CORRELATION BETWEEN CORTICAL CYTOARCHITECTONICS AND NEURONAL ORGANIZATION IN SOMATOSENSORY AREAS I AND II OF THE CAT'S BRAIN

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It has now been proved conclusively that sensory systems have a dual representation in the human and animal cortex [6, 14, 18, 19]. Somatosensory areas I and II of the cortex (S_I and S_{II}) have been investigated particularly fully by neurophysiologists.

The results of neurophysiological experiments, and also clinical observations [15] show that areas S_I and S_{II} are not duplicate systems, for definite functional differences exist between them. Area S_I is responsible for fine discrimination between sensations whereas area S_{II} probably plays no part in this process but is more likely to be concerned with the general integration of sensory information [15]. It has recently been shown that area S_{II} has a significant influence on conduction of afferent impulses through the nonspecific structures of the brain stem and thalamus [2], whereas area S_I influences mainly the conduction of impulses through the specific relay nuclei of the thalamus.

From a comparison of all the known facts concerning functional differences between areas S_I and S_{II} it seems likely that differences exist between the morphology of these areas. The extremely small number of investigations devoted to the cortical cytoarchitectonics of the cat, so widely used for experimental purposes, must be emphasized [9, 10, 17]. Unfortunately the special structural differences between the cortex of areas S_I and S_{II} have not yet been precisely described in the literature [9, 10, 16, 17].

The object of the present investigation was to compare the cytoarchitectonics and neuronal organization of areas S_I and S_{II} of the cat's cerebral cortex.

EXPERIMENTAL METHOD

Nissl's method was used for the investigation. Two portions of the cortex of areas S_I and S_{II}, identical as regards their sensory modality, in the zone of representation of the hind limb were studied. To determine structural differences more precisely, the cytoarchitectonic structure of these zones was drawn by means of the RA-1 apparatus under magnification of 400 times.

EXPERIMENTAL RESULTS

The study of the cytoarchitectonics of these portions of areas S_I (see figure A) and S_{II} (see figure B) revealed the following differences.

Layer I (molecular) of both somatosensory areas is clearly demarcated from the adjacent layer II and is approximately equal in width or slightly wider in area S_I.

Layer II (outer granular) is also equal in width in both areas, although differing in the size and distribution of its cells. In area S_I, for example, the nerve cells are smaller and more scattered, whereas in area S_{II} the neurons of layer II are large and relatively densely packed. The border between layers II and III is ill defined.

Layer III (the layer of medium-sized pyramids) is of considerable width in both areas although marked differences are seen in the distribution of the cells. In area S_I the medium-sized pyramids characteristic of this layer are arranged singly or in groups, a considerable distance apart, and the rest of the

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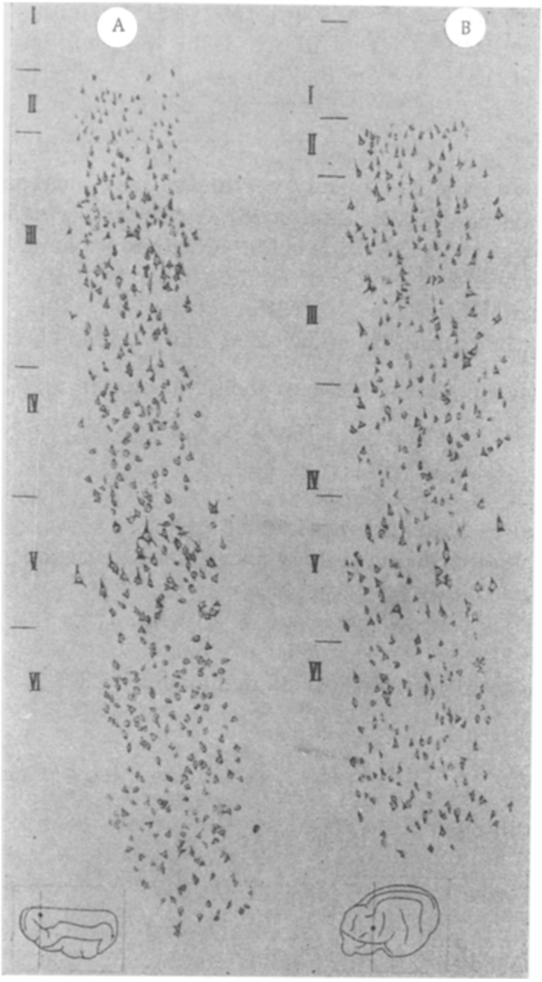

