

## GENERALIA

### Comparative Survey on Enzyme Localization, Ultrastructural Arrangement and Functional Organization in the Optic Tectum of Non-Mammalian Vertebrates

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**Summary.** The histochemical localization of some enzymatic activities is surveyed in the optic tectum of vertebrates from cyclostomes to birds. These data are compared with results arising from ultrastructural and experimental works in order to outline some possible connections between enzyme localization and functional organization of the optic tectum. The most interesting result derives from acetylcholinesterase which, in the majority of vertebrate species, is localized in tectal layers in which visual and other sensitive afferents discharge. Such a situation, together with some experimental and developmental results, suggests that cholinergic mechanisms play an important role in the function of the optic tectum and that these mechanisms are worthy of further and more detailed investigations.

#### 1. Introduction

In non-mammalian vertebrates, the dorsal part of the midbrain, the optic tectum, is usually a well developed region showing a very differentiated cortical structure. The optic tectum constitutes primarily the main end-station of retinal afferents but also other exteroceptive and, particularly in lower classes, olfacto-gustative fiber systems converge to the tectum.

Many workers have studied the structural organization of the optic tectum, and a general agreement exists upon the fact that this nervous center possesses a common organization plan in the majority of non-mammalian vertebrates. However, many structural studies are so descriptive and detailed that it is difficult to orientate them in the subdivision of tectal layers and sub-layers and in the terminology adopted. For this paper, I have used the nomenclature originally proposed for reptiles by HUBER and CROSBY<sup>1</sup>, and successively extended it to other vertebrate classes<sup>2</sup>, but in many cases reference has been made to the comparative study of LEGHISSA<sup>3</sup> or to more specialized researches on the different species<sup>4–13</sup>. Starting from the ventricular border, the layers of the optic tectum are the following: 1. stratum fibrosum periventriculare; 2. stratum griseum periventriculare; 3. stratum album centrale; 4. stratum griseum centrale; 5. stratum fibrosum and griseum superficiale; 6. stratum opticum. In teleosts the stratum opticum is overlaid by a conspicuous stratum marginale, and in some amphibians and reptiles by a thin stratum zonale, both free of optic terminals. In some vertebrates, the strati-

fication pattern is very rudimentary (urodeles) or more or less regressed (cyclostomes, selachians).

The aim of this paper is to provide a survey on the histochemical distribution of some important enzymatic systems in the optic tectum of non-mammalian vertebrates, and to correlate these data with the most significative results arising from ultrastructural and experimental works, in order to outline some features useful for an approach to the comparative description of vertebrate optic tectum in terms of structural and functional organization.

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<sup>2</sup> C. U. ARIENS KAPPERS, G. C. HUBER and E. C. CROSBY, *The Comparative Anatomy of the Nervous System of Vertebrates Including Man* (1936; reprinted by Hafner, New York 1960), vol. 2.

<sup>3</sup> S. LEGHISSA, *Archo ital. Anat. Embriol.* 67, 343 (1962).

<sup>4</sup> S. LEGHISSA, *Z. Anat. EntwGesch.* 118, 247 (1955).

<sup>5</sup> S. LEGHISSA, *Z. Anat. EntwGesch.* 120, 247 (1958).

<sup>6</sup> S. LEGHISSA, *Atti Accad. Sci. Bologna Memorie* 9, 123 (1962).

<sup>7</sup> GY. LAZAR and GY. SZEKELY, *J. Hirnforsch.* 9, 329 (1967).

<sup>8</sup> H. D. POTTER, *J. comp. Neurol.* 136, 203 (1969).

<sup>9</sup> J. H. LA VAIL and W. M. COWAN, *Brain Res.* 28, 391 (1971).

<sup>10</sup> J. J. O'FLAHERTY, *J. Hirnforsch.* 12, 387 (1971).

<sup>11</sup> D. G. SENN and R. G. NORTHCUTT, *J. Morph.* 140, 135 (1973).

<sup>12</sup> H. VANEGAS, M. LAUFER and J. AMAT, *J. comp. Neurol.* 154, 43 (1974).

<sup>13</sup> D. M. SCHROEDER and S. O. E. EBESSON, *J. comp. Neurol.* 160, 443 (1975).

## 2. Enzyme activities in the vertebrate optic tectum

**Acetylcholinesterase (AChE).** In the optic tectum of cyclostomes a weak to moderate reaction is present in a middle band<sup>14,15</sup> which corresponds to the stratum griseum centrale and lower part of the stratum fibrosum and griseum superficiale, or to the lower part of the superficial gray and fibrous zone of LEGHISSE<sup>3,6</sup>. In selachian optic tectum AChE reaction appears faint and lacking in clear laminar distribution<sup>16</sup>.

