INTERZONAL AND INTRAZONAL CONNECTIONS OF THE SOMATOSENSORY CORTEX

Z. V. Eliseeva, A. G. Rabin, and R. A. Durinyan

UDC 612.826.2

Morphological and electrophysiological investigations demonstrated the absence of connections between individual subdivisions in the first somatosensory area of the cortex. They also confirmed the existence of a strict somatotopical organization of the connections between the two somatic regions of the cortex and that these connections end principally in cortical layers IV and III.

The results of morphological and electrophysiological investigations indicate the existence of connections between the first and second somatic areas (SI and SII) in the cerebral cortex [1-3, 7, 9].

A more detailed analysis of these connections has been undertaken recently by morphologists who have examined the preterminal degeneration following extirpation of comparatively small areas of cortex [4, 5]. However, even in these investigations, considerable contradictions were discovered. In particular, connections were found between individual subdivisions of the sensory representation in the same cortical somatic area and differences between the degree of somatotopical organization of the connections were found between areas SI and SII.

It was accordingly decided to make a special morphological and electrophysiological analysis in order to clarify the character of the interzonal and intrazonal connections in the somatic cortex.

EXPERIMENTAL METHOD

The electrophysiological part of the investigation was carried out partly on unanesthetized, immobilized cats, and partly on cats anesthetized with nembutal under acute experimental conditions. The method of recording the focal cortical potentials and single unit responses was described previously [3].

Morphological investigations of intrazonal and interzonal connections were carried out on 4 cats from which small areas of cortex (about 2 mm in diameter), corresponding to the focus of maximal responses to stimulation of the skin of the hind limb, were extirpated in region SI by thermocoagulation. From 7 to 9 days after the operation, under nembutal anesthesia the brain was perfused, and the segment of cortex including the two somatosensory areas was cut into three blocks so that each corresponded to the representation of the hind limb, the forelimb, and the snout in area SII. The zones of representation of individual parts of the body were determined immediately before perfusion by the method of recording focal responses. The blocks were treated by the Nauta–Gygax method [8].

EXPERIMENTAL RESULTS

Results of the Electrophysiological Experiments. Recordings of focal interzonal responses of unanesthetized, immobilized animals showed that the region of spread of responses in SII to stimulation of

Laboratory of Physiology of Subcortical Structures, Institute of Normal and Pathological Physiology, Academy of Medical Sciences of the USSR, Moscow. (Presented by Academician V. V. Parin.) Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 72, No. 10, pp. 3-5, October, 1971. Original article submitted December 28, 1970.

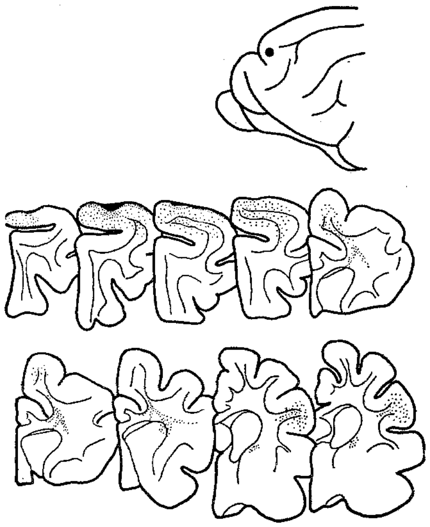

Fig. 1. Extent of degenerated fibers in frontal sections through the cat's brain after local thermocoagulation in the zone of the hind limb in region SI.

the cortex in the representation zones of the hind limbs and forelimbs in SI overlap considerably. Among the interzonal responses, differing in their configuration and temporal parameters, a local area could be distinguished in which focal responses characteristic of the place of ending of the interzonal associative connections appear. These responses possess the minimal latent period and duration of the positive-negative waves. The series of fast waves of potential always corresponded to the phase of development of the positive wave.

In animals anesthetized with nembutal, the zones from which focal responses to an interzonal cortical stimulus could be recorded were much narrower and hardly overlapped at all. In response to interzonal stimulation, only responses close in their configuration and temporal parameters to the responses of the zone of ending of the interzonal fibers were preserved.

