CORTICAL CONNECTIONS OF THE PARAFASCICULAR COMPLEX OF THE THALAMUS

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Thermocoagulation of the second cortical somatosensory area was carried out to study its connections with the parafascicular complex of the thalamus in the cat. Preterminal degeneration of cortical afferents in the parafascicular complex was found in frontal sections of the brain stained by the Fink–Heimer method. Degenerated drop-like fibers were much thinner in this structure than fibers running toward the ventrobasal complex. In all probability afferent fibers from the cortex form axo-dendritic and sometimes axo-somatic contacts. Most of the degenerated fibers were concentrated chiefly in the lateral part of the nucleus. However, local areas in which degeneration was concentrated could not be found in the nucleus. The precise topographic distribution of corticofugal fibers evidently is found at the primate level. The presence of direct connections between the second somatosensory area and the parafascicular complex suggests that the latter participates in the somatic functions of the brain.

Among the nuclei of the nonspecific system of the thalamus the centrum medianum (CM) is one of the most important. For most mammals, especially subprimates, CM is regarded together with the parafascicular nucleus (Pf) as a single complex, for at this stage of phylogeny CM is not yet distinguishable as an independent nucleus. In the cat, an object widely used in modern electrophysiological research, the parafascicular complex (CM-Pf) should therefore be distinguished [5].

It was held for a long time that after removal of the neocortex the nonspecific nuclei do not undergo retrograde degeneration, or such degeneration is extremely slight. As a result of the introduction of more accurate methods for detecting degenerated fibers in recent years convincing evidence has not been obtained on the existence of connections of the anterior zones of the cortex, notably the motor cortex, with the CM-Pf complex both in primates [6, 10, 11, 14, 17] and in cats [18]. In primates, moreover, the topographic distribution of these connections was found to be quite clear [6, 10].

The problem of the corticofugal projections of the somatosensory cortex in CM-Pf has not yet been solved although there is evidence of the existence of such connections [4, 7, 9, 15, 19].

The results of electrophysiological studies of corticofugal responses in CM-Pf [1-3], clearly detectable during stimulation of the second somatosensory area of the cortex, suggest that the somatosensory cortex, especially this part of it, must in fact have well-marked connections with the CM-Pf complex.

EXPERIMENTAL METHOD

Morphological investigations of corticofugal connections were carried out on six cats in which the cortex was removed by thermocoagulation over the whole of the second somatosensory area (the anterior ectosylvian gyrus). Under pentobarbital anesthesia 3-4 days after the operation the brain was perfused with 10% neutral formalin in physiological saline, after which frontal serial sections were stained by the Fink–Heimer method to reveal terminal degeneration.

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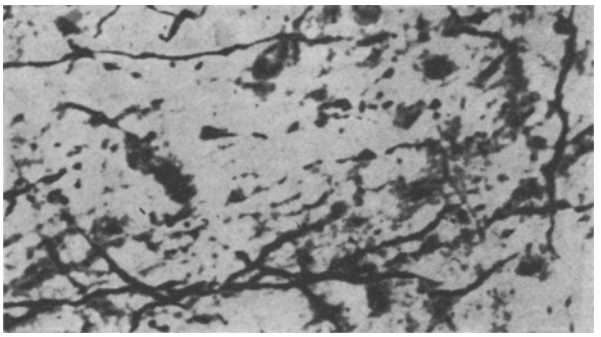

Fig. 1. Degeneration of thin fibers in the parafascicular complex after coagulation of the second cortical somatosensory area (photomicrograph, MBI-11 microscope, ocular 40, homal 2.5).

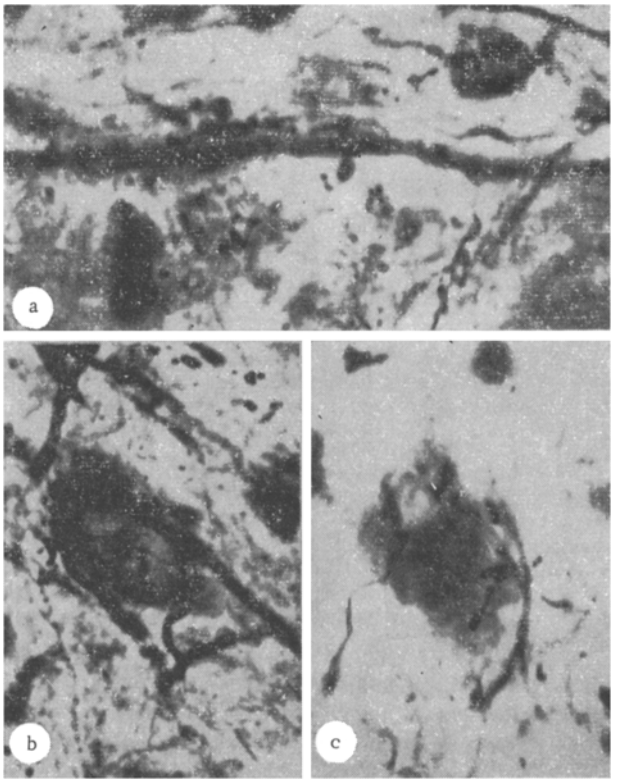

Fig. 2. Degeneration of preterminal fibers in the parafascicular complex of the thalamus after coagulation of the second somatosensory area of the cortex: a) degeneration of cortical afferents along the course of the dendrite of a neuron of the parafascicular complex (photomicrograph, MBI-11, ocular 60, homal 2.5); b) multiple degeneration against the background of a large neuron of the parafascicular complex (photomicrograph, MBI-11, ocular 40, homal 2.5); c) racemose degeneration against the background of a neuron of the parafascicular complex (photomicrograph, MBI-11, ocular, 60, homal 2.5).

