# *Visual Centers in the Brain*

By

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### Central Processing of Visual Information
### Part B

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# Anatomy and Synaptology of the Optic Tectum

By

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With 8 Figures

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After decussation in the chiasma the optic fibres become segregated to form the *accessory optic tract* and the *main* or *marginal optic tract*. The anterior part of the accessory optic tract is supposed to connect the retina with subthalamic and dorsal hypothalamic nuclei [45]. While a few recent observations seem to corroborate this early assumption [18, 47—49, 65, 71], the bulk of opposing data denies the existence of these connexions [1, 5, 9, 11, 12, 14, 27—29, 34—36, 46, 55, 57, 67, 76]. The posterior part of the accessory optic tract terminates in the mesencephalic basis and tegmentum (for details see Marg's Chapter 15, this volume). The marginal optic tract carrying nearly all the optic fibres, terminates in different diencephalic optic nuclei and in the mesencephalic optic tectum. It is now known that the diencephalic portion of this tract only partially decussates also in submammalian vertebrates [5, 6, 47, 55]. The aim of the present survey is to give a detailed account of the mesencephalic optic tectum and its connexions.

## I. Cytoarchitectonics of the Mesencephalic Roof

In view of the well known differences, both in structure and function, between the non-mammalian and mammalian optic tecta, it seems adequate to describe their structure in two separate sections. For brevity's sake the optic part of the mesencephalic roof will be denoted *optic tectum in non-mammals*, and *superior colliculus in mammals*.

## 1. Tectum Opticum

The optic tectum has a distinct stratified structure. The division of the strata and their terminology is far from being uniform in the literature. The first effort to introduce uniformity was made by KAPPERS et al. [45]. In their scheme of stratification six, alternating fibrous and cellular, layers are distinguished (Figs. 1a to c). Comparing the amphibian, reptilian and avian tecta, one finds that this scheme is readily applicable to these brains, there are, however, certain difficulties to obtain a proper matching between this scheme and the scheme of stratification proposed for the fish tectum by P. RAMÓN [69] and LEGHISSA [56]. From the excellent study of Leghissa on the teleost brain it appeares that not only the number, but also the order, of the cellular and fibrous layers is different in the fish tectum. This suggests that the structure of the fish optic tectum must be a different story, and cannot directly be compared to other submammalian tecta.

Beginning at the surface and passing towards the ventricle, the first stratum (overlaid by a thin *str. zonale*) is generally described as [1] *stratum opticum*, and is held to be the place of invading optic fibres. The subsequent [2] *stratum fibrosum et griseum superficiale* comprises alternating cellular and plexiform sheets. The cell population of this stratum is rather poor in amphibia; it contains more and more neurons in reptiles and birds. The stratum is regarded as the main recipient zone of optic and non-optic afferents. The next is the [3] *stratum griseum centrale*. It is barely discernible from the overlying stratum in the frog, it stands out clearly in reptiles and birds containing medium size and large neurons. These neurons are generally referred to as being the efferent elements of the optic tectum. Their axons descend to the underlying [4] *stratum album centrale* which constitutes the major efferent path of the optic tectum. The [5] *stratum griseum periventriculare*, situated internal to the stratum album centrale, varies in size and arrangement in the various submammalian classes. In the anuran optic tectum this stratum contains the majority of neurons arranged in definite layers with intervening fibrous bundles. The efferent elements of the tectum can be found here. In reptiles the periventricular gray substance has a similar appearence, it contains, however, relatively fewer cells. This stratum is greatly reduced in birds, more of the neurons having migrated superficially. The [6] *stratum album periventriculare* is a thin fibrous layer which can be found only in the reptilian and avian tecta between the periventricular gray and the ependyma. The large monopolar neurons of the mesencephalic trigeminal root can be found in strata 5 and 6 (Fig. 1a).

The following description of the characteristic types of neurons relies mainly on the Golgi study of LÁZÁR and SZÉKELY [54] made on the frog's optic tectum. These authors have distinguished *9 layers* (Fig. 3). Starting now from the inside the first layer is a single sheet of ependymo-glial cells, the characteristic supporting elements of the brain in lower vertebrates, with their long straight processes extending up to the surface. The branches of these processes terminate in expansions beneath the pia forming an external limiting membrane. In addition to these a few astrocyta-like glial cells can also be found scattered among the neurons especially in layer 9.

