

## ULTRASTRUCTURE INVESTIGATIONS ON THE CEREBRAL CORTEX OF THE SAND-LIZARD (*LACERTA AGILIS* L.)

A. ÁBRAHÁM

*Department of Zoology, Attila József University, Szeged*

(Received June 30, 1972)

### Introduction

The proper cerebral cortex appeared first at lizards although there are in the dorsal part of the forebrain of Amphibia some cell groups that may be considered as the precursors of the cerebral cortex.

In the cerebral cortex of lizards, going from the lateral wall of ventricle towards the surface of brain, the first layer is that of ependyma cells consisting of a single cell line. The cells are cylindric. Every cell is continued in an ependymal fibre that, going on upwards in the cerebral substance, is ramifying abundantly. The rami pass through the single layers and end, in the form of terminal heads, on the surface of brain. The ependymal fibres appear in the preparations impregnated according to GOLGI's method in so large numbers that cover the other layers of cortex almost entirely. The layer of ependyma cells is followed by the medullary layer.

The medullary layer is consisting of myelinated fibres. These are partly the neurites of the nerve cells of cortex, partly centripetal fibres originating from other cerebral regions, mainly from the olfactory region and ending in the cortex. The medullary layer is followed by the layer of pyramidal cells.

The pyramidal cells are forming more layers. They have got their name from their pyramid-like shape. Their cell body is triangular. The base of triangle is looking towards the cerebral ventricle. The cell part lengthened and directed towards the surface of brain is proceeding to a thick dendrite, the so called peak-dendrite ramifying abundantly. The rami becoming more and more thin enter the external molecular layer and end there. There originate from the base of pyramidal cells at about the middle region the neurite and from the corners the two basal dendrites. The latter ones are abundantly ramifying and their strongly thinned terminal rami develop the deep molecular layers (KRAUSE, 1921).

In the layer of pyramidal cells, apart from the typical pyramidal cells, there are other cell forms, too, of course, in a much lower number than the pyramidal cells. Cell forms like this are the triangular cells the peak of which is directed towards the ventricle of the brain and their two basal main dendrites towards the surface of the brain. Among the pyramidal cells there are bipolar cells, as well, occurring mainly in the dorsal and lateral regions of cortex. The layer of pyramidal cells is followed by the external molecular layer.

The external molecular layer consists overwhelmingly of terminal rami and centripetal fibres originated from the ramification of peak dendrites. In the layer, in addition to the fibres resp. fibre terminations, there can rarely be observed bipolar cells of rather large extent, as well, the longitudinal axis of which is parallel with the surface of brain. The outmost part of cortex is the tangential layer.

The tangential layer consists of fine unmyelinated fibres running parallel with the cerebral surface. A number of the fibres are centripetal fibres, others of them are the rami of the neurites originating from the pyramidal cells. The neurites of not all the pyramidal cells are namely directed towards the medullary layer, but there are also that are bending back, stepping in the external molecular layer, in that ramifying and the rami ending in the tangential layer.

For recognizing the ultrastructure of the cerebral cortex of lizards, we have carried out electron microscopic investigations on the cerebral cortex of the sand-lizard.

### Materials and Methods

For being investigated, small pieces were excised from the dorsal part of telencephalon, fixed in osmic acid buffered according to Millonig, dehydrated in alcohol of gradually increasing concentration and embedded in araldit. We made sections from the material with an L.K.B.-ultramicrotome and investigated them with electron microscopes TESLA D 242 and JEM 6. Some of the investigations were performed in the Biological Research Institute of the Hungarian Academy of Sciences at Tihany others in the electron microscopic laboratory of the Institute of Biochemistry, University Medical School, Szeged. In the following we sum up the results of our observations concerning some components of the cortex.

### Nerve cells

There are characteristic for the nerve cells: the narrow, margin-like cytoplasm (pericarion), a round nucleus of central position, as well as the processes, neurite and dendrites. In the cytoplasm, the endoplasmic reticulum, that is to be regarded as the largest organellum of the cell, appears in the form of various cisternal systems. Its shape and external form, the extent of the single cisterns, its course, connection in the various cells are very different, showing in some case a peculiarly different picture. There are cases where some parts of cisterns widen out extremely, forming very large cavities. On other occasions, the cavities resp. cavity systems of straight course, uniform in length and quasi identical in diameter, too, arranged beside each other are showing a form reminding us of the chords of lute. There are cases when the tubes of reticula are of proportionally narrow lumen, showing anyway in some places smaller or larger dilatations. The cisternal regions developed in this way, in which the dilatations and strictures are alternating with each other, take on a wavy shape and the tube systems that are parallel with one another are forming specific wave systems. Between the cisterns there appear sometimes some roundish formations limited by thin walls in the central substance of which there may be observed very small granules being electron-dense only in a low degree. (Fig. 1).

