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## NEURONOGRAPHIC ANALYSIS OF MEDIAL AND BASAL CEREBRAL CORTEX. I. CAT

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Reprinted from  
*J. Neurophysiol.*, 1953, 16: 312-323

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## NEURONOGRAPHIC ANALYSIS OF MEDIAL AND BASAL CEREBRAL CORTEX. I. CAT<sup>1</sup>

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(Received for publication July 22, 1952)

IN RECENT YEARS evidence has accumulated that portions of the medial and basal cortex of the cerebral hemispheres are implicated in "affective" ("emotional") processes (6, 7, 11). Comparative, ontogenetic, and cytoarchitectural studies have drawn a distinction between the cortex contained in the convolutions surrounding the hilus of each hemisphere, known as the great limbic lobe (2), and the rest of the cerebral mantle. Phylogenetically, this cortex appears to have differentiated before the neopallium. Ontogenetic and cytoarchitectural studies also attest to the primitive origin as well as to the primitive organization of the limbic cortex. These considerations, together with recent physiological and psychological findings, suggest that the limbic system represents an early neural development involved in affectively determined processes.

But it still remains to be ascertained whether or not the limbic system has holistic functions pertaining to affective behavior that distinguish it from the phylogenetically newer part of the forebrain. A logical formulation for further investigation presupposes the need for more detailed knowledge about the functional anatomy of the limbic system and its relationship with the rest of the nervous system. Essentially this involves an inquiry into the origin, transmission and destination of signals passing through this part of the brain. As part of this study the present investigation was undertaken to demonstrate the interrelationship of the limbic and extralimbic cortex. The method of physiological neuronography developed by Dusser de Barenne and McCulloch (4) provided an appropriate method for this purpose. A comparative study limited to two such easily available and commonly used laboratory animals as the cat and the monkey was decided upon in the hope of obtaining information regarding phylogenetic trends of the organization of this relationship.

Analysis of the neuronographic data obtained in the present experiments suggested that on the basis of their reciprocally related parts the limbic and extralimbic cortex could be divided into five large regions. This first paper reports the findings in the cat. Certain comparative aspects of the study will be considered in both this and the following paper on the monkey.

<sup>1</sup> Aided by a grant from the Veterans Administration, Contract No. VAM 23379-A.

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## MATERIALS AND METHODS

The method of physiological neuronography developed by Dusser de Barenne and McCulloch (4), and since modified by other workers, was selected for this study on the grounds that it gives one an estimation of the extent of functionally related cortex. There has been some doubt expressed as to whether or not activity induced in a *cortical* neurone by strychnine can pass *cortical* synapses.<sup>2</sup> Significant as this problem is, the fact remains that in a series of preparations where dial anesthesia is used, the firing patterns obtained from a particular area of the cortex are usually similar and do not exceed certain limits. The variations one may find within these limits could conceivably be related to a number of variables such as the size of the area strychninized, the anatomical differences among animals of the same species, the depth of anesthesia, fluctuations of homeostatic mechanisms, manipulative trauma, etc. It is the consistency of the limits beyond which no firing is obtained that gives one assurance that physiological neuronography is a useful method for demonstrating functionally related parts of the cortex.

*Application of method.* A small piece of filter paper (about 2×3 mm.) was soaked in a saturated solution of strychnine sulfate and applied to the cortex. Precautions were taken to prevent the accumulation and flow of cerebrospinal fluid from spreading the strychnine to the surrounding cortex. Silver chloride electrodes were used. The electrode used as a monitor of the spike activity in the strychninized area was referred to an electrode on the scalp. After rapid voltage fluctuations (spiking) appeared (usually within 1 to 5 minutes), the filter paper was removed. Bipolar electrodes whose points were 1.5–2.0 mm. apart were manually employed to explore the distribution of propagated potentials. In the repetition of some experiments where there had been a question regarding the nature of low-amplitude potentials obscured by the ink-writer, the findings were checked by means of an electronically switched double-beam cathode-ray oscilloscope which allowed one to compare in clearer detail the activity at the monitoring and exploring electrodes.

*Animals, anesthesia, and surgical procedures.* Eighteen cats were used in these experiments. Anesthesia was obtained by the intraperitoneal injection of dial with urethane in a dosage of 0.4 cc./kg. of body weight. Supplementary doses were given to maintain anesthesia. Access to the entire lateral aspect of the hemisphere was obtained by a procedure which involved the removal of the temporal muscle, the zygoma, the roof and contents of the orbit, and the calvarium. In those experiments requiring exploration of the medial surface, the sagittal veins were coagulated by electrocautery and then sectioned. Afterwards, gentle traction and packing with cotton patties resulted in an adequate exposure of the medial surface. To gain access to the entire frontomedial surface it was usually necessary to make a subpial resection of the opposite frontal lobe. In all the foregoing procedures, the head of the animal was placed in whatever position afforded maximum exposure of the region to be investigated.