AChE activity in teleost optic tectum shows the most complex laminar distribution described among vertebrates. In 8 seawater and freshwater teleosts, a common distribution pattern, with only minor species-dependent variations, has been described<sup>17-19</sup>; this pattern is characterized by alternate bands with strong or moderate reaction in cellular and plexiform layers and no reaction in fibrous layers (Figure 1). However, in 2 other teleosts, *Ictalurus* and *Gobius*, a different distribution pattern is present<sup>18,19</sup>: the laminar distribution of histochemical reaction is less distinct and the marginal layer, which in the other species appears lacking in enzyme activity, shows a strong

positive reaction. In another species, *Cottus bubalis*, the optic tectum seems deprived of AChE activity<sup>17</sup>.

Among the amphibians, in urodeles a strong reaction is present in outer tectal layers<sup>20-22</sup>, the retinal and neuropilar layers of LEGHISSE<sup>3,6</sup> where discharge of retinal afferents occurs. In anurans AChE activity is distributed with 2 or 3 bands in the stratum fibrosum and griseum superficiale<sup>22,23</sup>; the largest band corresponds to laminae C (partly), D and E of POTTER's<sup>8</sup> classification (Figure 2).

Also in reptiles<sup>24-26</sup>, AChE activity is mainly localized in the stratum fibrosum and griseum superficiale with very strong reaction in the stratum fusiforme retinum of LEGHISSE<sup>3</sup> (Figure 3). In the optic tectum of *Caiman*<sup>26</sup>, in connection with a more differentiated stra-

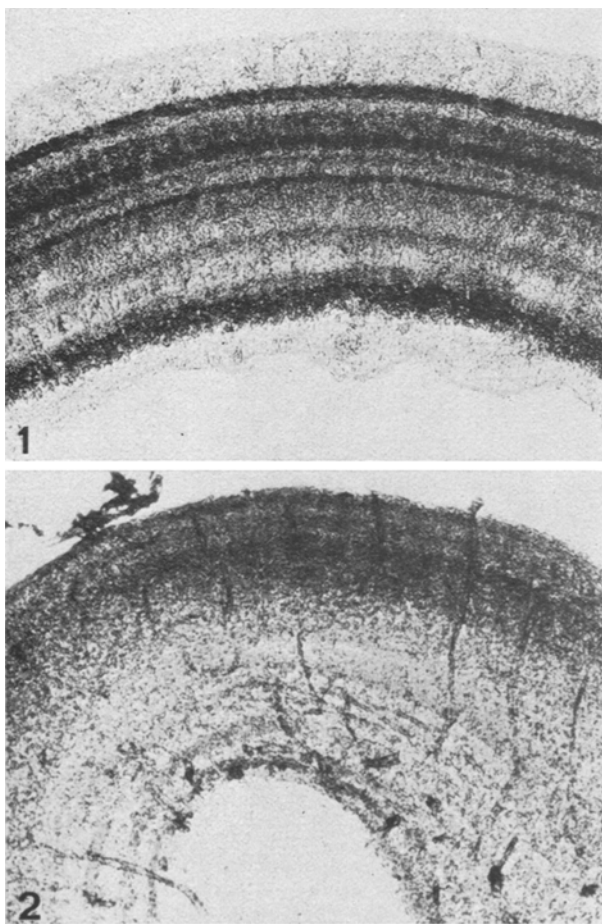


Fig. 1. AChE activity in the optic tectum of the rainbow trout, *Salmo gairdneri*. Karnovsky and Roots method.  $\times 50$ .

Fig. 2. AChE activity in the optic tectum of the frog, *Rana esculenta*. Karnovsky and Roots method.  $\times 55$ .