In the cytoplasm a particular place is taken by GOLGI's complexes. We have to say that in the course of our investigations covering almost every region



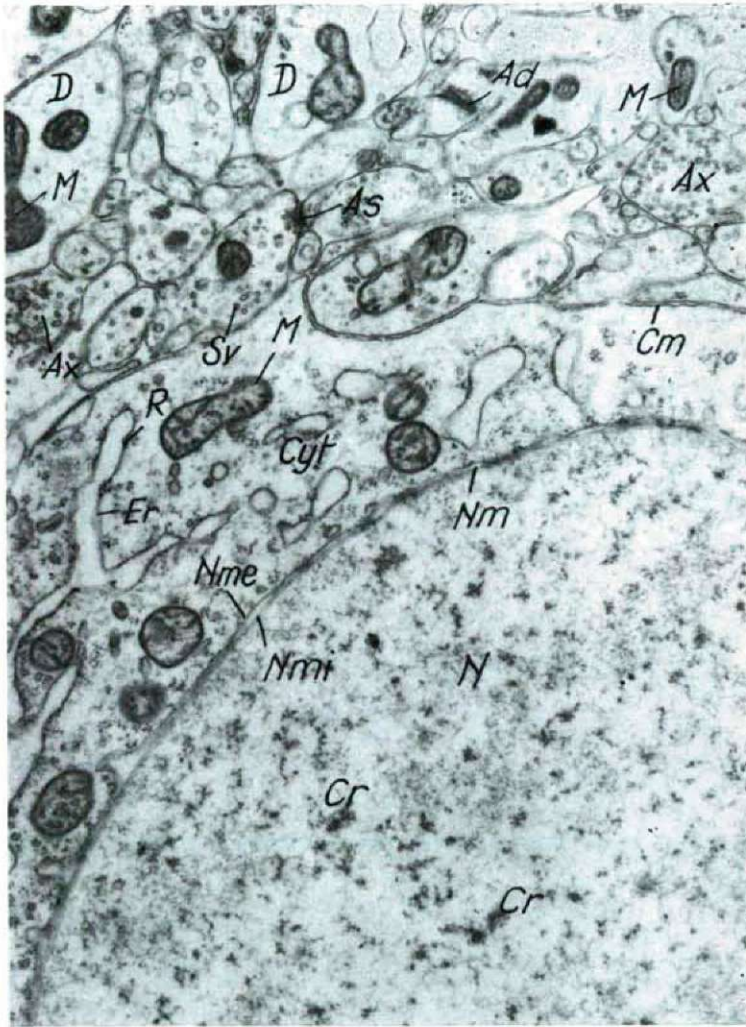


Fig. 1. *Lacerta agilis*. Cerebral cortex. Nerve cell. Cyt — cytoplasm, Cm — cell membrane, N — nucleus, Nm — nuclear membrane, Nmi — internal nuclear membrane, Nme — external nuclear membrane, Er — endoplasmic reticulum, M — mitochondrium, R — ribosoma, Cr — chromatin, Ax — axon, D — dendrite, Sv — synaptic vesicle, As — axo-axonic synapse, Ad — axo-dendritic synapse. Magnified: x 25.00.

of the brain we have found nowhere as many GOLGI's complexes as in the cerebrocortical nerve cells of the sand-lizard. There are microscopic pictures in which 5 to 6 and even more GOLGI's complexes can be observed showing interesting and specific formations. It is generally characteristic of these that the vesicular groupings are richer and more developed than the tubular region. The vesicles are comparatively large, showing a perfectly round form, and the many empty vesicles of equal size are followed at the edge of the field by

large electron-light cysts. The high number and conformity of vesicles, the association of vesicles of large size, the abundance in short tubes and cavity systems speak in the favour of the supposition that at lizards GOLGI's cerebral complexes may have a peculiar role. It is, of course, possible, too, that these marks do appear just at the sand-lizard that is extremely sensitive and moves incredibly fast (Fig. 2).

In the cytoplasm, both in the pericarion and in the dendrites, the multi-vesicular bodies appear not in a high number but in a sharp form and in a

