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A comparative study of the mammalian amygdala: a Golgi study of the basolateral amygdala

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*The lateral (LA), basolateral (BL) and basomedial (BM) amygdaloid nuclei were compared in the guinea pig (*Cavia porcellus*), rabbit (*Oryctolagus cuniculus*) fox (*Vulpes vulpes*) and pig (*Sus scrofa*) by using the Golgi techniques. The interspecific comparisons of the individual basolateral nuclei have shown that the neuronal structure in each of them is extremely stable and remains almost unchanged in the series of animals studied. The only difference is the size of the basolateral neurons, which increases with the increasing size of the brain. Moreover, the intraspecific comparisons revealed that in all the animals studied LA, BL and BM form a fairly homogenous mass of cells in which similar cell types are present. The most numerous neurons in all basolateral nuclei are the spiny cells that often show a pyramidal or semi-pyramidal appearance (the Type I cells). Many of these have conical cell bodies and easily recognisable "apical" and "basal" dendrites. The Type II neurons are the most common variety of non-pyramidal cell and have round cell bodies and smooth or sparsely spined dendrites. The axons of these cells often form a dense terminal field that remains in the vicinity of the parent soma. The Type III cells, which are only occasionally seen, are small spine-sparse neurogliaform neurons with a few extremely delicate beaded dendrites and a poorly branching local axon. These neurons were only located in LA and BL.*

key words: amygdala, basolateral nuclei, neuronal structure, comparative study

INTRODUCTION

The amygdala (CA) is a large almond-shaped structure, which, together with the striatum and the claustrum, forms one of the large nuclei of the telencephalon. This is an extremely complicated and highly organised collection of nuclei and cortical areas, differing with regard to cellular structure [9, 10, 12, 15, 16, 21, 41, 44], connections [13, 17, 18, 21, 35, 42, 44, 49, 54] and neurotransmitter expression patterns [4, 6, 30, 32, 36, 38, 39, 42, 44, 48, 54]. At present more than 10 separate structures are usually identified within the CA [9, 15, 21, 49, 54]. The cellular organisation of these areas is so diversified, that they require additional divisions [9, 15, 21, 49, 54].

The 3 prominent regions of the CA namely LA, BL and BM are particularly clearly delineated from the surrounding structures due to the bundles of fibres that encircle them and to large and well stained cells [5, 9, 15, 21, 27, 44, 52]. Both these features, as well as the implication of the basolateral nuclei (BLC)

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in various important physiological processes [11, 23, 25, 26], have made this brain region the focus of much attention in recent decades. It is also at present the most eagerly investigated amygdaloid area.

In spite of the large amounts of data concerning the connections [3, 19–21, 31, 33–35, 45, 49, 53, 54], physiology [11, 13, 23, 25, 26] and distribution of various neurotransmitters [4, 30, 32, 36, 38, 39, 44, 46, 48] in BLC, surprisingly little is known about the Golgi architecture in this region [5, 7, 10, 12, 16, 27, 28, 40]. Moreover, all of the Golgi studies performed so far have been restricted to single and selected mammalian species only [5, 7, 10, 12, 16, 27, 28, 40]. Detailed comparative reports have, to our knowledge, not yet become available.

It seems, therefore, to be of interest to compare directly LA, BL and BM in the guinea pig, rabbit, fox and pig by using the classical Golgi techniques. This is the proposed aim of the present study.

MATERIAL AND METHODS

The studies were carried out on 24 brains derived from adult representatives of 4 mammalian orders. The following species were examined: guinea pig (*Cavia porcellus*), rabbit (*Oryctolagus cuniculus*), fox (*Vulpes vulpes*) and pig (*Sus scrofa*). Each species was analysed on 6 brains.

The right brain hemispheres in each species were cut serially into 50 μm-thick coronal sections that were then stained with cresyl violet, according to the Nissl procedure. The left hemispheres in each were impregnated by silver nitrate according to the Golgi method and cut into 60 μm-thick strips.

Neurons that granted the conditions for impregnation quality and demonstrated the representative features of the cellular populations studied were chosen for the documentation. 512 × 512 pixel microscopic images of the single impregnated cells were digitally recorded by means of a camera that was coupled with a microscope and a computer. 50 to 100 such micrographs were taken at the different focus layers of one section for each neuron. The computerised reconstructions of the dendritic fields were performed on the basis of these series.

