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The neuronal structure of the inferior colliculus in the bank vole (*Clethrionomys glareolus*) — Golgi and Nissl studies

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The inferior colliculus (IC) of the bank vole is made up of 3 nuclei: the external and pericentral nucleus, which are located on the outer border of the IC, and the central nucleus, which is the largest part of IC and shows a laminated structure. On the basis of various morphological criteria 5 types of neurons have been distinguished in the bank vole IC: 1. The rounded cells (perikarya 10–15 µm) with 2–4 primary dendritic trunks. The dendritic tree has a spindle-like shape. The axon emerges from the soma or from the proximal portion of a dendrite. 2. The fusiform neurons (17–20 µm) with 2 primary dendrites arising from both poles of the perikaryon. The dendritic tree has the same shape as the previous type. The axon originates from the proximal dendritic trunk. The rounded and fusiform cells constitute the main neuronal type. 3. The pear-shaped neurons (10–13 µm) with 2 main stems or rarely 1. The axon emerges from the perikaryon or seldom from the dendritic trunk. 4. The multipolar cells (18–23 µm), which have from 4 to 6 primary dendrites radiating in all directions. The dendritic tree has a spherical shape. The axon emerges either from the proximal stem or directly from the soma. 5. The triangular neurons (15–18 µm) with 3 primary dendritic trunks. The axon originates from the perikaryon. The triangular cells are the least numerous. All types of neurons in the bank vole IC bear spines and protrusions.

key words: inferior colliculus, types of neurons, bank vole

INTRODUCTION

The inferior colliculus (IC) is one of the major centres in the auditory system. It receives afferent projections from the auditory cortex [6, 13, 27] and from the majority of the brainstem auditory nuclei as well [2, 5, 12, 14, 15, 19, 21, 27]. Other non-auditory neurons projecting to IC were observed in the pars lateralis of the substantia nigra [29] and in the globus pallidus [20]. Some papers [4] revealed that IC is involved in the integration of defensive reactions. Electrical and chemical stimulation of this structure causes fear and escape behaviour [4]. According to Bagri et al. [1] the ventral part of IC is more sensitive than the dorsal part, as lower intensities were needed to elicit wild running. Mascetti and Strozzi [16] found in the cat IC few neurons which were responsive to visual stimuli. They suggest that the visual input to IC participates in an integrated reflex-orienting behaviour, in which the visual information is important for the localisation of the sound source.

Although the distribution of projections to IC and from this structure [3, 6, 11, 13, 28] as well as the tonotopical organisation [10, 26, 30] were studied, there is little information concerning its neuronal

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structure. There have been studies of the neuronal morphology of IC in the rat [7, 24], cat [10, 23], squirrel monkey [8] and marmoset [9]. The aim of our studies was to describe types of neurons in the bank vole IC.

MATERIAL AND METHODS

The studies were carried out on 8 brains of adult bank voles. The preparations were made by means of the Nissl and Golgi methods. The brains were cut into 15 μm and 50 μm sections for the Nissl method and into 90 μm sections for the Golgi technique. The microscopic images of selected impregnated neurons were digitally recorded by means of a camera, which was coupled with a microscope and an image-processing system. From 50 to 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 the pictures in order to show the real microscopic images and then it was removed from each of them to clarify the neuron illustrations.

RESULTS

The inferior colliculus (IC) of the bank vole is a well-developed mesencephalic structure. The rostral part of IC is made up of a thin strip of cells that extends dorsally and borders gradually the superior colliculus, which is located between IC and the periaqueductal grey matter. Further caudally, the superior colliculus becomes smaller, disappears and is completely replaced by IC. At this level IC takes an oval shape and becomes a heterogeneous structure, consisting of 3 nuclei: the external nucleus and the pericentral nucleus, which are located on the outer border of IC, and the central nucleus, which is the largest one. On the medial side of the central nucleus lies the periaqueductal grey matter, while on the ventral side lie the nucleus cuneiform and the dorsal nucleus of the lateral lemniscus. The ventral part of the central nucleus is composed of the largest neurons, which are loosely packed, whereas the dorsal part of this nucleus shows the laminated structure. This structure was not noticeable on the Nissl material, but the tissue impregnated according to the Golgi method showed it distinctly. The caudal tip of IC has the shape of a small oval, which is bordered around by cerebellar tissue.

