AXODENDRITIC CONNECTIONS OF THE PYRAMIDAL NEURONS OF THE SENSORIMOTOR CORTEX OF THE CAT

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UDC 612.825:612.823.5-019

The dendrites of the nerve cells play an important role in the general activity of the cerebral cortex. They constitute the greater part of the gray matter of the cortex. In the pyramidal neuron, 90% of the surface is attributable to the dendrites [12].

Information concerning the axodendritic connections of the cortical neuron has mainly been obtained by the study of the dendritic spines [4,6], which are clearly revealed by the Golgi method. Opinions differ regarding the synaptic endings of the end-plate type. Difficulty in detecting synapses on the cortical neurons by the ordinary methods of silver impregnation has led some investigators to conclude that no synaptic plates are present here whatsoever [12], or that they do not stain [10,11], or that their dimensions lie outside the limit of resolving power of the optical microscope [13].

British investigators [10] explain the absence of synaptic plates in preparations of the cerebral cortex impregnated with silver by postulating that the synapses of the cortex, unlike the similar formations in the spinal cord, do not contain neurofibrils, and are therefore not revealed by neurofibrillary methods of impregnation with silver. A method of revealing synapses has been suggested [8,9], based on staining the synaptic mitochondria. However, this method has important disadvantages: not only the synaptic mitochondria, but also the mitochondria of the nerve cells, the dendrites, and the neuroglia are stained, and they are difficult to differentiate. It is impossible by this method to determine the true shape of the synaptic ending and of the afferent terminal fibrils.

Having adapted Deineka's method for demonstrating synapses in the brain stem [1,2], and having received reports that this method can be used to detect synaptic endings in the cortex [5,7], the authors decided to use Deineka's method of silver impregnation to study the interneuronal synapses in the sensorimotor region of the cortex.

The sensorimotor cortex has long attracted the attention of neurologists, although there is no information in the literature concerning the terminal synapses in this region.

The object of the present investigation was to discover how the dendritic spines and synapses of end-plate type are distributed on the apical dendrites of the pyramidal neurons of the sensorimotor cortex in the cat.

EXPERIMENTAL METHOD AND RESULTS

The cerebral cortex of healthy cats was investigated by the methods of Golgi and Deineka. Sections were cut of different thicknesses – from 13-100 μ. For convenience during the calculations, the dendrites together with all the synapses were drawn by means of a drawing apparatus.

The apical dendrites of the pyramidal neurons, treated by Golgi's method, had numerous dendritic spines (Fig. 1). The dendritic spines of the pyramidal neurons of the cortex differ from the spines of the neurons of the reticular formation of the brain stem [2].

In the cortex, the dendritic spines were uniformly distributed over the dendrites, they were identical in size, and all ended in fungiform heads (Fig. 1b). Examination of large numbers of pyramidal neurons stained by Golgi's method showed that the proximal portions of the apical dendrites possess no spines. The dendritic spines on the preparations in the present experiments began approximately 100 μ from the cell body. Remembering that the diameter of the apical dendrites remains approximately constant for a distance of 400 μ from the cell body, the number of spines for each 10 μ of dendrite length was calculated. Starting at 100 μ from the cell body and ending at the distal

Laboratory of Physiology of Afferent Systems, Institute of Normal and Pathological Physiology, Academy of Medical Sciences of the USSR, Moscow. (Presented by Active Member of the Academy of Medical Sciences of the USSR V. V. Parin.) Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 62, No. 8, pp. 101-103, August, 1966. Original article submitted August 2, 1965.

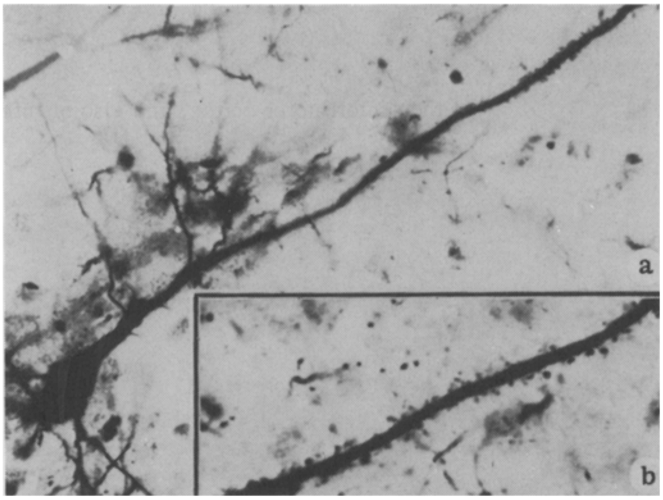

Fig. 1. Pyramidal neuron of the sensorimotor cortex of a cat. Golgi's method: a) dendritic spines are visible on an apical dendrite. The proximal part of the dendrite has no spine. MBI-6. Objective 40, ocular 7; b) fragments of the distal parts of an apical dendrite with dendritic spines. MBI-6. Objective 60, ocular 7.

