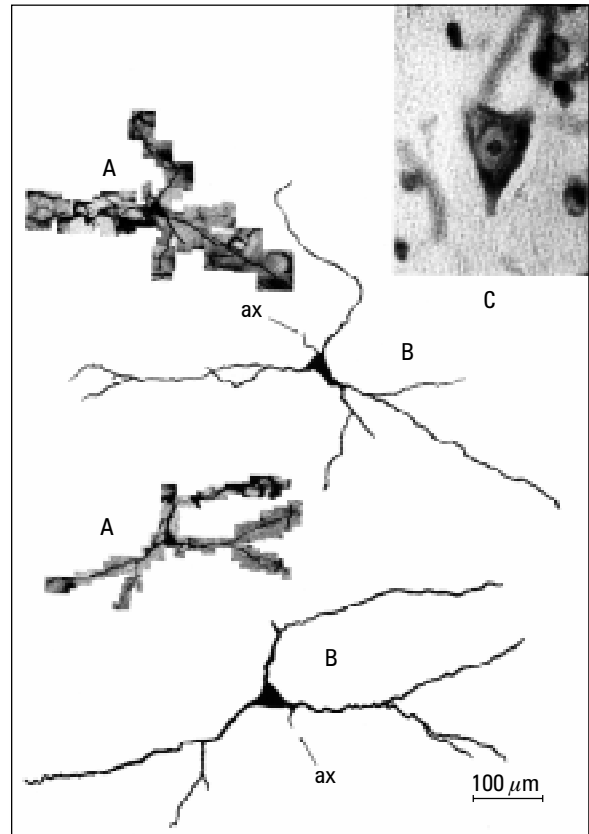


**Figure 1.** Bipolar neurons (the first kind of the bipolar neurons).  
A) Non-clarified Golgi impregnation.  
B) Clarified Golgi impregnation, ax — axon.  
C) The Nissl stained soma.

a wavy course and run for a long distance; some of them may be followed at the distance of about 600–700  $\mu\text{m}$  within the same sagittal section. They divide into quite long, thinner secondary dendrites after 15–40  $\mu\text{m}$  of their route and once again at various distances from the perikaryon. Bead-like protuberances and varicosities are sporadically observed on the secondary dendrites and their branches. Most of the dendrites of the fusiform cells (sagittal plane) run in a rostro-caudal direction and only some of them have a tendency to direct dorso-ventrally. The dendritic field has a stream-like form. The dendrites of the rounded or oval cells usually have a dorso-ventral course and show a dendritic field which is oval in shape. It is possible to notice that some dendrites from the pars compacta run into the pars reticulata of SN. An axon arises from the initial portion of the dendritic trunk or seldom directly from the perikaryon, and takes a dorsal or an antero-dorsal course. An axon can be seen at the distance of about 35–50  $\mu\text{m}$ . The fusiform cells have a large, elongated and centrally located nucleus. The tigroid



**Figure 2.** Bipolar neurons (the second kind of the bipolar neurons).  
 A) Non-clarified Golgi impregnation.  
 B) Clarified Golgi impregnation, ax — axon.  
 C) The Nissl stained soma.