To illustrate the relationships between various neuronal types in BLC of the animals under investigation, size measurements of a soma were also introduced. The data are presented in μm and in the following format: the major cell axis/the minor cell axis. All measurements were performed with the use of a calibrated image analysis system equipped with morphometric software (MultiScan 8.2, Computer Scanning Systems, Poland).

RESULTS

The interspecific comparisons of the individual basolateral nuclei have shown that the neuronal structure in each of them is extremely stable and remains almost unchanged in the series from the guinea pig to the rabbit and to the fox and pig. The only difference is in the size of the basolateral neurons, which increases with the size increase of the brain. Moreover, the intraspecific comparisons revealed that in all the animals studied LA, BL and BM together form a fairly homogenous mass of cells, in which similar cell types are present. According to the differences in the shape and size of the somata, the dendritic surface characteristics and the morphology of the axons, all the basolateral neurons in any of the species studied can be classified as belonging to one of 3 distinct subpopulations: Type I cells, which comprise the bulk of the cellular populations in all portions of BLC, and Type II and III cells, which are only occasionally scattered among the Type I cells.

Type I cells (Fig. 1) are pyramidal and semi-pyramidal neurons with a large or medium-sized somata and spine-laden dendrites. In all the animals studied they display similar morphology and form the basic cellular populations in LA, BL and BM. The soma and the adjacent portions of the primary dendrites are commonly devoid of spines. The more distal portions of the primary dendrites and their side branches are always densely covered with the pedunculated spines. Many spines have bulbous terminal knobs and the thread-like stems tilted at various angles to the parent process. The others show slender but thick stalks with an elongated enlargement on the top. The spines vary in density even in the single dendrite. The axon of the Type I cells is formed either from the cone-shaped mound on the soma or from the proximal portion of a thick primary dendrite. It gives off usually several thin collaterals at different distances from the origin. Despite the common general plan, the Type I cells differ from each other in several details including the size and shape of the soma as well as the dendritic arbour characteristics.

The size measurements in each of the species studied were performed in 6 different areas of BLC on 500 randomly selected Type I cells. The comparisons of the values indicated that the size of the Type I cells in the given species is highly interrelated (1) with the position of these cells in BLC and (2) the size of the brain. In all species the particularly prominent Type I neurons occur in the anterior part of BL (BLa). The medium-sized cells prevail in both parts of LA (LAa and LAp), the posterior region of BL (BLp) and the anterior part of BM (BMa). The smallest Type

