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MITRAL CELLS OF THE OLFACTORY BULB OF THE LIZARD *PODARCIS HISPANICA*

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RESUM

Als rèptils *(Podarcis hispanica)* i amb els mètodes d'impregnació de Golgi i microscòpia electrònica, s'ha estudiat l'estructura de les cèl·lules mitrals dels bulbs olfactoris principal i accessori. Al bulb principal s'ha observat l'existència d'un sol tipus de cèl·lules mitrals. En canvi, al bulb accessori s'han establert tres poblacions diferents en funció de la mida neuronal i de la distribució dels arbres dendrítics. Així doncs, les cèl·lules mitrals del bulb accessori mostren una diversitat morfològica més gran, probablement relacionada amb el gran desenvolupament del sistema vomeronasal dels rèptils.

RESUMEN

La estructura de las células mitrales de los bulbos olfatorios principal y accesorio de reptiles *(Podarcis hispanica)* ha sido estudiada mediante los métodos de impregnación de Golgi y microscopía electrónica. Mientras que en el bulbo principal se ha observado la existencia de un sólo tipo de células mitrales, en el bulbo accesorio se han podido establecer tres poblaciones diferentes en base al tamaño neuronal y a la distribución espacial de las arborizaciones dendríticas. Así, en el bulbo accesorio las células mitrales presentan una mayor diversidad morfológica, probablemente relacionada con el gran desarrollo del sistema vomeronasal en reptiles.

ABSTRACT

The structure of mitral cells in the main and accessory olfactory bulbs of the lizard *Podarcis hispanica*, was studied by means of the Golgi-impregnation method and electron microscopy. In the main olfactory bulb only one mitral cell type was observed, while in the accessory bulb three main populations of mitral cells were established on the basis of the neuronal size and spatial organization of the dendritic trees. Thus, the accessory olfactory bulb shows a great morphological diversity probably related to the great development of the vomeronasal system in reptiles.

Key words: Golgi method, olfactory system, reptiles, synaptology, ultrastructure.

INTRODUCTION

The olfactory bulbs constitute the most rostral portion of the telencephalon. A variety of typical behaviors, including odor detection and examination, spatial orientation, sexual and maternal behaviors, aggressivity, sodium uptake, memory and learning, have been found to depend on the olfactory bulbs (Shaffa, 1979).

The olfactory bulbs of most vertebrates are composed of two different areas or structures, the main olfactory bulb (MOB) and the accessory bulb (AOB). Both areas receive peripheral inputs from different sources and have separated central projections (Allison, 1953; Scalia and Winans, 1975). The MOB receives inputs from the olfactory mucosa, while the AOB receives afferents from the vomeronasal (or Jacobson's) organ (McCotter, 1912). These olfactory areas have a basic lamination pattern of six layers which, from the external to the ependymal surfaces, have been denominated: 1) nerve fiber layer, 2) glomerular layer, 3) external plexiform layer, 4) mitral cell layer, 5) internal plexiform layer and 6) granule cell layer. This laminar organization remains unchanged among vertebrates (Andres, 1970; Nieuwenhuys, 1967).

Mitral cells are the main integrating and relay units of the olfactory bulbs and their large somata are constituting the mitral cell layer of both olfactory areas. Generally they have primary dendrites extending into glomeruli, where they receive sensory information from olfactory or vomeronasal axons, and secondary ones which distribute mainly in the external plexiform layer where they contact with granule cells, the principal type of bulbar interneurons (Orona et al, 1984; Price and Powell, 1970a,c). Mitral cells have been largely studied in mammals (Kishi et al, 1984; Macrides et al, 1985; Macrides and Schneider, 1982; Mori et al, 1983) and fishes (Kosaka and Hama, 1982; Oka, 1983), but available data in the rest of vertebrates are very scarce.

The aim of the present report is to determine the morphology of the mitral cells of *Podarcis* by means of Golgi-impregnation methods, and their ultrastructure by conventional electron microscopy. Also, a comparison between data on main and accessory olfactory bulbs, as well as among reports on mitral cells of other vertebrates will be made.

MATERIALS AND METHODS

For this study, 37 adult specimens of *Podarcis hispanica* were used. All animals were anesthetized with ether and perfused transcardially.

Nissl-staining

Two animals were perfused transcardially with a phosphate-buffered 10 % formalin solution (pH 7,3). After extraction bulbs were dehydrated,

embedded in paraffin, cut into 9 μm-thick transversal serial sections and stained with cresyl violet using standard techniques.