*Layers 2, 4 and 6* are cellular layers, separated the one from another by thin plexiform layers 3 and 5, respectively. This region of the tectum corresponds to the stratum griseum periventriculare in the above scheme of stratification. The

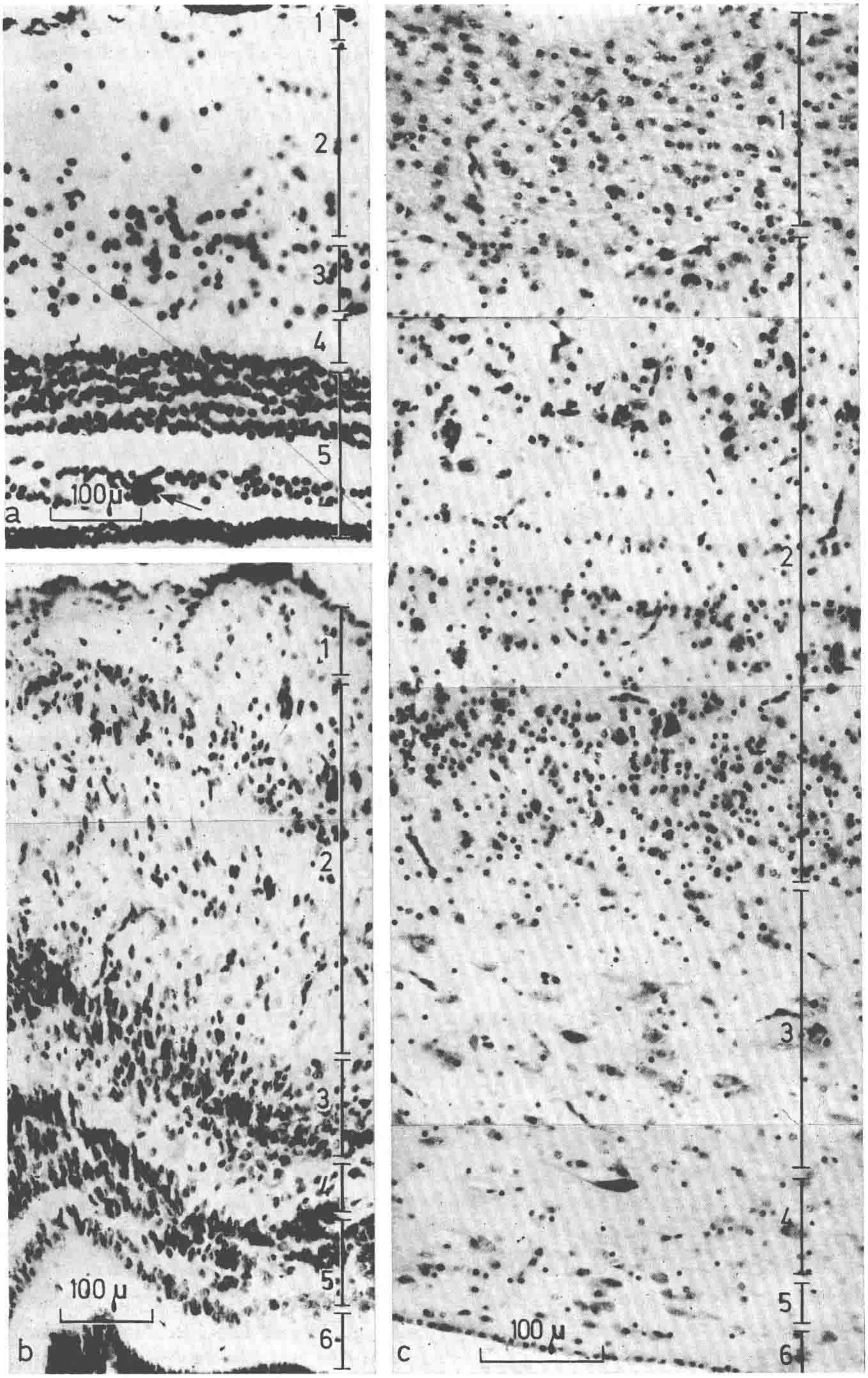

Fig. 1a—c. Stratification of the tectum opticum in three submammalian classes. a *Rana esculenta*; b *Lacerta muralis*; c *Gallus domesticus*. Vertical lines and numbers indicate the strata described in the text. In Fig. a an arrow points to a large neuron of the mesencephalic trigeminal root (Cross-sections, Nissl preparations)