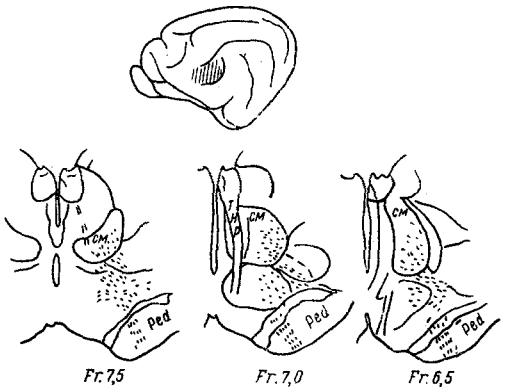

Fig. 3. Diagram of extent of cortical afferents from second somatosensory area in the parafascicular complex (coordinates taken from the atlas of Jasper and Ajmone-Marsan).

EXPERIMENTAL RESULTS

Considering that according to data in the literature [9] the removal of small areas of cortex does not yield positive results, it was decided to carry out complete coagulation of the second somatosensory area of the cortex throughout its depth.

Terminal degeneration was found in frontal sections through the cat brain in the region of the parafascicular complex of the thalamus. The degenerated fibers were varicose and fragmented. Many thin fibrils, broken up into droplets, could be seen in the field of vision and these were undoubtedly preterminals of corticofugal fibers (Fig. 1). The corticofugal projections in CM-Pf are evidently characterized by these thin fibers, as Japanese workers also point out [15]. Rinvik [19] also observes that corticofugal fibers of CM-Pf are thinner than fibers running toward the ventrobasal complex. This observation agrees with the electrophysiological data indicating a longer latent period of activation of neurons of the nonspecific nuclei in response to cortical stimulation than with the responses of the cells of the thalamic relay nuclei [12]. Accordingly it can be postulated that the duration of the latent period is explained by the caliber of the corticofugal fibers in CM-Pf and not by synaptic delay.

A degenerated fiber in some sections apparently broke up along the course of a large dendrite of a CM neuron (Fig. 2a). The afferent fibers from the cortex evidently form true axo-dendritic contacts. This agrees with data obtained by light-microscopic [20] and electron-microscopic [25] studies of the structure of the cat CM-Pf complex (without coagulation of the cortex). Together with axo-dendritic contacts, in all probability axo-somatic contacts also are occasionally found. For instance, degenerating fragments of fibers could be traced against the background of large cells (Fig. 2b, c). Degenerated terminals could be observed more often in the neuropil of the nucleus, against the background of nuclei of glial cells.

Many undegenerated axons also were found in CM-Pf. This indicates that CM-Pf has extensive connections with other brain structures. Of these the most important are connections of CM-Pf with the motor (anterior cruciate gyrus) [6, 10, 11, 14, 17], the motor-associative (gyrus proreus), and the somatosensory (gyrus coronalis) areas of the cortex [4, 15, 19].

Most of the degenerated fibers were concentrated chiefly in the lateral part of the nucleus (Fig. 3), roughly coinciding with the part of CM in which axons of cells of the frontal cortex terminate [18]. However, no sufficiently local area could be identified in the nucleus in which the degeneration was concentrated; the degenerated fibers were spread in separate groups without any distinct focus. This pattern has also been emphasized by other workers. A more localized topographical distribution of the representation of corticofugal fibers has been observed in CM of primates [18], particularly for projections of the frontal cortex.

This investigation revealed the presence of direct connections between the second somatosensory area and the parafascicular complex of the cat thalamus although the precise topography of these corticofugal projections could not be established. The results of these investigations, like the data in the literature cited above, suggest that the CM-Pf complex participates in the somatic functions of the brain. In all

probability, in primates, anthropoid apes, and man further specialization has taken place through evolution and CM has differentiated as an independent nucleus, adapted chiefly for somatic functions. It will be recalled that a similar view was expressed as long ago as in 1865 by Luys, who first distinguished CM as an independent structure.

However, the view has long been accepted in the literature that the parafascicular complex and, in particular, CM is instead an intrathalamic connector and that it has no direct relation to cortical functions. This view is based on a series of investigations [8, 16, 23, 24] in which no connections between the cortex and CM could be established, although some evidence to the contrary had been found at that time [21, 22]. These contradictions can be attributed to technical difficulties. The retrograde degeneration method does not permit changes in the cellular composition to be demonstrated (or they are largely masked) if bifurcating axons are present, and these are particularly numerous in the axonal system of CM [20]. The contradictions affecting this problem can also be explained by different approaches used by the authors concerned to define the boundaries of CM-Pf [13].

Finally, having regard to the thinness of the CM fibers, direct degeneration methods such as the Marchi method could not yield positive results and not until the introduction of modern impregnation methods could degeneration of the thin axon terminals in the cat CM-Pf be revealed, especially after removal of the second cortical somatosensory area.

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