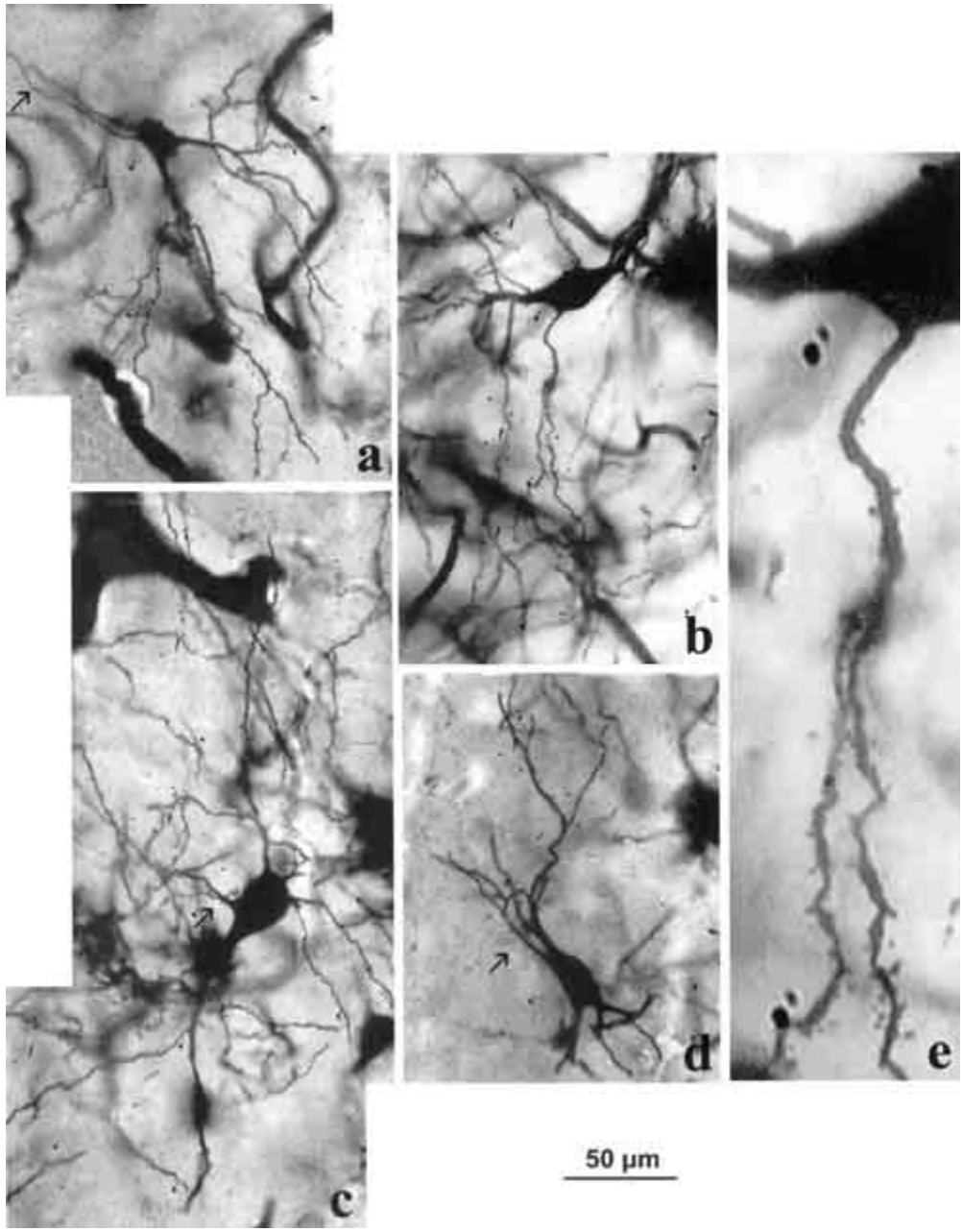

Figure 1. The spiny Type I neurons. **A.** Type I cell in LA of the fox; **B.** Type I cell in BLa of the rabbit; **C.** Type I cell in BL of the fox; **D.** Type I cell in BM of the fox; **E.** Higher magnification of the spiny dendrite from Figure 1B. Golgi impregnation. Axons are marked by arrows.

I neurons can be found in the caudal portion of BM (BMp). For instance, in the fox the average size of the Type I cells in BLa is 30.9/20.3 μm, whereas in BMp it drops to 23.7/16.7 μm. In LAa, LAp, BLp and BMa the size parameters accept the intermediate values i.e. 24.5/15.6 μm, 25.7/17.9 μm, 26.1/18.9 μm and 25.6/16.5 μm respectively. It should be noted that the size variations between the Type I cells can be observed in any part of BLC, even among the neighbouring cells. In LAp of the fox the sizes of the major cell axes vary from 14.3 μm to 37.6 μm, in BLa they are in a range from 17.5 μm to 43.6 μm and in BMp from 16.3 μm to 33.5 μm. On the other hand, the average size of the Type I cells also increases with the increasing size of the brain. For example the average size of the Type I cells in BLa of the guinea pig is 22.3/16.8 μm, whereas in the pig it reaches 33.1/ /23.3 μm. In the rabbit and fox the size parameters of BLa neurons accept the intermediate values i.e. 25.2/18.9 μm and 30.9/20.3 μm respectively.

The shape variation among the Type I cells can be observed in any part of BLC. In all the animals

studied and in all the nuclei the multipolar, triangular and fusiform neurons were observed most often, whereas the rounded cells were seen only occasionally. The shape of a soma can be expressed in a number as the ratio of the major and minor axes (a shape factor). This coefficient seems to be a useful tool in the intraspecific and interspecific shape variability evaluations. The distribution of the Type I cells according to shape in the BLC of the given species is well characterised by the following example. The shape factor values of the Type I cell in the LAp of the fox are in a range from 1.07 to 2.53, in BLa they vary from 1.21 to 2.64, whereas in BMp they are dispersed between 1.03 and 2.12 (the value for a circle is 1). The average values of the shape factor in all these 3 regions are: 1.47 in LAp, 1.59 in BLa and 1.44 in BMp. On the other hand the average shape factors of the Type I neurons in LAp of the guinea pig, rabbit, fox and pig are 1.38, 1.33, 1.47 and 1.42 respectively.

