

# The nerve cells of the neostriatum in the common shrew (*Sorex araneus*) and bank vole (*Clethrionomys glareolus*): a Golgi comparative study

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[Received 8 August 2006; Received 23 November 2006; Accepted 23 November 2006]

*The studies were carried out on 12 brains derived from adult representatives of two mammalian orders, Insectivora and Rodentia. The neostriatum was compared in the common shrew (*Sorex araneus*) and bank vole (*Clethrionomys glareolus*). Three main types of striatal neuron were distinguished in the common shrew and five types of neurons in the bank vole. The fifth type of bank vole neurons was additionally divided into two subtypes with respect to dendritic pattern.*

**Key words:** neuronal structure, silver impregnation, caudate nucleus, putamen, Insectivora, Rodentia

## INTRODUCTION

The mammalian neostriatum consists of the caudate nucleus and putamen. It receives afferent connections from the cortex, substantia nigra, thalamus, corpus amygdala, claustrum, globus pallidus and nucleus accumbens [10, 23, 26, 30, 33, 34, 42, 43, 45, 47, 49, 51]. The efferent fibres of the neostriatum project to various structures, such as the globus pallidus, nucleus entopeduncularis, substantia nigra and the neocortex [14, 19, 37].

The neostriatum is a complex structure known for its role in motor function. It has also been shown to play an important part in the learning and memory processes [18, 21, 27, 36, 50, 53].

By using the Golgi technique an analysis of the neuronal structure of the neostriatum has been carried out in the rat [4, 25, 31, 46, 48], cat [3, 15], monkey [13, 15, 16, 17] and man [5, 20, 55]. Single studies have been made of the European bison [41], mouse [24], guinea pig [44] and rabbit [15]. In the available literature there is a lack of studies concern-

ing the neuronal structure of the neostriatum in the common shrew (Insectivora) and bank vole (Rodentia), and therefore the aim of our study was to provide the full morphological characteristics of and a comparison between the striatal neurons in the two species analysed, which represent different mammalian orders.

## MATERIAL AND METHODS

The studies were carried out on 12 brains derived from adult representatives of two mammalian orders, Insectivora and Rodentia. The neostriatum was compared in the common shrew (*Sorex araneus*) and bank vole (*Clethrionomys glareolus*). The neostriatum of the each species was analysed on the basis of 6 brains. The brains were fixed in 10% neutralised formalin for not less than three months. One brain was cut into 50- $\mu$ m coronal sections that were then stained with cresyl violet, according to the Nissl procedure. The 5 brains for the Golgi impregnation were placed first in a solution of 2.5% potassium

dichromate for 7 days and then in a 3% silver nitrate for 3–7 days. After impregnation the paraffin blocks were cut into 120  $\mu\text{m}$  scraps. The microscopic images of the selected impregnated cells were digitally recorded by means of a camera and an image processing system (MultiScan 8.2, Computer Scanning System, Poland). Between 60 and 100 digital microphotographs were taken at the different focus layers for each neuron. The computerised reconstructions of microscopic images were made on the basis of these series of microphotographs using the Corel Photo-Paint 9 software. The neuropil was kept in all the pictures in order to show the real microscopic images but was then removed from each to clarify the picture.