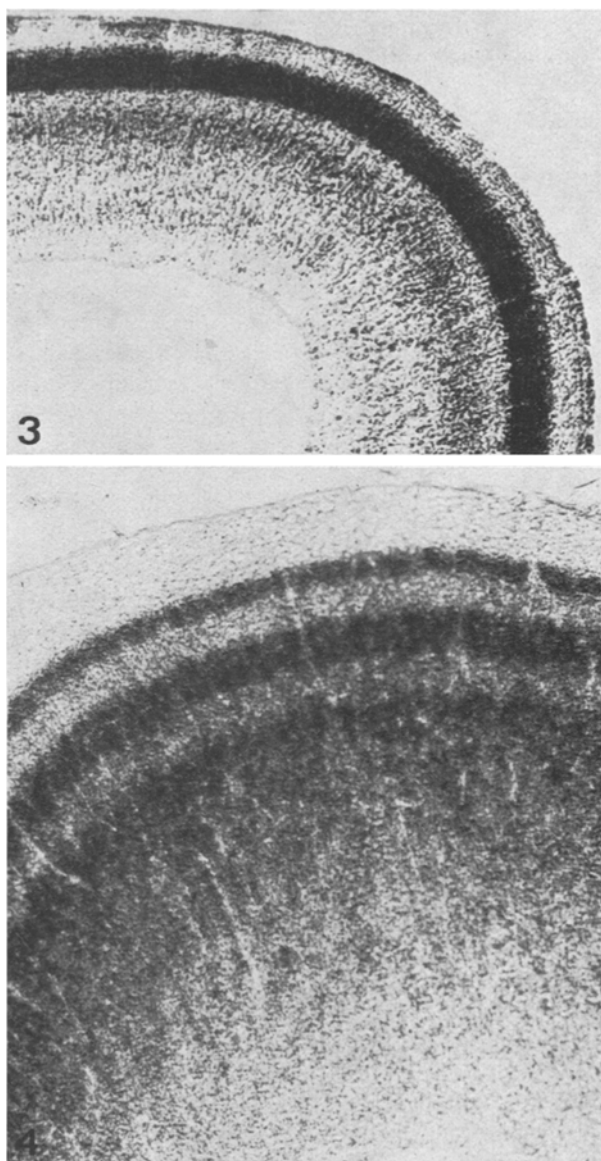


Fig. 3. AChE activity in the optic tectum of the turtle, *Pseudemys scripta*. Gerebtzoff method.  $\times 50$ .

Fig. 4. AChE activity in the optic tectum of a 40-day-old pigeon. Gerebtzoff method.  $\times 45$ .

tification of the stratum fibrosum and griseum superficiale, AChE activity shows a three-laminar distribution pattern which seems to prelude the pattern present in birds.

The optic tectum of birds is characterized by great development and laminar differentiation of the stratum fibrosum and griseum superficiale. In this layer, AChE activity exhibits a clear three-laminar distribution<sup>24,27-29</sup> (Figure 4). The 2 more superficial bands seem to correspond to the laminae where the majority of optic terminals discharge<sup>9</sup>, while the third is wider and corresponds to deeper cellular and plexiform sublayers of the stratum fibrosum and griseum superficiale.

**Monoamine oxidase (MAO) and monoamine terminals.** MAO activity in the optic tectum is prevalently localized in fibrous and sometimes in plexiform layers with noticeable differences among vertebrate classes<sup>24-26,28-31</sup>. The highest MAO activity has been found in the stratum album centrale and in the stratum opticum of teleosts and birds (Figures 5 and 7). The histochemical reaction is noticeably weaker in anurans (Figure 6) and reptiles, while it is absent in urodeles and shows a distribution pattern restricted to the outer half of the tectum in selachians.

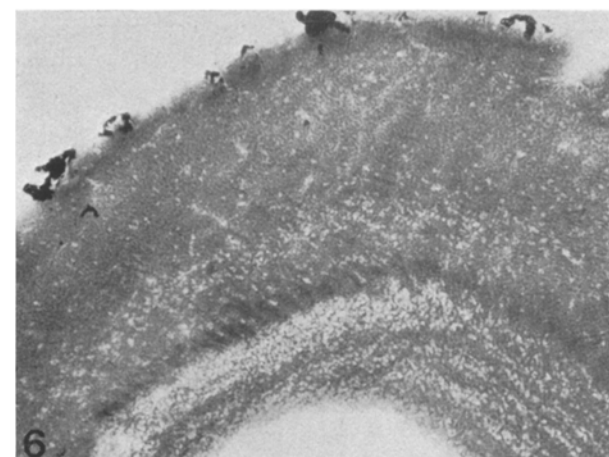
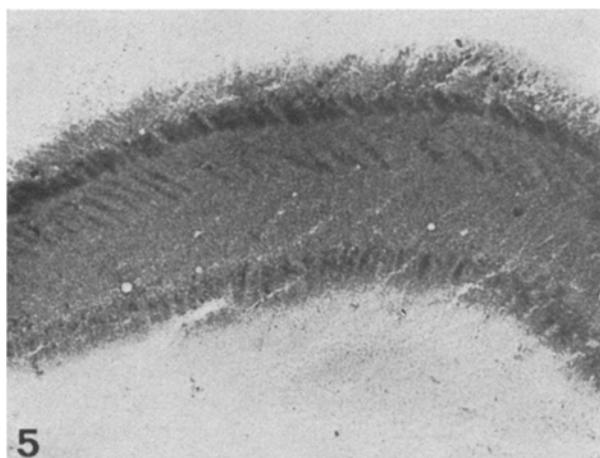


Fig. 5. MAO activity in the optic tectum of the teleost, *Poecilia sphenops*.  $\times 70$ .