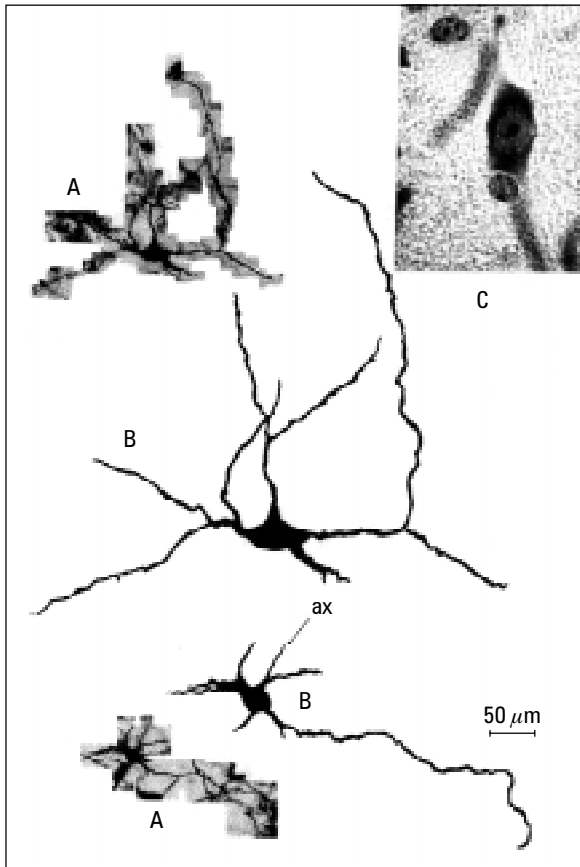
**Figure 3.** Triangular neurons.  
 A) Non-clarified Golgi impregnation.  
 B) Clarified Golgi impregnation, ax — axon.  
 C) The Nissl stained soma.

substance has the form of thick and medium-size granules which are concentrated at the poles of the cell body and enter deeply into the initial portion of the dendritic trunk. The rounded or oval cells have a spherical, centrally localised nucleus and contain medium-size granules of the tigroid substance, which do not penetrate into the dendritic trunks.

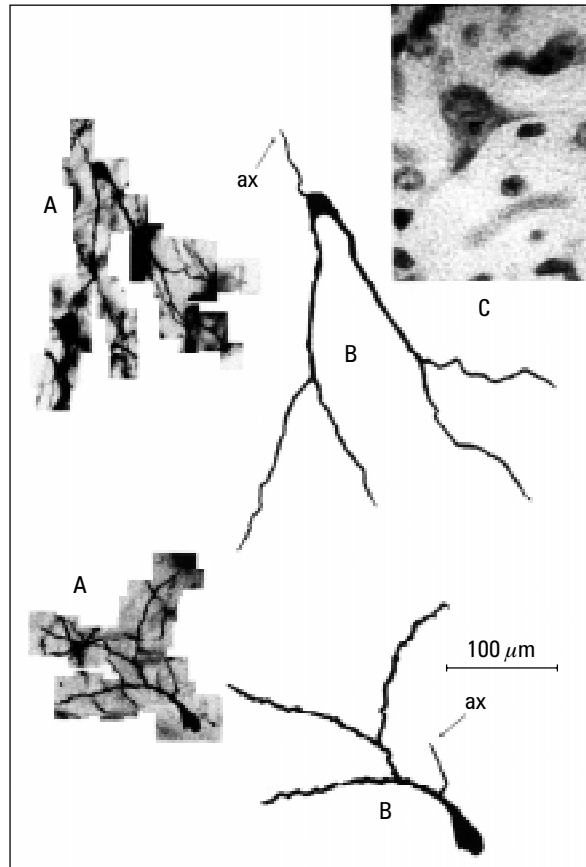
Triangular neurons (Fig. 3). Their cell bodies measure from 20 to 35  $\mu\text{m}$ . They have 3 primary dendrites which arise conically from a perikaryon. Most of them bifurcate for the first time near the cell body, and the second time at a different distance from a perikaryon. In our material we also observed neurons with dendrites that divide only once at the distance of about 70–100  $\mu\text{m}$  from a soma. Some dendrites do not bifurcate but only give off collaterals. The secondary and tertiary dendrites have a slightly wavy course and may be observed for a relatively long distance (400–500  $\mu\text{m}$ ). These dendrites are smooth along their whole extent but the secondary dendrites and their branches are sometimes covered with delicate varicosities. The dendrites run in ros-

tral, caudal, ventro-caudal, and dorsal directions causing the dendritic field to have a form of a three-pointed star. An axon emerging directly from the soma or from the proximal portion of the primary dendrite takes a dorsal or ventral course. The triangular cells have a centrally-located, large, spherical nucleus and the coarse granules of the tigroid substance, which are densely packed in the neuroplasma and deeply penetrate into the cones of the dendritic trunks. These neurons are the most often met kind of neurons in the pars reticulata of SN.