The microelectrode investigations showed that neurons with a short latent period, indicating that endings of interzonal cortical connections were present on these cells, were recorded in the other somatic regions only from a local area in which interzonal responses characteristic of the focus appeared. The latent period for the monosynaptically activated cortical cells was 1.4-1.8 msec. Cells involved antidromically in the response, with a latent period of discharge of 0.7-1.2 msec, could be found in the same localized areas. For example, the area in which short-latency discharges appeared in region SII to stimulation of the zone of representation of the hind limbs in region SI did not exceed 1.5-2 mm in diameter. In areas of the cortex surrounding the local zone of short-latency unit responses, the latent period of the unit responses indicated the presence of several intracortical synaptic relays in their course.

Analysis by the method of recording interzonal focal responses showed that the zones of representation of individual areas of the body in region SI are not interconnected.

Interzonal responses in region SII to stimulation of region SI are more marked than responses in region SI to stimulation of region SII.

Results of the Morphological Experiments. In 3 of the 4 animals injury in the zone of representation of the hind limb in region SI was restricted to the layers of the cortex and did not affect the underlying structures. In the immediate vicinity of the region of injury, degenerated fibers running tangentially in layers I, III, and V could be found. The zone of spread of this degeneration was limited to the region of representation of the hind limb and did not affect the zone of representation of the forelimb in the same region. The only exception was one case in which the area of injury was more extensive and included the white matter immediately beneath the site of coagulation.

The course of the degenerated fibers was followed in the white matter as far as region SII (Fig. 1), where they were located in a small area limited to the zone of representation of the hind limb. They climbed up to cortical layer III. The dimensions and direction of the course of most of the fibers in layers VI and V suggest that they were fibers passing through into layers IV and III, in which they appeared as tiny, scattered granules, characteristic of preterminal degeneration. In the zones of representation of the forelimb and snout, no degeneration was found.

Jones and Powell [4] found no connections between individual subdivisions of the representation of sensation in region SI, although other investigators [6, 10] consider that such connections exist. This point of view has been confirmed recently by Kawamura and Otani [5]. Having regard to the importance of this fact to the understanding of the organization of connections and interactions in neuronal systems receiving afferent impulses from the limbs, it was decided to make repeated observations of the results of analogous operations. The zone of representation of the hind limb, which is relatively circumscribed and local, and remote from region SII, was chosen for injury. In all 3 cases in which the area of injury was small and did not affect the white matter, no connections could be clearly distinguished between the zones of representation of the hind limbs and forelimbs with region SI. This was also shown by the results of recording focal cortical responses. The spread of fibers into other subdivisions of the same region in the experiments of Kawamura and Otani [5], and also the considerable spread of degenerated fibers into neighboring cortical zones, can evidently be explained by injury to the white matter. Similar results also were observed in one of the present experiments in which the white matter was damaged.

The results of the present morphological and electrophysiological investigations confirm the existence of a strict somatotopical character of organization of the connections between the two somatic areas of the cortex, and they show that their endings are mainly in layers IV and III of the cortex. The results of the electrophysiological experiments, both under acute experimental conditions and on waking animals with implanted electrodes, are in agreement with the conclusion of Kawamura and Otani [5] regarding the relative dominance of connections from region SI to region SII.

LITERATURE CITED

1. R. A. Durinyan, Neirofiziologiya, 2, 155 (1970).
2. V. Yu. Ermolyaeva, Byull. Éksperim. Biol. i Med., No. 3, 114 (1963).
3. A. G. Rabin, Byull. Éksperim. Biol. i Med., No. 3, 3 (1969).
4. E. G. Jones and T. P. S. Powell, Brain Res., 9, 71 (1968).
5. K. Kawamura and K. Otani, J. Comp. Neurol., 139, 423 (1970).
6. E. Kawana and T. Kusama, Folia Psychiat. Neurol. Jap., 18, 337 (1964).
7. H. Nakahama and M. Saito, Jap. J. Physiol., 6, 200 (1956).
8. W. J. H. Nauta and P. A. Gygax, Stain Technol., 29, 91 (1954).
9. W. Spencer, Am. J. Physiol., 163, 749 (1950).
10. C. N. Woolsey, Fed. Proc., 6, 437 (1947).