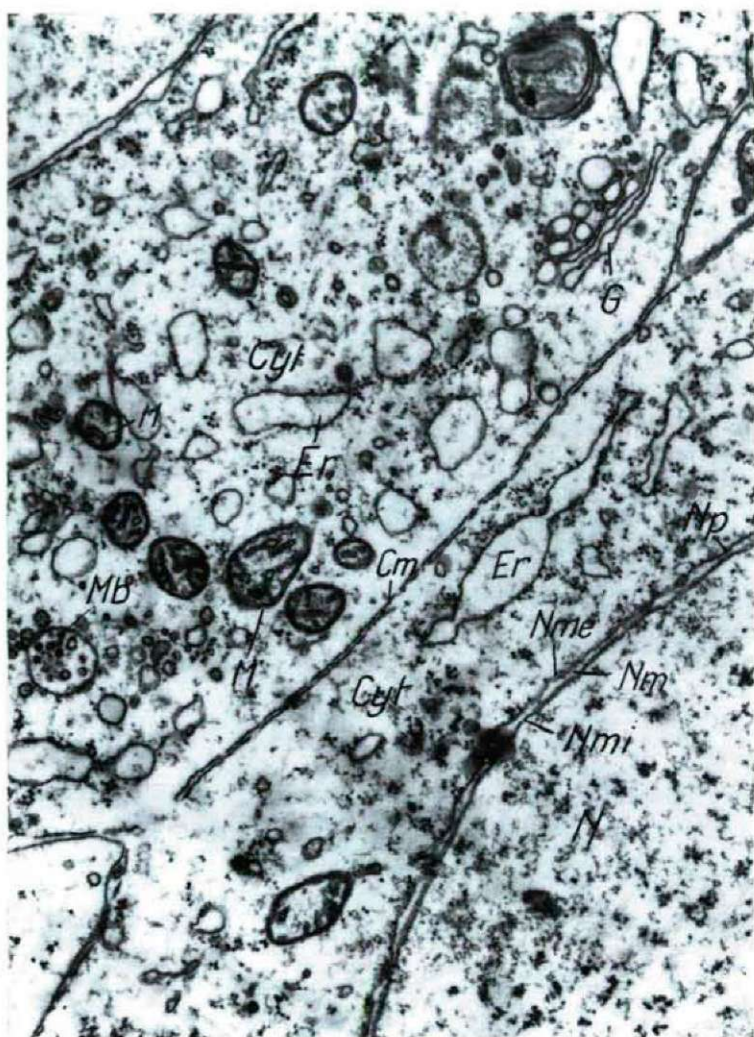


Fig. 2. *Lacerta agilis*. Cerebral cortex. Nerve cells. Cyt — cytoplasm, Cm — cell membrane, G — Golgi's complex, Mb — multivesicular body, Er — endoplasmic reticulum, M — mitochondrium, N — nucleus, Nm — nuclear membrane, Nmi — internal nuclear membrane, Nme — external nuclear membrane, Np — nuclear pore. Magnified: x 30.000.



comparatively large size. They are generally roundish or long-shaped, their wall is thick, homogeneous, and within them, limited from one another well, several vesicles of comparatively equal size may be seen. The latter ones do not touch one another, their stroma is of loose construction.

In the cytoplasm, ribosomes can be seen in large numbers. Their locations and groupings are different. There are some microscopic pictures in which the ribosomes arranged in lines beside the endoplasmic cisterns are following exactly the course of the latter ones. Besides these pictures there are some others, too, and not rarely, in which the ribosomes form groups, and even the general situation is that in the same picture both formations are to be found. In the middle of the groups the ribosomes are nearly touching one another but near the border of the group they become strongly rarified.

Some characteristic components both of pericarions and of processes are the mitochondria. They belong to the crista type. In their structure we can distinguish well the double membrane and the central matrix in which the cortex of the crests engendered by the invagination of the internal membrane and the central light part always appear sharp. Between the crests we see here as well as generally in the mitochondria everywhere an electron-light matrix substance. The shape of mitochondria is extremely interesting and various. Most of them are manifesting the usual ellipsoid resp. elliptical forms although there occur sporadically also those of them that may be included in the spheric type. Apart from them, the peculiar forms are not rare, either. There are remarkable those showing abnormality in width or length. Mainly the longitudinal overgrowth seems to be a rather frequent appearance. The shapes of a crescent or of an expressed shepherd's crook are not rare, either. There are, however, rare the forms referring to a division. The shape, size and direction of crests is manifold, their grouping is peculiar (Fig. 3).

The cell nucleus is generally big, it constitutes almost three-quarters of the cell. It is an electron-dense granulated body, surrounded only by, a very narrow pericarion border. Its substance is loose, the chromatin clots are formless, forming sporadically larger knots. In the nucleus is to be found the nucleolus, usually of excentric location. Its shape is irregular, sometimes roundish. Its substance is much more electron-dense than that of the nucleus, consisting of round knots arranged close to one another. The nucleus is surrounded by a double nuclear membrane distinctly visible. The area between them is proportionately wide and in every case sharply conspicuous. The two nuclear membranes — here as well as generally — adhere sporadically close to each other, later however getting farther. In these places the nuclear pores are to be seen. It is not rare either, that the external nuclear membrane gets into a great distance from the internal one, folding into the pericarion. As the process repeats in the course of the external nuclear membrane, peculiar cavity systems develop called herniae of the nuclear membrane.

The neurite is a thin process of an unvarying thickness, limited sharp by the highly conspicuous but proportionately thin axolemma towards the adjacent tissue components. In the axoplasm we can see, even if not always, the neurofilaments of various thickness, located generally longitudinally. Among the latter ones there are some, as well, the course of which is not parallel with that of the axis of axon. We have come to this conclusion from the fact

that in microscopic pictures they appear in cross-section. The synaptic vesicles are special ingredients of neurites. These are empty vesicles of 150–300 Å diameter that, as proved by our pictures, fill in completely not only the axon terminals but also other axon regions having no synapses at all. Such a mass of vesicles never occurs in dendrites. This mark enables us to distinguish the dendrites of various sizes from neurites and to find our way in the different forms of the synaptic connections, resp. contacts.

Dendrites are cellular processes of the most various size and dimension. Their structure is agreeing with that of pericarian. Their substance is loose.