Multipolar neurons (Fig. 4). The cell bodies are mostly quadrangular (sometimes oval) in shape, and measure from 22 to 35  $\mu\text{m}$ . From a soma there originate 4–5 thick dendritic trunks which spread out in all directions. The primary dendrites divide usually into secondary dendrites near the cell body after 15–30  $\mu\text{m}$  or rarely at the distance of about 50–80  $\mu\text{m}$  from a perikaryon. The secondary dendrites sporadically ramify into tertiary branches at various distances from the first bifurcation. The dendritic branches have a slightly wavy course and may be followed at



**Figure 4.** Multipolar neurons.  
A) Non-clarified Golgi impregnation.  
B) Clarified Golgi impregnation, ax — axon.  
C) The Nissl stained soma.



**Figure 5.** Pear-shaped neurons.  
A) Non-clarified Golgi impregnation.  
B) Clarified Golgi impregnation, ax — axon.  
C) The Nissl stained soma.

the long distance of about 400–500  $\mu\text{m}$ . The dendritic trunks are smooth and they are devoid of protuberances, whereas the secondary and tertiary dendrites have bead-like protuberances and varicosities. The dendritic field is oval or round in shape. An axon arises from the proximal part of the dendritic trunk or from the soma, and usually directs dorsally. The soma contains a large, round nucleus which is surrounded by coarse granules of the tigroid substance. They penetrate into the initial segments of the dendritic trunks. Both parts of the SN have a similar number of the multipolar neurons.

Pear-shaped neurons (Fig. 5). Their cell bodies measure from 15 to 25  $\mu\text{m}$ . These neurons have one or two dendritic trunks, which arise from one pole of the cell body. The dendrites divide dichotomically into secondary branches usually at the distance of 60–100  $\mu\text{m}$  from the perikarya. Some dendrites, especially the dendrites of the neurons which possess only one dendritic trunk, bifurcate near the cell body (after 10–30  $\mu\text{m}$  of their route). The secondary den-

drites may branch once again at a different distance from the soma. The dendritic branches on their whole length are smooth but they have moderately distributed varicosities and bead-like protuberances. The dendrites are oriented dorsally or ventrally and the dendritic tree has a fan-like shape. An axon usually arises from the opposite side of the cell body, or rarely from the initial portion of the dendritic trunk and takes a rostro-dorsal direction. The neuroplasma contains medium-size and thick granules of the tigroid substance which enter into the initial portion of the dendritic trunks. The pear-shaped neurons are more often observed in the pars compacta than in the pars reticulata of SN.

## DISCUSSION

In the substantia nigra of the guinea pig four distinguished types of neurons are present in the pars compacta (PC) and in the pars reticulata (PR), but PC is mainly made of the fusiform and pear-shaped neurons, whereas the triangular neurons are the com-

