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CORTICAL EFFERENTS OF DIFFERENT PARTS OF THE CAT ORBITOFRONTAL CORTEX

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As the result of a combined approach, several functional differences have been discovered in the frontal regions [2, 6]. The anterior zone of the frontal neocortex is known as the orbitofrontal cortex (OFC) [13, 14]. In the process of evolution there is a progressive increase in the complexity of the structure and functions of OFC, which is the precursor of the anterior zone of the human frontal cortex [5, 11], with its higher integrative functions.

In the cat the term OFC is taken to mean the proreal gyrus and the anterior part of the orbital gyrus, adjacent to the presylvian sulcus. Efferent connections of this cortex in the cat after destructuion of OFC in its entirety have been described in one or two publications [7]. There is no information in the literature on efferent connections of different parts of OFC, although such information could be important for our understanding of its structural-functional organization. In view of these considerations it was decided to undertake the present investigation.

EXPERIMENTAL METHOD

Experiments were carried out on 29 adult cats subjected to unilateral subpial extirpation of different parts of OFC under intraperitoneal pentobarbital anesthesia: the medial part (P_1), and superior (P_2) and inferior (P_3) zones of the dorsolateral part of the proreal gyrus (PfG) and the anterior zone of the orbital gyrus (G). The animals were killed 6-8 days later. The brain was fixed for 3-4 weeks in neutral formalin. Series of frontal brain sections were impregnated by Nauta's method and its modifications (Fink—Heimer and Kawamura—Niimi). The depth of injury to the cortex was verified in preparations stained by Nissl's method.

EXPERIMENTAL RESULTS

Destruction of the cortex of P_1 (part of area 8 on the medial surface of the hemisphere) was accompanied by the appearance of fragmented preterminals in the cortex of the posterior sigmoid gyrus (PSG) and the superior part of the coronal gyrus (CG, area 4) of both hemispheres in layers III-V, and of the anterior sigmoid gyrus (ASG, area 6) of the injured hemisphere. A moderate number of altered preterminals was observed in the cortex of the anterior suprasylvian gyrus (ASSG, area 5) in layers III-V of both hemispheres. Massive destruction of fibers was discovered in the cortex of the gyrus cingulus (GC, area 24), mainly ipsilaterally. Endings of axons from P_1 were identified also in the presubiculum (Ps), the entorhinal region (ErR), the piriform cortex (PiC) of the injured hemisphere, and in the cortex of the dorsolateral part of the proreal gyrus (area 8) of both hemispheres.

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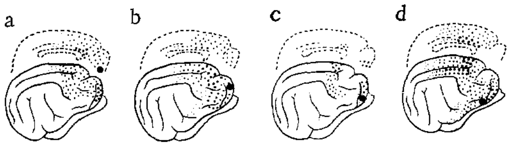

Fig. 1. Scheme of efferent cortical connections of different parts of OFC. a) Medial, b) superior, c) inferior part of proreal gyrus, d) anterior zone of orbital gyrus. Dots of different sizes indicate abundance of connections.

Destruction of P_2 (superior part of area 8 on the lateral surface of the hemispheres) caused degeneration of fibers in the middle layers of the cortex of ASG (area 6) of the injured and, to a lesser degree, of the opposite hemispheres. Many disintegrating axons were found in the cortex of PSG and the upper part of CG (areas 4 and 4b), mainly on the side of operation. Massive disintegration of fibers was found in the cortex of the inferior part of CG (area 4b) and the anterior ectosylvian gyrus (AEC, area 2) on the side of operation. Altered fibers were observed in the cortex of the middle part of LG on the side of the operation. A moderate number of fragmented fibers could be traced in the anterior part of the middle suprasylvain gyrus (MSG, area 5) and the anterior part of LG (area 53) in layers III-V. Altered preterminals were found in smaller numbers in the cortex of ASSG (area 5) in layer V, and in the cortex of the middle part of GC on both sides, more marked on the boundary between areas 24 and 23. A moderate number of connections was found with the cortex of P_1 in layers III-V on the side of the operation. Such connections were more numerous with the cortex of OG.