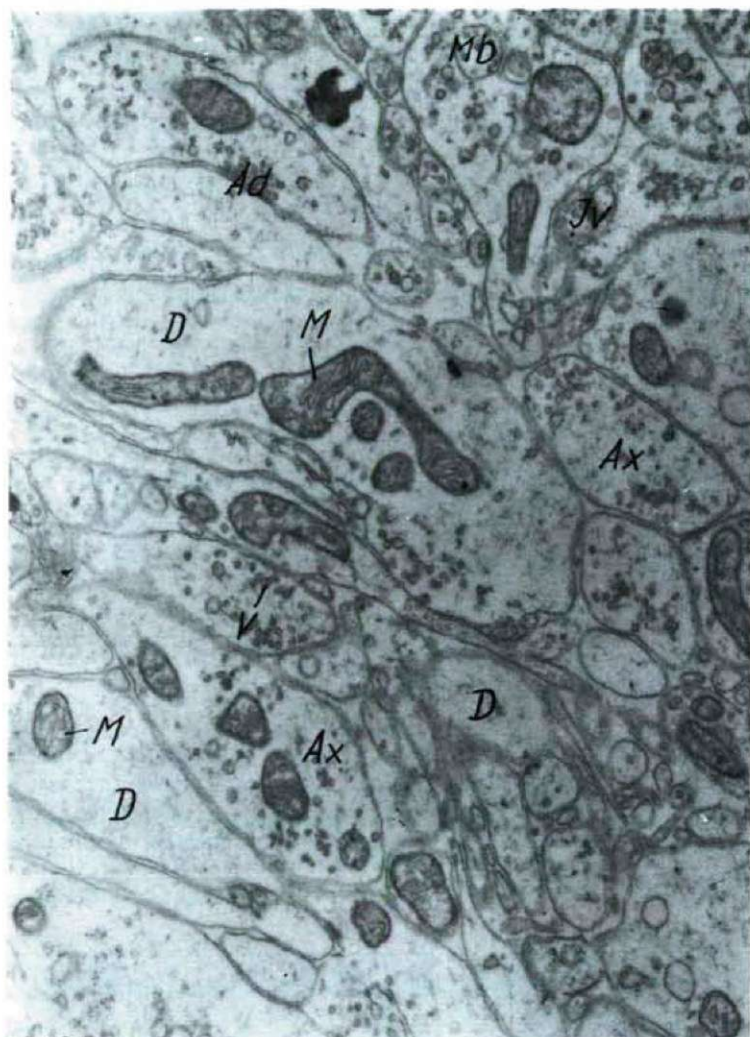


Fig. 3. *Lacerta agilis*. Cerebral cortex. External molecular layer. Ax — axon, D — dendrite, V — vesicle, M — mitochondrion, Ad — axo-dendritic synapse, Iv — invaginated synapse, Mb — multivesicular body. Magnified: x 25.000.



They are characterized by the neurotubules located longitudinally and transversely, and by microvesicular bodies. The synaptic vesicles are completely missing. The diameter is variable. The limiting membrane (dendrolemma) is very conspicuous well limited electron-dense membrane. In the dendroplasm there are to be seen sporadically major electron-light vesicles too (Fig. 4).



Fig. 4. *Lacerta agilis*. Cerebral cortex. External molecular layer. Ax — axon, D — dendrite, Al — axolemma, V — vesicle, M — mitochondrion, Er — endoplasmic reticulum, Mb — multivesicular body, Ad — axo-dendritic synapse, Si — intersynaptic space, Sv — synaptic vesicle, Dl — dendrolemma, Nt — neurotubule. Magnified: x 25,000.

## Glia cells

They are structurally close to the nerve cells (ROBERTIS, GERSCHENFELD and GOMEZ, 1961). In the pericarion there are to be seen about the same cell organella as in the nerve cell. Characteristic differences are manifested in form and arrangement of the cisternae of the endoplasmic reticulum. The tubules are ramifying, their course is irregular. Multivesicular bodies appear often, the number and location of the vesicles differing highly. There is a very great difference in the arrangement of ribosomes. The latter ones are forming groups that are not limited sharp from one another. Every group has a centre where there are more ribosomes, and a peripheral part where the number is strongly diminished and the single shapes are far from one another. Sometimes the cytoplasm is so much full of ribosomes that it seems to be a real granulated electron-dense substance divided into peculiar pieces by the endoplasmic cisternae and GOLGI's complexes forming peculiar systems. The accumulation of glycogenic clots is characteristic of glia cells. The situation is, namely, that glycogen is transported for the nerve cells, resp. neurons by glia cells.

The nucleus of glia cells is showing, as well, some characteristic feature. This manifests itself first of all in the fact that the electron density is fainter than in the nerve cells and round the internal nuclear membrane there are no circularly located polymorphous electro-dense areas. It is to be considered as characteristic, as well, that the nucleus of glia cells is long-shaped and the two nuclear membranes are very close to each other. The hernia-like protrusions that always occur in nerve cells can in glia cells never be found.

The glia fibres are as much characterless as the glia cells are. They are usually thick, the rami are rougher and the substance within the glia membrane is homogeneous. In that, there are to be seen neither any filaments nor any vesicles, although in some cases in the apparently empty substance some vesicles of larger dimension can be observed connected with one another with thin canal pieces.

## Synapses

The synaptic contacts are characteristic of the cerebral cortex and, within it, first of all of the fibrous layers. Their number is generally high. Four to six and possibly more synapses can be distinguished in each picture. They are structurally chemical synapses the components of which are, according to PALADE and PALAY (1954), ESTABLE, REISSING and ROBERTIS (1954), PALAY (1956, 1958), FERNANDEZ-MORAN and BROWN (1958), ROBERTIS (1955, 1958, 1959), LORENZO (1959), ROBERTIS and IRALDI (1961), WHITTACKER and GRAY (1962), LOOS (1963), WESTRUM (1966), JONES (1969), the presynaptic plasm, the presynaptic membrane, the synaptic space, the postsynaptic membrane and the postsynaptic plasm (Fig. 5).

The components of the presynaptic plasm are the presynaptic organella. There belong to them the synaptic vesicles, the mitochondria, as well as the neurofilaments and neurotubuli. From among the synaptic vesicles the empty vesicles appear in the largest quantity. Their size varies between 250 and 600 Å. It is interesting that not only the axon terminals are full of empty synaptic vesicles but also the parts of axons that are not in synapsis.



