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Structural Organization of the Optic Tectum of Barbus meridionalis Risso. II. Outer Strata (SFGS, SO and SM)

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With 11 Figures

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Summary: The present work deals with the histological organization of the three outer strata of the optic tectum of *Barbus meridionalis*. As far as general features are concerned, of noteworthy interest are the absence of myelin in the SM and the ordered pattern of myelinic distribution of the SO. The SFGS shows a more irregular appearance than the SM and SO. It was only possible to observe with clarity several neuronal types in the SO and SFGS, whereas in the SM no clear neuronal types could be seen. The SFGS was seen to contain pyramidal neurons with spiny dendrites in the SM, together with fusiform, multipolar and horizontal neurons. In this latter type we have described neurons with ascending axons emerging from the soma or from the base of a principal dendrite. The SO contains neurons whose dendrites are distributed mainly on the horizontal plane, in each case showing certain particular features.

Introduction

The higher strata of the optic tectum of Teleosts are involved in two large groups of afferences; those originating in the retina, which run through the stratum opticum (SO) and leave most of their terminals in the stratum fibrosum et griseum superficiale (SFGS), and those which originate in the torus longitudinalis; these are the almost exclusive axonic component of the stratum marginale (SM), in which their synaptic sites may also be found (Vanegas et al. 1984; Airhart and Kriebel, 1984).

The SFGS contains a dense neuropil composed of dendrites stemming from neurons located in different strata and a large amount of fibres and axonic terminals which originate in the retina (Meek, 1981; Ito, 1971). In nearly all the species of Teleosts studied, the most representative cell type of this stratum are the pyramidal or fusiform neurons with a spiny dendritic tree in the SM. Studies have been carried out on this type of neuron using Golgi techniques (P. Ramón, 1899; Leghissa, 1955; Vanegas, 1975) and electron microscope procedures (Ito, 1971; Meek, 1981; Lara and Aijón, 1983); similar details were observed in all such studies. Horizontal and multipolar neurons have also been found in this stratum.

The thickness of the SFGS depends on the quantity of the retinal terminals, as in the case with the SO, and is consequently fairly reduced in blind species of Teleosts or those with limited vision (SCHROEDER and VANEGAS, 1977).

The SO may be distinguished by its notable ordering of myelin bundles running from dorsal to ventral regions, such that the dorsomedial and dorsoventral regions are the most abundantly myelinized ones, whereas the dorsolateral regions are sometimes confused with the SFGS (Choms et al., 1981; Lara, 1982).

The great majority of fibres which follow a tangential course in the SO originates in the retina (Campbell and Ebbesson, 1969; Sharma, 1972; Landreth et al., 1975; Schmidt, 1979, 1982). This stratum is also crossed by some telencephalic-tectal fibres, especially in its upper zone (Vanegas, 1975; Meek, 1983), and by tectal efferences whose fate is in diencephalic centres (Grover and Sharma, 1979; Ebbesson and Vanegas, 1976; Vanegas, 1975).

The cell types with soma in the SO mainly correspond to T shaped cells and fusiform or pyramidal neurons with a characteristic spiny dendritic tree in the SM (P. Ramón, 1899; Leghissa, 1955; Vanegas et al., 1974; Schroeder and Vanegas, 1977).

The SM is a very homogeneous neuropil mainly composed of the unmyelinated marginal fibres originating in the torus longitudinalis (Ito and Kishida, 1978; Meek, 1981), the spiny dendrites of the neurons of the SFGS and SO (Meek and Schellart; 1978; Lara and Aijón, 1983; Meek, 1983; Vanegas, 1983) and the terminal portions of the ependymocytes (Kruger and Maxwell, 1966). Only a few authors (P. Ramón, 1899, in *B. fluviatilis*;

LARA, 1982, in C. carpio) described neuron somata in this stratum.

The present work studies the cytoarchitecture of the SFGS, SO and SM of the optic tectum of Barbus meridionalis in an attempt to relate the morphological data obtained from Golgi preparations to their possible functional implications.

