MORPHOLOGY AND PATHOMORPHOLOGY

DISTRIBUTION OF VARIOUS TYPES OF SYNAPSES ON THE PYRAMIDAL NEURONS OF THE SENSORIMOTOR AREA OF THE RAT'S CORTEX

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In connection with recent advances in neurophysiology in the study of the synaptic transmission of excitation in the central nervous system, investigations of the structural organization of the synaptic apparatuses have assumed great importance.

The foundations of synapsoarchitectonics have been laid on the numerous facts concerning the structure and distribution of synapes in various parts of the brain obtained by the methods of optical microscopy. The neurons of the motor cortex are known to form numerous connections both with each other and with other parts of the central nervous system. These connections are made through a complex system of interneuronal contacts, well known from the data of optical microscopy [3-8, 11, 12, etc.], for their polymorphism. The results of electron-microscopic investigations have not only confirmed our ideas of the fine structure of the synapic contacts but have extended and deepened them [14, 15, 16, 18].

The object of the present investigation was to analyze the organization of the synapses on the neurons of the sensorimotor cortex of albino rats.

EXPERIMENTAL METHOD AND RESULTS

The investigations were carried out by means of optical (staining by the Golgi and Golgi—Deineka methods) and electron microscopy.

The authors have shown [10] that the sensorimotor cortex of rats and the human cerebral cortex [4] are characterized by the presence of two types of neurons, differing in the structure of their dendrite apparatus and the distribution of the spines, the points of contact between the neurons.

In this communication a more detailed description is given of the distribution of the various forms of synapes on the pyramidal cells of the rat's cortex. On these neurons axo-somatic, axo-dendritic, and, more rarely, axo-axonal connections were discovered. Axo-somatic synapses are comparatively rare in the sensorimotor cortex. The results of neurohistological investigations show that the bodies of the neurons in the sensorimotor cortex are surrounded by plexuses of thin nerve fibrils, and only here and there can single synapses be found in the form of rings and loops. Nerve fibrils may also be seen forming pin-head enlargements on the bodies of the neurons. It has been shown electron-microscopically that most nerve fibers touching the body of a nerve cell or approaching close to it do not form interneuronal contacts with the nerve cell, and synapses are present only between individual fibers and the cell body.

Axo-somatic connections are represented by type II synapses (after Gray [14]), i.e., with a large and active (thickened) part of the contacting synaptic membranes with pre- and postsynaptic membranes of approximately the same thickness; the width of the synaptic space is of the order of 250 A.

The synapses on the dendrites are distributed unevenly, and variations are seen in the density of their distribution and in the form of the synapses along the course of the dendrites of the pyramidal cells. On the basal dendrites, mainly two zones, and on the apical dendrites three zones may be distinguished, in which the density of distribution of the synapses is different.

Sarkisov [7] has previously shown that the overwhelming majority of interneuronal contacts in the motor cortex are axo-dendritic. They consist of two main types: synapses on the trunks of dendrites and synapses on the spines of the dendrites.

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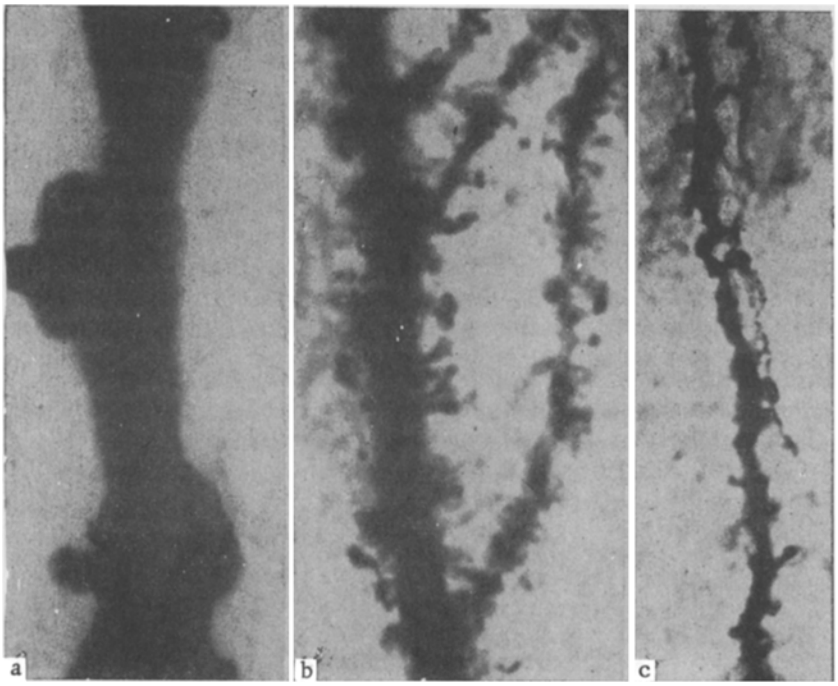

Fig. 1. Structure of an apical dendrite of a pyramidal neuron of layer V of the sensorimotor cortex in a rat. a) Zone I—(initial part of dendrite); b) zone II—with an increased number of spines; c) zone III— with few spines and uneven contours of the trunk of the dendrites. Golgi's method. Magnification 1,500.