neurons which build up the cellular layers have more or less conical perikarya. The tip of the perikaryon gives rise to the long apical, or shaft, dendrite which extends toward the periphery of the tectum. The dendrites are devoid of typical spines, but at the terminal arborization they generally bear grape-like spheroid protrusions. At the base of the cell several short basal dendrites emerge, and they terminate in one of the adjacent plexiform layers. On the basis of the dendritic arborization and the course of the axon, two groups of these neurons can be distinguished. Neurons in the first group have relatively large pyramidal bodies measuring 14 μ at the base and 26 μ in height *(large pyramidal neurons)*. They can be found mainly in layer 6, a few occuring also in layer 4. The strong apical dendrite, before reaching layer 8, breaks up into 2–4 main branches (Fig. 2a). On their course toward the surface they give off several secondary and tertiary branches, covering altogether a triangular area with a tangential spread of 160–180 μ. Relatively few basal dendrites leave the cell body. The axon arises from the apical dendrite not far from the perikaryon, enters layer 7 and runs mostly laterally. Occasionally initial collaterals can be observed returning to layers 5 or 3. These neurons are held to be main efferent elements of the frog's tectum. The neurons in the second group have a rounded, often pear-shaped, sometimes spheroid perikaryon *(large pear-shaped neurons)*. The area occupied by the branches of the apical dendrite is much smaller than in the case of pyramidal neurons, and it is of cylindrical shape. The number and length of basal dendrites is very variable. There are neurons with few and short basal dendrites, in other cases they may arise from the whole circumference of the perikaryon and extend as far as 70–150 μ from the cell. The axon originates from the shaft dendrite. It either ascends vertically parallel to the apical dendrite and terminates in layer 9 (Fig. 2c), or it takes an arched course in the horizontal direction and terminates in the neighbourhood of the neuron, or it may enter layer 7 in which it courses in one case medially, in the other case laterally. These cells are, obviously, associative neurons establishing interconnexions both in the vertical and in the horizontal directions. Layers 3 and 5 contain parallel running fibres. In addition to basal dendrites and recurrent axon collaterals, the axons of some superficial tectal neurons and terminals of non-optic afferents of tegmental origin can be found here.

*Layer 7* contains thick myelinated fibres running parallel to the surface. Laterally, at the tecto-tegmental border, this layer leads directly into the white substance of the mesencephalon. It clearly corresponds to the stratum album centrale. In addition to tectal efferents it carries afferent fibres of tegmental and diencephalic origin.

Layer 8 consists of loosely placed cells in the dendritic and axonal tangle of the deeper neurons. It seems to correspond to the stratum griseum centrale, which is poorly developed in the frog, and to the lower part of the stratum fibrosum and griseum superficiale. Two basically different types of neurons can be found in this layer. The first is composed of *small pyramidal* and *pear-shaped neurons*. These look like the minor counterparts of the large ones in deeper layers. The arborization pattern of their dendrites is also similar, although there are great variations in the course of their axons. These may descend to layer 6 (Fig. 2g), or make a downward loop and return to layer 9 (Fig. 2f), one can observe axons running along an arched horizontal course, ascending straight to the surface (Fig. 2d) or arborizing close to