Fig. 6. MAO activity in the optic tectum of the frog, *Bufo bufo*.  $\times 50$ .

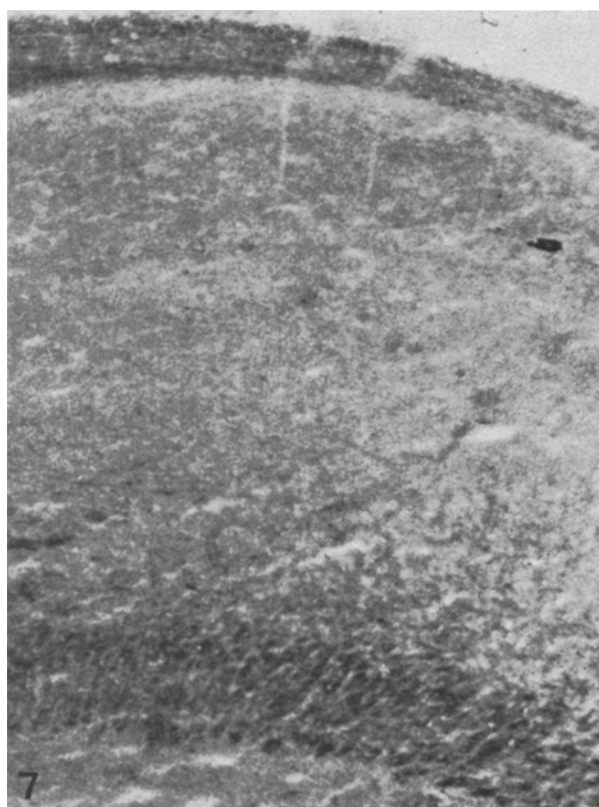


Fig. 7. MAO activity in the pigeon optic tectum.  $\times 55$ .

In addition to MAO, also monoamine containing nerve terminals have been traced with the method of formaldehyde induced fluorescence. In cyclostomes, this method reveals a fine network of serotonin containing axons in the optic layer and scattered catecholamine containing varicose terminals in more internal layers<sup>32</sup>. In other vertebrates, monoamine containing axons and nerve terminals reveal different features in the distribution pattern among tectal

<sup>14</sup> K. WACHTLER, *Cell Tiss. Res.* 152, 259 (1974).

<sup>15</sup> K. WACHTLER, *Cell Tiss. Res.* 159, 109 (1975).

<sup>16</sup> T. KUSUNOKI, Y. TSUDA and F. TAKASHIMA, *J. Hirnforsch.* 74, 13 (1973).

<sup>17</sup> M. WAWRZYNIAK, *Z. Zellforsch.* 58, 234 (1962).

<sup>18</sup> A. CONTESTABILE and N. ZANNONI, *Histochemistry*, 45, 279 (1975).

<sup>19</sup> A. CONTESTABILE, *Experientia* 32, 625 (1976).

<sup>20</sup> G. MINELLI and A. QUAGLIA, *Riv. Biol.* 67, 63 (1968).

<sup>21</sup> G. MINELLI and A. QUAGLIA, *Riv. Biol.* 62, 255 (1969).

<sup>22</sup> A. CONTESTABILE and I. MUSSONI, *Experientia*, 32, 94 (1976).

<sup>23</sup> S. C. SHEN, P. GREENFIELD and E. J. BOELL, *J. comp. Neurol.* 102, 717 (1955).

<sup>24</sup> G. MINELLI, *Riv. Biol.* 63, 61 (1970).

<sup>25</sup> T. KUSUNOKI, *Yokohama med. Bull.* 22, 1 (1971).

<sup>26</sup> A. CONTESTABILE and S. CUPPINI, in preparation.

<sup>27</sup> G. FILOGAMO, *Archs Biol., Liège* 71, 159 (1960).

<sup>28</sup> T. KUSUNOKI, *J. Hirnforsch.* 77, 475 (1970).

<sup>29</sup> S. LEGHISSA, A. CONTESTABILE and A. POLI, *Atti Accad. Sci. Bologna, Serie XII*, 10, 26 (1973).

<sup>30</sup> T. KUSUNOKI and H. MASAI, *Arch. hist. jap.* 27, 363 (1966).

<sup>31</sup> T. KUSUNOKI, H. ISHIBASHI and H. MASAI, *J. Hirnforsch.* 9, 63 (1967).