Material and Methods

The studies were performed on the Cypriniform Teleost Barbus meridionalis Risso, employing several staining and impregnation techniques. Those details about procedures employed have been given in the previous paper.

Results

Stratum Fibrosum et Griseum Superficiale

Both with Hematoxylin-Eosin and/or Nissl staining techniques and with techniques for demonstrating the presence of myelin, this stratum appears as a complex neuropil, relatively low in density of neuron somata and with an irregular distribution of isolated fibres and myelinic and unmyelinic bundles (Figs. 2 and 5). Its maximum width is seen at dorsomedial level, after which it becomes progressively thinner as one advances in a ventral direction until it finally disappears almost completely at the ventrolateral limit. B. meridionalis displays a relatively thin SFGS compared with other strata and some of the neuron types found are similar to those found in the SO. Accordingly, horizontally developed neurons and fusiform or pyramidal neurons are seem to produce a spiny ramification in the SM. Although the SFGS sems to certain fewer horizontal developed neurons than the SO, it is possible to distinguish a subtype of such cells which is well represented in the SFGS; their most salient characteristic is that they exhibit an ascending axon. Such neurons show a approximately half-moon shaped soma, with a concavity towards the tectal surface, and dendrites which stem from both sides of the cell body and extend horizontally through the SFGS along a long trajectory which gives rise to thick branches when it bifurcates (Fig. 11h). The axon stems from the soma (Fig. 9), or from areas very close to it at the base of the principal dendrite (Fig. 8).

A type of fusiform vertical neuron can be observed with a basal dendritic trunk which descends and bifurcates on the medial plane of the SGC, giving rise to horizontal branches. From the apical pole stems a thick and equally bifurcated dendrite which branches within the SO (Figs. 5 and 10).

The pyramidal neurons (Fig. 4) exhibit a thick dendrite ascending trunk (Fig. 11g) which reaches as far as the SO-SM limit without branching; from here on it branches dichotomously until it reaches the surface of the SM (Fig. 11g). After first bifurcation, all the branches are densely populated by spines, synaptic sites with the marginal fibres.

A type of multipolar neuron may be observed with two thick horizontal dendrites displayed in the SFGS together with other fines dendrites which ascend to the SO and, thereafter, follow a horizontal and fairly prolonged course (Fig. 11e). The axon stems from the basal pole of the soma to follow a sinuous and recurrent pathway. Other multipolar neurons observed, besides being infrequent, exhibit dendritic morphologies which are difficult to identify with any single cell type.

We emphasize the presence of neurons with a monopolar aspect with a thick dendrite stemming from a rounded soma and following an approximately horizontal course (Fig. 11f).

Stratum Opticum

In the stains for demostrating the presence of myelin, of interest was the ordered distribution pattern of myelin fibres of this stratum. In Barbus meridionalis, it is clearly differentiated from the SFGS in the ventral and dorsomedial regions (Figs. 1 and 2), where its thickness is notable, while in the lateral and dorsolateral regions, the degree of myelinization is low and the stratum may even be confused with the SFGS (Fig. 3).

The SO reveals a clear predominance of neuron types with soma and dendrites, both horizontally arrayed. Somata may also be observed of pyramidal and fusiform neurons with spiny dendrites in the

Fig. 1. Section stained by Kluver-Barrera method in which the great thickness of the SO in dorsomedial regions is observed. The SM is very thin. Kluver-Barrera 160×.

