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# The morphological types of neurones of the medial and lateral mamillary nuclei in a newborn guinea pig: Nissl, Klüver-Barrera and Golgi studies

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*The studies were carried out on the hypothalamus of 5 newborn (P0 stage) guinea pigs. The sections were impregnated according to three modifications of the Golgi technique or stained according to the Nissl and Klüver-Barrera methods. On the basis of the shape and size of perikarya, dendroarchitecture, pattern of axon as well as the inner structure of neurones, in the medial (Mm) and lateral (Ml) mamillary nuclei four morphological types of nerve cells were distinguished: cap-like with two subtypes (33% of the cell population), fusiform (35%), triangular (12%) and rounded unidendritic (21%) neurones. The majority of them possessed spines on their dendrites. The spiny cells, both cap-like and fusiform ones, were observed preponderantly, in the medial mamillary nucleus, whereas in the lateral mamillary nucleus there were mainly seen the triangular and fusiform neurones, either spiny or aspiny cells. The spineless rounded unidendritic cells were dispersed throughout the mamillary region, but they were twice as numerous in Mm as in Ml, where they were the least numerous.*

**key words: medial mamillary nucleus, lateral mamillary nucleus, types of neurones, Nissl and Klüver-Barrera methods, Golgi impregnation, newborn guinea pig**

## INTRODUCTION

The philogenetically old mamillary nuclei and, related to them, the main nervous bundles appear at an early stage in ontogenetic development [4, 17, 40]. They come into existence in rat on 15–17 embryonic days [4], whereas the specific period of rat's brain growth occurs during the postnatal period [11]. This specific period differs in its timing in relation to birth in various animals; in guinea pig it occurs in prenatal life [11, 25], whereas perinatally in man [11]. The neurogenesis may also occur postnatally [39], but always it is followed by morphological, functional and neurochemical cell differentiations. It was found, for example, in mouse that dopamine D3 receptors, involved in ontogenic processes, appear at postnatal day 8 in the medial mamillary nucleus [9]. In the human mamillary complex, in newborns and infants, the topographical distribution of benzodiazepine binding sites was similar, whereas their densities had a tendency to increase during postnatal development [24]. The cell differentiation depends on genetic as well as environmental (extrinsic) factors [21, 25]. For example, the presence of the mamillothalamic tract depends

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on the expression of *Pax-6* gene during embryonic period [40], whereas the normal structure of the mamillary body is related to an appropriate level of thiamine during all the life span in man [5, 6, 26]. It is well-known that cytoarchitectonics, types of neurones and kinds of various neurotransmitters are different in analogical nuclei of various sexually mature animals (rat, mouse, guinea pig, monkey) [2, 3, 12, 32, 34], and also between the young and adult individuals even within the same strain of species, including man [12, 22, 25, 26]. The structural, cytological and morphometric parameters of the mamillary nuclei also change during postnatal development [23, 31]. The types of mamillary neurones are briefly described in 20-day-old guinea pig [33], but there are no data on newborns. The aim of this study is to examine the types of neurones in the mamillary nuclei at P0 stage in guinea pig using the Golgi technique as well as the Nissl and Klüver-Barrera methods. On the other hand, the focus on the mamillary bodies is worthwhile, since their distortions are related to loss of some forms of memory and other disorders [5, 6, 11, 13, 20, 36]. The mamillary bodies are relay stations with various neural connections [1, 10, 12, 14, 15, 18, 27, 34] and multiple neurotransmitters [2, 15, 16, 24, 35], but the linkup and processing of information by their responsive cells is not well known yet, with scarce exceptions [13, 19].

## MATERIAL AND METHODS

The studies were carried out on the brains of 5 newborn (P0) guinea pigs, Dunkin-Hartley strain. The animals were overdosed with sodium pentobarbital and perfused transcardially with phosphate and then formaldehyde buffered solutions at pH 7.4. The sections preparations (10 $\mu$m thick) were stained according to the Nissl and the Klüver-Barrera methods. The blocks containing the hypothalamus were processed according to the Stensaas, Bagiński or Golgi-Kopsch techniques, and then cut into 60 $\mu$m thick sections, both in sagittal and transversal planes. The microscopic images of selected, impregnated neurones were digitally recorded by means of a camera that was coupled with microscope and image processing system (VIST-Wikom, Warsaw). From 20 to 100 such digital microphotographs were taken at different focus layers of the section for each cell. On the basis of these series the computerised reconstructions of neurones were made (Figs.1–4a). The neuropil was removed to clarify the picture (Figs.1–4b).

