

DISTRIBUTION OF DEGENERATED FIBERS IN THE CORTEX  
OF THE MEDIAL AND LATERAL SURFACES OF THE DOG'S BRAIN  
AFTER DESTRUCTION OF THE ANTERIOR LIMBIC AND MOTOR AREAS

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The representation of the internal organs in the premotor, motor, and limbic areas of the cerebral cortex has been established by numerous investigations [1-4, 6, 7, 10, 13, 14]. Detailed studies have been made of the connections between the various parts of the limbic system (the limbic cortex, the hippocampus, the septum, and so on). However, the relationship between the limbic cortex and the other areas of the cortex has not yet been investigated. The literature contains only isolated reports of the abundant associative connections of the limbic region [15, 17, 18]. Previously [20] we showed that destruction of the sigmoid gyrus in cats leads to degeneration of a certain part of the fibers on the medial surface of the brain. In these circumstances mainly the thin radial fibers emerging from the white matter of the gyrus fornicatus and passing up to the first layer of the cortex degenerated. A large number of thin horizontal fibers in a state of fragmentation was found in the first layer of the cortex, especially in the superior and inferior walls of the cruciform and splenic fissures. Destruction of the anterior limbic region in cats caused, besides degeneration of the fibers of the posterior and retrosplenial portions of the limbic region, very intensive degeneration of the fibers of the anterior and posterior divisions of the sigmoid gyrus. The changes affected a large number of fibers of all calibers and directions, in all the layers of the cortex (mainly the lower layers).

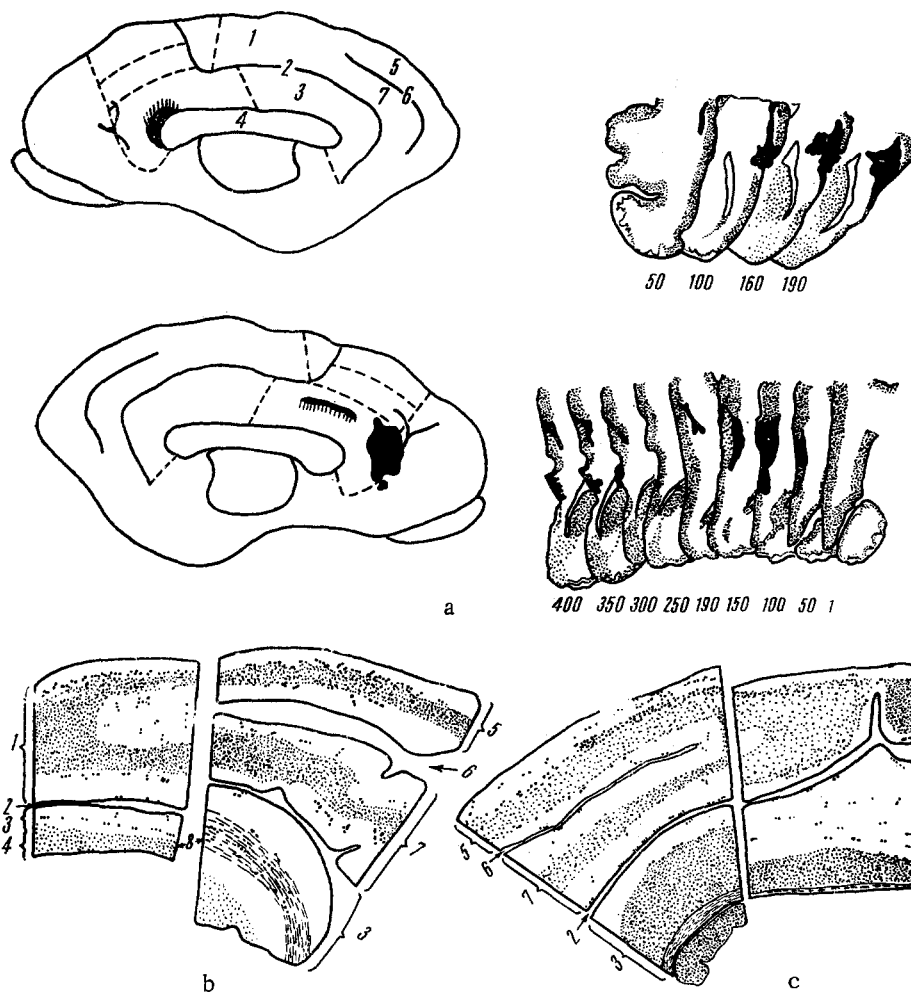
In this article we describe an investigation of these and also of other cortical areas in dogs after injury to the anterior limbic and motor areas.