<sup>32</sup> H. G. BAUMGARTEN, *Progr. Histochem. Cytochem.* 4, 1 (1972).

layers<sup>33-36</sup>. The areas provided with higher density of monoamine containing terminals are the periventricular and inner layers in amphibians, and the stratum opticum and the stratum fibrosum and griseum superficiale in reptiles.

*Enzymes of energy metabolism: succinate dehydrogenase (SDH) and lactate dehydrogenase (LDH).* The histochemical localization of these enzymes has been studied in the optic tectum of selachians<sup>16</sup>, teleosts<sup>30,37</sup>, amphibians<sup>37</sup>, reptiles<sup>24,25</sup> and birds<sup>24,28</sup>. Noticeable differences in the characteristics of histochemical picture obtained can be seen in presumable connection with the level and the type of metabolic processes present in brain tissue of a given species. Apart from these differences, a common pattern exists in SDH and LDH localization in the optic tectum of the vertebrates, since these enzymes appear more concentrated in those tectal layers in which AChE activity is prominent.

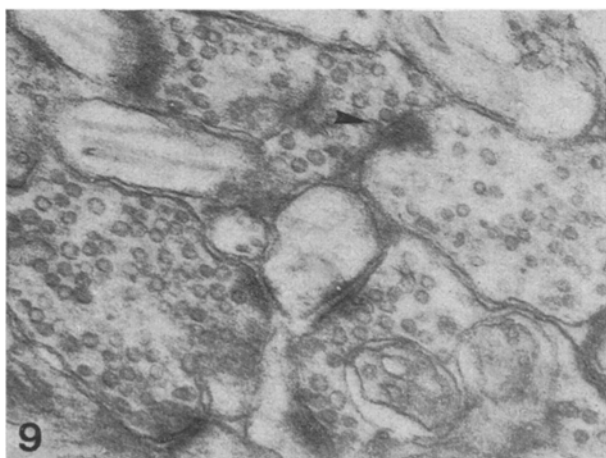


Fig. 8. Marginal layer of the optic tectum of the teleost, *Poecilia reticulata*. The terminal dendrite of a pyramidal neuron receives 2 synapses (arrowheads) from parallel fibres on its dendritic spines.  $\times 45,000$  (specimen and photograph of F. CIANI and L. VILLANI).

Fig. 9. Stratum fibrosum and griseum superficiale of the optic tectum of *Poecilia reticulata*. Afferent axons, presumably retinal, make synapse on fine dendritic branches of tectal neurons. An axo-axonic contact (arrowhead) is also present.  $\times 40,000$  (specimen and photograph of F. CIANI and L. VILLANI).

*Biochemical data.* Quantitative studies on concentration of acetylcholine, monoamines and of related enzymatic systems in the brain of non-mammalian vertebrates are relatively scarce and only few works have considered separately the optic tectum. In amphibians, biochemical proofs confirm the AChE distribution pattern observed with histochemical methods<sup>23</sup>. Other biochemical research suggests that in several species the optic tectum possesses substantial, even if species dependent, amounts of acetylcholine, monoamines, MAO, AChE and choline acetylase<sup>32,38-40</sup>.

### 3. Remarks on enzyme activities in the optic tectum

The prominent AChE activity is the most striking feature among enzymatic patterns of the optic tectum. In all vertebrates examined, with the exception of selachians and one teleost, AChE shows distribution patterns which seem strictly related to the level of structural and functional organization reached by the optic tectum. The negative results achieved in selachians and in *Cottus* need further confirmation since these results derive from the use of the Koelle method or its Gerebtzoff modification<sup>16,17</sup>; some recent findings on teleost brain<sup>18,41</sup> have pointed out characteristic discrepancies derived from the use of different methods in cholinesterase histochemistry.

A common feature exists in AChE localization in the vertebrate optic tectum: the layers provided with stronger enzyme activity are usually those in which retinal afferents discharge. Several experimental works<sup>9,42-54</sup> have traced the distribution fields of optic terminals in the tectum of different species. The main receptive layer of these afferents corresponds to the stratum fibrosum and griseum superficiale, which is differently developed in the different classes of vertebrates. In the same layer, other sensitive tracts discharge, even if the opinions concerning the actual importance and disposition of these tracts are not in agreement among different authors<sup>2,3,55</sup>. The presence of high AChE activity in this layer strongly suggests that cholinergic mechanisms are involved in reception, control and propagation of the sensitive input and in particular of the visual one.