## RESULTS

**Nissl study (Figs. 1–4)**

At P0 in the guinea pig the mamillary body is relatively well myelinated and main bundles are easily distinguishable. The medial mamillary nucleus has a small-celled well outlined posterior sector (cell sizes from 6 $\mu$m), and a less uniform middle-anterior sector, which as a rule contains smaller cells in its ventral part and larger cells (up to 22 $\mu$m) in its dorsal part, whereas the largest cells (over 30 $\mu$m in long axis) were observed in the lateral mamillary nucleus.

The majority of Mm cells, especially in its posterior part, are rounded or oval-shaped, small and lightly stained neurones. They contain a small amount of the tigroid substance, which sometimes occupies only one side of the cell nucleus or is distributed around it forming a thin ring. Inside the cell nucleus, two nucleoli were often observed. In the middle and anterior parts of Mm, the cells stain more darkly and contain a large, lightly stained nucleus and a relatively large amount of the cytoplasm with irregularly distributed tigroid substance. Ml cells are the darkest stained neurones. They contain a lot of coarse grains of the tigroid substance, which form bands or nests and often enter the proximal portion of dendritic trunks. In general, the sizes of cells in the Nissl picture are smaller than those of impregnated cells in the Golgi preparation, but there is a coincidence as regards the distribution of their sizes in the medial and lateral mamillary nuclei.

**Golgi study**

In the present study, 80 well impregnated cells in the two mamillary nuclei at P0 stage in guinea pig were examined. These cells were categorised into 4 types of neurones: cap-like (they constitute 33% of the cell population), fusiform (35%), triangular (12%) and rounded unidendritic (21%) cells. The types of neurones were distinguished on the basis of the shape and size of perikarya, the number of dendritic trunks and their arborisation as well as the pattern of axon. Taking into account the appearance of dendritic spines, the cells which had a lot of spines were named the spiny cells (S-cells). Aspiny nerve cells (A-cells) were devoid of spines, although they may have varicose dendrites with protuberances. The spineless cells (L-cells) are intermediate cells between S- and A-cells. They possessed a different number of spines, which may be sporadically observed on whole dendrites or may be located in small groups usually on the distal dendritic branches. The dendritic spines

were classified into: i) the knob-like spines; they have rather short and thin trunks with small, rounded expansion on their tips; ii) the rose-thorn spines having a triangular form; iii) the filiform spines, which are similar to the knob-like spines, but they have no enlargement on their tips.

**Cap-like neurones (Fig. 1)**

They measure from 12–22 $\mu$m in long axis. Cap-like neurones are either bipolar or multipolar cells, thus they were segregated into 2 subtypes: a) typical cap-like cells (bipolar) with 2 dendritic trunks; b) transitional cap-like cells (multipolar) with 3 dendritic trunks. The cells of the two subtypes: a and b constitute 21% and 11% of the whole cell population, respectively.

The cap-like bipolar cells have irregular semilunar shapes and usually 2 dendritic trunks, which conically emerge from the base of perikarya. They measure from 12 to 18 $\mu$m. Their characteristic feature is polarised distribution of the dendritic trunks, which create a pen-shaped dendritic tree. From the