Golgi-impregnation

For the Golgi impregnation study, 30 lizards were perfused with 5 % glutaraldehyde in 0,1 M phosphate buffer. Olfactory bulbs were removed and postfixed in the same fixative solution overnight. Bulbs were processed according to the Golgi-Colonnier method (Colonnier, 1964) and incapsulated in paraffin. 150 μm-thick transversal sections were dehydrated and mounted between two coverslips in Araldite.

Electron microscopy

For the conventional electron microscopy, five lizards were employed, perfused with a 3 % paraformaldehyde, 4 % glutaraldehyde and 0,05 % calcium chloride in 0,1 M phosphate-buffered solution (pH 7,3). Olfactory bulbs were carefully removed and inmersed in the fixative solution during 4 hours. After, they were sectioned and postfixed in 2 % osmium tetroxide for 2 hours, stained in block with 2,5 % uranyl acetate, dehydrated and embedded in Araldite. Sections of 1 μm-thick, were stained with toluidine blue. Ultrathin sections were also obtained with a LKB-III ultramicrotome, stained with lead citrate and examined with a Hitachi HU-12 A electron microscope.

RESULTS

Olfactory bulbs of *Podarcis hispanica* occupy the most rostral portion of the telencephalon and join the cerebral hemispheres by two long peduncles. Each bulb is composed of two distinct structures, the main and accessory olfactory bulbs, being the latter mediocaudally located to the former (Fig. 1).

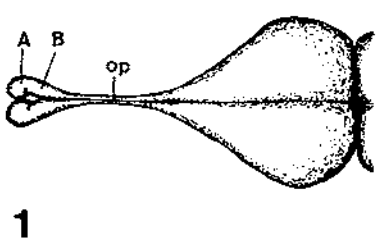

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Figure 1. Scheme of the telencephalon of *Podarcis hispanica*. A: main olfactory bulb, B: accessory olfactory bulb, op: olfactory peduncles.

Although, the main olfactory bulb (MOB) and the accessory bulb (AOB) are composed of six similar major layers, the transition between them can be easily recognized by the location of bulbar ventricles: while in the MOB all layers are concentrical to the ventricle (fig. 2), in the AOB the

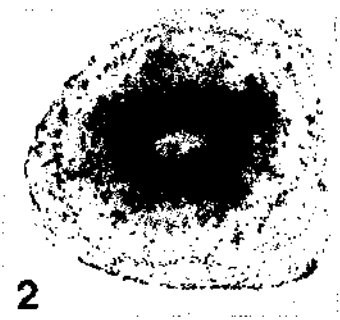

Figure 2. Nissl-stained transverse section of the MOB. See the concentric arrangement of cellular layers around the ventricle (V). Arrows indicate the mitral cell layer which is composed of parallelly oriented mitral somata. X85

bulbar ventricle is displaced laterally restricting the cellular layers to the medial wall of the bulb (fig. 3).

In transversal sections stained with the Nissl method, the mitral cell layer (MCL) in both MOB and AOB presents some remarkable differences: the MCL of the MOB is better defined than that of the AOB, and mitral cell somata, which usually are parallely arranged to the bulbar surface in the MOB, show in the AOB diverse orientations.

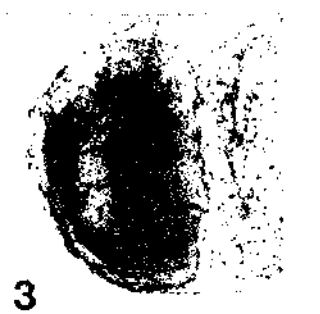

Figure 3. Nissl-stained transverse section of the AOB. Note as the ventricle (V) is displaced laterally being the cellular layers restricted to the medial wall of the bulb. The mitral cell layer is not well-defined (arrows), showing mitral cell bodies diverse orientations. X85

GOLGI OBSERVATIONS

Mitral cells of the MOB

In the MOB all mitral cells are generally distributed throughout the MCL and arranged parallelly to the bulbar surface. Displaced mitral cell bodies could be occasionally observed in the external plexiform layer.

Mitral cell bodies are fusiform or, occasionally, spherical in shape measuring 20 μm in mean diameter. Their dendritic trees are very long and can encircle an appreciable fraction of the circumference of the olfactory bulb.

Mitral cells have two distinct types of dendrites, primary and secondary ones. A single primary dendrite, in all mitral cells of the MOB, arises from the cell body or from a proximal portion of a secondary dendrite, travels upwards through the external plexiform layer and forms a tuft (fig. 4A) within a single glomerulus. From each somatic pole 1 to 2 secondary dendrites emerge and branch out sparsely. The secondary dendrites never contribute to the glomeruli formation. Mitral dendrites are thick and lack spines although present some varicosities especially at their distal portions.