A clear evolutionary sequence is shown by the anuran-reptile-bird series in which the progressive lamination of AChE activity corresponds to the progressive complexity in the differentiation and arrangement of cellular and plexiform bands of the stratum fibrosum and griseum superficiale<sup>2,3</sup>. In teleost optic tectum, a wider AChE distribution is present suggesting that cholinergic mechanisms play a different and presumably more important role in comparison with other vertebrates. This suggestion is in agreement with interpretations pointing out that the teleost optic tectum, even if related to fundamental plan of other vertebrates, might possess structural and functional

characteristics of peculiar type<sup>55</sup>. The unusual AChE distribution pattern adds further indirect evidence to this hypothesis supported by original structural features, as the presence of a highly developed marginal layer, and by results of experimental works, as the close relationship observed between the development of the stratum griseum periventriculare and the arrival of optic fibres<sup>56</sup>.

There is no evidence that monoaminergic mechanisms play an important role in the function of vertebrate optic tectum, even if biochemical and fluorescence

histochemical studies indicate that these mechanisms are active at certain levels of the tectum. The results of BRAAK et al.<sup>34</sup> and BRAAK<sup>35</sup> suggest that the optic tectum might be connected with an integrated serotonine pathway starting from serotonine containing neurons of the nucleus reticularis mesencephali. However, the differences in monoaminergic terminal distribution, the preferential MAO localization at level of fibrous layers of the tectum together with scarcity and erratic distribution of synaptic endings provided with dense-cored vesicles, presumably monoaminergic in function<sup>51, 57-60</sup>, constitute a lot of data not univocal and quantitatively inadequate which, at present, cannot help to explain the actual importance of monoaminergic mechanisms for optic tectum function.

The similarity between distribution patterns of AChE and LDH or SDH seems to constitute a common feature in vertebrate optic tectum and is in agreement with the situation observed in the majority of nervous centers in the vertebrate brain<sup>61</sup>. ITO<sup>57</sup> has pointed out the parallelism between layers with strong SDH activity and the number of mitochondria in teleost optic tectum. Thus the energy requirement of a given layer appears strictly related to the level of nervous mechanisms and in particular to metabolic supply for chemical synapse function.



Fig. 10. Stratum fibrosum and griseum superficiale of the optic tectum of the green lizard, *Lacerta viridis*. Synaptic contacts (arrowheads) are present between afferent axons and dendritic branches with different orientation.  $\times 35,000$  (specimen and photograph of F. CIANI and L. VILLANI).

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- <sup>37</sup> H. MASAI and S. MATANO, *Yokohama med. Bull.* **72**, 271 (1961).
- <sup>38</sup> M. H. APRISON, R. P. SHANK and R. A. DAVIDOFF, *J. Neurochem.* **11**, 341 (1964).
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- <sup>43</sup> S. O. E. EBESSON and J. S. RAMSEY, *Brain Res.* **8**, 36 (1968).
- <sup>44</sup> C. B. G. CAMPBELL and S. O. E. EBESSON, *Brain Behav. Evol.* **2**, 415 (1969).
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- <sup>50</sup> T. M. SCOTT, *J. Anat.* **114**, 261 (1973).
- <sup>51</sup> GY. SZEKELY, G. SETALO and GY. LAZAR, *J. Hirnforsch.* **14**, 189 (1973).
- <sup>52</sup> M. LAUFER and H. VANEGAS, *J. comp. Neurol.* **154**, 97 (1974).
- <sup>53</sup> R. G. NORTHCUTT and A. B. BUTLER, *J. comp. Neurol.* **157**, 453 (1974).
- <sup>54</sup> B. P. HAYES and K. E. WEBSTER, *J. comp. Neurol.* **162**, 433 (1975).
- <sup>55</sup> G. SZEKELY, in *Handbook of Sensory Physiology* (Ed. R. JUNG; Springer Verlag, Berlin 1973), vol. 7/3B, p. 1.
- <sup>56</sup> E. SCHMATOLLA, *J. Embryol. exp. Morphol.* **27**, 555 (1972).
- <sup>57</sup> H. ITO, *J. Hirnforsch.* **12**, 325 (1971).
- <sup>58</sup> M. LAUFER and H. VANEGAS, *J. comp. Neurol.* **154**, 61 (1974).
- <sup>59</sup> F. CIANI, S. LEGHISSA and L. VILLANI, *Riv. Biol.* **68**, 5 (1975).
- <sup>60</sup> B. P. HAYES and K. E. WEBSTER, *J. comp. Neurol.* **162**, 447 (1975).
- <sup>61</sup> R. L. FRIEDE, *Topographic Brain Chemistry* (Academic Press, New York 1966).