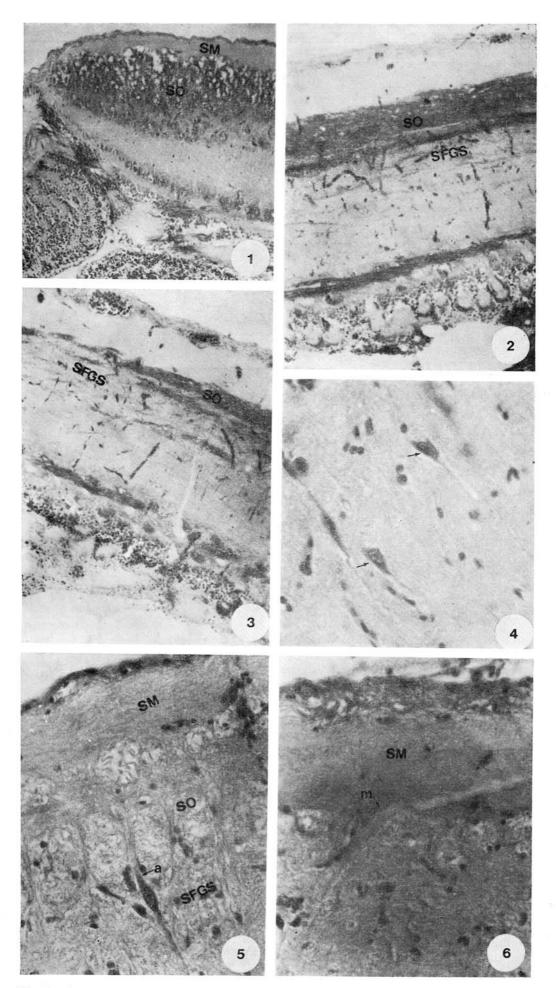
Fig. 2. Dorsal region of the tectum opticum with thick SO and scattered myelinization in the SFGS. Kluver-Barrera 160×.

Fig. 3. Dorsolateral transition region of the SO in which the scant myelinization towards lateral region is observed. Kluver-Barrera 160×.

Fig. 4. Pyramidal neurons of the SFGS (→). Hematoxylin-Eosin 400 x.

Fig. 5. Fusiform neuron of the SFGS with a thick dendritic shaft advancing the direction of the SO. a = dendritic shaft.

Fig. 6. Amyelinic bundle entering the SM (m). Hematoxylin-Eosin 400×.



Figs. 1-6

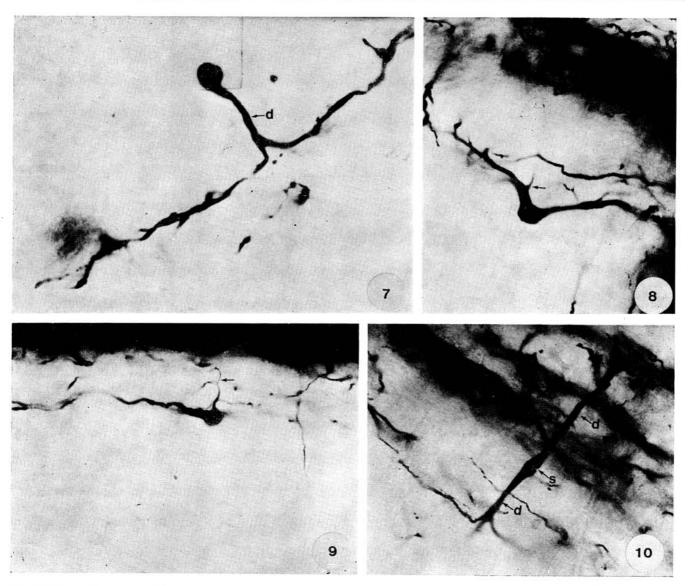


Fig. 7. T-shaped neuron with relatively long principal dendritic trunk (d). Golgi-Colonnier $400 \times$. Fig. 8. Horizontal neuron of the SFGS with ascending axon (\rightarrow) stemming from the base of a dendrite Golgi-Colonnier $400 \times$. Fig. 9. Horizontal neuron of the SFGS with the ascending axon (\rightarrow) emerging from the soma. Golgi-Colonnier $400 \times$. Fig. 10. Fusiform neuron of the SFGS. s = soma; d = dendritic shafts. Golgi-Colonnier $400 \times$.

SM. The horizontal neurons sometimes display a voluminous soma and their dendrites may extend along the horizontal plane for a quarter the length of one hemitectum on a transverse cut. Some of the neurons show dendrites which penetrate into lower strata, sometimes after sharp changes in direction (Fig. 11a), though they are most commonly found restricted to the SO (Fig. 11d). Occassionally it is possible to observe axons starting a descending course from the basal pole, though it has been impossible to follow their subsequent course. In many cases, the somata are located at the upper limit of the SO.