On the basis of various morphological criteria, such as the shape and size of perikarya, number and arborisation of dendritic trunks, presence of dendritic

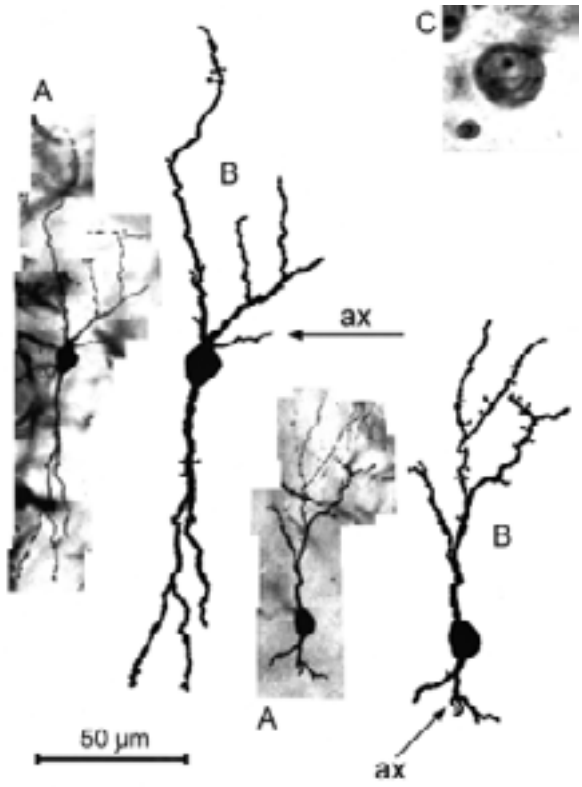

Figure 1. The rounded neurons; A — non-clarified Golgi impregnation, B — clarified Golgi impregnation, ax — axon, C — the Nissl stained soma.

spines and protrusions as well as appearance and location of the axon, 5 types of neurons were distinguished in the bank vole IC.

The rounded neurons (Fig. 1). Their perikarya measure from 10 to 15 μm. These cells have 2–4 primary dendritic trunks, which usually arise from both sides of the cell body. The primary dendritic trunks are smooth or bear few big spines. They branch dichotomously at the distance of 10–25 μm from the perikaryon. The secondary and tertiary dendrites are covered with bulbous spines and they form a spindle-like dendritic tree. The axon emerges directly from the soma or from the proximal portion of a dendrite. The rounded neurons are predominant in the bank vole IC and they were found in all nuclei of IC.

The fusiform neurons (Fig. 2). The cell bodies measure from 17 to 20 μm. A thick and spineless primary dendritic trunk arises from both poles of the perikaryon and ramifies into secondary branches, which narrow into thinner distal dendrites. The big, knob-like dendritic spines are irregularly dispersed over their surface. The dentritic tree is similar to the previous type and takes the form of a spindle. The