## RESULTS

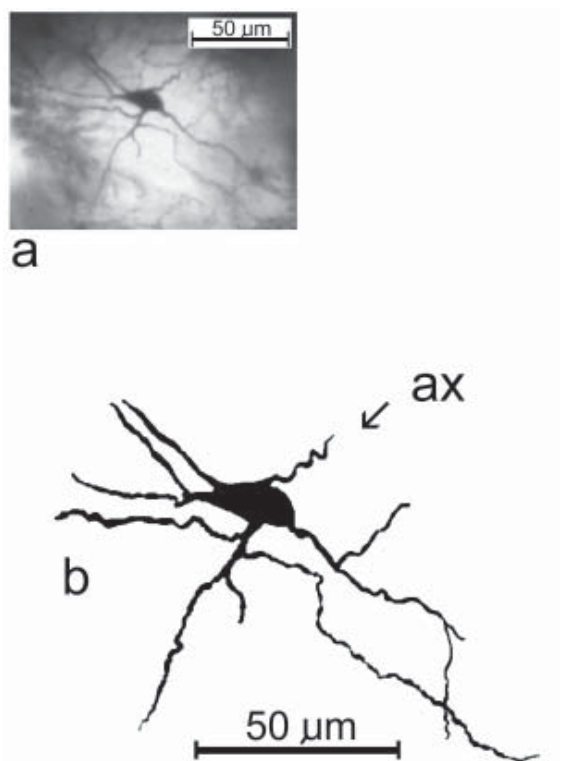
The comparison of the neostriatum of the common shrew with the neostriatum of the bank vole revealed some differences in neuronal structure. On the basis of such criteria as the shape and size of the soma, the number and arborisation of the dendrites, axon location and the presence of dendritic spines the following types of neurons were distinguished.

### Large neurons — L (Fig. 1, 2)

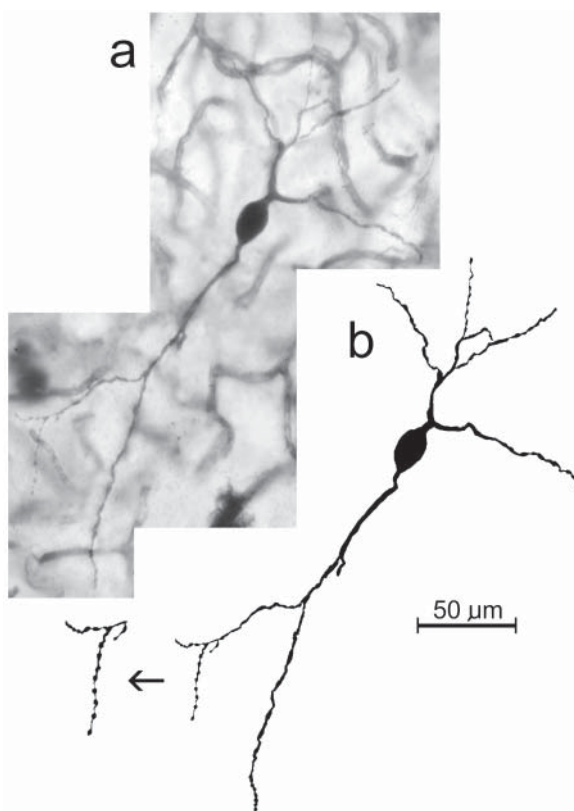
Large neurons were observed in both the species studied. The long axis of the perikarya measures from 16.2 to 22.4  $\mu\text{m}$  (average  $18.30 \pm 2.07 \mu\text{m}$ ) in the common shrew (Fig. 1) and from 23.4 to 36  $\mu\text{m}$  ( $26.78 \pm 2.41 \mu\text{m}$ ) in the bank vole (Fig. 2). The large neurons have elongated, multipolar and triangular perikarya. From the cell body arise 2–5 smooth dendrites in the common shrew and up to 6 dendritic trunks in the bank vole. In both animals the dendrites are poorly ramified and possess irregular swellings, especially on the terminal portions. The dendrites usually bifurcate up to third-order branches. An axon originates either from the initial portion of the dendritic trunks or from the soma. These neurons are not numerous in the neuronal population of the striatum in either mammal. In the bank vole the multipolar neurons are mainly seen in the central part of the neostriatum. The long axis of the elongated perikarya is situated parallel to the fibres of the corpus callosum.