*Experimental procedure.* Restrictions on time and materials made it impracticable to explore the cortex in the depths of the sulci and fissures. In the cat, the superficial limbic cortex is contained in the subcallosal, cingulate, parasplenial, and hippocampal gyri and the pyriform area. The plan in these experiments was to strychninize successive areas of the limbic cortex around the hilus of the hemisphere and to map in each instance the distribution of the propagated potentials. Both negative and positive findings were recorded on brain maps. The extralimbic areas shown to be "fired" in these experiments were then strychninized and the findings similarly recorded. In this way it could be ascertained what portions of the limbic and extralimbic cortex had unidirectional, reciprocal, or no connections. In order to be assured of good preparations, as well as to allow adequate recovery of the nervous elements between strychninizations, only three to four strychninizations were performed on each cat. Whenever possible, successive strychninizations were done on parts of the brain remote from each other.

*Explanation of terminology and figures.* In keeping with the nature of these experiments, a description of the results will be given in terms of the external morphology of the cat's

(Continued on page 320)

<sup>2</sup> A discussion of this problem is precluded here, but at least in regard to the so-called "association" neurones it should be pointed out that there are cytoarchitectural and physiological considerations that suggest their circuitry is such that they are unable, by themselves, to initiate firing of effector neurones (3).

<sup>3</sup> Each cc. contained 0.1 g. of diallylbarbituric acid, 0.4 g. of urethane, and 0.4 g. of monoethylurea.

FIG. 1A, B: The pyriform area fires itself and the cortex of the hippocampal gyrus. Exploration was difficult, but as far as could be determined, no potentials were propagated into the gyrus rectus or the subcallosal gyrus. It will be noted in Fig. 6A and B, however, that these latter structures fire into the pyriform area. Above the rhinal fissure the pyriform area fires into the coronal, orbital, and anterior sylvian, temporal polar and fusiform gyri. It will be seen in the following figures that there is a reciprocal relationship of the pyriform area only with extralimbic cortex contained in the orbital, anterior sylvian and temporal polar gyri. It is the reciprocal connections among all this limbic-extralimbic cortex that define the frontotemporal region. Strychninization of the part of the fusiform gyrus immediately adjacent to the temporal polar gyrus, as well as the more caudal portion (see Fig. 2B), results in no firing of the pyriform area. It is the failure of the fusiform gyrus to reciprocate connections with the pyriform area that determines the caudal limits of the frontotemporal region. Similarly, the rostral margin of this region is established by the finding of no reciprocity of connections of the pyriform area with the coronal gyrus or with the gyrus rectus and subcallosal gyrus.

FIG. 1C: The orbital gyrus overlies the most rostral part of the claustrum. Some investigators consider it to be the homologue of the posterior orbital area of primates. Its inclusion in the frontotemporal region rests on its reciprocal relations with the limbic cortex of the pyriform area and with the extralimbic cortex of the anterior sylvian and the temporal polar gyri (cf. B, D, E). Its other extralimbic connections include those with the anterior ectosylvian, coronal, suprasylvian, and anterior and posterior sigmoid gyri as shown in the diagram.

FIG. 1D: The inferior portion of the anterior sylvian gyrus corresponds to at least part of the insula of higher forms. Its inclusion as part of the frontotemporal region is evident from its reciprocal connections with the limbic cortex of the pyriform area and the extralimbic cortex of the orbital and temporal polar gyri (A, B, C, E). It fires the proximal portions of the sylvian gyri, and in some preparations potentials were propagated into discrete parts of the sigmoid, coronal, and anterior ectosylvian gyri as indicated in the figure.

FIG. 1E: The temporal polar gyrus belongs to the frontotemporal region because of its reciprocal relationship with the limbic cortex of the pyriform area and the extralimbic cortex contained in the orbital gyrus and inferior portion of the anterior sylvian. It fires the greater extent of the sylvian gyri, the contiguous part of the fusiform, and the inferior portion of the posterior ectosylvian.