#### EXPERIMENTAL METHOD

A morphological analysis was made of nine cerebral hemispheres from adult dogs (in 7 following destruction of the anterior limbic region, in 2—of the sigmoid gyrus). The cortex was destroyed surgically in sterile conditions. The animals were sacrificed 5-6 days later by electrocution. The limits of injury were determined in a series of sections of the area of operation on the brain, passed through alcohols and stained with cresyl violet. The rest of the brain was placed in 10% formalin solution. Each area of the brain, starting from the site of injury and ending at the occipital region inclusively, was impregnated by the Bielschowsky—Gros and Nauta methods. Laterally, the limits of the area investigated extended as far as the coronary and lateral fissures. The sections were cut in the frontal and sagittal planes. Hence, the following areas were investigated for the presence of fragmented fibers: the pre- and postcoronary areas (Areas 6 and 4), the parietal (Areas 1, 2, 5, and 7) and occipital areas (Areas 19, 18, and 17), and the posterior limbic and retrosplenial areas (Areas 23, 29, 30, and 31).

#### EXPERIMENTAL RESULTS

Destruction of the anterior limbic region. Microscopic analysis of the region of injury showed that in all cases the genual gyrus was destroyed and the genu of the corpus collosum injured. In some dogs, in addition, areas of destruction were present in the proreal gyrus and the medial part of the sigmoid gyrus. The depth of injury varied from



Distribution of degenerated fibers in cortex of medial and lateral surfaces of the brain of a dog after injury to the anterior limbic regions. a) Localization of injury, left—scheme of medial surfaces of right and left hemispheres of dog undergoing operation, right—frontal sections through these hemispheres, destroyed area shaded black; b and c) sagittal sections through right (b) and left (c) hemispheres of the same dog. The dots indicate fragmented fibers: 1) presplenial gyrus; 2) splenic fissure; 3) gyrus cinguli; 4) corpus callosum; 5) suprasplenial gyrus; 6) suprasplenial fissure; 7) splenic gyrus; 8) fasciculus cinguli.

total destruction of the white matter to destruction of the fibers lying just beneath the cortex only. The area of injury occupied from  $\frac{1}{4}$  to  $\frac{2}{3}$  of the width of the medial surface of the cortex at the level of the genual fissure, and varied in length from 4 to 9 mm.

Examination of the preparations treated by the methods of Nauta and Bielschowsky—Gros revealed a large number of degenerated fibers on the lateral surface between the coronary and cruciform fissures (the posterior sigmoid gyrus, Area 4). Horizontal and obliquely running thick fibers were predominant in the lower layers of the cortex. Swollen argentophilic synapses and bulb-shaped endings were frequently seen. In the upper layers of the cortex no degenerated fibers were seen. In the part of the cortex between the cruciform fissure and the medial surface of the brain the number of fragmented fibers was appreciably reduced (anterior sigmoid gyrus, Area 6). On the medial surface of the brain (anterior sigmoid gyrus, medial part of Area 6) the degeneration of the thick fibers of the lower layers of the cortex had almost disappeared. At the same time varicosity and fragmentation of the thin fibers of the first layer were found in the cruciform fissure and on the medial surface. The total number of degenerated fibers was appreciably reduced. Hence, when injury was caused to the medial surface, the process of degeneration spread with greater intensity over the lateral surface of the brain than over the medial. This character of the distribution of the degenerated fibers, and their quantitative and qualitative characteristics remained constant

when the parietal region was compared with the posterior limbic region and the occipital with the retrosplenial. Investigation of these areas was carried out mainly in sagittal sections, for the degenerated fibers were mainly fronto-occipital in direction.

In preparations of the parietal and posterior limbic regions of the brain (the presplenial gyrus and the gyrus cinguli) the following distribution was found; the degenerated fibers were most numerous in the lateral portion of the presplenial gyrus. They were similar in character to the degenerated fibers of the posterior sigmoid gyrus and they were situated in the lower layers of the cortex. In the upper layers no degenerated fibers were present or only odd ones were seen. In the medial portion of the presplenial gyrus the changes observed were of the same character, but the fragmented fibers were much smaller, and degeneration of the first layer of the cortex also was observed (superior wall of the splenial fissure). Hence, the character of the degenerative changes in this part of the cortex was apparently intermediate. In the gyrus cinguli the horizontal degenerated fibers of the lower layers were completely absent. Only isolated, thin, radial fibers running from the fasciculus cinguli and the horizontal fibers of the first layer of the cortex (inferior wall of the splenial fissure) were fragmented. Large numbers of degenerated fibers could be seen running in the fasciculus cinguli. In the corpus callosum no fragmented fibers were present. Large numbers of varicose and fragmented fibers were seen in the subcallosal tract. Crossing into the occipital and retrosplenial regions, the phenomena just described did not disappear, but mostly increased in intensity in Areas 18 and 19 (see figure, b and c). Here, too, the main mass of fibers in a state of fragmentation were concentrated in the lower layers of the lateral portion of the suprasplenial gyrus (the direct continuation of the presplenial gyrus). In the lower layers of this part of the cortex, in a brain with one extensive but superficial injury of the genual gyrus, destruction of nearly all the fibers was observed, but was absent from the upper layers, where a large number of degenerated fibers appeared (see figure, b). In order to determine the degree of spread of the process of intensive degeneration over the lateral surface, the ectolateral gyrus was impregnated in addition. It was found that in this area of the brain, also, numerous fragmented fibers were present.