#### 4. Ultrastructural and functional organization of the optic tectum

In spite of different degrees of structural complexity observed in non-mammalian vertebrates, several publications have pointed out that the optic tectum seems to possess similar functional organization and common features in ultrastructural arrangement and synaptic pattern. The majority of these publications are concerning only with the retinal projection to the tectum on account of its relative topographical constancy and the facility to interfere by experimental means with this projection and to achieve the consequent responses. Even bearing in mind this restriction, one must consider that retinal projection is by far the most important sensitive input to the optic tectum, and it is reasonable to suppose that the structural and functional organization of this nervous center is primarily shaped in relation to visual input.

In this connection, some important features seem common to most vertebrate species. The first of these features is the prevalent topography of optic terminals in the stratum fibrosum and griseum superficiale which develops and differentiates in close relation to the development of retinal projection<sup>9,42-50</sup>. The second common feature is the ordered projection upon the tectum of the different quadrants of the retina according to a precise retinotopic relationship<sup>62-65</sup>. A third important feature is the peculiar cellular arrangement and in particular the presence of neurons whose radially oriented dendrites constitute the main receptive elements of the optic tectum. These neurons,

fusiform, pear-shaped or pyramidal, extend and ramify their apical dendritic branches in superficial tectal layers and receive at different depth optic terminals, other afferent terminals and intrinsic terminals derived by tectal neurons. Ultrastructural observations have revealed the complex organization of synaptic endings on dendrites of radially oriented tectal neurons<sup>48,51,57-60,66,67</sup>.

In the frog, SZEKELY<sup>55</sup> and SZEKELY et al.<sup>51</sup>, on the basis of a very detailed ultrastructural analysis, have emphasized the presence of characteristic glomerular-like synaptic structures at level of optic terminals; these glomeruli are formed by 3 different types of axon terminals (almost one of which is intrinsic, i.e. derived from a tectal neuron), which make axo-axonic synapses among them and axo-dendritic synapses with dendritic branches of deeper tectal neurons. The glomerular apparatus is presumedly associated with a structural-functional unit, the so-called 'tectal column', which derives from radial orientation of receptive neurons. The 'tectal column' works by means of a co-ordinate complex of excitatory and inhibitory synapses and might be provided with other synaptic structures able to prolong its activity by reverberating circuits and to inhibit the activity of adjacent columns.

Other ultrastructural studies on the optic tectum of teleosts<sup>57-59</sup>, reptiles<sup>48,67</sup> and birds<sup>60</sup> could not reveal similar precise relationships among the different tectal neurons and intrinsic and extrinsic synaptic endings. However, the neuron arrangement, the distribution pattern of synaptic endings and the reciprocal relationships among the different layers appear basically similar in all vertebrates with well developed optic tectum (Figures 8-11). The ultrastructural differences recorded might reflect a different organization of mechanisms of enhancement and inhibition in the vertebrate optic tectum. In teleosts, for example, a peculiar feature is the presence of a conspicuous marginal layer whose structure strictly resembles that of cerebellar molecular layer<sup>58</sup>. In the marginal layer, each pyramidal neuron of the stratum fibrosum and griseum superficiale receives on its dendritic spines tens of thousands of synaptic endings from parallel fibres which run along the marginal layer in parasagittal planes<sup>58</sup>. This peculiar arrangement suggests that the activity of pyramidal neurons, as the Purkinje cells of the cerebellum, is controlled by parallel fibre synapses on their terminal branches. In birds, a recent study has outlined interesting ultrastructural features in the retino-receptive

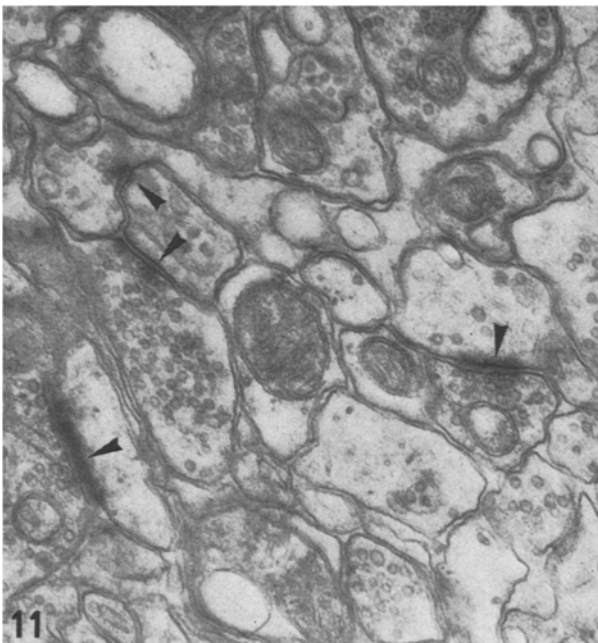


Fig. 11. Different types of synaptic contacts (arrowheads) in the stratum fibrosum and griseum superficiale in the optic tectum of the quail, *Coturnix coturnix japonica*.  $\times 35,000$ . (Specimen and photograph of F. CIANI and L. VILLANI.)