monest cell type observed in the pars reticulata. The multipolar neurons are uniformly distributed in both parts of SN. These bipolar, triangular, multipolar and pear-shaped neurons of the guinea pig correspond most probably to the large fusiform (type I), small and medium-sized triangular (type II), large and medium-sized multipolar (type III) and small and medium-sized pyriform and rounded neurons (type IV), respectively, described in bison by Szteyn et al. [43]. In general, these cells show similar shape of cell bodies, number and arborisation of dendrites and the dendritic fields. The neuronal structure of SN was also investigated in primates [13,34,35,50], rat [7,23] and kitten [33]. In the primates, Siddiqi and Peters [35] distinguished three types of SN neurons: large multipolar, medium-sized bipolar and small multipolar neurons, but other authors [34,50] described two types of nigral neurons: large and small neurons. The cell bodies of these neurons present a wide variety of shapes; they are fusiform, pyramidal, triangular, polygonal, mitral or ovoid [34,50]. In the rat SN, Juraska et al. [23] described large, medium-sized and small neurons, but Danner and Pfister [7] distinguished polygonal (spiny or aspiny), fusiform and triangular neurons. These neurons are considered to be nigral projection cells, whereas small spherical, spindle-shaped and neurogliform neurons are reported to be interneurons [7]. The fusiform, triangular and multipolar neurons of the guinea pig resemble the large neurons of the primates [34,50] and also the medium-sized and large fusiform, trigonal and polygonal neurons of the rat [7,23], respectively. They may differ only in details. The dendrites observed in our material have usually a slightly wavy course and can even be seen at the distance of 700  $\mu\text{m}$  (especially dendrites of the bipolar neurons). Some authors [27,50] observed dendrites of SN (in the opossum and in the primates) at the distance of more than 1000  $\mu\text{m}$ . Most dendrites of SN of the guinea pig have a rostro-caudal or dorso-ventral direction, and only some dendrites of the pars compacta neurons run downward into the pars reticulata. This was also reported by Juraska et al. in the rat [23] and by Schwyn and Fox [34] in the primates. "The terms pars compacta and pars reticulata, which are used to describe regions of SN, do not separate this nucleus into two regions containing neurons belonging exclusively to the one part or the other of SN" [34]. The pars reticulata contains most of the receptive structures in the SN and Schwyn and Fox [34] suggest that the pars reticulata should be regarded as the plexiform layer,

whereas the pars compacta as the ganglionic layer. Due to the fact that in Golgi scraps the cytoarchitectonic limit between the PC and PR is not visible [34], Francois et al. separated these two subdivisions according to the presence of the pigmented cell bodies in the PC of the human and according to the density of cell bodies observed after counterstaining in macaques [13]. Many nigral neurons in rat have dendritic varicosities, which are not found on the thick dendritic trunks, but they are located slightly further from the cell body [23], and in the primates Schwyn and Fox [34] observed varicosities and occasionally dendritic spines on the terminal portion of dendrites. In the opossum Ma and Hazlett [27] described neurons which were moderately spinous and neurons which possess only sparsely spinous dendrites. Some authors [23,33] observed more spines on the soma and dendrites in the youngest animals than have been reported in the adult [23,34]. Schwyn and Fox [34] as well as Phelps and Adinolfi [33] came to the conclusion that most of these spines observed in the SN newborn infant disappear during the early stages of development. A significant loss of dendritic spines and dendrites was also observed in the human SN neurons, especially in the oldest cases [6]. In our material no typical spines but varicosities and bead-like protuberances were observed, only on the secondary dendrites and their branches. The absence or presence of the varicosities may result from the fact that the same dendrite may receive differential input. Electron microscopic studies [10, 26] indicate that pallidal terminals form symmetric synaptic contacts with the perikarya and proximal dendrites, whereas the striatal terminals contact with the distal dendrites. These terminals contain large synaptic vesicles of the type I [34]. According to some authors [23,35], large and medium-sized neurons in the pars compacta contain dopamine, and these cells are probably the origin of the dopaminergic nigro-neostriatal tract [23]. On the other hand the triangular, multipolar, fusiform and oval perikarya of the pars reticulata are the source of the nigrostriatal projections [10].

In the guinea pig in all types of neurons an axon arises either from the soma or from the initial portion of the dendritic trunk and in all the types of neurons usually takes a dorsal or rostro-dorsal direction. Sometimes, especially in the triangular neurons, an axon may run in a ventral direction. The same observations were reported by Juraska et al. [23] in rat. In our material an axon is impregnated only in its initial segment. This fact corresponds to

the results presented by Schwyn and Fox [34] in the primates. In guinea pig no collaterals were seen to arise from an axon, contrary to the results presented by Juraska et al. [23] and Yelnik et al. [50]. The results of our paper indicate that in various species of mammals in SN obvious differences are present. The greatest number of similarities in the neuronal structure of SN exist between SN of rats and guinea pigs, which may result from the fact that these mammals belong to the same order.

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