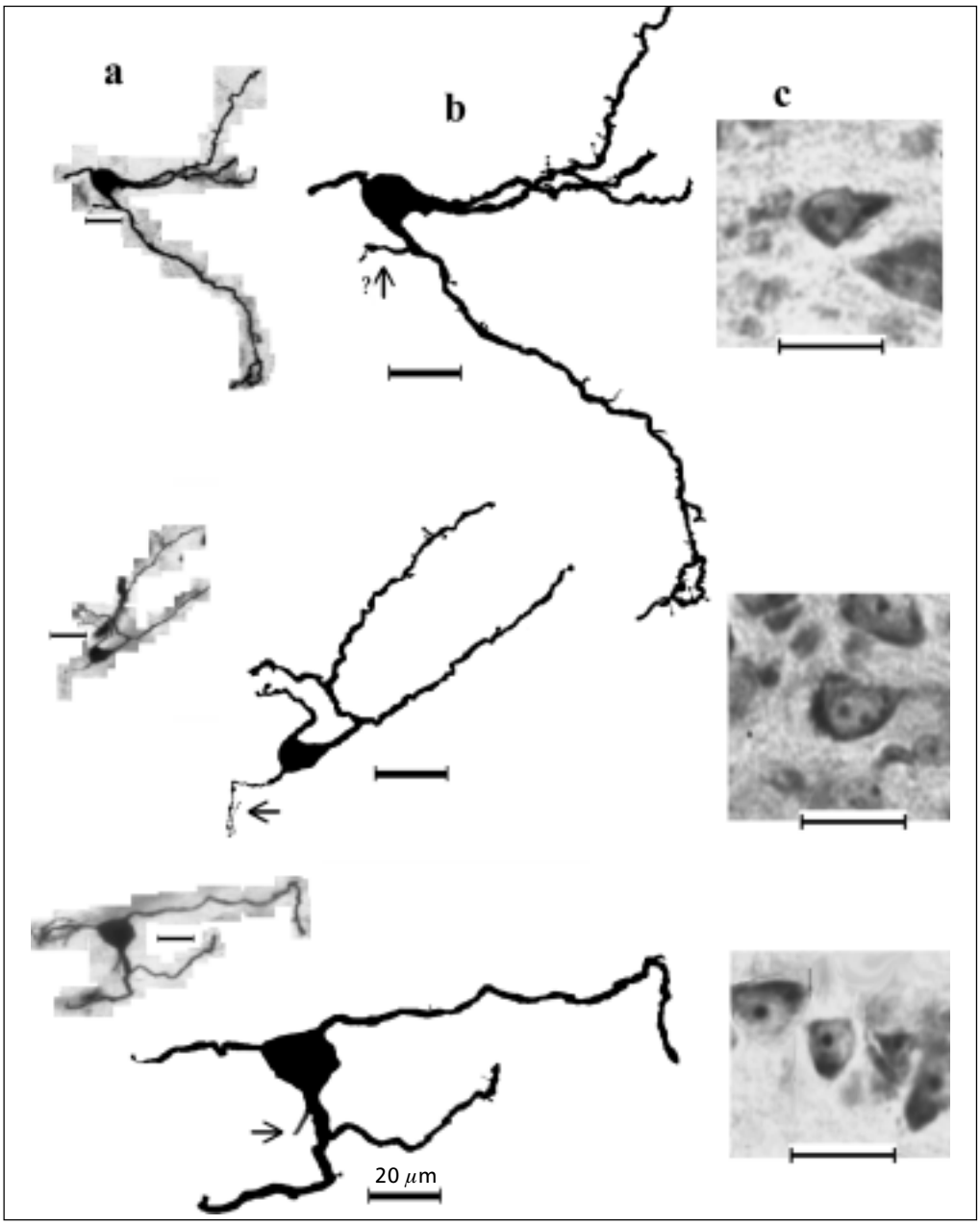


**Figure 1.** Cap-like neurones (Mm cells: subtype a — above and in the centre, subtype b — at the bottom): **a)** Golgi impregnation (non-clarified montage), **b)** Clarified reconstruction of impregnated neurone, **c)** Klüver-Barrera method; arrow — axon.

opposite, convex, apical pole of the soma the axon arises or sometimes the third dendritic trunk, which seldom could be observed on the same section. The basilar dendritic trunks dichotomously divide into quaternary order branches, but one of the two may remain undivided. Usually, for the first time the dendritic trunks divide in the vicinity of the soma within a radius of 6-25 $\mu$m, whereas the next time at different distances from the first point, i.e. about 40 $\mu$m or even 100 $\mu$m after their courses. These dendrites run in a specific way, sometimes create loops, bend and wrap themselves. In general all dendrites possess protuberances and varicosities. Additionally, many of them (S-cells) are covered with numerous various spines, but the knob-like spines preponderate. In this subtype there were observed L-cells; their dendrites occasionally were covered with only a few spines. Sometimes, on tips of the distal dendritic branches there are present widening expansions, which send thread-like processes. Probably they are "growing" dendrites. The L-cells usually have a more weakly developed dendritic tree than S-cells, but the first point of division of the primary dendrite was located mainly at the distance of about 6 $\mu$m from the soma. A-cells in this subtype were rare.

An axon arises alone from an apical side of the cell body or together with a primary basilar dendrite. The initial segment of an axon is well impregnated for a relatively short distance (about 25 $\mu$m) and usually has an equal diameter of about 2–2.5 $\mu$m. Sometimes it is observed that further forward the axon rapidly becomes thinner; it gives off collaterals and forms rounded expansions on their route like a synaptic button "en passant". Typical cap-like cells constitute about 25% of cells in Mm and 16% in Ml.

The subtype b contains slightly bigger cells (17––22 $\mu$m) than subtype a. Their perikarya have various transitional shapes but quite often take a piriform or globular contour, which is different from the triangular multipolar shapes. These cells usually possess 3 dendritic trunks (similar to the triangular cells), whereas their patterns of arborisation resemble those of the typical cap-like neurones. Some dendritic trunks divide once at the distance of 12–37 $\mu$m from the soma, but either primary or secondary undivided dendrites about 160 $\mu$m in length were also observed. The b subtype mainly consists of aspiny and spineless cells, but L-cells were in the majority. Dendrites possess many protuberances, but only single spines, knob-like in appearance. The axonal pattern is similar to the pattern of spiny cap-like cells, but the initial thick segment of an axon was impregnated for a distance of 10–30 $\mu$m. The synaptic buttons were more often observed in the cells of Ml, whereas collaterals in the Mm cells. The neurones of subtypes b constitute about 8% of cells in Mm and 13% in Ml.

