

THALAMIC PROJECTIONS OF SOMATOSENSORY  
CORTICAL AREAS

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The results of morphological investigations of degenerated fibers show that the first somatosensory cortical area is connected by descending cortico-thalamic fibers with the posterior ventral nucleus of the thalamus. The second somatosensory area is connected simultaneously with the caudal part of the posterior ventral nucleus and with the posterior group of thalamic nuclei. These cortico-thalamic connections are distributed on a somatotopic principle.

KEY WORDS: somatosensory cortical areas; thalamic relay nuclei; cortico-thalamic projections; somatotopic principle.

Somatosensory systems of the brain, like other systems (visual, auditory), are represented in the cortex in two separate regions. For the somatic systems these are somatosensory cortical areas I and II (SI and SII). Investigations in the writers' laboratory [3, 4, 11] and data in the literature [6, 20, 22, 31] show that the two regions of somatic representation in the cortex are not identical, duplicate systems, but they differ in a number of functional and morphological respects. Ascending thalamo-cortical projections to areas SI and SII differ in their origin. Area SII receives afferents from two different groups of thalamic nuclei: the posterior ventral nucleus (n.VP) and, partly, from the nuclei of the posterior group, whereas area SI receives afferents from n.VP only. These facts are based both on morphological observations [15, 16, 20, 21, 25] and on electrophysiological analysis of antidromic responses of thalamic relay neurons [2, 24]. The distribution of ascending afferent projections in the thalamic relay nuclei led to the hypothesis that a double organization of somatic systems exists at the thalamic level also in rats [12] and cats [7]. Similar data with respect to the human thalamo-cortical system have recently been published [8].

The question accordingly arose of relations between the cortical and thalamic areas of somatic representation, and in the investigation described below the character of descending (cortico-thalamic) connections of cortical areas SI and SII with the corresponding thalamic nuclei was determined.

## EXPERIMENTAL METHOD

Experiments were carried out on cats. Under pentobarbital anesthesia the cortical surface was exposed in areas SI or SII and the focus of representation of the forelimb was determined electrophysiologically by the evoked potentials method; the focus was then destroyed by thermocoagulation, with the result that an area of local coagulation (2 mm<sup>2</sup>) was produced in all the animals in the same cortical projection. The coagulation affected all six layers of the cortex but not the subjacent white matter. The animals were killed 4-9-14 days after the operation by intravital perfusion with 10% formalin, the brain was removed and fixed, and frontal serial sections were cut and treated by the Fink-Heimer [14] and Nauta-Gygax [26] methods to detect preterminal degeneration of corticofugal nerve fibers. Parallel sections were stained with thionine to identify the thalamic nuclei by reference to the stereotaxic atlas of Jasper and Ajmone-Marsan [17].