### Medium-sized spiny neurons — MS (Fig. 3, 4)

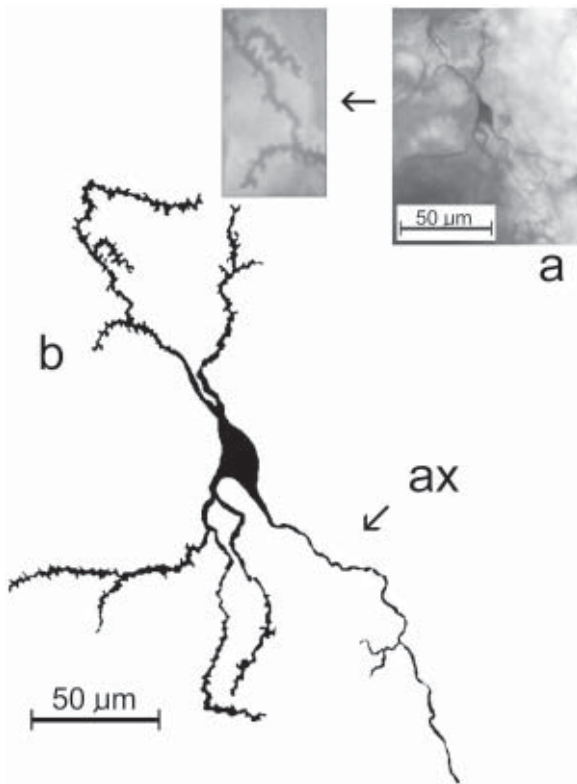
In both the species studied the medium-size spiny neurons display a similar morphology and form the basic cellular populations in the neostriatum. The long axis of the perikarya of medium-sized spiny



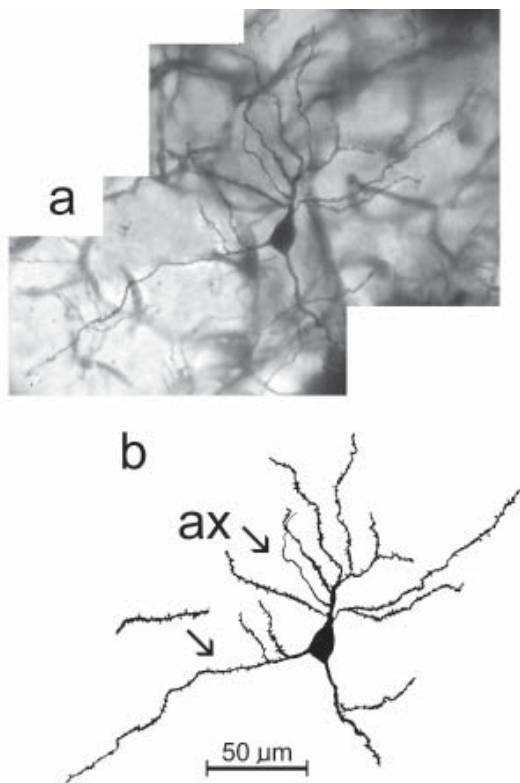
**Figure 1.** Large neurons (L) in the common shrew: **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation; ax — axon.



**Figure 2.** Large neurons (L) in the bank vole: **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation.



**Figure 3.** Medium-sized spiny neurons (MS) in the common shrew: **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation; ax — axon.



**Figure 4.** Medium-sized spiny neurons (MS) in the bank vole: **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation; ax — axon.

neurons measures from 8.4 to 15.5  $\mu\text{m}$  ( $11.38 \pm 1.76 \mu\text{m}$ ) in the common shrew (Fig. 3) and from 16.2 to 22.6  $\mu\text{m}$  ( $19.45 \pm 1.87 \mu\text{m}$ ) in the bank vole (Fig. 4). The perikarya are polygonal and rounded in shape. In the bank vole triangular and fusiform cell bodies were seldom observed. In the common shrew the cells have 2–6 smooth dendritic trunks and most divide two or three times, with a fourth bifurcation sometimes observed. In the bank vole the cells even have 8 long dendrites which are greatly ramified. The dendrites usually bifurcate up to sixth-order branches. In both animals the dendrites spread out, making the dendritic field oval in shape. They are differentiated as regards shape and size and bend at various angles to the mother branch. The dendrites are covered with various spines and are knob-like, mushroom and filiform in shape. The highest density of spines was observed on the terminal portions of the dendrites. The dendritic spines occur in greater number in the bank vole than in the common shrew. An axon emerges from the cell body or from the initial portion of the dendritic trunk. The axonal collaterals were observed and these branch within the dendritic domain.