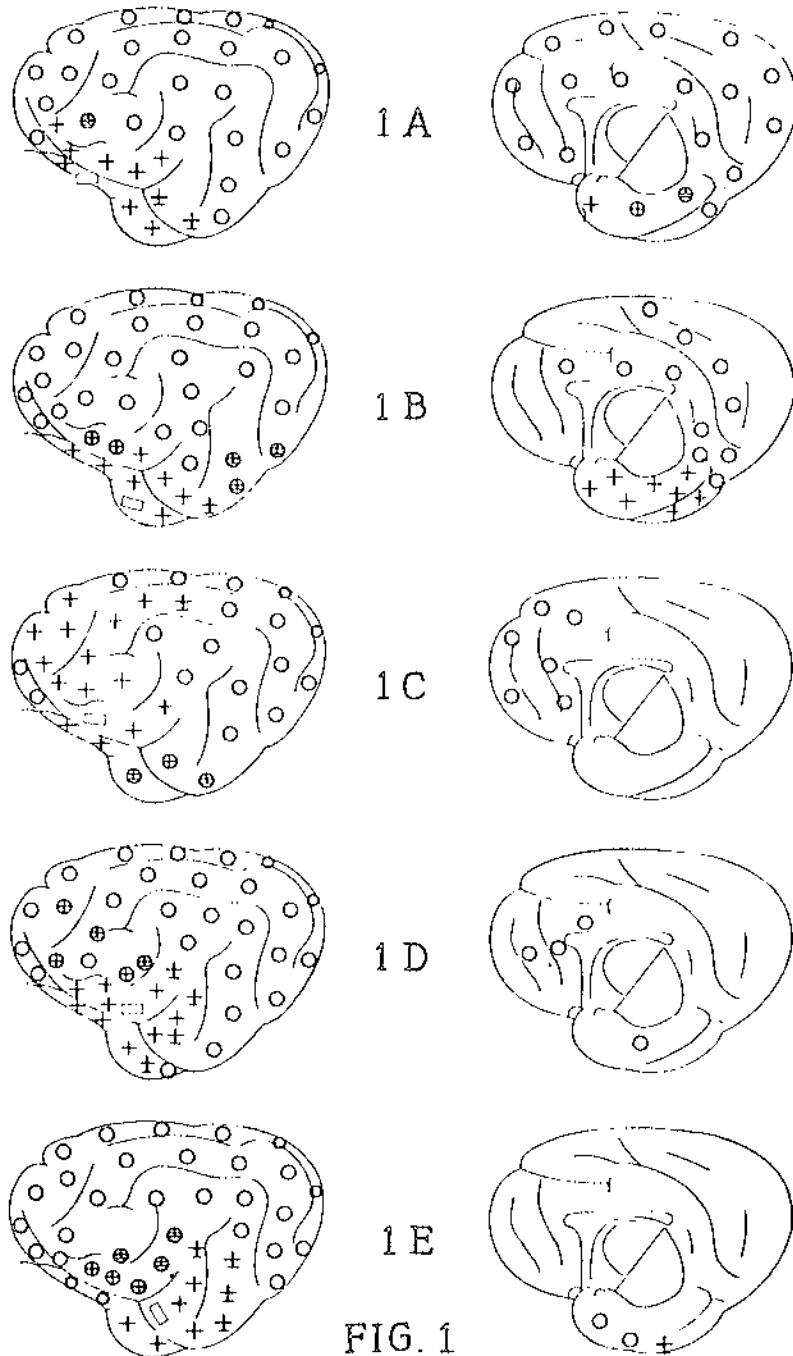


FIG. 1

FIG. 1. FRONTOTEMPORAL REGION.

FIG. 2A: The reciprocal connections of the hippocampal gyrus provide the basis for identifying a limbic-extralimbic region in this part of the brain which may be called the medial occipitotemporal region. As exemplified by the strychninization shown here, this gyrus relates only to the extralimbic cortex of the fusiform and hippocampal fusiform gyri (cf. B, C) which in turn reciprocate connections. Its limbic connections extend forward into the pyriform area, and caudally as far as the parahippocampal gyrus.

FIG. 2B: The fusiform gyrus together with the hippocampal fusiform gyrus (cf. C) comprises the extralimbic portion of the occipitotemporal region, reciprocating connections with the hippocampal gyrus. Reference to 1E shows that there is remarkably little overlap of connections between the fusiform and temporal polar gyri, allowing one to draw a fairly sharp line of demarcation between these contiguous areas in cat. It will be seen in the following paper that an analogous situation holds for monkey (12). Otherwise its extralimbic connections are striking in their extent, including almost the entire suprasylvian gyrus, the inferior portion of the posterior ectosylvian and the entire hippocampal fusiform gyrus.