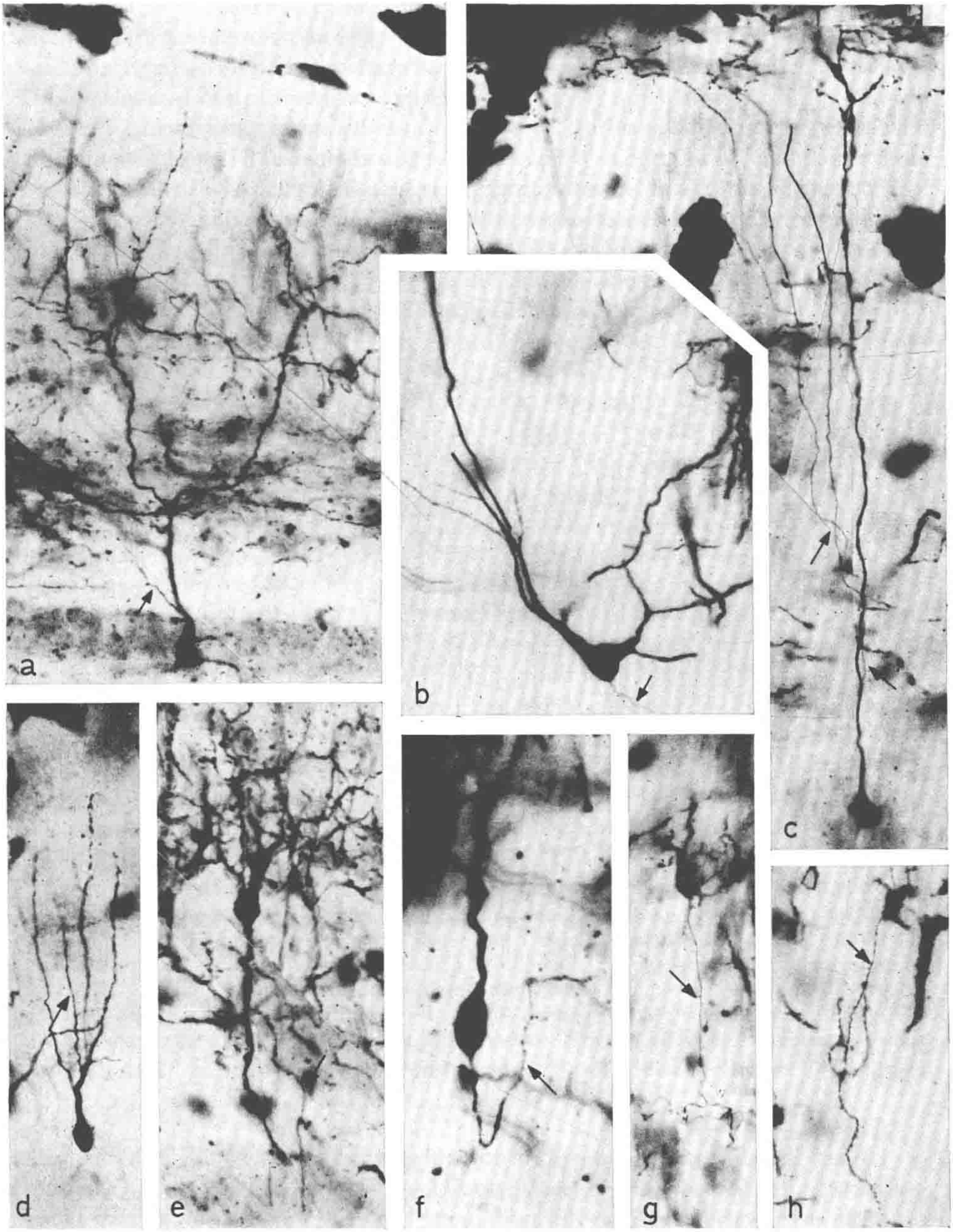

Fig. 2a—h. Types of neurons in the frog's optic tectum. Golgi preparations. Arrows indicate the axons. a Large pyramidal neuron; b large ganglionic neuron; c large pear-shaped neuron with ascending axon; d small pear-shaped neuron with ascending axon; e vertical bipolar neuron with descending axon; f small pear-shaped neuron with recurrent axon; g small pearshaped neuron with descending axon; h stellate neuron with descending axon and two recurrent axon-collaterals (Figs. a to g are from Lázár and Székely [54])

the parent neuron. Obviously, these neurons establish horizontal and vertical interconnexions within short distance. The second type of neurons consists of *large ganglionic cells*. They are situated in the lower part of the thin 8th layer and also on the top of layer 6 (Fig. 2b). The triangular perikaryon is remarkably large (30–40 μ). The dendrites rise up gently toward the surface embracing a conical area which may be as large as 500 μ in the longest diameter. Other ganglionic cells extend their dendrites in the horizontal plane measuring 250–800 μ from one end to the other. The axon either descends to layer 7 or recurs to layer 9.