**Fusiform (bipolar) neurones (Fig. 2)**

Their perikarya are fusiform and oval in shape, measuring from 15 to 40 $\mu$m in long axis. The biggest cells were observed only in the lateral mamillary nucleus. The fusiform cells have usually 2 thick (up to 5 $\mu$m in diameter) dendritic trunks, rarely 3 (in these cases two of them arise together from one pole of the soma). The primary dendrites of the small fusiform S-cells divide for the first time close to the soma or within its radius of about 25 $\mu$m. The secondary and tertiary dendrites sequentially ramify into daughter branches at similar intervals of 20–25 $\mu$m. In the biggest fusiform cells some dendritic trunks remain undivided or divide twice. The first point of a dendritic branching of the bigger S-cells lies nearer the soma (about 7–10 $\mu$m) than in the smaller ones, whereas the second point of division may be located at a distance even about 150 $\mu$m from the first point. Dendrites branches follow wavy courses and have a tendency to form an oval-shaped dendritic tree on one side of the perikaryon. S-cells of the fusiform type possess mainly filiform and rose-thorn spines; the latest spines occasionally were present on the dendritic trunks and perikarya. The knob-like spines were less numerous and irregularly distributed. The spineless and aspiny cells were also present, but mainly in Ml. The primary dendrites of fusiform, A-cells usually divide once at the distance of about 17–40 $\mu$m, whereas the trunks of the bigger aspiny cells branch at a similar distance to the big fusiform S-cells described above.

In all observed neurones of the fusiform, bipolar cell type, an axon goes away from a soma close to the dendritic trunk, or from the latter (mainly in A-cells), usually at the distance of about 4 $\mu$m from the perikaryon. The well impregnated axon was seen at a distance of about 50–63 $\mu$m. Sometimes very fine arborisation of an axon was seen. The cells of this type constitute about 36% of cells in Mm and 33% in Ml, but S-cells were threefold more often observed in Mm than in Ml.

**Triangular (multipolar) neurones (Fig. 3)**

The typical multipolar neurones possess triangular perikarya (17–30 $\mu$m), which send three dendritic trunks in all directions. Other shapes of soma