FIG. 2C: The firing pattern of the hippocampal fusiform gyrus is essentially similar to that shown for the fusiform in the preceding figure, except that it extends into the lingual and suprasplenial gyri and does not involve so much of the posterior ectosylvian. Homologies are immediately suggested when one compares the firing patterns of both this and B with those obtained by Petr *et al.* (10) in their strychninization of the areas they label "TPO" and "TF" in monkey.

FIG. 3A: The parahippocampal gyrus is differentiated from contiguous limbic areas because of reciprocal extralimbic connections that are exclusively confined to the suprasplenial gyrus. This region of reciprocally related limbic-extralimbic cortex may be designated the medial parieto-occipital region. Strychnine applied to any portion of the parahippocampal gyrus results in firing of the whole gyrus (limbic cortex) as well as the proximal portion of the suprasplenial gyrus. If strychnine is placed at the caudal part of the gyrus, as indicated in the figure, there is also firing into the hippocampal gyrus.

FIG. 3B: As stated for A, the extralimbic cortex forming part of the medial parieto-occipital region is contained in the portion of the suprasplenial gyrus lying in proximity to the parahippocampal gyrus. The results of the particular strychninization shown here not only exemplify the reciprocity of connections of this extralimbic cortex with the entire parahippocampal gyrus, but also illustrate the extent of its peripheral firing into the rest of the suprasplenial gyrus forward of the occipital pole and into the lateral gyrus.

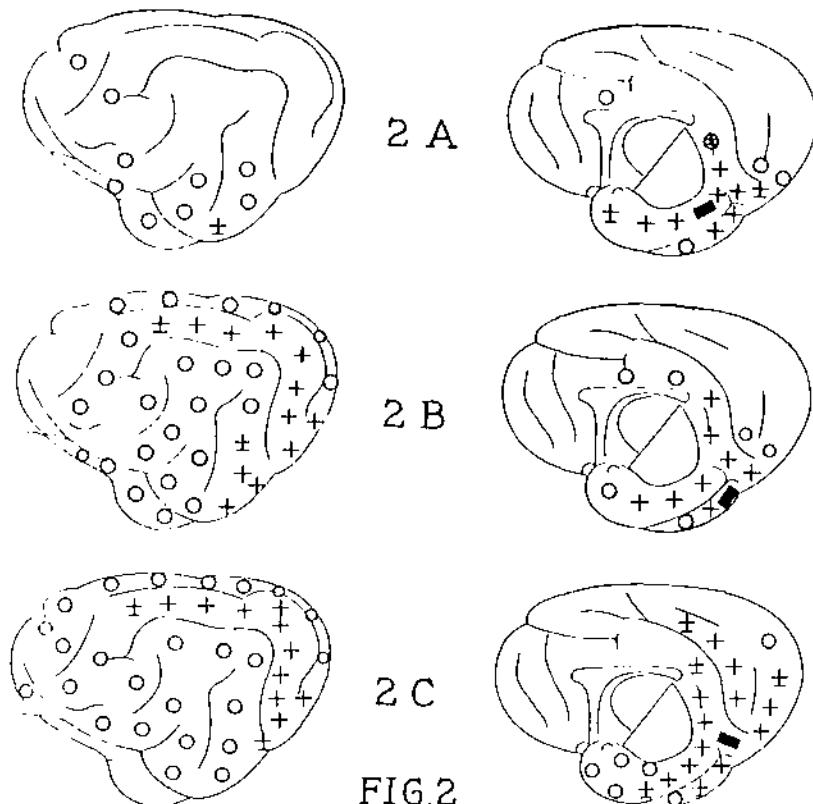


FIG. 2.

FIG. 2. MEDIAL OCCHIPOTEMPORAL REGION.

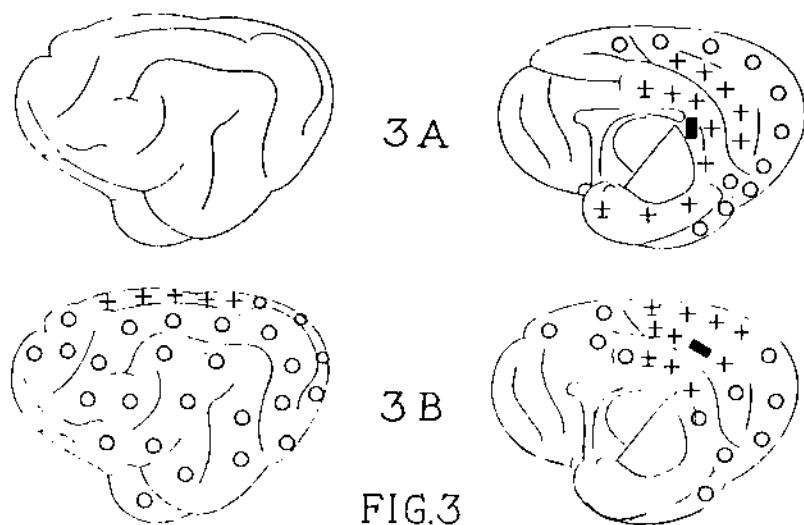


FIG. 3.