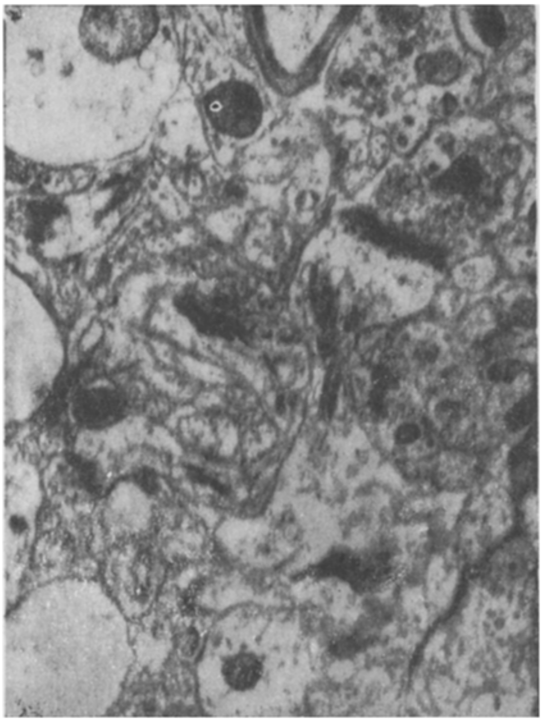

Fig. 2. Synapse on a spine of a dendrite from the sensorimotor cortex of a rat. The spine is cut longitudinally. Magnification 32,000.

The initial part of the apical dendrites, for a distance of about 50-100 μ from the bodies of the neurons, possesses comparatively few synapses on the trunks of the dendrites and synapses on the spines of the dendrites.

In this region the synapses on the trunk of the dendrite are very similar in structure to the axo-somatic synapses. In most cases, they are formed by axons passing through, and their synaptic membranes are of considerable size (up to 1 μ).

In this same region of the dendrite, single large round spines are found, and like the synapses on the trunk of the dendrite, these have contacting synaptic membranes over a considerable area.

The authors consider [1] that the spines may be grouped into three main groups. Group 1 are the most widely distributed in the cerebral cortex and consist of large, rod-shaped spined with a well developed spinal apparatus and a comparatively small area of synaptic membranes. Group 2 includes the large spines with a basal diameter equal to or even greater than the height or length of the spine; group 3 includes small, multiple spines, with an ill-defined synaptic apparatus and arranged one after the other like a palisade. In the initial regions of the dendrite mainly spines of group 2, and less commonly spines of group 1 are found. In these parts of the dendrite, as a rule, the spines have the appearance of bulges or thickenings, or they may be mushroom-shaped and so on (Fig. 1a). As a rule, these spines

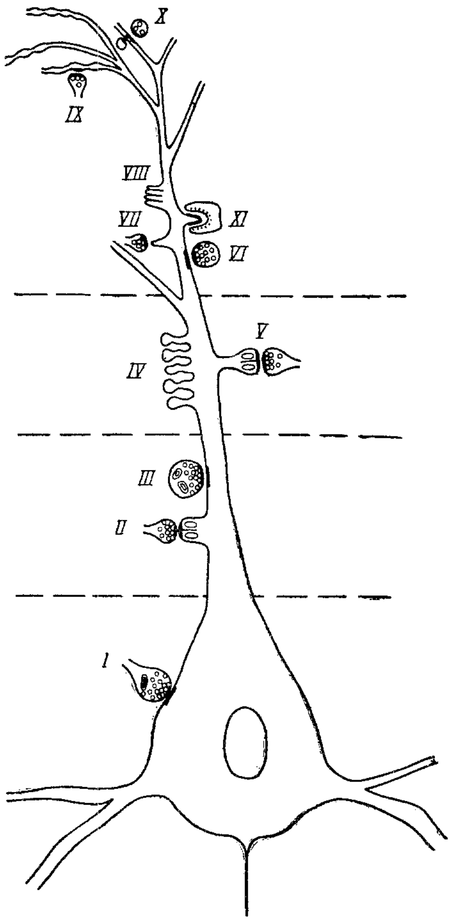

Fig. 3. Scheme of distribution of synapses of different types on the pyramidal neuron of the motor cortex of the rat. I—Axo-somatic synapse; II—synapse on a short wide spine (type II); III—synapse on the trunk of a dendrite similar in structure to an axo-somatic synapse; IV—large spines following one another and as a rule forming synapses with a passing axon; V—synapse on a single long spine (Type I); VI—synapse on the trunk of a dendrite similar in structure to a synapse on the spine; VII—synapse on a small branch of a dendrite or small spine; VIII—multiple small spines (type III); IX—synapse on various thickening of a branch of a dendrite; X—multiple synapses on terminal branches of a dendrite; XI—synapse on an invaginated branch or spine of a dendrite.