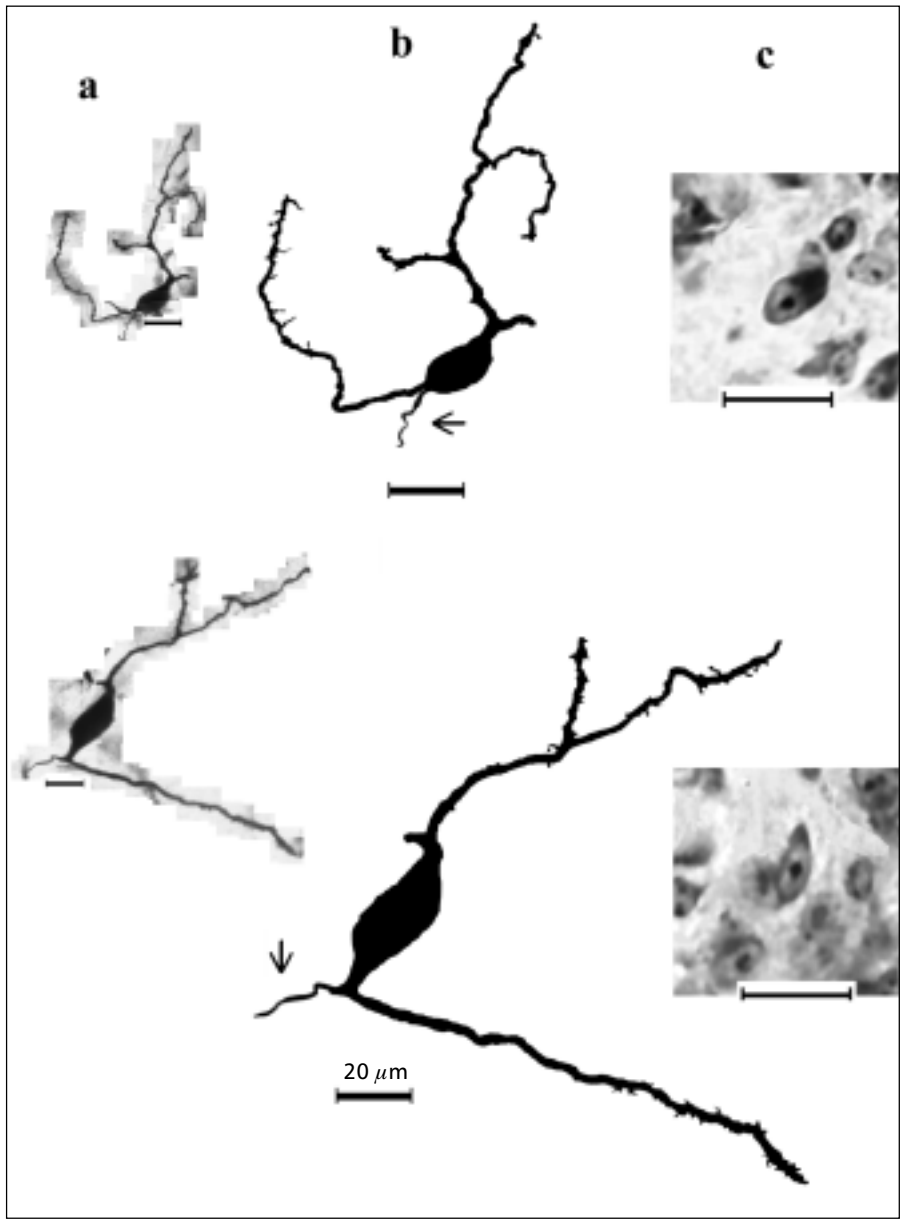


**Figure 2.** Fusiform neurones (Mm cell — above, Ml cell — at the bottom): **a)** Golgi impregnation (non-clarified montage), **b)** Clarified reconstruction of impregnated neurone, **c)** Klüver-Barrera method; arrow — axon.

and fourth dendrite may seldom be observed. The dendritic trunks rarely divide more than twice; for the first time at the distance of 6–15 $\mu$m from the soma, and the second time at various distances (25–50 $\mu$m) from the first point. Sometimes the primary dendrite at first gives off collaterals or an axon and then divides into secondary branches. There are also undivided dendritic trunks, which run for a distance of about 125 $\mu$m. Dendrites follow a slightly wavy course and form a rounded or an oval-shaped dendritic tree. They have irregular, varicose surfaces, which are covered with spines of various numbers and shapes: knob-like, rose-thorn and filiform (the latest are slightly longer than analogue spines in cap-like and fusiform types). An axon conically arises from the perikaryon, or from a dendritic trunk (mainly in S-cells). In a few L-cells a delicate arborisation, after 25 $\mu$m of the axon's route, was seen. The S-cells are not numerous and are observed only in the lateral mamillary nucleus. The type of the triangular multipolar cells contains mainly L- and A-cells, which only sporadically appear in Mm. The triangular cells constitute about 25% of cells in ML, and only 3% in Mm.