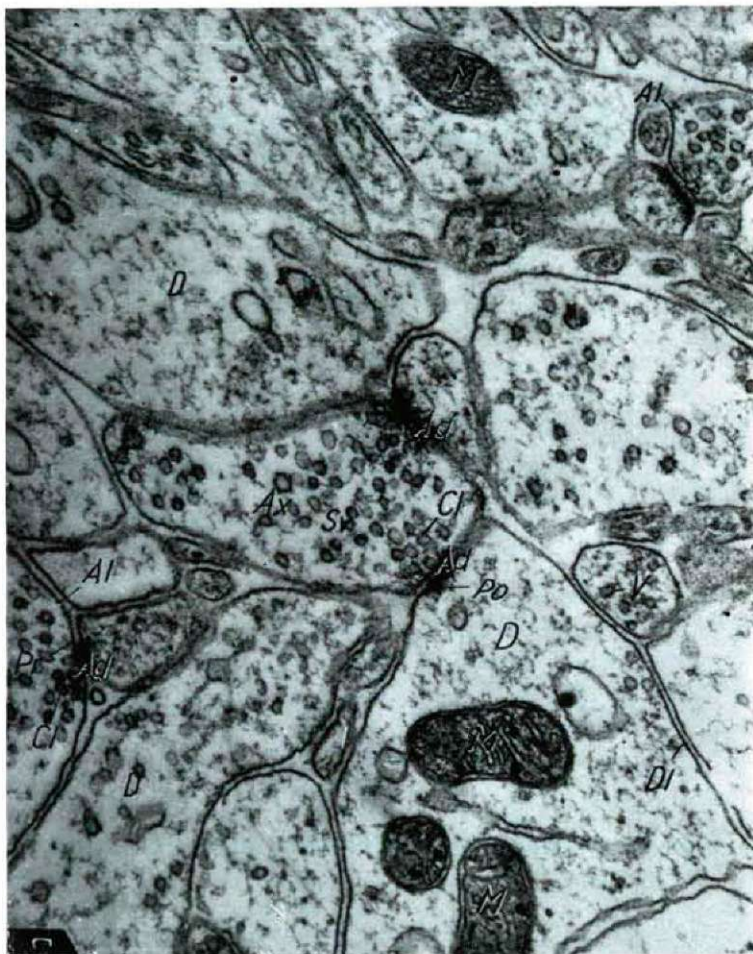


Fig. 5. *Lacerta agilis*. Cerebral cortex. Nerve-fibre layer. Ax — axon, D — dendrite, Al — axolemma, Dl — dendrolemma, Ad — axo-dendritic synapse, V — vesicle, Sv — synaptic vesicle, Pr — presynaptic membrane, Po — postsynaptic membrane, Cl — cluster, M — mitochondrium. Magnified:  $\times 48,000$ .

Fullness is singularly characteristic of the cerebrum of this animal. It is not excluded, and even it seems to be probable, that the cause of this particular richness is, as already mentioned, the strong agility and high sensitivity of this animal. If the transmitter material is transferred by the empty vesicles then that is natural because they need for the fast movements many stimuli, and for releasing the way of the impulse conduction depolarizing the postsynaptic membrane they need much transmitter material. As soon as we have fixed the cerebral cortex of the sand-lizard we had the thought that here the vesicle system must be richer and denser than in other animals moving slower and more sluggishly. It is to be mentioned as a peculiarity that that some empty vesicles exactly of the same appearance as that of those filling

both the terminal and the praeterterminal regions of axons may be observed in dendrites, too, anyway not in large numbers, only in a few cases. And even it occurs that these show some groupings in the immediate vicinity of the postsynaptic membrane. In the presynaptic plasm it is sometimes possible to see, apart from the empty synaptic vesicles, electron-dense vesicles of a thickness of 1000 Å, as well. Without going into functional explanations, we have to refer to that the dense-core forms occur everywhere and in every axon in the animal kingdom, in smaller or larger quantity, both in the synaptic region and in the presynaptic axon sections. In connection with the phenomenon, we should like to emphasize only, in addition, that the structure of these vesicles is the same in the animal kingdom everywhere and in each organ.

It is mentioned repeatedly that one of the characteristic features of the presynaptic protoplasm is that in it the mitochondria accumulate, forming a



Fig. 6. *Lacerta agilis*. Cerebral cortex. External molecular layer. Ax — axon, — D — denrite. V — vesicle, Sv — synaptic vesicle, Ad — axo-dendritic synapse, As — spine synapse, Pr — presynaptic membrane, Po — postsynaptic membrane, Si — intersynaptic space, M — mitochondrion, Cr — cristae mitochondriales, Mn — mitochondrial membranes, Cl — cluster. Magnified: x 48.000.



group close to the presynaptic membrane. This statement cannot be referred at all to our material. We had investigated a great many synapses and found so that the number of mitochondria varied between 0 and 3. Reckoning by and large, we have found numbers 0 and 1, to be equal the most of them being number 1. In a sense like this, in our case it is not to be thought of the accumulation of mitochondria.

In our pictures from among the organelle of the presynaptic protoplasm the less obvious ones were the fibrous components of the axons, the neurofilaments. In our opinion, the cause of this is to be sought for in the fact that the pieces of these fibres are intermingled among the synaptic vesicles past recognition, the latter appearing in every case in very large numbers and unusually sharp.

The presynaptic membrane is an everywhere sharply separated, structurally homogeneous membrane. Thickening is always conspicuous. It is generally not thick. It is interesting and in our case characteristic, too, that along a few longer presynaptic membranes there are smaller or larger interruptions in the thickness dividing the membrane into two or three parts. It is interesting in this division that in the presynapse the cumulation of vesicles, the so-called cluster is showing a double resp. triple division, as well (Fig. 6).