In the medial portion of the suprasplenial gyrus the number of degenerated fibers was reduced, and in the gyrus cinguli they were found only in the fasciculus cinguli.

Destruction of the sigmoid gyrus. The morphological control of the zone of injury showed that it was bounded by the white matter of the anterior and posterior portions of the sigmoid gyrus. Impregnation of the parietal and posterior limbic, and occipital and retrosplenial regions of the brain revealed that the distribution of the degenerated fibers was similar to that observed following destruction of the anterior limbic region. In the lower layers of the cortex of the parietal zones, many fragmented fibers were present. In the gyrus cinguli solitary fragmented radial fibers were encountered. In the first layer of the cortex (the walls of the splenial fissure) many long, degenerated, tangential fibers were counted. Fibers with gross changes were observed only in Areas 18 and 19 of the occipital region, possibly as a result of division of the fronto-occipital associative pathways.

It may be concluded from these findings that injury to the anterior limbic and motor areas of the cortex leads to two types of distribution of the degenerated fibers in the cerebral cortex. One type—degeneration of a large number of thick, mainly horizontal fibers of the lower layers of the cortex on the lateral surface—may be described as the "lateral" type of degeneration. The other—degeneration of solitary thin, mainly radial fibers and of thin horizontal fibers of the first layer of the cortex on the medial surface—is the "medial" type of degeneration. Between these two zones of the cortex lies a third, "intermediate" area, in which the first type of degeneration is observed but the number of degenerated fibers in the lower layers of the cortex is appreciably smaller here, and at the same time some fragmentation of the fibers of the first layer of the cortex is present. Corresponding to the "lateral" type, changes occurred in the fibers of the lateral portion of the presplenial and suprasplenial gyri (the lateral portions of the motor, parietal, and occipital areas), corresponding to the "intermediate" type—in the medial portions of the same gyri and areas, and corresponding to the "medial" type—in the gyrus cinguli (limbic areas). This pattern of distribution of the degenerated fibers was observed in all nine cases which we investigated. It must be stated, however, that destruction of the genual and not of the sigmoid gyrus leads to a more marked degeneration of the fibers in accordance with the "lateral" type.

Evidence against the suggestion that the phenomena which we observed were caused by injury to the anterior cerebral artery was given, firstly, by the absence of severe bleeding during the operation, and secondly, by the fact that in this case the region of maximal fragmentation of the fibers must have been situated in the gyrus cinguli, supplied exclusively by the anterior cerebral artery [5], and not on the lateral surface of the brain, in a zone of col-lateral circulation [8].

It is difficult to explain the relationships between the areas which we investigated. The connections between the motor and limbic areas are the easiest to interpret, for they both possess motor and visceral functions and require a mutual interchange of fibers. It is more difficult to understand why premotor Area 6 does not possess such connections, despite the fact that it lies immediately above the site of operation and is functionally close to Area 4, whereas in the parietal and, in particular, in the frontal portions of the visual areas massive degeneration of deeply lying fibers was observed. After destruction of the anterior limbic and motor areas, no disturbance of the conditioned cutaneous and pupillary reflexes is known to occur. This may perhaps be explained by the fact that the cells with which the degenerated fibers are connected have no direct relationship to the afferent function of these particular regions. The possibility is not ruled out, however, that in order to reveal defects in the working of these analyzers, the conditions under which the experiments are performed will have to be improved.

#### SUMMARY

Damage to the anterior limbic and motor regions of the brain cortex results in two types of distribution of degenerated fibers over the brain cortex in dogs. The first "lateral type" is characterized by a predominant fragmentation of a large number of thick horizontal or diagonal fibers of the lower cortical layers on the lateral surface; the second type, known as "medial," by the fragmentation of single slender radial fibers and horizontal fibers of the first cortical layer on the medial surface.

The "lateral-type" degenerated fibers are distributed over the cortex of the sigmoid, presplenial, suprasplenial and ectolateral convolutions (motor, parietal and occipital fields). They are most numerous in the motor (4) and optic (19, 18) areas. The "medial-type" degeneration is characteristic of the cingulum (gyrus cinguli) (limbic fields).

An injury to the anterior and posterior portions of the sigmoid convolution causes a less extensive "lateral-type" degeneration than an injury to the genu convolution.

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