The mitral cell axon arises from a dendritic portion close to the soma and runs through the internal plexiform layer towards caudal regions. Near the soma one collateral branch running back towards the external plexiform layer can be observed. At the AOB level, most mitral cell axons coming from the MOB are constituting the lateral olfactory tract, that is laterally situated in the AOB and courses caudally towards the retrobulbar region.

Mitral cells of the AOB

The mitral cell layer of the AOB of *Podarcis* is not well-defined since the mitral cell bodies are distributed in a wide area. At rostral levels, mitral somata are often parallelly arranged to the medial surface, but at more caudal levels, perpendicular or tangential orientations can easily be observed.

In the AOB mitral cells can give rise to more than one primary dendrite and corresponding tuft (fig. 4B,C) in the glomerular layer (one tuft within one single glomerulus). Each tuft is constituted by branches from one mitral dendrite or by several dendritic stems from the same mitral cell. Also, secondary dendrites are present in these neurons. The mitral dendritic trees are long, aspinous and sparsely branched, showing varicosities especially in their distal portions.

Three main types of mitral cells were established on base of differences in size and spatial organization of dendritic trees. Two types correspond to big mitral cells with distinct secondary dendritic distributions. The third type is the smallest one in the AOB.

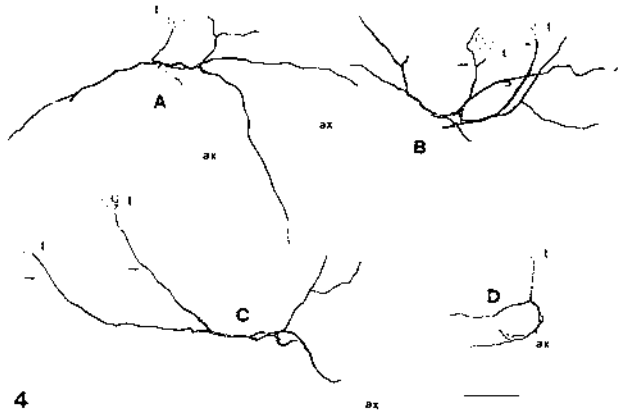

Figure 4. Camera lucida drawing of Golgi-impregnated mitral cells in the olfactory bulb of *Podarcis*. Mitral cell of the MOB (A) having only one dendritic tuft (t). Outer (B) and inner (C) mitral cells of the AOB showing primary dendrites (arrows) originating some dendritic tufts (t) at the glomerular layer. Small mitral cell (D) of the AOB, which is characterized by present no typical mitral dendritic tufts (t). Axon (ax) of mitral cells. Scale bar, 50 μm.

Outer mitral cells

This category comprises the biggest mitral cells of the AOB. Their somata are fusiform or spherical measuring 22 μm in mean diameter. They are predominantly distributed in dorsomedial portions of the external plexiform layer. At rostral levels, the long axis of most of these somata were parallelly arranged to the medial surface of the bulb, while at more caudal sections, diverse orientations could be distinguished. Generally four dendritic trunks emerge from the soma when it is spherical, while two or three trunks emerge from the fusiform ones. All of these neurons give rise to more than one tuft in the glomerular layer (fig. 4B). Their dendrites are the thickest ones of all mitral cell types and at distal portions their courses take a rostrocaudal direction.

Inner mitral cells

These neurons have mostly spherical, occasionally fusiform and usually smaller cell bodies than the outer mitral cells, measuring about 17 μm in diameter (fig. 4C). They are mainly distributed throughout the mitral cell layer and extend 2 to 3 main dendritic trunks comparable in size and thickness with those of the first category of mitral cells. Their major dendritic portions are oriented parallelly to the transversal sections of the bulb. Generally, these dendrites follow a dorsoventral course in the

external plexiform and mitral cell layers, most of them being also traced in the outer portions of the internal plexiform layer.

The neurons belonging to this type extend typical mitral tufts (more than one) in the glomerular layer (fig. 4C).

Small mitral cells

This category of mitral cells represents the smallest ones in the AOB. They are distributed throughout the external plexiform and mitral cell layers. Somata are oval or spherical, measuring approximately 12 μm in diameter. Main dendrites emerge from each cell body pole, but run towards the same direction and branch out sparsely at their distal portions (fig. 4D). They can be oriented parallelly, tangentially or perpendicularly to the medial surface of the AOB. Their dendrites are considerably thinner than those of the other mitral cell categories of the AOB.

In our Golgi material, mitral cells of this group do not have typical tufts, but present a great number of very short ramifications at their dendritic ends.