<sup>62</sup> M. JACOBSON, Q. Jl. exp. Physiol. 47, 170 (1962).

<sup>63</sup> T. HERIC and L. KRUGER, J. comp. Neurol. 124, 101 (1965).

<sup>64</sup> H. O. SCHWASSMANN and L. KRUGER, J. comp. Neurol. 124, 113 (1965).

<sup>65</sup> J. I. MCGILL, T. P. S. POWELL and W. M. COWAN, J. Anat. 100, 5 (1966).

<sup>66</sup> G. MINELLI and A. QUAGLIA, Archo ital. Anat. Embriol. 73, 203 (1968).

<sup>67</sup> T. V. DAVYDOVA, Tsitologiya 13, 433 (1971).

layer of pigeon optic tectum<sup>60</sup>. Some of these features, such as the differences in synaptic endings, the triadic arrangement of some synaptic arrays and the presence of characteristic types of axo-axonic and dendrodendritic synapses, recall the organization pattern described in the frog. In birds a peculiar function in regulating the optic tectum activity seems to be performed by the neurons of the stratum fibrosum and griseum superficiale with horizontally oriented dendrites<sup>60,68</sup>. Ultrastructural studies showed that some of these neurons receive optic terminals and that their dendrites make synapses with the dendrites of radially oriented neurons which are the main receptive elements for visual input; a similar arrangement might constitute the structural basis of control mechanisms in the optic tectum of birds.

In addition to ultrastructural similarities, other experimental researches have revealed common features in the type of potentials evoked in the tectum by optic stimulations, in the differences of conduction velocity among different types of retinal fibres, in laminar distribution of optic terminals along radially oriented dendrites of receptive neurons and in the presence of mechanisms for inhibition or facilitation of tectal circuits<sup>68-73</sup>. In particular these studies seem to extend the concept of columnar organization for visual reception in the tectum and to emphasize the importance for central integration of the spatio-temporal segregation of visual input due to laminar distribution of optic terminals and to differences in conduction velocity among different groups of retinal fibres<sup>72</sup>.

#### 4. Conclusions

As previously pointed out, the peculiar AChE localization in receptive layers of vertebrate optic tectum suggests that cholinergic mechanisms might be involved in reception, modulation and integration of visual input and possibly also of other sensitive modalities. In the frog optic tectum, a cholinergic inhibitory system has been revealed by means of physiological and pharmacological studies<sup>74</sup>; this system controls synaptic discharge of optic terminals on tectal elements and can be easily related to high concentration of AChE at the same level. However, at the moment, physiological evidence of this kind of correlation is lacking in the majority of vertebrates. The application of histochemical methods to electron microscopic analysis of the optic tectum appears necessary in order to achieve more precise details on AChE and other enzyme localization at level of the different synaptic contacts and different tectal elements.

Indirect evidence of the functional importance of enzyme activities derives also from comparative developmental studies on AChE and MAO localization in the optic tectum of nidifugous (quail) and nidicolous

(pigeon) birds<sup>75</sup>. In the quail, AChE activity in the optic tectum develops during embryonic life and the new-born shows a histochemical picture similar to that of the adult; in the pigeon on the contrary, AChE activity starts to develop at hatching and reaches the adult pattern only after 20-30 days. The temporal gap between the appearance and development of MAO activity in the quail and pigeon is noticeably shorter. These results seem to indicate that AChE and MAO play different roles in the optic tectum and that AChE is more strictly related to the differentiation and the integration level reached by the nervous center.

Further useful data could be derived from more detailed ultrastructural and physiological studies of the optic tectum of species belonging to the same class and showing different patterns in AChE distribution. This is the case of teleosts, which can exhibit two patterns of AChE distribution, the main difference regarding the enzyme activity in the marginal layer and in marginal neurons of the optic layer<sup>18,19</sup>. Since these structures are not directly involved in visual reception but probably in mechanisms of control and modulation of sensitive input<sup>12,58</sup>, it seems particularly interesting to verify if differences in ultrastructural and functional organization correspond to different patterns of AChE distribution. In addition, the study of cholinergic mechanisms in teleost optic tectum might be of particular interest on account of peculiar AChE distribution which suggests that these mechanisms are quantitatively, and perhaps qualitatively, different from those of other vertebrates.

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