Destruction of P_3 (inferior part of area 8 on the lateral surface of the hemisphere) was accompanied by destruction of its axons in layers III-V of the inferior part of CG (area 4b), in layers III-V of AEC (area 2), and in the anterior part of LG (area 53) of the ipsilateral hemisphere. Fragmentation of fibers was observed in layers III-V of ASSG (area 5) on the side of the operation, and also in the anterior part of GC on the boundary between areas 25 and 24 in layers III-V on the side of the operation, and to a lesser degree, of the intact hemisphere. Relatively unchanged fibers were found in the middle part of GC (area 23) of both hemispheres. Fragmented preterminals also were found in the cortex of P_1 and P_2 (area 8) in layers III-V, of both hemispheres.

Destruction of the cortex of the anterior zone of OG (area 43) was accompanied by changes in the axons in the cortex of PSG and CG (areas 4 and 4b) of both hemispheres. Many fragmented axons were found in the region of the coronal sulcus (area 4b) in the middle layers of both hemispheres, fewer in layers III-V of the cortex of the middle and posterior parts of LG (areas 17 and 18) on the side of the operation, and fewer still in layers III-V close to the anterior ectosylvian sulcus (area 50) of both hemispheres. Many degenerated axons of OG neurons were found in the cortex of the anterior part of LG (area 53), ASSG, and MSG (areas 5 and 7), and also in the cortex of GC (areas 23, 24, and 30), the parasplenial gyrus and PiC of the ipsilateral hemisphere.

A definite pattern can thus be distinguished in the distribution of intercortical efferents of the different parts of OFC. Their number increases in the rostro-caudal direction with the transition from P_1 and P_2 and P_3 and to the anterior zone of OG (Fig. 1).

Although long association connections become well marked only in primates [1], the functional role of the small number of efferents of OG in the cortex of area 17 may be great. This suggestion is valid for two reasons. First, we traced connections of OG with the majority of subcortical structures which process visual information. Second, OG occupies a special place among the other zones of OFC in the number of its sources of afferentation [1, 8], possible evidence of the important role of this zone in the integration of different flows of impulsation. In particular, some workers [7] found single fibers in cats running from PrG to the parietal areas, and consider that connections of this kind become significantly abundant only in dogs. According to our data, all parts of OFC in cats project to the parietal cortex. This fact seems important, for according to recent data the parietal areas are the components of the association cortex in which different kinds of sensory information are concentrated [1, 3, 4, 10] and may be directed into OFC along existing systems of connections [7]. Compared with results obtained by other workers [15], our own data are evidence of more extensive connections of the different parts of OFC with the limbic cortex. Differences in the projections, according to our data, are that the dorsolateral part of PrG is connected with the anterior zone of GC, whereas P_1 and the anterior zone of OG project, besides to GC, to the parasplenial gyrus, PiC, and ErR; connections in the reverse direction also are present [15].

Efferents of OFC which we observed in the parietal and limbic cortex perhaps regulate the flow of impulses arriving in OFC from important zones, and if necessary, they determine the priority of one input. An essential addition to this description may be provided by data in the literature showing the presence of connections between the parietal cortex and GC in cats [4, 10]. These characteristics of the neocortical connections of the cat brain which we have examined permit a wide exchange of information between three functionally important zones of the cortex: association — parietal, limbic — GC, and integrative-triggering — OG. Excitation from each of the above-mentioned sources can circulate between these structures along independent systems of connections in opposite directions. This special feature of the organization of these connections may perhaps be of definite importance for memory processes [1].

This comparison of our own data and those published in the literature suggests the presence of morphologically based "circles" between OFC, the parietal cortex, and the limbic cortex, which can be classed as strict [1] horizontally organized brain systems. No such "circles" are found with other parts of the neocortex. Analysis of studies of intracortical connections in monkeys [4, 9, 12], moreover, has shown that similar, although evidently more highly organized, "circles" exist in these animals also.

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