Several varieties of the Type I neurons can be recognised according to the differences in the dendritic arbour morphology. They can be found in various configurations in all portions of BLC and in any species. Many Type I cells have a single thick, long "apical" dendrite that arises from one pole of the cell body and several shorter, thinner "basal" dendrites, which originate from the opposite side. This distinctiveness of the primary dendrites results in these cells taking on the typical pyramidal shape (the pyramidal variety of the Type I neurons). In these cells the soma gradually blends into the stout main dendrite, which gives off irregular side branches at short intervals. The secondary dendrites bifurcate close to their origin. In some neurons the main dendrite may divide dichotomically at various distances from the soma. On rare occasions two separate thick dendrites can coexist in one neuron. The other Type I neurons are more irregular in appearance. Most of them seem to be simply the modifications of the regular pyramidal cells (the semi-pyramidal variety of Type I neurons). In these cells 4–8 smooth dendritic trunks emerge from the soma, which give rise to several densely spiny secondary dendrites. The additional side branches (tertiary dendrites) were also often observed. The dendritic field, like that in the pyramidal cells, is not homogenous and in a set of the thinner smaller primary dendrites several thicker ones can be seen. However, the distinction between the "apical" and "basal" dendrites is less clear than in the pyramidal Type I neurons. The third subtype comprises stellate Type I cells with all the dendrites of equal diameters and lengths (the non-pyramidal variety of the Type I neurons).

Type II cells (Fig. 2) are the non-pyramidal neurons characterised by the spine-sparse dendrites and the rich local axonal arbourisation. In all the animals studied they demonstrate a similar morphology and can be found in small proportions in all basolateral nuclei.

Most often 2–7 relatively thick, smooth and not frequently branching dendritic trunks emerge from the rounded small or medium-sized soma. These bifurcate close to the parent soma and give rise to the secondary branches, which are almost devoid of spines. The diameter of the dendrites is considerably reduced at each branching point. The secondary dendrites and their side branches often bend back and follow a tortuous course close to the parent soma. Only the delicate terminal branches of the dendrites show a varicose outline. The appearance of the other Type II neurons is very similar to that described above, but they differ in some peculiar features. The proximal dendritic trunks can be very short, in the form of dichotomically divided broad stems. From these stalks bifurcate the beaded secondary branches. Each ramification produces thinner and more varicose dendritic branches. The spindle shaped varicosities differ in size and length and are irregularly distributed on the dendrites. Occasionally, the spindle-shaped Type II neurons can be observed with a few thick and extended dendrites that ramify infrequently. The diameter of these processes is relatively constant. Sometimes, the stout dendrites can give off relatively thin branches that follow a tortuous course. The dendritic surface is slightly irregular due to the protrusions, but the real spines are rarely seen as they are isolated and randomly distributed. The varicose outlines of the dendrites were not observed in the spindle-shaped, sparsely spiny cells. In all subtypes of the Type II cells a thin axon emerges either from the soma or from one of the dendritic trunks. Within the dendritic domain it often bifurcates into fine, beaded processes. In close vicinity to the parent soma these collaterals sometimes make several very delicate loops. The fine axonal branches always show a varicose outline.

The average size of the Type II neurons in the given species is considerably smaller in comparison with the Type I cells. In BLa of the fox the mean size values of both these of these cell are 16.8/13.2 μm and 30.9/20.3 μm respectively. However, the size variability of the Type II cells is also extremely wide in all nuclei. In BLa of the fox the size values of the major