The synaptic space is a conspicuous, electron-light substance of the same breadth that shows, magnified weakly, no division or structure at all. In pictures, however, magnified rather strongly, it is full of parallel ridges perpendicular to the synaptic membranes. According to our observations, it is of the same breadth in every synapse. In our material, the synapses cannot be classified on the basis of the synaptic space.

The postsynaptic membrane always shows some fringing towards the postsynaptic plasm, resp. it is not limited towards the central region of the postsynaptic plasm. In a great part of cases it is thicker than the presynaptic membrane (Fig. 7). This phenomenon was noticed first by GRAY (1959), in the course of investigating the synaptic linkages of the cerebral cortex. Later on, seeing that in a part of the cerebral synapses the synaptic membrane is thicker than the presynaptic one, in other ones however the thickening of both membranes is the same, he divided the cerebrocortical synapses into two groups. He arranged into the first group those with a thicker postsynaptic membrane, into the second one those with the same thickening of both membranes. At a later date, the former one was named the synapsis of type GRAY I, the latter one that of type GRAY II. Both forms were found in our material, too, although – after having observed the pictures magnified more strongly – it could be said, as well, that all the forms of synapses belonged to the type GRAY I. The situation is namely in almost every case that the postsynaptic membrane is much thicker, darker and the fring-like appendages penetrate deep into the postsynaptic plasm. In most part of the cases it is so that in both forms of synapses one axon is in contact with one dendrite but it occurs, too, and even not rarely, that a axon piece is connected with two dendrites (Fig. 5).

The postsynaptic plasm is showing no peculiarity at all. The empty vesicles and the neurotubules do appear sporadically here, too, but the former ones in an extremely low number. Mitochondria are found in it only occasionally.

## Axodendritic synapses

In our material, 95 to 96 and perhaps even more per cent of the chemical synapses appearing extremely sharp and in large numbers belong to the axo-dendritic forms. Their shape and size are highly different. Both are a result of meeting forms. There are cases when the synaptic endings getting into contact are by and large of the same form. The situation is, however, generally so that the axon terminal is of larger extent than the surface of dendrite that is in contact with it. There occur, anyway, some cases, too, when the dendrite surface is larger than the detail of axon. The junctional axon ending is



Fig. 7. *Lacerta agilis*. Cerebral cortex. External molecular layer. Axo-dendritic synapse. Ax — axon, D — dendrite, Al — axolemma, Dl — dendrolemma, V — vesicle, Sv — synaptic vesicle, Pr — presynaptic membrane, Si — intersynaptic space, Po — postsynaptic membrane, Sr — synaptic fringes, M — mitochondrium, Cr — cristae mitochondriales, Mm — mitochondrial membranes, Il — intersynaptic ridges. Magnified: x 100.000.



usually straight or rounded. In this case, it is embedded in the excavation of the dendrite. There are anyhow also some cases when the excavation is in the axon ending and in that is lying the dendrite ending or some part of the dendrite. There are interesting the synapses in which the side of a longer axon ending or that of a longer preterminal piece is in contact with a small dendrite ending or a preterminal piece of lesser extent of a dendrite. These pictures are favourable the opinion that the transmission of stimuli is not limited to the endings. That means that in the transmission of stimuli there can have a role from both parts some fibre-regions that are far from the endings.

A peculiar form of the axo-dendritic synapses appearing rather rarely is the invaginated synapse. It is a form of contacts when we see in the cross-

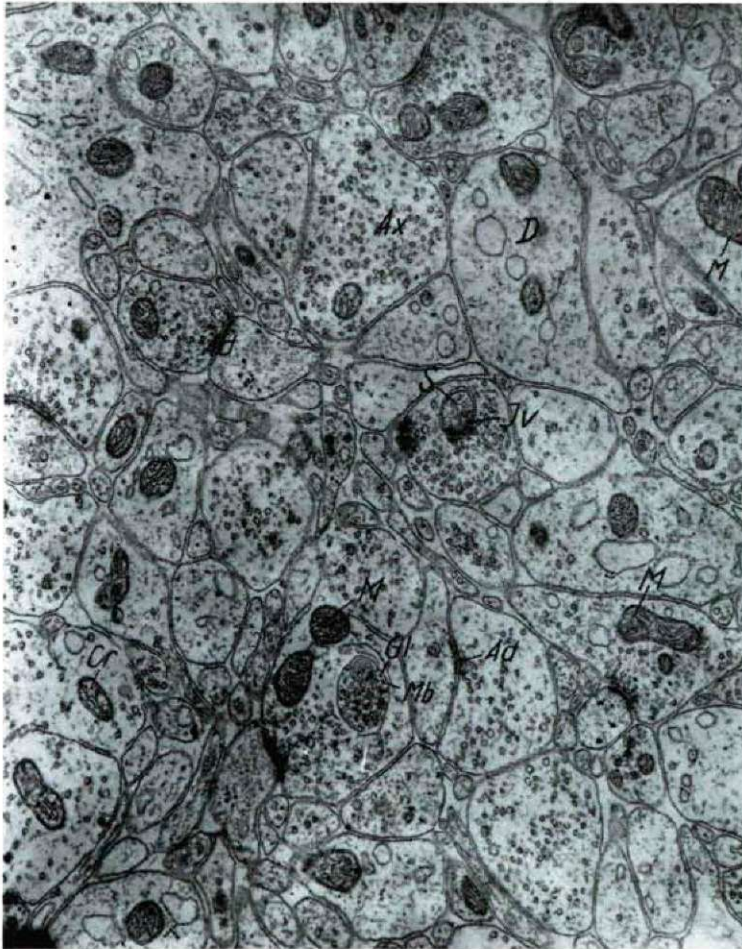


Fig. 8. *Lacerta agilis*. Cerebral cortex. External molecular layer. Invaginated synapse. Axo-dendritic synapses. Ax — axon, D — dendrite, S — dendrite-spine, M — mitochondrion, Mb — multivesicular body, Ad — axodendritic synapse, Iv — invaginated synapse, Cr — cristae mitochondriales, Gl — glycogen. Magnified: x 25,000.