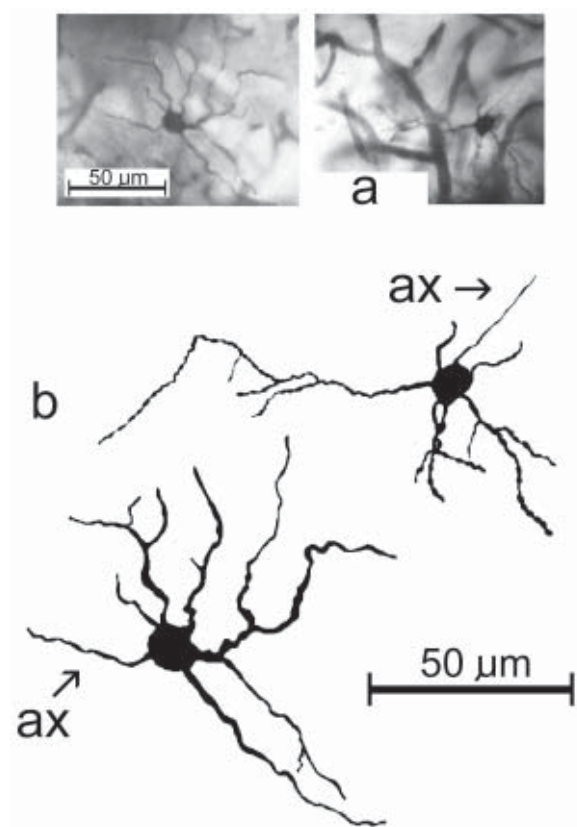
#### Medium-sized aspiny neurons — MA (Fig. 5, 6)

The medium-sized aspiny neurons have polygonal, triangular, spindle-shaped and rounded perikarya. The long axis of the cell bodies measures from 8.4 to 12.4  $\mu\text{m}$  ( $10.33 \pm 1.51 \mu\text{m}$ ) in the common shrew (Fig. 5) and from 17 to 21.6  $\mu\text{m}$  ( $20.13 \pm 1.74 \mu\text{m}$ ) in the bank vole (Fig. 6). From the perikarya arise 2–5 long dendrites in the bank vole and up to 6 dendrites in the common shrew. The dendrites have a straight or wavy course. In the bank vole some dendrites bifurcate even up to fourth-order branches. The dendritic field is ellipsoidal in shape. The primary dendrites are smooth or bear few swellings. The swellings are irregular in shape, but on the terminal portion they have a bead-like form. A short axon emerges from the soma.

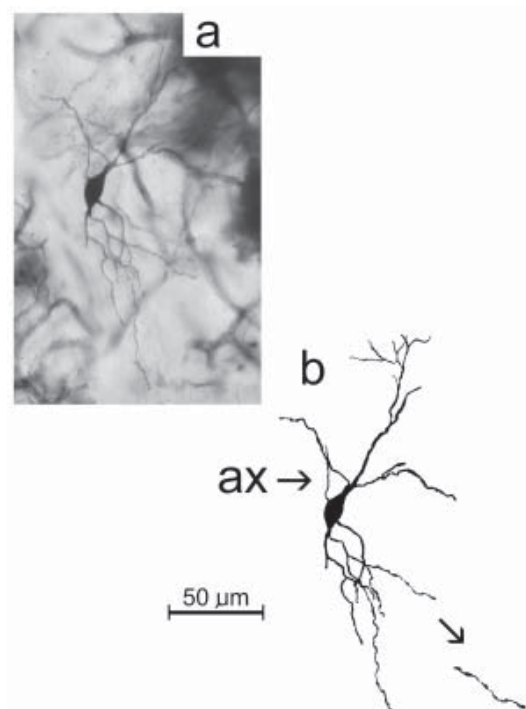
Only in the bank vole were small spiny and aspiny neurons observed in the neostriatum.