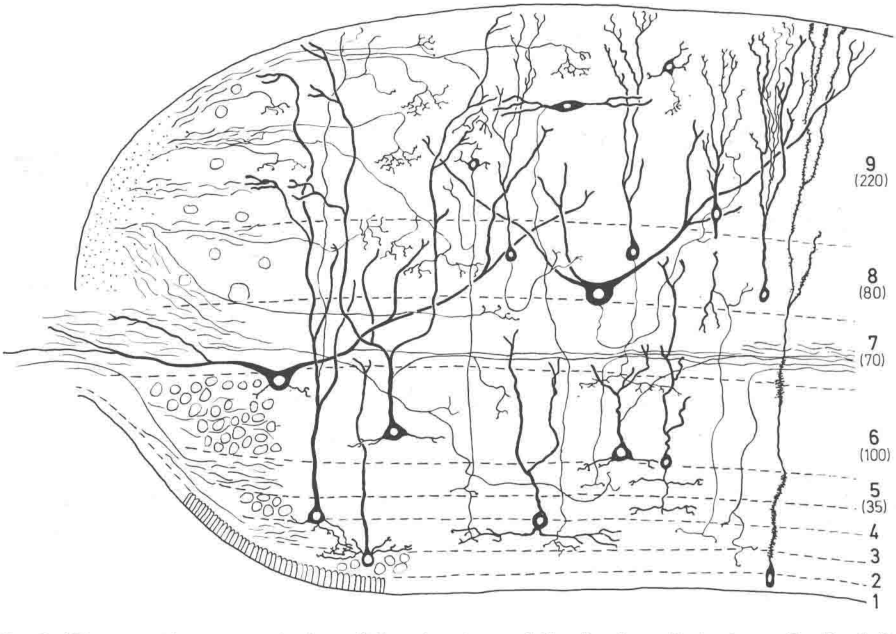

Fig. 3. Diagramatic representation of the structure of the frog's optic tectum. On the left is the medial border of the tectum; here it continues into the contralateral tectum through the commissura tecti. At this margin a combined cytoarchitectonic and fibre picture is shown obtained from Nissl and reduced silver stained sections. Scattered dotts indicate the medial division of the optic tract. The types of neurons are drawn from Golgi preparations. On the right an ependymo-glial cell is shown. Numbers indicate the layers, and numbers in parentheses the thickness of the respective layers

Layer 9 includes the stratum fibrosum and griseum superficiale and the stratum opticum, and it occupies about one third of the thickness of the tectum in the frog. Its structure is rather intricate. Besides being the main recipient of afferent pathways, this layer contains the dendrites of practically all kinds of tectal neurons. It can be subdivided into six alternating cellular and plexiform sheets. The constituents of the cellular sheets are the *bipolar* and *stellate neurons*. The long axis of the former type of neuron may be oriented either vertically (Fig. 2e) or horizontally. The axon originates from one of the dendrites and descends straight towards deeper layers. The stellate neurons are typical Golgi II type of neuron, the axons of some of them, however, may be quite long reaching down as far as layer 3 (Fig. 2h). Their dendritic arborization can be best seen in horizontal sections. The plexiform sheets are composed of the terminal arborizations of apical dendrites, the vertical ascending axons of pear-shaped neurons, and of the optic and non-optic afferent fibres. The intricate structure of this layer will be discussed in more detail in a following section.

The types of neurons and their arrangement in the reptilian optic tectum is very similar to that in the frog. The main difference follows from the outward migration of neurons. As a consequence of this, the stratum griseum periventriculare contains many fewer cells than layers 2, 4 and 6 in the frog. Their shape, dendritic and axonal arborizations of these cells appear identical in the figures of P. RAMÓN [69] and HUBER and CROSBY [39]. The stratum griseum centrale is rich in cells. Its deepest portion is occupied by the large pyramidal and pear-shaped neurons; these neurons become smaller towards the surface. Among them the *grands neurons ganglionaires* [69] can be found, which are similar to the large ganglionic cells in the frog. The area occupied by the stratum griseum and fibrosum superficiale and stratum opticum is wider and richer in neurons than in the frog. P. RAMÓN [69] distinguishes 8 layers in this part of the tectum, composed of similar types of neurons as described in the frog. The optic terminals reach the middle part of the stratum griseum and fibrosum superficiale [5].