section of an axon the cross-section of a dendrite piece with which the axon is forming synapse. But the same axon synaptizes with another dendrite piece, as well, that is lying outside the substance of neuraxon. According to our opinion, the matter in question is here an invaginated form of synapse that is forming an axon with a dendritic spine. The peculiar picture is the demonstration of a situation when the knife is cross-cutting a dendritic spine located in the cavity of an axon ending forming a synapse with



Fig. 9. *Lacerta agilis*. Cerebral cortex. External molecular layer. Synaptic vesicle, diapedesis. Ax — axon, D — dendrite, V — vesicle, Sv — synaptic vesicle, Cl — cluster, Pr — presynaptic membrane, Po — postsynaptic membrane, Si — intersynaptic vesicle diapedesis, Ad — axo-dendritic synapse, M — mitochondrion, Cr — cristae mitochondriales, Er — endoplasmic reticulum, Mb — multivesicular body. Magnified: x 25.000.



the spine. In our picture this would be the central synapse. The other one that in our case could be said to be a peripheric synapse does exist – as concluded from the situation – similarly between the axon and a dendrite spine. That may be concluded, apart from others from the fact, too, that round the peripheral synapse, and generally between the axon endings, there is everywhere a large number of smaller or bigger dendrite spines (Fig. 8).

Like of a peculiarity, we have to speak of an axodendritic form of synapses in which in the synaptic space, between two clusters a synaptic vesicle of large size is located. The situation is essentially that the presynaptic membrane is broken and in the space of the rupture, there is a larger vesicle in transition, pushing before itself the postsynaptic membrane. Supposedly, there is here a real diapedesis in the course of which the vesicle gets inside the dendrite. We cannot answer the question what is the cause of this peculiar phenomenon. It may be supposed that this vesicle of striking size is containing another material than the lesser ones ranging themselves along the membrane. It is, however, possible, as well, that it is containing the same material but more of it than the others do. At any rate, the phenomenon is interesting, the problem needs being clarified. This synaptic form is characterized, apart from the facts outlined above, also by that among the synaptic vesicles forms of dense-core type can be observed, as well (Fig. 9).

#### Axo-somatic synapses

Apart from the extremely numerous axo-dendritic synapses, we have found a few forms of synapses, too, where the axon is in synaptic contact with the soma of the nerve cell. These usually show the common form but we have found some of them, too, that – owing to its peculiar structure as well as to the peculiarity of its supposed function – will take some more explaining. In this synaptic form that belongs structurally to type GRAY II, there are two subsynaptic membranes parallel with and close to, each other, immediately under the postsynaptic membrane. The two membranes surround a narrow cavity along the whole length of the contact. One end of the canal is open, the other one is leading into an endoplasmic cistern (Fig. 10). The structure is unparalleled, unknown in the literature. To-day, when there is much discussion about the place, media and material basis of memory that can be seriously in question in this relation, we have the following ideas concerning the functioning of this system. Is it true, as said and written, that the basis of memory is protein, then our synapse may play the following part. The synaptic vesicles lining up along the presynaptic membrane in the axon terminal, with the acetylcholine contained by, resp. connected with, them – if that is, indeed, the transmitter in the cerebral cortex – make the postsynaptic membrane permeable and then the stimulus is transferred to the subsynaptic canal, resp. to both subsynaptic membranes. From these it gets to the membrane of the endoplasmic cistern where it transmits informations to the ribosomes lined up there, then the protein production begins and together with that the corresponding change in the situation, quantity and the strength of memory. Nobody knows if it is so or not, at any rate, the idea seems undoubtedly to be plausible. That is confirmed by the structure, placing at disposal plenty of the supposed morphological bases for adventures of this kind.



Fig. 10. *Lacerta agilis*. Cerebral cortex. Axo-somatic synapse, Ax — axon, V — vesicle, M — mitochondrium, Ad — axo-dendritic synapse, As — axo-somatic synapse, Cyt — cytoplasm, Cm — cell membrane, Er — endoplasmic reticulum, Pr — presynaptic membrane, Sm — subsynaptic membrane, Ec — endoplasmatic cistern, Cc — subsynaptic canal, Sv — synaptic vesicle, Cl — cluster, R — ribosome. Magnified:  $\times 48,000$ .

### Axo-axonic synapses

In our material we have met this synaptic form extremely rarely. It occurred generally in the vicinity of nerve cells where the axon terminals becoming very thin form rich groups along the cell membrane. As to the structure of these synaptic forms, the situation is generally that from among the axon terminals running across one another, at the end of one of them there is an excavation and the end of the other one is rounded. The synaptic vesicles can be seen in both axon terminals scattered, sporadically in smaller groups distinctly visible. In the presynapse, the cluster manifests itself in a sharp form.