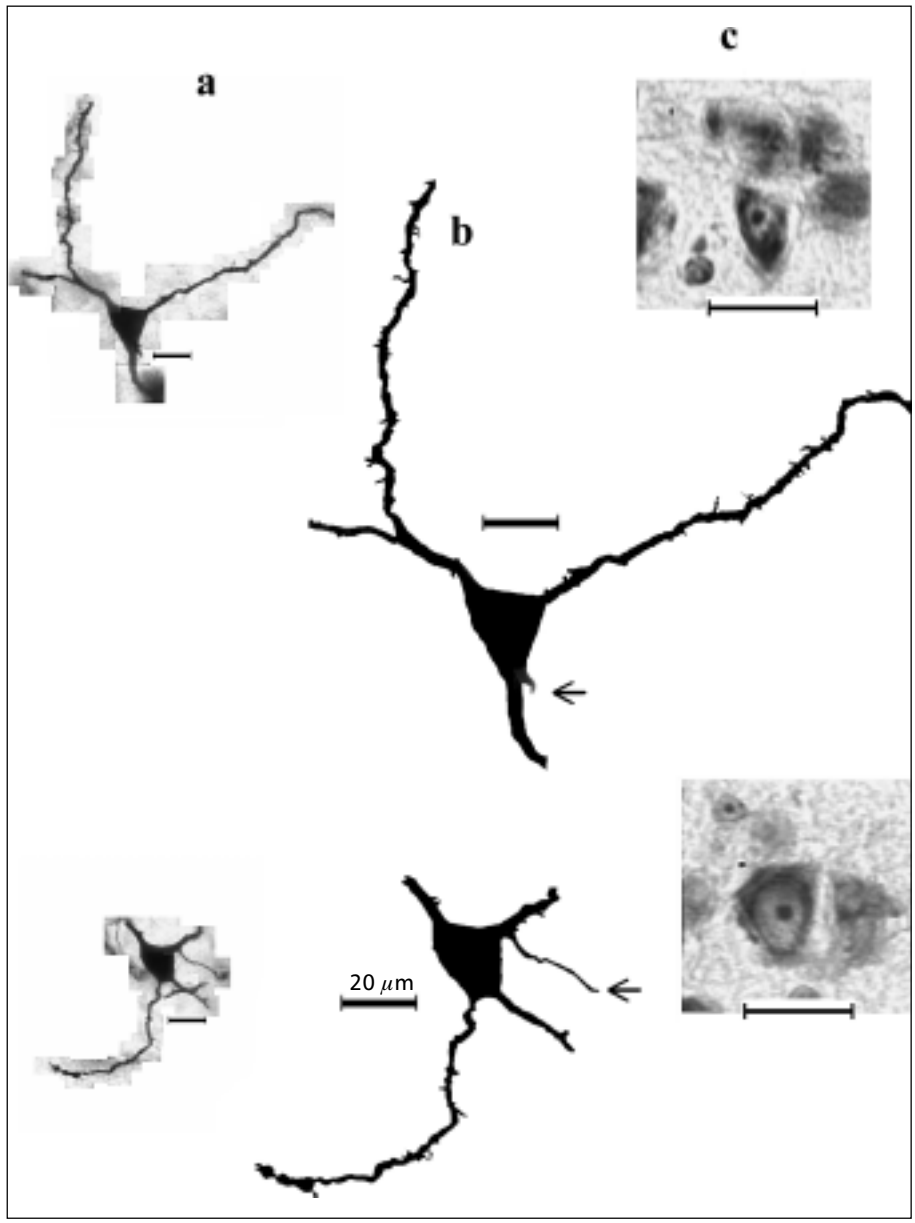


**Figure 3.** Triangular neurones (MI cells): **a)** Golgi impregnation (non-clarified montage), **b)** Clarified reconstruction of impregnated neurone, **c)** Klüver-Barrera method; arrow — axon.

**Rounded (unidendritic) neurones (Fig. 4)**

They have perikarya which are round or oval in shape, measuring from 10 to 20 $\mu$m, and one usually thick dendritic trunk. The trunk may run for a relatively long distance (110–140 $\mu$m) without branching, or divides and gives off thinner collaterals. For the first time they divide near the soma, usually within a radius of about 5 $\mu$m. Secondary dendrites divide once again but at various distances up to 42 $\mu$m, but usually 12–17 $\mu$m after their routes. Usually, a dendritic tree is stream-like in shape. Most dendrites possess varicosities and various spines. The rose-thorn spines were often seen on the dendritic trunk, whereas the knob-like ones mainly on dendritic branches. However S-cells were rarely observed. This cell type in majority is made up of aspiny and spineless neurones, which possess only single spines. The final portions of dendrites may possess irregular, small extensions and lacunes. An axon conically arises from the dendritic trunk near the soma or from a different place of the perikaryon. The axon dividing like a dendrite occasionally was seen, but more often axons send a thread-like process or arborise in the vicinity of the soma (after about 20 $\mu$m). In gen-