The axons of all mitral cells of AOB usually emerge from an initial dendritic segment, or occasionally, directly from the soma. They follow a descending course through the internal plexiform layer and bend to continue towards the retrobulbar region. The rarely observed collateral branches often run back towards the outer layers. However, only short axon courses could be followed in our transversal sections.

ELECTRON MICROSCOPY

Mitral cells of the MOB

Mitral cells of the MOB usually are very large (fig. 5) and contain a voluminous nucleus displaced to the periphery, which occasionally shows

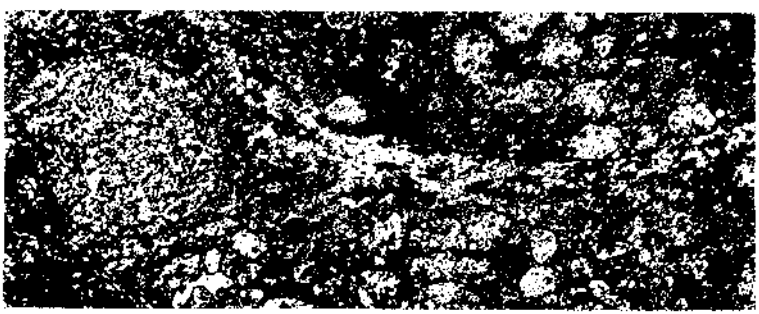

Figure 5. A mitral cell soma. Note the great amount of cytoplasmic organelles. A thick dendritic trunk arising from the cell body is also seen. X3400.

small indentations and a great amount of nuclear pores, being the perinuclear cisterna a little dilated. The chromatin is spongious and a well-developed nucleolus can be centrally observed.

The cytoplasm of mitral cells is rather pale and contains numerous cisternae of rough endoplasmic reticulum, short and a little dilated, which are little associated forming very small clumps of Nissl substance. Golgi complexes are very abundant throughout the cytoplasm and at the beginning of dendrites. They are composed of 3 to 6 very long and rather dilated saccules and a diverse population of vesicles in their surroundings, some of them being coated vesicles. Microtubules, mitochondria and polyribosomes are also observed. Lysosomes, some dense bodies and small spherical vesicles of 40-45 nm in mean diameter are also distinguished.

Mitral cell dendrites are clearly recognized by their large diameter, regular outline and wide ependymoglial covering. They show numerous microtubules aligned along of dendrites, elongated mitochondria and small groups of spherical vesicles of 40-45 nm in diameter close to the plasma membrane.

These dendrites establish reciprocal synaptic contacts (fig. 6) with terminals showing spherical vesicles of 45-50 nm in diameter. These synapses are asymetric when the mitral dendrite acts as the presynaptic element, and symmetric in the opposite direction. This kind of synaptic contact can also be made by the mitral cell somata of the MOB.

Figure 6. Reciprocal dendro-dendritic synaptic contact between a mitral cell dendrite (M) and a gemmule (G) belonging to the granule cell. Arrows indicate the direction of synapses. X28000.

Mitral cells of the AOB

Mitral cell somata of the AOB can present big or small diameter. Large somata are similar to those of the MOB, but they are distinguished by their very indented nuclear surface and greatest amount of Golgi complexes. There is no differences between mitral cell dendrites of MOB and AOB.

Small mitral cell somata are qualitatively similar to large ones. However, they contain less cytoplasmic organelles, scarce nuclear indentations and less synaptic contacts on their somata.

DISCUSSION

The main and accessory olfactory bulbs of *Podarcis* have similar lamination patterns, as it has been reported for other reptiles (Andres, 1970; Crosby and Humphrey, 1939; Halpern, 1980; Nieuwenhuys, 1967). Nevertheless, the mitral cell layer of the AOB is worse defined than that of the MOB. Neither in the olfactory bulb of teleosts (Oka, 1983) and turtles (Orrego, 1961) nor in the AOB of mammals (Lohman and Lammers, 1967) the mitral cell layer shows clearcut boundaries. Mitral cell layer of both olfactory areas are mainly composed of the large mitral cell bodies which, while in the MOB are arranged parallelly to the bulbar surface (García Verdugo et al., 1986), in the AOB show diverse orientations.