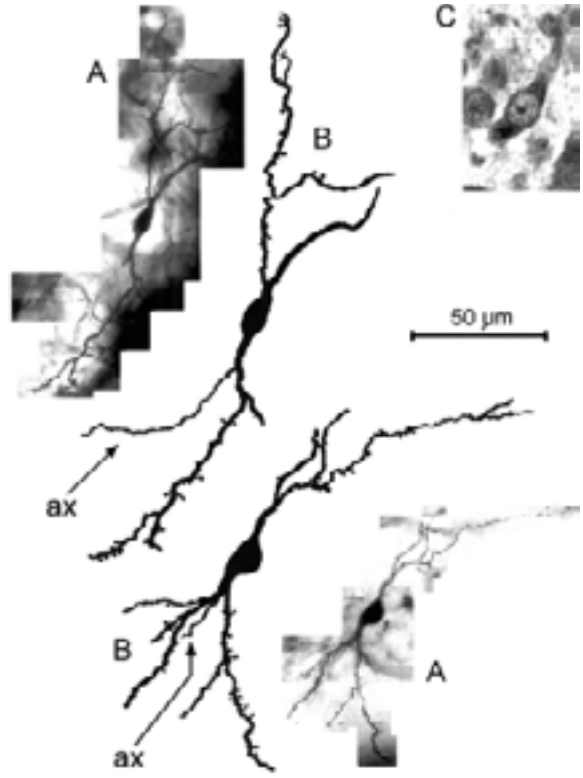

Figure 2. The fusiform neurons; A — non-clarified Golgi impregnation, B — clarified Golgi impregnation, ax — axon, C — the Nissl stained soma.

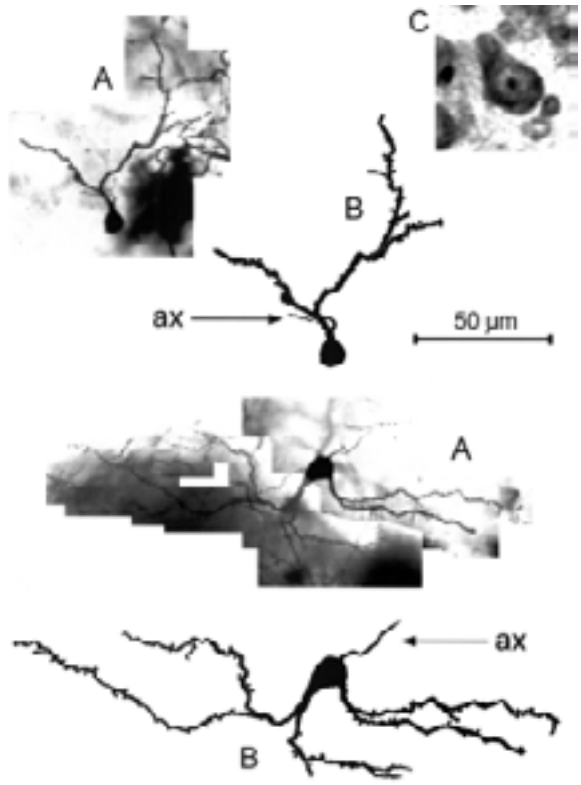

Figure 3. The pear-shaped neurons; A — non-clarified Golgi impregnation, B — clarified Golgi impregnation, ax — axon, C — the Nissl stained soma.

axon originates from the proximal dendritic trunk and it is usually directed along the long cell axis. The fusiform neurons are distributed throughout IC, constituting together with the rounded cells the main neuronal type. In the dorsal part of the central nucleus both types of neurons form a characteristic laminated structure. Their dendritic trees are oriented in parallel layers forming individual laminae. In the external nucleus these cells are primarily located along the outer surface of IC whereas in the pericentral nucleus they are situated in the dorso-ventral direction.

The pear-shaped neurons (Fig. 3). These cells are small sized, their cell bodies range from 10 to 13 μm. 2 main stems or rarely 1 emerge from the soma and after a short distance of their route divide into secondary and next into usually thinner distal branches. The dendritic tree is densely covered with big, knob-like spines, only the principal trunks remain smooth. The axon emerges from the perikaryon or seldom from the primary dendritic trunk. The pear-shaped cells occur mainly in the central and external nuclei. Their cell bodies were observed in the border tissue between these 2 nuclei, sending their dendrites into either central or external nucleus.

The multipolar neurons (Fig. 4). The perikarya of these cells measure from 18 to 23 μm. From 4 to 6 spineless primary dendrites of various thicknesses radiate in all directions. Long secondary dendrites give off thinner distal branches, which are covered richly with bulbous spines and which form a spherical dendritic field. The axon originates either from the proximal stem or directly from the soma. The multipolar neurons occur mostly in the central nucleus. In the ventral part of this structure the largest cells were observed, but they were less numerous and more loosely packed than the multipolar neurons in the dorsal part. In frontal sections of the dorsal part of the central nucleus, the radially spreaded dendrites of multipolar cells do not form laminae. They seem to be perpendicular to the dendritic branches of the rounded and fusiform cells.