#### Small spiny neurons — SS (Fig. 7)

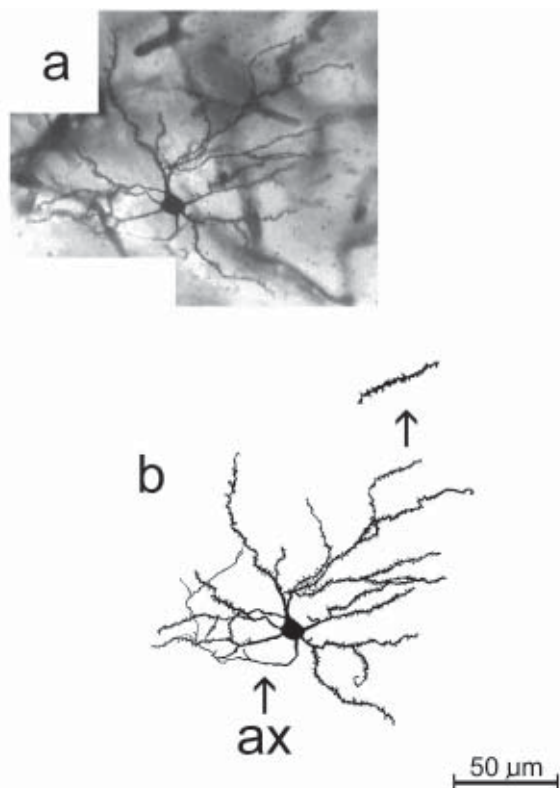
The perikarya of these cells measure from 10.8 to 16.2  $\mu\text{m}$  ( $13.53 \pm 1.53 \mu\text{m}$ ) along the long axis. The small spiny neurons have rounded multipolar and triangular perikarya and have 2–6 dendrites, which bifurcate even up to fifth-order branches. The surface of the cell body and primary dendrites are devoid of spines and other protrusions. Long secondary dendrites give off thinner distal branches,



**Figure 5.** Medium-sized aspiny neurons (MA) in the common shrew: **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation; ax — axon.



**Figure 6.** Medium-sized aspiny neurons (MA) in the bank vole: **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation; ax — axon.



**Figure 7.** Small spiny neurons (SS) in the bank vole: **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation; ax — axon.

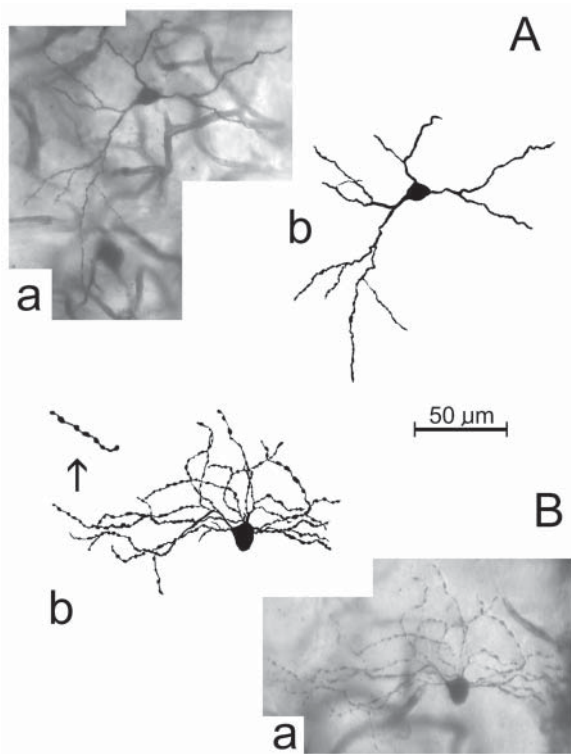
which are densely covered with spines. A long axon arises mainly from a cell body. The axon collaterals were observed within the dendritic domain.