Cytoarchitectonics of the cortex of areas S_I (A) and S_{II} (B) in the zone of representation of the hind limbs. Drawn with the RA-1 apparatus. I-VI) Cytoarchitectonic layers of the cortex. The diagrams in the bottom corners of the figure show parts of the cortex chosen for investigation. Objective 40, ocular 10.

space is occupied by small cells. In area S_{II} on the other hand, the medium-sized pyramids are much larger and are scattered throughout the layer. They are easily distinguished by their size from the background of small cells and are appreciably larger than the medium-sized pyramids of area S_I. In contrast to area S_I, these large pyramidal cells are particularly conspicuous in a sublayer of layer III.

Marked differences are observed between layer IV (inner granular) in the two areas. In area S_I this layer is more clearly demarcated from the other layers than in area S_{II}, in which the cells are densely packed. In area S_{II} the cells of layer IV are less dense, so that this particular layer is less clearly defined than in area S_I.

The low cell density of layer IV is also stressed by Gurevich and Khachaturyan [9]. According to Hassler's observations [10], area S_{II} occupies Area 2_{pri}. We consider that it would be more correct, taking into account the data of electrophysiology, to include in this zone part of the inferior portion of Area 2, where layer IV is also less dense, narrower, and not clearly demarcated from neighboring layers.

Characteristic differences are also found during the comparison of layer V (ganglionic). In area S_I this stands out more clearly against the background of the whole section of the cortex than in area S_{II}. The most characteristic feature is that in area S_I, layer V contains very large pyramids, distributed singly or in pairs among small and medium-sized pyramids. In area S_{II} no such large pyramids are found. In layer V of this area large cells are seen, but they are not as large as the large pyramidal cells observed in area S_I. In the classification of Gurevich and Khachaturyan [9], area S_{II} occupies Area 2, characterized by the presence of two bands of equally large cells in layers III and V, in agreement with our observations.

Layer VI (layer of polymorphic cells) is slightly wider in area S_I, where the cells are small in size and densely packed. In area S_{II} these cells are less compactly arranged.

Comparison of the neuronal structure of the cortex in areas S_I and S_{II}, which we studied previously with the aid of Golgi's method [3], with the results of the present investigation confirmed the cytoarchitectonic structural differences between these areas. For instance, the cells of layer II are much larger in area S_{II}. In layer III the cells in area S_{II}, like the cells in layer II, are larger than in area S_I. The pyramids here are mainly large, with a thick apical dendrite and powerful basal cytoplasmic processes, extending over a long distance. In area S_I the pyramids of layer III are smaller and more delicate in their pattern. The neurons of layer IV are of approximately the same small size, but in area S_I the stellate neurons vary in size. In layer V the largest cells are seen in area S_I. They possess thick apical dendrites running into the molecular layer. Numerous basal dendrites of these cells spread out far and wise in a horizontal direction. In area S_{II} the pyramidal cells of layer V are more elongated in shape and smaller than the analogous cells of area S_I. The results may be summarized by saying that layers IV and V attain their highest development in the cortex of area S_I and layer III in the cortex of S_{II}.

It has been found [7, 11] that a dense plexus of terminal ramifications of ascending afferent fibers lies in the inner granular layer of the cortex. As Lorente de Nó [12] first showed, the ascending afferent fibers reach the projection cortex from the thalamus and terminate on cells in layer IV. This was later investigated more fully by Chang [8], G. I. Polyakov [4, 5], and others.

Our observations show that the axons of the cells in layer IV are in contact with the basal dendrites of the cells in layer V. Taken as a whole, these cells, together with the afferent fibers of the thalamic nucleus (VP), constitute point projections. The local distribution of these projections in area S_I is evidently due to the fact that the cells of layer III, being smaller than those in area S_{II}, have shorter dendrites and can thus detect excitation only from a localized area of the cortex.

Because of this structural organization, the excitation therefore spreads only vertically over a narrow restricted portion of the cortex, as Mountcastle has recently pointed out [13]. In area S_{II}, on the other hand, layer III is particularly well developed. The cells here are larger, with many branching dendrites extending far and wide. In G. I. Polyakov's opinion [4], afferent neurons of this type give rise to the principal system of intercortical fibers; the terminal ramifications of these fibers, joining different regions and areas of the cortex, extend throughout layer III and form a dense plexus in its upper part and in layer II.

This associative structure of layer III of the cortex in area S_{II} may be the morphological basis for the wider overlapping of afferent projection zones in this area.*

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