The triangular neurons (Fig. 5). Their cell bodies measure from 15 to 18 μm. These neurons give off 3 primary dendrites, which subdivide dichotomously into distal branches. The knob-like spines are poorly distributed over the spherical- or triangular-shaped dendritic tree. The axon emerges from the perikaryon, sometimes very close to one of the primary den-

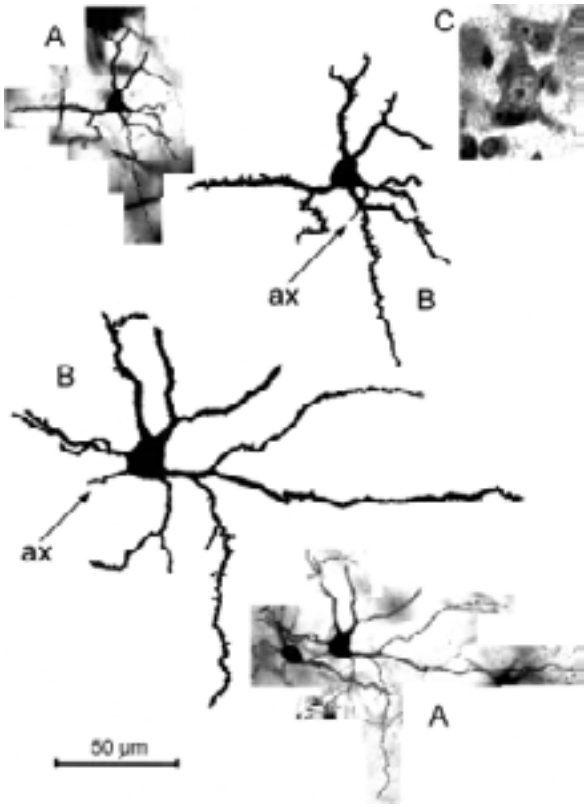

Figure 4. The multipolar neurons; A — non-clarified Golgi impregnation, B — clarified Golgi impregnation, ax — axon, C — the Nissl stained soma.

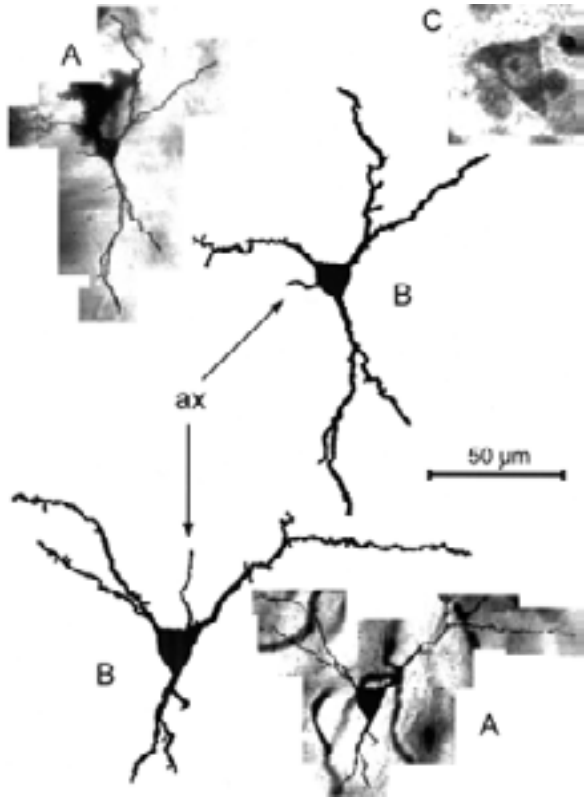

Figure 5. The triangular neurons; A — non-clarified Golgi impregnation, B — clarified Golgi impregnation, ax — axon, C — the Nissl stained soma.

drites. The triangular cells are the least numerous and they have been mainly observed in the pericentral nucleus. Most of these neurons show a dorsoventral direction.