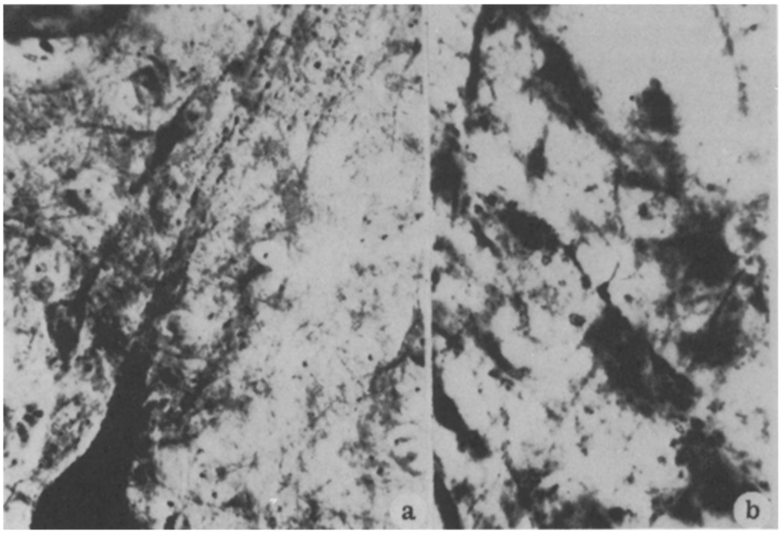

Fig. 2. Pyramidal neuron from the sensorimotor cortex of a cat. Deineka's method: a) apical dendrite with synaptic plates. MBI-6. Objective 60, ocular 5; b) fragments of an apical dendrite. Synaptic loops can be seen. Some synaptic plates have afferent fibrils. MBI-6. Objective 90, ocular 12.5.

segment of the dendrite, 400 μ away, the number of spines per unit length (10 μ) remained constant and was approximately 8.

By means of Deineka's method, many synapses were revealed on the bodies and dendrites of the pyramidal cells (Fig. 2). The synaptic plates on the pyramidal neurons of the cortex differed only very little from the typical synapses of the spinal cord [3] and reticular formation [1,2]. The synapses were shaped like loops. They measured 1.5-2.0 μ. Sometimes thin afferent fibrils could be seen (Fig. 2b).

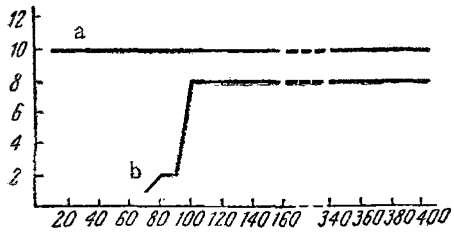

Fig. 3. Graph showing distribution of synaptic contacts on an apical dendrite of the sensorimotor cortex of a cat: a) distribution of synaptic contacts of the end-plate type (Deineka's method); b) distribution of synaptic contacts of the dendritic spine type (Golgi's method). Along the axis of abscissas – distance from cell body (in μ); along the axis of ordinates – number of synapses per 10 μ length of dendrite.

Deineka's method reveals neurofibrils very clearly [1,7]. The ring-shaped appearance of the synapses, and also the clearly defined afferent fibers (Fig. 2b) demonstrated the possibility of revealing neurofibrillary components. Because of these findings in the synapses of the sensorimotor cortex, and also of information in the literature concerning the synapses of the optic cortex [7], care must be taken when interpreting the results of those investigations denying that synapses can be detected in the cortex by neurofibrillary methods. Ten dendrites, 400 μ in length, were chosen arbitrarily and the number of synapses on each 10 μ length of dendrite was calculated. This showed that the number of synaptic plates per unit length was the same on the proximal and distal segments (10 synapses per 10 μ). The density of synaptic plates per 100 μ^2 surface of dendrite was calculated. The synaptic density (23 synapses/ 100 μ^2) also remained constant on the proximal segment of the dendrite and the segment situated 300-400 μ from the cell body.

The results of all the calculations are summarized in Fig. 3, which clearly shows the character of distribution of the synaptic contacts of different types and the fraction of the dendritic spines and end-plates on the proximal and distal portions of the dendrite.

The results described above show that the axodendritic connections of the pyramidal neurons of the cortex are effected both by synaptic end-plates and by dendritic spines. Both these forms of communication exist simultaneously. It would be a serious mistake to explain the whole variety of axodendritic connections by only one of these types.

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