#### Small aspiny neurons — SA (Fig. 8)

These are the least numerous cells in the neuronal population. The cell bodies of the small aspiny neurons measure from 12.6 to 16.2  $\mu\text{m}$  ( $14.22 \pm 1.33 \mu\text{m}$ ) along the long axis. In this type two subtypes (A and B) were distinguished with respect to the pattern of the dendrites and the dendritic tree.

**Subtype A neurons — SA<sub>A</sub> (Fig. 8A).** The perikarya of these are rounded, polygonal and triangular in shape and the dendritic trunks (2–5) have a straight or wavy course. The surface of the cell body and primary dendrites is smooth, whereas the secondary dendrites have bead-shaped swellings.

**Subtype B neurons — SA<sub>B</sub> (Fig. 8B).** These neurons have rounded perikarya with up to 8 tortuous dendrites, which bifurcate near the cell body, so that the dendritic tree has a bushy form. The secondary dendrites have swellings similar in form to the swellings of the SA<sub>A</sub>.



**Figure 8.** Small aspiny neurons (SA) in the bank vole: **A.** Small aspiny neurons with a straight or wavy course of the dendritic trunks (SA<sub>A</sub>); **B.** Small aspiny neurons with tortuous dendrites bifurcating near the cell body (SA<sub>B</sub>); **a.** Non-clarified Golgi impregnation; **b.** Clarified Golgi impregnation.

## DISCUSSION

The major neuronal population in the neostriatum of both the animals studied is represented by the spiny projection neurons. According to Kemp and Powel [31], these account for almost 95% of total striatal cells. In both the mammals analysed the medium-sized spiny neurons correspond to the type I neurons in the monkey [13], humans [5], European bison [41] and guinea pig [44] and the type II neurons in the cat [15]. In the common shrew and bank vole the medium-sized spiny neurons possess axonal collaterals. Kawaguchi et al. [29] described how in the rat the axonal collaterals of the medium-sized projection neurons arborise profusely according to two different patterns. The first consists of local axonal arborisations restricted to the dendritic domain of its cell of origin. The second pattern consists of much larger and more extended axonal arborisation that goes far beyond the dendritic domain [29]. In both the species examined by us the axonal collaterals of the medium-sized spiny neurons branch according to the first pattern. Bolam et al. [2] reported that axon collat-

erals of the medium-sized spiny neurons terminate within the neostriatum onto both the striatal interneurons and other medium spiny cells. An extensive network of axon collaterals originating from the spiny neurons is an important intrastriatal source of  $\gamma$ -aminobutyric acid (GABA) [32, 38]. According to Parent et al. [37], the spiny neurons are the main integrating element of the primate neostriatum. The medium spiny neurons are the major target of both local and extrinsic afferents when compared with the aspiny interneurons, which receive only a sparse innervation. The extrinsic afferents arise principally from the cerebral cortex, thalamus and substantia nigra *pars compacta* and contact mainly the distal portion of the dendritic arbour of medium spiny neurons. Virtually all medium spiny neurons use GABA as their main neurotransmitter [35, 40] but also co-express a number of neuroactive peptides, such as substance P, enkephalin, dynorphin and neurotensin [1, 22].

The small spiny neurons that were observed only in the bank vole correspond to the type III neurons of the rabbit, cat, monkey and humans [15]. The efferent long axonal small neurons together with the medium-sized spiny neurons form the principal cell group of the neostriatum of these mammals.

According to Kawaguchi et al. [28] about 5% of striatal cells consists of aspiny interneurons containing, alternatively, acetylcholine, somatostatin, NADPH-diaphorase (enzyme nicotinamide adenine dinucleotide phosphate-) or GABA associated with parvalbumin or calretinin.