In the chick optic tectum the stratum griseum periventriculare is very thin and contains small cells mostly with short axons; some of the neurons send their axons to the stratum zonale [69]. The neural picture of the stratum griseum centrale is dominated by large and medium size, polygonal neurons with radial dendritic arborization, and only a few pear-shaped neurons can be found here [16]. These large neurons are held to be the efferent elements of the tectum. The bulk of the pyramidal and pear-shaped neurons are shifted to the lower part of the stratum fibrosum and griseum superficiale which froms the largest portion of the tectum's cross-section. JUNGHERR [44] divides it into 6, COWAN et al. [14] into 10 layers. With the exception of the large ganglionic neurons, the neuronal picture of this region resembles very much that of the frog's tectum. On approaching the surface the small pyramidal and pear-shaped neurons appear, and they are followed in the region of the strata opticum and zonale by the bipolar and stellate neurons. As revealed in P. RAMÓN's drawings these neurons are basically similar to those of the frog, but are much more differentiated in form. The optic fibres reach down as far as the middle part of the stratum fibrosum and griseum superficiale [14].

## 2. Colliculus Superior

The superior colliculus occupies a relatively much smaller portion of the brain and its structure is greatly reduced in complexity as compared to the submammalian optic tectum. The laminar distribution of neurons and the radial arrangement of the principal dendritic branches are barely recognizable (Fig. 5). Owing, probably, to the indistinct stratification, the superior colliculus is subdivided differently by various observers, including in many cases the substantia grisea centralis which is clearly delimited from the superior colliculus. In the present account the scheme of stratification suggested by HUBER and CROSBY [40] will be used as a basis for description. Disregarding the insignificant looking stratum zonale and the strata for the substantia grisea centralis, one finds that, at least in terminology, the tectal and collicular stratification may be brought close to each others. We are, however, not inclined to follow the scheme of analogy proposed by HUBER and CROSBY between tectal and collicular layers. The following description of the characteristic types of neurons relies entirely on the Golgi studies of RAMÓN Y CAJAL [69] and VIKTOROV [90, 91] making also extensive use of TÖMBÖL'S [88] unpublished Golgi-Kopsch material of the cat. The following strata and types of neurons may be recognized.

**(1) Stratum Zonale and (2) Stratum Griseum Superficiale.** As revealed by cell staining methods (Fig. 4a) these two superficial strata are the richest in neurons; the distribution of neurons, hovewer, does not allow an obvious distinction between the strata. In Golgi pictures the shape and form of neurons are rather diverse. Close to the surface, in the stratum zonale, small neurons may be seen with various dendritic arborization pattern (Fig. 4b). Their axons are short, and are limited to this stratum. A little deeper small bipolar neurons in horizontal orientation may be found (Fig. 4d). Still deeper the neurons tend to be larger. The perikaryon is frequently triangular or ovoid, from which a large dendrite extends towards the surface and a number of smaller dendrites arise from the opposite pole. These are similar to the small pyramidal and pear-shaped neurons described in the submammalian optic tectum. Other ovoid perikarya with their long axes vertical to the surface give origin to two main, richly arborizing dendrites (Fig. 4c). Still other neurons send the dendrites toward the surface and only the axon originates from the internal pole. There are also a number of stellate neurons with radially oriented dendrites (Fig. 4e). The axons of these various forms of neurons may be either short, terminating in their own strata, or they may be longer terminating in the deep strata and giving rise to several collaterals in their courses. As in the optic tectum, this superficial part of the colliculus is the principal recipient of optic afferents. In addition to optic fibres one part of the cortico-collicular projections terminates here; it also contains a number of ascending axons of deeper lying neurons.

**(3) Stratum Opticum** is a lamina of white matter with indistinct borders containing also a few smaller neurons. The superficial part of this stratum contains the optic fibres which arrive from the brachium of the superior colliculus. The fibres make a knee-bend towards the surface and after a curving course they terminate in bushy terminal formations in the overlying stratum (Fig. 5). The closer they terminate to the surface, the larger is the area covered by these ter-