Characteristic of this stratum is the type of T-shaped neurons, distinguishable by their pyriform or round soma with a descending basal dendrite

which may branch immediately after its exit from the soma (Fig. 11c) or may follow a short trajectory as far as the upper limit of the SFGS where it suddenly bifurcates into two horizontal branches (Fig. 7).

Another peculiarity of the SO is the presence of neurons with a large basal dendrite which reaches the SFGS, thereafter branching, and of another two dendrites of similar calibre which exit from both sides of the soma and cross the SO tangentially. From one of the branches resulting from the bifurcation of the basal dendritic tree stems a descending axon which crosses the SFGS (Fig. 11b).

There are also some of pyramidal or fusiform neurons similar to those found in the SFGS, though the dendritic tree contained in the SM is larger.

Stratum marginale

The SM is the most extensive of the strata and occupies approximately 1/5 or 1/6 of the whole of the tectum in lateral portions, after which it becomes progressively thinner towards the dorsal and ventral regions. It is mainly composed of unmyelinized fibres stemming from the torus longitudinalis, of dendritic trees of the pyramidal neurons of the SFGS and SO and of the terminals of the long prolongation of the ependymocytes.

According to Golgi techniques, it was not possible in this study to distinguish any corpuscle identifiable as a neuron; however, with Hematoxylin-Eosin or Nissl techniques, it was possible to observe somata with the aspect of neurons clearly located in the SM, with large rounded nuclei, fairly euchromatic, and a very pronounced nucleolus.

In some preparations, bundles of amyelin fibres may be observed to penetrate into the SM from adjacent strata (Fig. 6).

Discussion

Stratum Fibrosum et Griseum Superficiale

Of the neuron types that we have described, the pyramidal neurons have also been reported by the majority of authors working with different species of Teleosts (P. RAMÓN, 1899; LEGHISSA, 1955; VANEGAS, 1975; SCHROEDER and VANEGAS, 1977; MEEK and Schellart, 1978; Kishida, 1979), whereas the fusiform neurons, which are less common, were not described by Leghissa (1955) in Cyprinus carpio and Carassius auratus; however, both MEEK and Schellart (1978), working in C. auratus, and VANEGAS et al. (1974) in E. plumieri, described a similar type. Meek and Schellart (1978) drew attention to the scarcity of fusiform neurons compared with the pyramidal variety and it has even been established that in this stratum, the pyramidal neurons receive few synaptic contacts, whereas the fusiform neurons would exhibit a much higher synaptic density (VILLANI et al., 1981).

Regarding the multipolar neurons with dendrites on two planes and a sinuous axon (Fig. 11e), only MEEK and SCHELLART (1978), working with C. auratus, describe a similar element in the upper zone of the SGC, in part coinciding with a type described by Leghissa (1955) in the SFGS.

A singular feature of our observations is that of horizontal neurons with an ascending axon (Figs. 8 and 9), only described hitherto by P. Ramón (1899). Both the axons of these cells and the collaterals stemming from axons originated in the upper dendritic

portions of the pyriform neurons of the SPV may have some relation with either the torus longitudinalis or the retina. A similar suggestion regarding the neurons of the SGC was put forward by Ito and Kishida (1978), and physiological experiments conducted to show the relationship between the torus longitudinalis and the Optic Tectum have demonstrated that interconnections exist between both structures. Accordingly, some of these neurons with ascending axons might be expected to play a role in these circuits. It should be remembered that the torus longitudinalis is responsive to light stimuli and also seems to be closely related to eye movements (ITO and KISHIDA, 1978; NORTHMORE et al., 1983).

Another salient feature is that of the neurons of monopolar aspect and horizontal development. Only one neuron type with similar features has been described by Romeskie and Sharma (1979) in C auratus.