## Capillaries

In connection with the ultrastructure of the cortex we have to discuss the structure of capillaries, as well, being essentially the same as anywhere in the organism of Vertebrata. Some characteristics of certain degree can only be observed in the shape of the endothelial cells and in their connection with one another. It may be called as a characteristic, apart from some others, that in the same capillary cross-section the endothelial cells appear in the most various shapes. On their surface, a great number of peculiar protrusions and hollows may be seen, that are showing, even in the same picture, a strongly varying form. The most characteristic parts of cells are the long processes hanging down into the lumen and showing, both in their shapes and situation, a great variety. In the cytoplasm, there are many empty round vesicles, arranged in a line. Complicated tubule systems are formed by the endoplasmic reticulum, and the mitochondria are forming groups. The ribosomes are arranged sporadically into lines, somewhere else they form indefinite and varying groups. The nucleus is a long-shaped, electron-light body. The chromatin clots form sporadically loose knots. The nuclear membranes are close to each other. The basal membrane is showing an oblique striation.

## Summary

As a result of the ultrastructure investigations carried out in the cerebral cortex of the sand-lizard (*Lacerta agilis* L.) the following have been established.

1. The pericarion of the nerve cells is a narrow cytoplasm border, the cell membrane is sharp, the nucleus is big, roundish, the nucleolus is ovoid and of excentric location.

2. The cisterns of the endoplasmic reticulum are forming branchy systems. The vesicle grouping of GOLGI's complex is richer than the tubular region. There are many multivesicular bodies and ribosomes. Shape and size of the cristic mitochondria is strongly changing.

3. The substance of nucleus is loose, the chromatin clots are forming dispersed, irregular knots, the nucleolus consists of a large number of small, roundish granules. The nuclear membrane is double, the site and lumen of the nuclear pores is changing.

4. The glia cells are structurally close to the nerve cells. The tubules of the endoplasmic reticulum are ramifying, the multivesicular bodies are frequent, there are many ribosomes and glycogenous clots. The nucleus is longshaped, the space between the nuclear membranes is narrow.

5. The synapses are chemical synapses. The components manifest themselves completely and in a sharp form. They belong overwhelmingly to the axodendritic type but a low number of axo-somatic and axo-axonic forms may be observed, as well.

6. There are not rare among the axo-dendritic synapses the invaginative forms, either, in which the excavation of the axon terminal is forming a double synapse, one with the dendrite spine in it and another with a dendrite piece beside it.

7. Under the postsynaptic membrane of one of the axo-somatic synapses we have found a subsynaptic canal opening into the cistern of the endoplasmic reticulum. The structure, that is new for the literature, seems to be usable for the analysis of problems connected with the memory.

### References

- ESTABLE, C., REISSING, M., and ROBERTIS, E. De (1954): Microscopic and submicroscopic structure of the synapsis. — *Exp. Cell. Res.* 6, 255—262.
- FERNÁNDEZ—MORÁN, H. and BROWN, R. (1958): The submicroscopic organization and function of nerve cells. — *Exp. Cell. Res. (Suppl.)* Academic Press, New York.
- GRAY, E. G. (1959): Axo-somatic and axo-dendritic synapses of cerebral cortex: an electron microscope study. — *J. Anat. (Lond.)* 93, 420—433.
- GRAY, E. G. (1959): Electron microscopy of synaptic contact on dendrite spines of the cerebral cortex. — *Nature (Lond.)* 1592—1593.
- JONES, D. G. (1969): The morphology of the contact region of vertebrate synaptosomes. — *Z. Zellforsch.* 95, 263—279.
- KRAUSE, R. (1921): *Mikroskopische Anatomie der Wirbeltiere in Einzeldarstellungen.* — Berlin und Leipzig.
- LORENZO, de A. J. (1959): The fine structure of synapses. — *Biol. Bull. Woods Hole* 117, 390—399.
- LOOS, H. van DER (1963): Fine structure of synapses in the cerebellar cortex. — *Z. Zellforsch.* 60, 815—825.
- PALADE, G. E. and PALAY, S. L. (1954): Electron microscope observations of interneuronal and neuromuscular synapses. — *Anat. Rec.* 118, 335—336.
- PALAY, S. L. (1956): Synapses in the central nervous system. — *J. Biophys. Biochem. Cytol. (Suppl.)* 2, 193—202.
- PALAY, S. L. (1958): The morphology of synapses in the central nervous system. — *Exp. Cell. Research. Suppl.* 2, 275—293.
- ROBERTIS, E. De (1955): Submicroscopic organization of some synaptic regions. An electron microscope study of the synapse. — *Acta neurol. latino-americana* 1, 3—15.
- ROBERTIS, E. De (1958): Submicroscopic morphology and function of the synapse. — *Exp. Cell. Res. Suppl.* 5, 347—369.
- ROBERTIS, E. De (1959): Submicroscopic morphology of the synapse. — *Internat. Rev. Cytol.* 8, 61—66.
- ROBERTIS, E. De and GERSCHENFELD, H. M. (1961): Submicroscopic morphology and function of glial cells. — *Internat. Rev. Neurobiol.* 3, 1—65.
- WESTRUM, L. E. (1966): Synaptic contacts on axons in the cerebral cortex. — *Nature (Lond.)* 210, 1289—1290.
- WHITTAKER, V. P. and GRAY, E. G. (1962): The synapse: biology and morphology. — *Brit. med. Bull.* 18, 223—228.

Address of the author:

Prof. Dr. A. ÁBRAHÁM

Department of Zoology, A. J. University,  
H—6701 Szeged P. O. Box 428,  
Hungary