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Fig. 4a—i. Stratification and types of neurons of the colliculus superior in the cat. a Nissl preparation of the colliculus. Numbers and vertical lines indicate the strata described in the text. The substantia grisea centralis is bordered by neurons of the mesencephalic trigeminal root. b small triangular neuron in stratum 2; c vertical and d horizontal bipolar neurons in stratum 2; e stellate neurons in stratum 2; f large multipolar neuron in stratum 4; g middle size neurons in stratum 4; h pyramidal-like neuron in stratum 6; i fibre terminals in the outer part of stratum 4. Photographs b to i were made from TÖMBÖL'S unpublished Golgi-Kopsch material

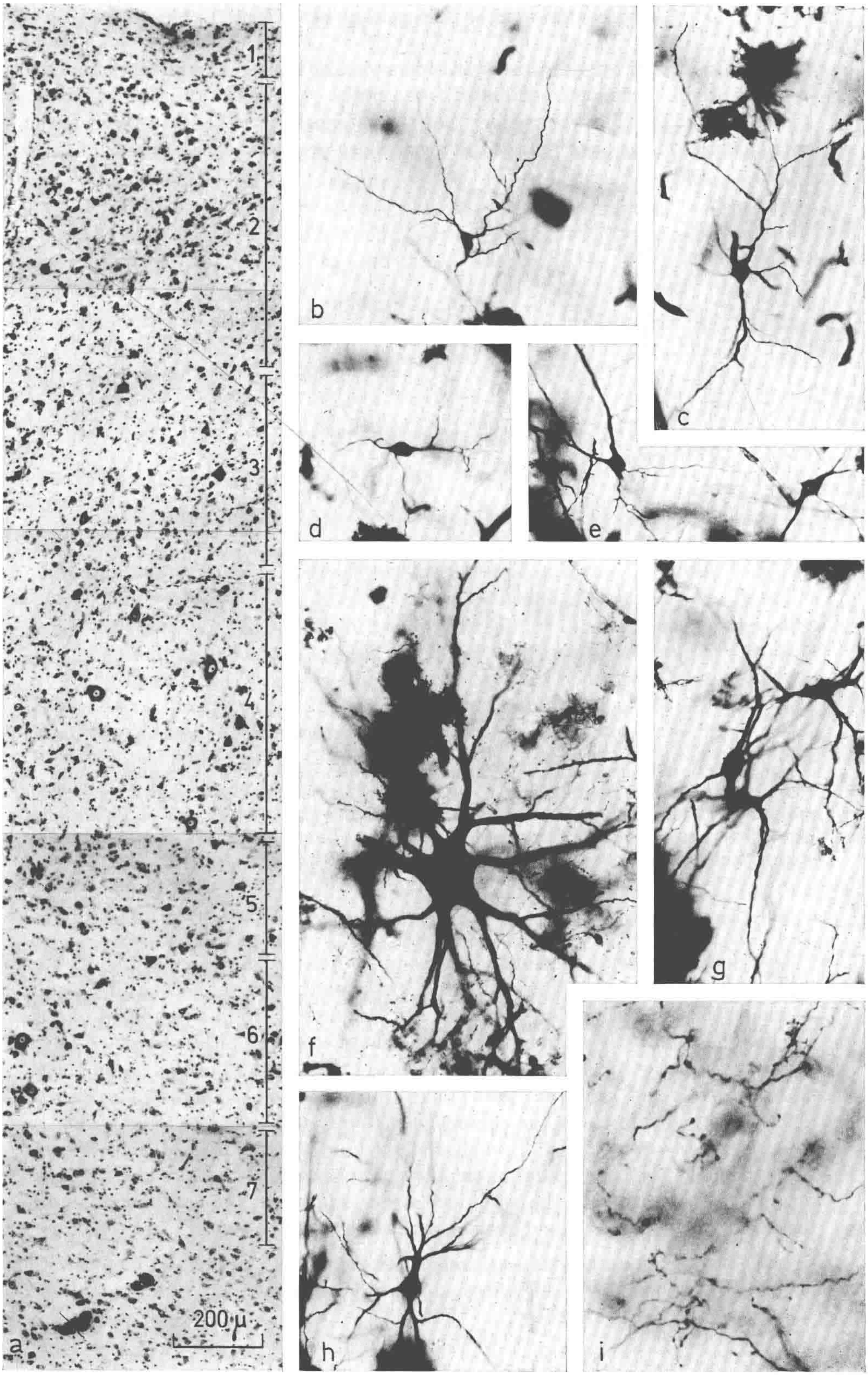

Fig. 4