Stratum Opticum

From the cytoarchitectural point of view, two neuron types are outstanding in this stratum, as has been reported in studies on E. plumieri (VANEGAS et al., 1974); C. auratus (LEGHISSA, 1955; MEEK and SCHELLART, 1978) and C. carpio (LARA et al., 1980); two similar types may be observed in B. meridionalis. On one hand there are the horizontal neurons whose opposed dendrites extend along the same plane as the soma, observed by P. Ramón (1899) in B. fluviatilis; on many occasions these neurons have been found in the upper limit of the stratum, which could be related to the presence of retinal terminals in the upper zone of the SO (MEEK, 1983). Certain neurons observed by us are bigger than those described by other authors (P. RAMÓN, 1899; VANEGAS, 1975; MEEK and SCHELLART, 1978; KISHIDA, 1979); the extension of the dendrites may be greater than a quarter part of one hemitectum cut transversally. In this study it was also possible to detect the initial portion of an axon which stems from the base of the soma, reaches the SFGS and does not appear to be assimilated to the axons which, immediately after their origin, follow a course parallel to that of the dendrites, as described by P. Ramón (1899) and Romeskie and Sharma (1979).

Numerous inverted T shaped neurons have also been observed, these have only been described previously by P. RAMÓN (1899) and LEGHISSA (1955) as usual elements of this tectal stratum.

The neurons displaying a bifurcated descending dendritic trunk and opposed lateral dendrites and

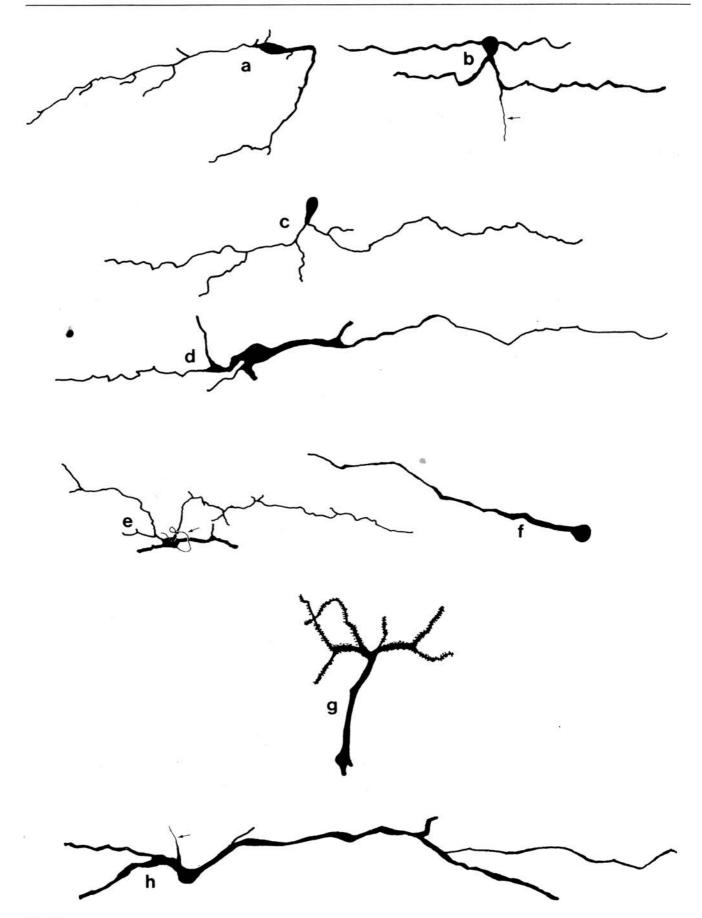


Fig. 11

of horizontal development described in this work exhibit a similar morphology to those described by P. Ramón (1899) in B. fluviatilis; no other reference has been found in the literature consulted. Our own observations confirm that the axon of this neuron type is descending and that it originates in one of the dendrites resulting from the bifurcation of the basal dendritic trunk.

Stratum Marginale

The thickness observed in the SM of B. meridionalis, slightly less than 20% of the whole optic tectum in the lateral zones, seems greater than that observed in other Cyprinids (KISHIDA, 1979; CHOMS et. al., 1981).

P. RAMÓN (1899) and LARA (1982), using Golgi techniques, reported the existence of neurons in the SM of B. fluviatilis and C. carpio, respectively. However, the other authors consulted make no reference to them. In B. meridionalis, corpuscles of a clearly neuron-like aspect in the SM could be observed with certain techniques.