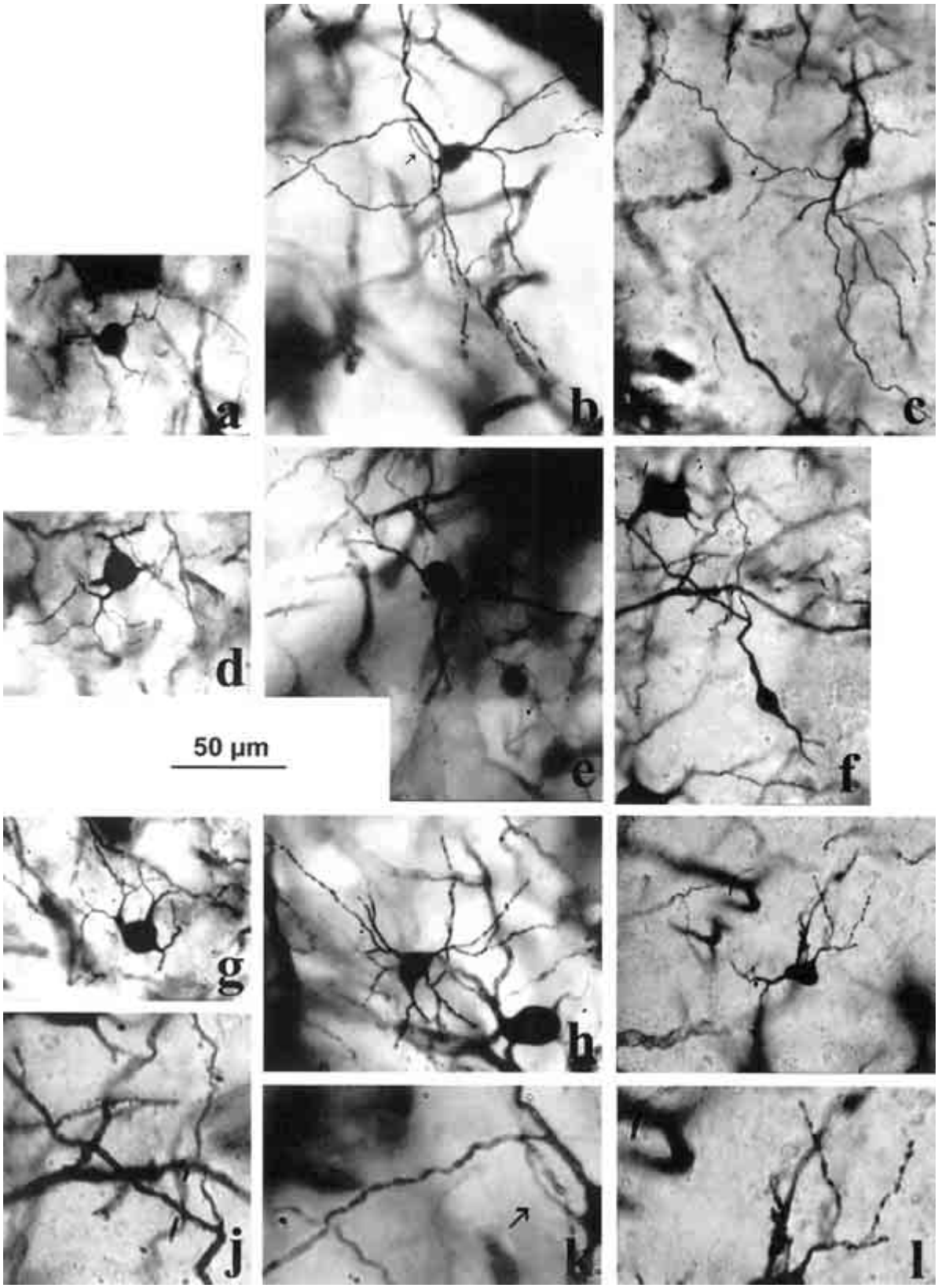

Figure 2. The sparsely spiny Type II neurons. **A–C.** Type II cells in LA of the guinea pig, rabbit and fox respectively; **D–F.** Type II cells in BL of the guinea pig, rabbit and fox respectively; **G–I.** Type II cells in BM of the guinea pig, rabbit and fox respectively; **J–L.** Higher magnifications of the dendrites from Figures 1F, B, I respectively. Golgi impregnation. Axons are marked by arrows.

cell axis vary from 12.7 μm to 33.5 μm. In contrast to the spiny Type I cells, the average size of the Type II neurons seems to be independent of the location in BLC. In all nuclei small and medium-sized cells predominate. The large Type II neurons were encountered in all basolateral areas but on rare occasions. In the fox the mean sizes of the Type II cells in LAa, LAp, BLa, BLp, BMa and BMp are 15.4/13.1 μm, 16.1/13.5 μm, 16.8/13.2 μm, 15.7/12.8 μm, 16.4/12.5 μm and 14.9/11.7 μm respectively. It should be noted that, similarly to Type I neurons, the size of Type II cells increases with the enlargement of the brain. For example, the mean size values in BLa of the guinea pig and pig are 13.4/11.9 μm and 18.7/16.3 μm respectively.