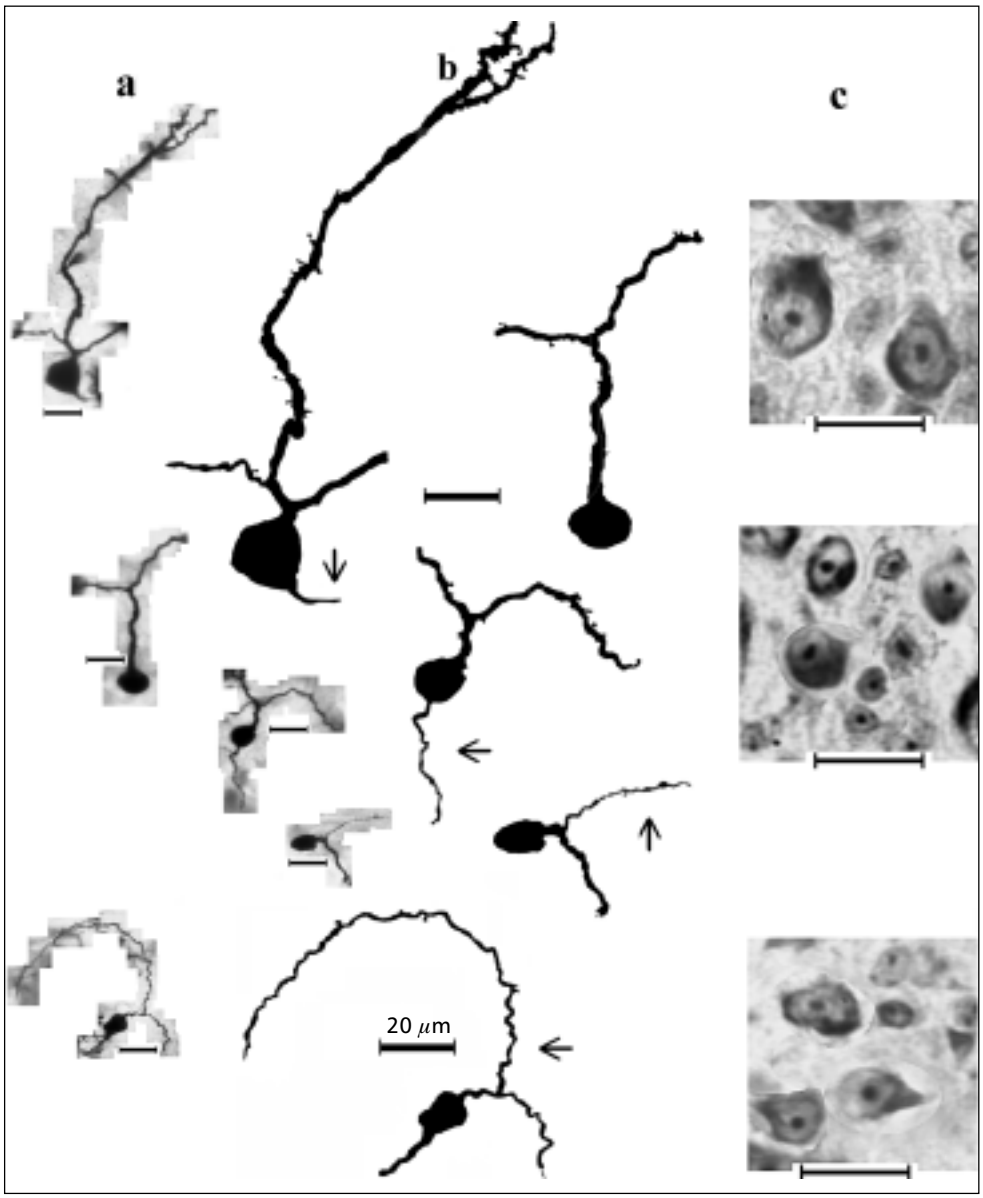


**Figure 4.** Rounded unidendritic neurones (Mm cell with the bifurcated axon – at the bottom; the bigger Ml cell – in the left upper corner): **a)** Golgi impregnation (non-clarified montage), **b)** Clarified reconstruction of impregnated neurone, **c)** Klüver-Barrera method; arrow — axon.

eral, L- and A-cells have smaller perikarya than S-cells. The unidendritic neurones constitute about 28% of cells in Mm, and 13% in Ml.

## DISCUSSION

The medial and lateral mamillary nuclei share the large and discrete connections with many brain areas [18, 27, 34, 35]. Probably, these connections are related to the cell segregation and subdivisions, which are observed within Mm [4, 32, 34]. The cells constituting Ml and subdivisions of Mm in the prenatal period vary in their sizes and times of origin (in rat four ontogenetic classes of cells are distinguished) [4]. In general, in mammals the lateral mamillary nucleus is formed earlier than the medial mamillary nucleus, and in a newborn guinea pig they have about 1100 and 450 microns in length, respectively [31]. Postnatally, Ml starts to enlarge after P10, whereas Mm as soon as after birth [31, 33]. Based on Golgi preparations, the mamillary nuclei in guinea pig (at P0) consist of 4 neuronal types of cells, which are listed in Table 1.

Comparing the neuronal types and their percentage contribution in the population of Mm and Ml,

**Table 1.** The neuronal types in mamillary nuclei of the guinea pig, in newborn (the present study) and adult stages (Robak 2000)

| Type of cells in: | | Mm | | MI | |
|---|---|---|---|---|---|
| Newborn | Adult | Newborn | Adult | Newborn | Adult |
| Fusiform (bipolar) | Bipolar | 36% | 40% | 33% | 40% |
| Rounded unidendritic | Unidendritic | 28% | 26% | 13% | 7% |
| Cap-like (bipolar and multipolar) | Multipolar (cap-like and transitional form) | 33% | 30% | 29% | 8% |
| Triangular | Multipolar (typical) | 3% | 4% | 25% | 45% |