Mitral cells are the biggest neurons of olfactory bulbs of *Podarcis* and they are larger than in teleosts (Kosaka and Hama, 1982) and turtles (Orrego, 1961), but a little smaller than in mammals (Macrides and Schneider, 1980; Price and Powell, 1970c). Mitral cells of the MOB of *Podarcis* have only one primary but several secondary dendrites, the former giving rise to a unique tuft at the glomerular level, as it has been described for the mammalian MOB (Macrides and Schneider, 1982). Nevertheless, mitral cells of the AOB of *Podarcis* show several primary and secondary dendrites, like it occurs in the AOB of mammals (Lohman and Lammers, 1967). In turtle olfactory bulbs (Mori et al, 1981) the existence of more than one tuft per mitral cell has been also demonstrated. In teleosts, mitral cells lack secondary dendrites (Kosaka and Hama, 1982; Nieuwenhuys, 1967; Oka, 1983). On the other hand, tufts of mitral cells of *Podarcis* are considerably smaller than those of mammals (Macrides and Schneider, 1982; Mori et al., 1983), but bigger than teleostian ones (Kosaka and Hama, 1982; Oka, 1983).

Shepherd (1966) observed that secondary mitral dendrites of the mammalian olfactory bulbs are mainly distributed along the rostrocaudal axis of the bulb. Mitral cell dendrites of the MOB of *Podarcis* extend principally in the transverse plane of the bulb, but secondary mitral dendrites of the AOB, belonging mainly to outer and small mitral cells, are oriented in a rostrocaudal direction.

Mitral cells of the MOB of *Podarcis* could be grouped in only one morphological type. However, three main types of mitral cells, on the basis of differences in size and spatial organization of dendrites, were established in the AOB. This fact might be related to the great development of the vomeronasal system in most reptiles. Moreover, the existence of several mitral cell types in the AOB of *Podarcis* might indicate a possible functional diversity, since in the AOB of mammals subgroups of vomeronasal axons showing segregated terminations were demonstrated (Imamura et al. 1985).

Inner mitral cells of the AOB are the most morphologically similar to those of the MOB in *Podarcis*. On the other hand, if one accepts the suggestion that the size of the neuronal soma is correlated with the amount

of stimulation received by the cell (Hickey et al. 1977), the outer mitral cells may correspond to the main neuronal type in the AOB of *Podarcis*. Finally, small mitral cells of the AOB are the smallest mitrall cell type in the olfactory bulbs and they do not extend typical mitral tufts. A possible explanation might be in relation to that observed in the cat olfactory bulb where it has been reported that histologically different groups of glomeruli receive inputs from topographically defined groups of olfactory receptors (Jastreboff et al. 1984).

The axon of mitral cells of *Podarcis* arises from the soma or from a proximal region of a secondary dendrite and runs towards the internal plexiform layer as it happens in most vertebrates (Kishi et al., 1984; Nieuwenhuys, 1967; Orrego, 1961). All mitral cell axons in our Golgi material were impregnated only in a short course, probably the unmyelinated part of the axon. In mammalian olfactory bulbs mitral cell axons becoming myelinated, as they pass caudally throughout the granule cell layer, were observed (Price and Powell, 1970c).

The somata of mitral cells of the MOB and AOB were easily recognized by their large size in conventional electron microscopy. The main ultrastructural differences between mitral cells, of both olfactory areas, are the very indented nuclear surface and greatest amount of Golgi complexes of the large mitral cells of the AOB. However, in the AOB a third type of mitral cells presenting few cytoplasmic organelles and scarce nuclear indentations could be distinguished. Since these neurons show smaller cell bodies than those of the other mitral cell types, they might possibly correspond to the small mitral cells recognized by the Golgi-impregnation method. On the other hand, general ultrastructural characteristics of mitral somata of *Podarcis* are very similar to those of mammalian olfactory bulbs (Price and Powell, 1970c; Willey, 1973). The only differences observed are those related to size and number of organelles.

Mitral cell dendrites of the MOB and AOB show the same ultrastructural features. They have a regular outline and a big diameter, showing numerous neurotubules, large mitochondria and small groups of spherical vesicles. Although, some myelinated dendrites of mitral cells have been recognized in mammalian olfactory bulbs (Remahl and Hildebrand, 1985; Pinching, 1971; Willey, 1973), in our material no myelinated dendrites were observed. Nevertheless, mitral cell dendrites show a profuse ependymoglial coating. Dendrites, and less frequently cell bodies, of mitral cells of *Podarcis* make characteristic reciprocal dendrodendritic synaptic contacts. These synapses were asymmetric when the mitral cell acts presynaptically, and symmetric in the opposite direction. This kind of synapses have been also described in most vertebrates (Ichikawa, 1976; Kosaka and Hama, 1982; Oka, 1983; Price and Powell, 1970b,c; Rall et al. 1966).

In mammalian olfactory bulbs it has been demonstrated that these reciprocal synapses occur between mitral cell dendrites, or somata, and gemmules of the granule cells (Price and Powell, 1970a,b,c; Rall et al., 1966).

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