In all species the shape variability of the Type II neurons is smaller than that of the spiny Type I cells and it is similar in all basolateral nuclei. Multipolar and rounded neurons were observed most often. Fusiform and triangular forms were rarely impregnated.

Type III cells (Fig. 3) are represented by particularly small and rarely distributed neurons, with a few short, delicate and varicose dendrites. The axon, which presents a similar appearance to the dendrites, impregnates very seldom and is hard to identify. It originates either in the cell body or from a primary dendrite and splits up poorly close to the parent soma. The general morphology of the Type III neurons is reminiscent of the glia cells. The Type III neurons were observed in LA of the rabbit, fox and pig as well as in BL of the rabbit. They were not found in BM.

DISCUSSION

This is the first investigation to provide a detailed Golgi analysis of the mammalian basolateral amygdala in 4 different species. Some of our findings are indicated in what follows.

The present results have demonstrated that the neuronal structure in each of the individual basolateral nuclei is extremely stable and remains almost unchanged in the line from the guinea pig to the rabbit and to the fox and pig. This is consistent with previous Golgi studies in a variety of different mammalian species [5, 7, 16, 28, 40]. In the rat [28], cat [16] and human [5] similar cell types have been found in all basolateral nuclei. This is not surprising since the neuroanatomical investigations in the basolateral amygdala indicate strong similarities between various mammalian species in the connections [21, 49, 55] and chemocytoarchitecture [29, 46, 48] of this brain area.

Furthermore, the intraspecific comparisons of LA, BL and BM revealed that they form in each of the species studied in a fairly homogenous mass of cells, in which similar cell types are present. The only difference between the individual basolateral nuclei is in the average size of the neurons that build their cellular populations. Similar findings have also been reported by other authors [5, 16, 28, 40]. Kamal emphasised the impacting uniformity of BLC in the Golgi method [16]. Braak has also considered LA, BL and BM as a compact area with a homogeneous cellular structure [5]. Both these authors have drawn up a detailed cytoarchitectonic analysis of the individual BLC nuclei, regarding the morphological differences among the neurons in these cellular populations as not important [5, 16].

In all the species studied the basic cellular populations in LA, BL and BM form the spiny cells that often present a pyramidal or semi-pyramidal appear-

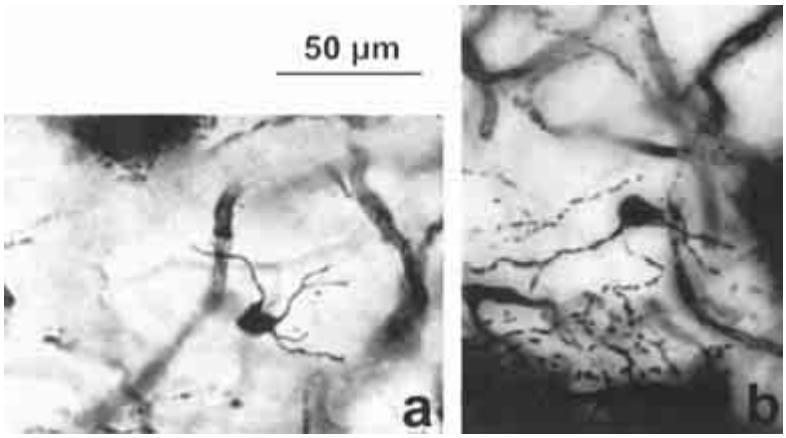

Figure 3. The sparsely spiny Type III neurons. **A.** Type III cell in LA of the fox; **B.** Type III cell in BL of the fox. Golgi impregnation.