are not more than 2 μ wide and 0.5-0.9 μ high. Electron-microscopically, the synapses on the spines of the dendrites have all the features distinguishing the synapses of Gray's type I, namely, widening of the synaptic space and the presence of electron-dense material in it, and also a considerable thickening of the postsynaptic membrane compared with the presynaptic on account of an increase in the osmiophilia of the adjacent layer of cytoplasm. In the spines the "subsynaptic reticulum" is well marked, gradually changing into a thickening of the postsynaptic membrane. A similar pattern of structure of the synapses is observed also in the initial part of the basal dendrites.

In the next zone the number of spines on the dendrites is much greater. This zone occupies a distance of approximately 100-180 μ for the apical dendrites of the neurons in layer III and 340-390 μ for those in layer V. On the basal dendrites the dimensions of this zone vary.

In this zone there are practically no synapses on the trunks of the dendrites, for they are all situated on the spines of the dendrite. The shape and size of the spines situated on the same dendrite vary, but most possess a pedicle and a well defined head (Fig. 1b). Most of the spines in this part of the dendrite belong to group 1 (the height of the spine is greater than the area of its space, the spinal apparatus is well defined, and the area of synaptic contact is small; Fig. 2). The spines are fairly densely distributed, especially on the front of the apical dendrites of the neurons in layer V. The mean dimensions of the spines are as follows: length usually 1.8-2 μ, diameter of base 0.3-0.7 μ.

Most of the synapses of this zone are formed by axons passing through, but synapses are also found, formed by terminal branches of an axon. It is important to note that it is in this region of the dendrite that multiple contacts are found, formed by one axon with the heads of several successive spines.

On the apical dendrites yet another zone (the third) may be distinguished in which the number of synapses is greatly increased on account of axo-dendritic synapses on the terminal branches of the dendrite, whereas the number of synapses on the spines is greatly reduced (Fig. 1c). The synapses along the trunks of the dendrites in this zone differ sharply from the synapses on the trunks of the dendrites near the cell body. On their electron-microscopic picture they resemble axo-dendritic synapses on the spines of the dendrites. The spines in this zone are small, usually rod-shaped, and lie singly or in small groups. At the site of their synaptic apparatus thin filaments can be seen, resembling protoneurofibrils (type III spines).

The synapses on the spines in this zone are often formed by terminal branches of axons. It is interesting that the terminal branches of the dendrites may often be uneven in outline and may possess varicose thickenings. Electron-microscopically, the terminal branches of the dendrites which are varicose in appearance are the location of the synapses on the branches of the dendrites. In the region of the terminal branches of the dendrites, many synapses are also seen between several axons and a dendrite, the axons enveloping a branch of the dendrites like a sleeve.

The results of this investigation can be summarized in a scheme (Fig. 3), showing the main varieties of synapses found on the pyramidal neuron of the sensorimotor cortex.

This scheme, like the scheme of the distribution of synapses of different types on the pyramidal cells of the rabbit's hippocampus suggested by Hamlyn [15], extends our ideas of the synapsoarchitectonics of the brain and helps us to understand the functional significance of the different types of synapses. According to G. I. Polyakov [4], the body and initial parts of the dendrites of the pyramidal neurons are the locations of the terminal contacts, whereas, the region of the dendritic branches, supplied with spines, is adapted mainly for tangential contact. Polyakov considers that the terminal contacts maintain communications within strictly defined groups of neurons, whereas, the tangential contacts mediate impulses to a particular cell from many other cells.

Other hypotheses confirming the functional role of the axo-somatic and axo-dendritic synapses have been put forward [13, 17, 19, etc.], but the significance of the various types of synaptic contacts has not yet been explained.

All that is known for certain is that the great variety of forms of synapses in the cerebral cortex is associated with the complexity of the functional activity of the cortex and it demonstrates the specificity of function of the interneuronal connections at a particular level of the cerebral cortex.

This conclusion is confirmed by results obtained by S. A. Sarkisov and co-workers, showing that following administration of certain neuropharmacological agents [5, 6, 9], and also during the action of other factors on the cortex [2], a certain selectivity of the changes in the structure of the various forms of synapses can be detected.

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