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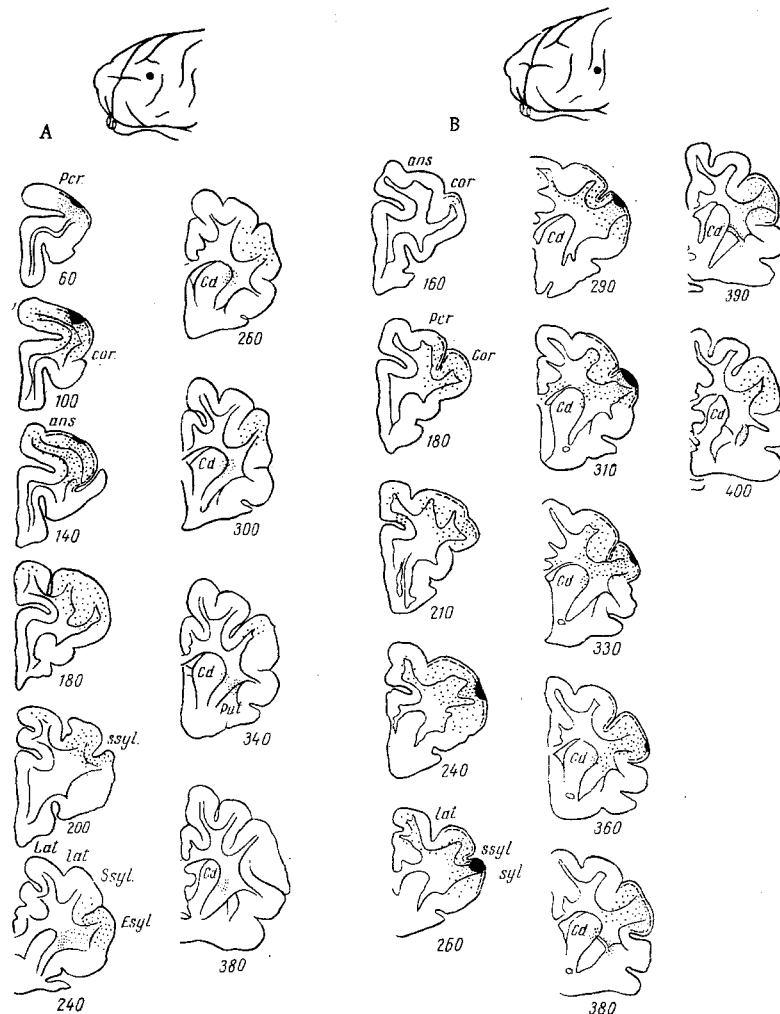


Fig. 1. Projection of frontal sections through anterior zones of the cat cerebral hemispheres after coagulation of areas SI (A) and SII (B). Foci of coagulation of cortex are shaded; dots denote areas of spread of degenerated fibers; broken line marks boundaries of spread of degenerated fibers from focus of coagulation in cortical layer I.

#### EXPERIMENTAL RESULTS

In areas SI or SII many degenerated fibers were observed around the focus of injury in all layers of the cortex. However, in cortical layers II and III in area SII degeneration of tangential fibers, which spread over longer distances, was more intensive. Clear degeneration of nerve fibers also was observed in the stratum zonale of both cortical regions. However, degeneration in layer I of area SI, although extending over a long distance, did not go beyond the boundary of that gyrus, whereas in area SII degenerated fibers were found in neighboring gyri also (Fig. 1). Besides degeneration of tangential fibers, in both cortical areas degeneration of U-shaped intracortical fibers, distributed by the somatotopic principle, also was seen. These results, in conjunction with data in the literature, were discussed in more detail in an earlier paper [5].

The course of degenerated projection fibers from both areas was largely identical both in the conducting systems (internal capsule - Ci) and in the striopallidary system, and also in the reticular nucleus of the thalamus (n.R). On involvement of the striopallidary system (lateral part of the head of the caudate nucleus - n.Cd and part of the putamen - Put) in the process of degeneration it could be seen that projections from area SI lie more rostrally in the putamen, whereas those from area SII are caudally and rather more numerous (Fig. 1). This observation is in agreement with those of Ermolaeva [5], although the topography of the projections is a little different.