in newborn and adult stages, it is easy to note that the neuronal structure of the lateral mamillary nucleus shows more pronounced changes than the medial mamillary nucleus. In MI the number of triangular cells increases from P0 to adult by 25% to 45%, whereas cells of the unidendritic and cap-like neurones decrease after birth by 13% to 7%, and by 29% to 8% respectively. The small number of polygonal cells in MI was also noted at P20 stage [33]. It may be supposed that unidendritic and cap-like cells in MI undergo cell death (apoptosis), or they differentiate in other neuronal types (perhaps in typical multipolar cells). "Transient polyinnervation" and the programmed death of buffer neurones are well-known phenomena [38]. The percentages of types of neurones constituting Mm at P0 and adult stage are different, but not in a wide range (Table 1). The striking feature of the morphology of neurones at P0 stage is the abundant presence of various dendritic spines, which were rarely observed at P20 stage [33] and were almost absent in adult specimens [32]. Millhouse suggests that in the adult hypothalamus the spines are not plentiful and the large spiny neurones are rather atypical [22]. On the other hand, the majority of both spiny and aspiny (or spineless) neurones possess varicose dendrites both in newborn and adult guinea pigs. The dendritic varicosities are more pronounced in the older brains [22], and their distribution has an electrical consequence [29]. Perhaps the varicosities, like the dendritic processes, may store and release a neurotransmitter substance and play a role in local modulatory influences [8, 12]. Comparing the morphology of neurones in newborn and adult guinea pigs, it is possible to deduce that postnatally dendritic trunks become shorter (the first division lies nearer the soma with the small exception of the cap-like and unidendritic cells), dendrites lose spines (no S-cells in adult), whereas dendritic trees lose distal dendrites (smaller number of dendritic divisions). The present results share the view that the pattern of the dendritic tree is age-related; in older brain dendrites become thinner [22] and the dendritic tree undergoes atrophy [23]. Parallelly, the biochemical properties of neurones also change [9, 12, 24, 36]. On the other hand, at P0 it was possible to observe synaptic buttons and arborisation of some axons, which were impregnated for a relatively long distance, probably due to lesser myelination than in adults. It was thought that the sequence of myelination of neurones occurs in the same order as their time of origin [4, 40]. The axons of mamillary cells, creating the mamillary peduncule [27] and principal mamillary tract [17, 32, 40], give off collaterals and project to the pontine and spinal nuclei [1, 10, 18] and the thalamic nuclei [34], respectively. Other studies reveal that axons of Mm cells forming the mamillothalamic tract have no wide collateralisation [28]. In newborn guinea pig, the axon collaterals were mainly seen in the cap-like cells (within two subtypes). In other neuronal types, usually fine axonal arborisations were seen. Around the fornix and mamillary peduncle, the serotonin and histamin perikarya were observed, whereas in the mamillothalamic tract enkephalin fibres were found [cit after 32]. There exist significant local circuits between mamillary nuclei and surrounding centres [14]. The mamillary nuclei receive input from the tuberomamillary nucleus (the histamine-containing cells colocalised with met-enkephalin or GABA, and P-positive cells in a guinea pig [2]), the premamillary nucleus and supramamillary nucleus (dopaminergic cells), which also establish the local TH-pathway [15]. On the other hand, GABA--immunoreactive fibres and terminals in the mamillary nuclei have symmetrical synaptic contacts [16]. The nonsynaptic interactions are proposed between the enkephalic axons and incoming dopaminergic terminals [8]. Probably, the aminergic terminals in CNS are influenced by local circuit interneurones, which may act also in nonsynaptic way. It is suggested that fibres of Mm cells reaching the muscarinic receptors of thalamic nuclei [35] may act as the presynaptic inhibition. Some researchers indicate that projecting neurones may give off early collaterals forming a local circuit pathway [37]. In the present studies unidendritic and caplike neurones are the smallest within the cell population of the mamillary nuclei. In

the primate brain, similar small cells contain catecholamines [12] as well as $\alpha$-ketoglutarate dehydrogenase complex [7], whose activity in Mm is reduced by thiamine deficiency [5, 26]. The cap-like cells (the present study) morphologically are similar to the cells, which were described in rat's Mm [Fig. 3 in 34] or classified as islet and stalked interneurones in the spinal cord [cit. after 8]. In the mamillary nuclei they correspond to the allodendritic cell type, which are characteristic for nuclei with monopolised function [30]. A variation in function is related to variations in neuronal number and neuronal morphology [38], but a feature of the class-characteristic shapes results largely from interactions between the environmental factors and cells [21].

Summing up, based on the previous [32] and present results obtained from Golgi studies, the main characteristic features of the morphological maturity of neurones in a guinea pig are the lack of dendritic spines and a poorly developed dendritic tree. It is possible that during postnatal development to adult stage some afferents do not form synapses on dendritic spines, or may preferentially establish synaptic and non-synaptic contact on varicosities. It is also possible that synapses formed in the newborn individuals on distal dendrites are eliminated at latter stages from dendrites leaving them naked to adulthood, or they are eliminated together with dendritic branches of a higher order.

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