The large neurons that were found in the neostriatum of both the animals examined correspond to the giant aspiny neurons described in the rat [9], cat [15, 31], rabbit, monkey and humans [15], the large neurons in the European bison [41] and the type I AChE-positive (acetylcholinesterase-) neurons in the rat [4]. The large striatal neurons, especially the neurons that do not have numerous dendrites, are very similar to the type I pallidal neurons of the rabbit [52]. Large aspiny neurons are cholinergic interneurons in the rat neostriatum [4, 54]. Although they only account for less than 2% of the neuronal population in the neostriatum [39], these neurons exert great influence on the function of the basal ganglia by modulating the synaptic transmission of the spiny projection neurons and interneurons [6]. It has been postulated that the main role of the large cholinergic interneurons is the regulation between inputs arising from dopaminergic afferents and the activity of projection spiny neurons [6, 7]. Current neuroanatomical data

indicate that the acetylcholine innervation of the neostriatum is essentially intrinsic, arising mainly, if not exclusively, from the large aspiny interneurons [6].

The medium-sized aspiny neurons in both the animals studied and also the SA<sub>A</sub> neurons in the bank vole correspond to the type I aspiny neurons in the monkey [11, 13], the type IV aspiny neurons in the cat [15] and the aspiny nerve cells (with dendritic swellings) in the European bison [41]. The medium-sized aspiny striatal interneurons are known to modulate the activity of the medium-sized spiny neurons [8]. According to Cicchetti et al. [8], axons of interneurons terminate predominantly onto the proximal somatodendritic domain of projection neurons, where they make symmetrical synaptic contacts. In our study an axon of the medium-sized aspiny neurons impregnates only at a short distance, but within the cell population of the SA<sub>A</sub> no axon was visible.

The small aspiny neurons of the subtype SA<sub>B</sub> (observed only in the neostriatum of the bank vole) seem to be similar to the type VI neurons in the cat [15]. The morphological features of these neurons also probably correspond to the type V neurons distinguished in humans [5]. However, in our material we could not precisely detect the axons of these cells.

Different types of striatal neurons exist and several classifications have been proposed in different mammals. The neurons have often been classified, for example, on the basis of cell body size [31], the presence of dendritic spines [11, 16, 17] or the length of the axon [12]. In our study we used identical criteria in order to compare the neuronal structure of the neostriatum in different mammals. We distinguished in the common shrew three main types of striatal neurons and five types in the bank vole, including two subtypes of small neurons. Sztejn et al. [44], using the Golgi technique, described four types (with two subtypes) of neurons in the neostriatum of the guinea pig, whereas in the European bison Równiak et al. [41] distinguished 5 types of neurons: 4 types of aspiny and 1 spiny nerve cells. Takagi et al. [46] observed in the rat neostriatum only aspiny neurons and divided them into 3 types. Éder et al. [15] described 6 types of neurons in the rabbit caudate nucleus, 7 in the cat and 9 in humans. In the series of neostriata of these mammals an increase in the number of interneurons has been noticed and the authors have concluded [15] that the number and variety of the types of neurons tend to increase during phylogenesis. Our studies support this view, as the neuronal structure of the neostriatum in the bank vole is more complex than this structure in the com-

mon shrew. The bank vole neurons have more dendritic trunks that divide more often than the neurons of the common shrew. The complexity of the striatal architecture in the bank vole also involves the small neurons, especially the aspiny neurons, which we did not observe in the common shrew neostriatum. The more complex structure of the neostriatum in the bank vole may result from the fact that this species belongs to a phylogenetically younger order (Rodentia) than the common shrew (Insectivora). When the number of cell types in the neostriatum of rodents is taken into account, it should be pointed out that mammals even within one order (Rodentia) show a wide diversity in this respect (for example, the rat, guinea pig and bank vole). In the light of the assumption made by Éder et al. [15], the neostriatum of the bank vole seems to be more advanced than that of the rat, whereas the neostriatum of the guinea pig occupies an intermediate position.

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