ance (Type I cells). Although, these cells differ in several details, including the size and shape of the soma as well as the organisation of the dendritic tree, similar morphological variability was observed among the cells of different nuclei, within the single nucleus and even in the discrete part of it (BLa, LAp etc.). The Type I neurons seen in our material correspond more probably to the class I cells of McDonald [27], the spiny nerve cells of Braak and Braak [5] and to the projecting neurons of Kamal and Tombol [16] and Milhouse and DeOlmos [40]. The second subpopulation of BLC neurons form Type II cells that are characterised by round cell bodies and smooth or sparsely spined dendrites [present research and 5, 7, 16 28, 40]. These occur in all the nuclei under examination but in each of them they are greatly outnumbered by the Type I cells. The Type II neurons seen in our material are comparable in description to the class II cells of McDonald [27] and Braak and Braak [5] as well as to the type "a" interneurons of Kamal and Tombol [16]. The third cellular type is reminiscent of the glia cells according to the general morphology (the Type III neurons) and in the present study it was observed exclusively in LA and BL. However, McDonald [27, 28] has described similar neurons in BL and BM only. These discrepancies in the location of the Type III cells can be due to their sporadic impregnation and the specificity of the Golgi technique [28]. The Type III neurons seen in our material are comparable to the class III cells of McDonald [27] and Braak and Braak [5] as well as to the type "b" interneurons of Kamal and Tombol [16].

In all the species studied the morphology of Type I and Type II basolateral neurons share many common features with the pyramidal and non-pyramidal cells respectively in the cerebral cortex. The remarkable similarities in the cellular structure between BLC and the cortex have been emphasised by many authors [5, 7, 16, 27, 28, 40]. Furthermore, the immunohistochemical studies, just like the cellular structure, suggest the cortical-like character of LA, BL and BM [8, 29, 30, 32, 38, 48, 54]. The basic neurotransmitter found in the Type I basolateral neurons, just as in the cortical pyramidal cells, is glutamic acid [36, 37, 54]. The basolateral cells that contain GABA and miscellaneous peptides display most often all the morphological features of the Type II and III neurons [1, 29, 30, 32, 38, 48, 54]. The clear domination of the glutamatergic Type I cells in the basolateral nuclei as well as the density, distribution and morphology of the GABA-ergic Type II neurons echo the typical relations observed in the cortical areas [1, 29, 30, 32, 38, 48, 54].

The average size of the Type I cells in the given species depends on the location in the basolateral amygdala, whereas the mean size of the Type II and III neurons is quite similar in all portions of BLC. In all the animals examined BLa contain the largest Type I cells in BLC. Both parts of LA and BMa are composed of Type I neurons mostly of medium-size. The smallest basolateral Type I cells populate BMp. The similar size segregation of the Type I cells in BLC has been reported by other authors [9, 12, 15, 16, 21, 52]. The distribution of the Type II neurons in BLC is different. In all basolateral nuclei the average size and the size variability are quite similar. Furthermore, the shape variability of the Type II neurons is also similar in all BLC regions. This uniformity of the Type II cell distribution gives the impression that these neurons form the single cellular population that penetrates the individual basolateral nuclei. Interestingly, recent embryological investigations indicate that at least the most sparsely-spiny GABA-ergic interneurons of the adult cerebral cortex are actually generated in the medial and lateral ganglionic eminences at the early stages of development [2, 22, 47]. From these sites these cells migrate dorsally to the cortex at subsequent stages. The origin of the aspiny cells of the cortex seems then to be striatal-like and different from that of the cortical pyramidal cells. Since the morphology of the basolateral Type II neurons and the cortical interneurons is very similar and both of them use GABA as a transmitter, it may be that their origin is also the same. The similarity of the Type II neurons in all portions of BLC to those in the cortex would be then justified.

The average size of the neurons in LA, BL and BM constantly increases in the line from the guinea pig to the rabbit and to the fox and pig. The positive correlation between the size of the cells and the size of the brain has also been described in the limbic cortex of several Cetacean species [43].

In all species the Type I cells in LA and BM show particularly strong morphological similarity (compare the cells of both nuclei in Fig. 1, 2). Interestingly, hodological and morphometric studies confirm that LA and BM may be closely related anatomically [14, 38, 45, 51]. The projections of the ventral prefrontal cortices to BLC mainly targeted LA and BM, whereas the input to BL, which lies between LA and BM, was very weak [14, 38, 45]. Furthermore, LA and BM, but not BL, have strong interconnections with each other and the superficial nuclei of CA [21, 45, 49]. Finally, contrary to BL, both nuclei receive afferents from the posterior thalamic region that process the auditory and somatosensory stimuli [24] as well as those

from the perirhinal cortex that probably process the visual and auditory signals [31]. In the light of the morphometric studies both these regions display a similar pattern of size evolution that is strikingly different from that of BL [51]. It should be noted that this view has received also some support from the studies of the expression of the homeotic genes during the development [50].

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