DISCUSSION

Most authors agree in distinguishing three main parts of IC in different species. However there is some difference in the nomenclature of these nuclei. Garey and Webster [9] defined the central nucleus, dorsal and lateral cortex, Faye-Lund and Osen [7] the central nucleus, dorsal and external cortex, FitzPatrick [8] the central, pericentral and external nuclei whereas Meininger and Baudrimont [18] described the ventral, dorso-medial and lateral parts. Despite the nomenclature differences these nuclei correspond to themselves and the organisation of the mammalian IC seems to be uniform. IC of the bank vole does not differ from this scheme either. Some authors do not regard the central nucleus, which is the largest structure of IC, as a uniform neuronal centre [23, 25, 30]. They define from 2 to 4 subdivisions by anatomical and physiological criteria. On the basis of the cytoarchitecture, the bank vole IC may be divided into 2 parts: dorsal and ventral. Tokunaga et al. [27] suggest that IC has a dual function. According to them, the central nucleus acts as a relay station in the main auditory system, while the cortical zone, with its converging auditory, visual and somatic inputs, may act as a subcortical integration centre for acousticomotor behaviour.

Neurons of IC are usually assigned by most authors to one of two major classes, the disc-shaped (bipolar) and stellate (multipolar) cells, which are defined by the three-dimensional form of their dendritic fields. In the cat, Oliver and Morest [23] subdivided the disc-shaped cells into large, medium, medium-large, small neurons and the stellate cells, which were less common, into simple, complex and small ones. FitzPatrick [8] described disc-shaped cells, which make up about 70–80% of the stained neurons in the central nucleus, and modified disc-shaped cells that are oriented perpendicular to the principal layers. The stellate neurons [8] were subdivided into type 1 with one or more dendrites oriented in the same direction as the disc-shaped cells and one or more additional dendrites perpendicular to the first.

The neurons of the stellate type 2 have dendrites which arise randomly from the soma and ramify in all directions. In the central nucleus of the marmoset [9] there were found bitufted or bipolar and multipolar neurons, whereas the cortex is composed of a variety of bipolar and multipolar cells. Roberts and Ribak [24] observed 4 types of GABAergic neurons in the central nucleus of the rat: small, medium-sized and large multipolar cells, as well as medium-sized bipolar neurons. The apparent discrepancies among the types of neurons in the bank vole and other mammals result from the fact that in the present study emphasis has been mainly placed on the shape of the perikarya instead of the form of dendritic fields. Thus the bank vole cells bear a strong resemblance to IC neurons of other species, showing a very similar branching pattern. As a result the rounded, fusiform and pear-shaped cells which were found in our material may be easily rated among the disc-shaped cells, whereas the multipolar and triangular neurons may be equated with the stellate cells of different mammals. It is suggested [22] that many of these cell types send their axons to the medial geniculate body. According to Meininger and Baudrimont [17] the characteristic orientation of the dendritic tree of cells observed in IC of the adult cat is established only after the first postnatal weeks.

Most authors described the very specific laminar pattern of the central nucleus, which is consistent with our results. In the bank vole the laminar organisation was mainly observed in the dorsal part of the central nucleus. The ventral part was characterised by the overall larger size and the smaller packing density of cells than in the dorsal part of this nucleus. Roth et al. [25] presume that the laminated division of IC probably consists of anatomically, physiologically and functionally distinct subdivisions and some aspects of auditory sensation may be encoded or represented separately. Faye-Lund and Osen [7] reported that both parts of IC cortex in the rat consist of 3 layers, which show a different neuronal structure. In our material we did not notice any laminae and the cortical nuclei seem to be homogeneous.

In most studies the presence of dendritic spines was not taken into account as a criterion. In the present study there have been commonly observed neurons with spinous dendrites, whereas spineless cells were not seen. All neurons in the cat [10, 23] and squirrel monkey [8] also have protrusions or spines. Even though one of the cell types in the cat [10] was called the aspinous disc-shaped type, these neurons bear very few dendritic spines. The authors [10] suggested that neurons in the central nucleus attain morphological maturity at the end of the first month of life and the density of dendritic spines is higher in the immature cats than in the adult.

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