Regarding the unmyelinized fibres which are integrated into the SM from lower strata, our results agree with those found by Ito and KISHIDA (1979) concerning the close relationship of those axons with the torus longitudinalis.

Two kinds of tectal efferences have led to conflicting results in the literature: the retinopetal projections and those which link the optic tectum and the torus longitudinalis. In both cases, electrophysiological data point to the existence of such projections (SANDEMAN and ROSENTHAL, 1974; NORTHMORE et al., 1983). However, the result of anatomical studies by HRP and cobalt labelling

Fig. 11.

a) Horizontal neuron of the SO with a lateral dendrite curving suddenly towards inner strata.

- b) Neuron with lateral horizontal dendrites and basal bifurcated dendritic trunk from which emerges a descending $axon (\rightarrow)$.
- c) T-shaped neuron of short basal dendritic shaft.
- d) Large horizontal neuron of the SO.
- e) Multipolar neuron of the SFGS with sinuous axon (\rightarrow) .
- f) Monopolar neuron of the SFGS with a thick, apparently non-branching dendrite.
- g) Pyramidal neuron of the SFGS with spiny dendritic tree in the SM.
- h) Large horizontal neuron of the SFGS with the axon (→) stemming from the base of a principal dendrite.

Projected drawings from Golgi preparations.

seem to be much less conclusive and according to different authors and species studies show considerable disparity in their results, above all with respect, to the retinopetal projections (Peyrichoux et al., 1977; SCHMIDT, 1979, 1982; MEYER and EB-BESSON, 1981). Certain authors deny the existence of optic tectum-retina connections (Peyrichoux et al., 1977), whereas others attribute the origin of such afferences to different tectal cell types in each case. Some workers have attempted to assign specific fates to the axons of each neuronal type of the optic tectum; thus, specific fates have been attributed to the type VI, XII, XIII, and XV neurons of MEEK and SCHELLART (1978) (VANEGAS and ITO, 1983; Meek, 1983). Some results seem to show that the retinopetal fibres run through the SO (SANDEMAN and Rosenthal, 1974) such that, in view of what has been reported above, we suggest that some of the horizontal cells of the SFGS whose axon ascends to the SO sould be considered as the origin of tectoretinal projections; confirmation of this hypothesis would require the employment of intracellular label-

It is also possible that the axons of these horizontal cells together with the colaterals stemming from the upper portions of the dendrites of periventricular neurons could intervene in afferences of the optic tectum towards the torus longitudinalis. With respect to such an idea, and according to the results of other authors (Vanegas and Ito, 1983; Meek, 1983), we propose the existence of a feedback circuit between the optic tectum and the torus longitudinalis, which would probably be involved in the visuostatic control of equilibrium. It is known that the torus longitudinalis mainly receives afferences from the valvula cerebelli (Ito and Kishida, 1978) and that such structures are involved in the control of equilibrium in Actinopterig fish active at different depths or which inhabit turbulent waters (KISHIDA, 1979). The response of the torus longitudinalis to eye movements and light stimuli has also been reported (Northmore et al., 1983); in the latter case with almost visuotopic representation in the torus longitudinalis (Northmore et al., 1983) and the necessary relay in the optic tectum (ITO and KISHIDA, 1978).

Finally, one cell type of the optic tectum, the pyramidal neurons of the SFGS, relate, by means of their spiny dendrites located in the SM, the afferences of the torus longitudinalis to the medial level of the SGC; on this plane may be found a dendritic plexus providing from types X, XII and XIV neurons described by MEEK and SCHELLART (1978), which are considered as the origin of efferent axons (MEEK, 1983). We therefore propose that the responses

derived from the tectal afferences would be controlled visuostatically by the pyramidal neurons, in turn influenced by the marginal fibres whose neurons originating in the torus longitudinalis would integrate visual information from the retina, through the neurons of the optic tectum, which we assume able to send their axons to the torus longitudinalis, with the static information arising from the valvula cerebelli.

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