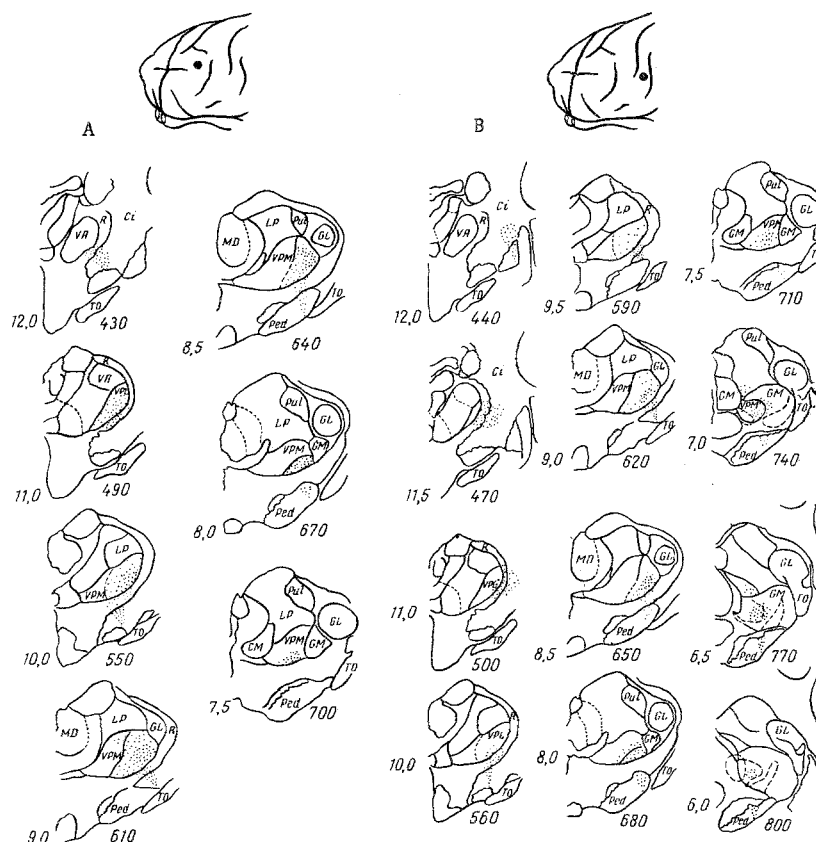


Fig. 2. Projections of frontal sections through thalamic nuclei of cat brain after coagulation of areas SI (A) and SII (B). Areas of spread of degenerated fibers are shown by dots.

These topographical features distinguishing the projections of areas SI and SII in the striopallidary nuclei can be regarded as indirect evidence of differences in functional relations between the somatic cortex and these subcortical nuclei.

A double picture of fiber degeneration is found in the reticular nucleus of the thalamus (n.R), which suggests that some of them terminate here on the neurons of n.R whereas others pass through into the thalamic nuclei. The possibility of endings of corticofugal fibers in n.R has been discussed some time ago in the literature [9, 27, 28]. The results of the present experiments showed that the degeneration process does not affect all fibers in n.R but only fibers of the middle part of the rostral pole and the ventral part of the more caudal zone (Fig. 2), thereby demonstrating not the diffuseness, but rather the definite topography of distribution of these fibers. Consequently, after selective removal of different parts of the cortex, different segments of n.R degenerate [1, 9, 27, 28].

The most substantial degeneration was found in the thalamic relay nuclei, receiving fibers that pass through n.R (Fig. 2). In the rostral part of n.VP, a compact zone of degenerated fibers appeared after coagulation of area SI. This zone coincided with the zone of the nucleus where representation of the forelimb was demonstrated by the evoked potentials method [3] and which gives ascending projections to cortical area SI, in the zone of representation of the forelimb. The degenerated fibers had the appearance of densely packed and deeply stained granules and larger masses. The zone of maximal degeneration was concentrated approximately in the middle part and displaced slightly medially at rostral levels, whereas at more caudal levels it was located in the ventral part of the nucleus. Consequently, the homonymous somatotopic zones of n.VP and area SI in the cortex are linked by two-way projections.

After coagulation of area SII the focus of degenerated fibers was found in the caudal parts of n.VP and in the nuclei of the posterior group (Sg, LP). Single diffuse fibers were observed in the rostral part of the nucleus. Coagulation of a local zone in area SII gave rise to degeneration in the lateral part of the nucleus and was located more caudally in n.VPM. Evidence of differences in the distribution of somatic

cortical projections at the rostro-caudal level in n.VP is also given by Kusama et al. [22] and de Vito [10]. Similar results have been obtained by other workers also [19, 29].

It is interesting to note that a similar organization has also been observed by analysis of ascending thalamo-cortical projections [20, 21, 23, 30]. Consequently, descending projections of area SII run into those regions of the thalamic relay nuclei that are connected by ascending projections with cortical area SII [13], and are designated the second somatosensory region of the thalamus.

Two-way connections (direct ascending and reciprocal descending), distributed by the somatotopic principle, thus exist between the thalamus and cortex in the somatosensory system.

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