FIG. 3. MEDIAL PARIETO-OCCIPITAL REGION.

FIG. 4. This is included to illustrate the nature of the restricted firing that resulted whenever strychnine was applied to any part of the cortex forming the transition between the parasplenial and anterior cingulate gyri. A similar situation appears to obtain in monkey (12). These findings therefore supplied an added reason for dividing the limbic-extralimbic region just considered from the medial frontoparietal region now to be described.

FIG. 5A: The application of strychnine to the part of the cingulate gyrus indicated here resulted in firing of all the limbic cortex comprising this gyrus. The distribution of the extralimbic connections extends forward, superiorly, and caudally across the genui, cruciate, and intercalary sulci, respectively. Only the extralimbic cortex contained in the superior frontal gyrus (cf. B) reciprocated connections with this area, however, and thereby provided a basis for differentiating a limbic-extralimbic region referred to here as the medial frontoparietal region. The schematic representation of the firing pattern has a form that is reminiscent of the "cingular belt" described by Bailey *et al.* (1) in monkey.

FIG. 5B: As just noted, the superior frontal gyrus was the only extralimbic cortex found to have reciprocal connections with the cingulate gyrus. Its firing pattern has the same "belt-like" distribution of the latter, and extends to include the anterior and posterior sigmoid and middle frontal gyri. The comparison of the results of strychninizing the superior frontal and cingulate gyri in cat with those obtained from the same named areas in monkey (12) suggests a striking homology between the limbic-extralimbic regions referred to as the medial frontoparietal in the two species.

FIG. 6A: It is extremely difficult to get access to the subcallosal gyres. Strychninization of this limbic cortex results in firing of the medial surface of the frontal lobe up to the level of the ventral bank of the cruciate sulcus. On the lateral surface, potentials are propagated into the superior banks of the presylvian and anterior rhinal sulci, respectively, as well as into the pyriform cortex and the most caudal part of the inferior frontal gyrus (gyrus proreus). Reciprocal connections with the extralimbic cortex of the ventromedial polar area (cf. B) served to differentiate a limbic-extralimbic region called the medial frontal region.

FIG. 6B: The ventromedial frontal polar area represents the outer extent of the extra-limbic cortex having reciprocal connections with the subcallosal gyrus. Along with the latter it comprises the medial frontal region which is the last of the five limbic-extralimbic regions distinguished in this study. Laterally, the ventromedial frontal polar area fires the inferior frontal gyrus (gyrus proreus) and the cortex just across the presylvian sulcus. In one instance there was firing of the pyriform area.

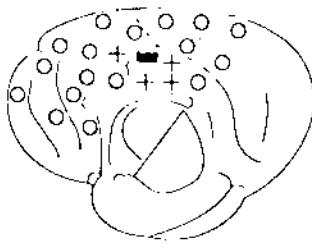
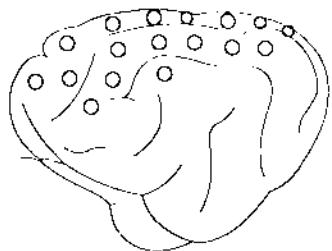
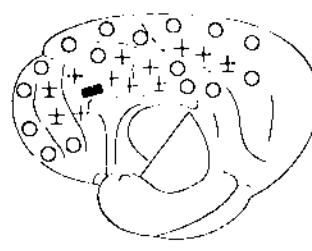
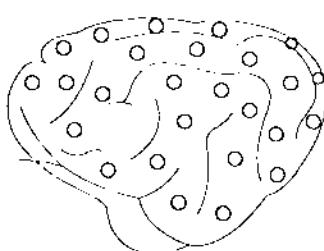
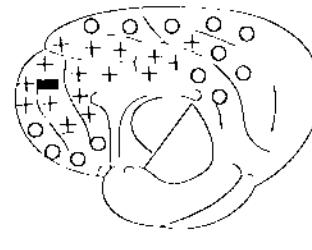
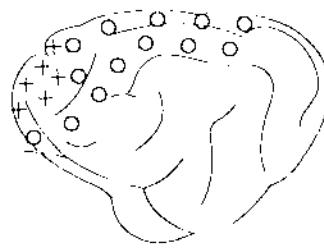


FIG. 4

FIG. 4



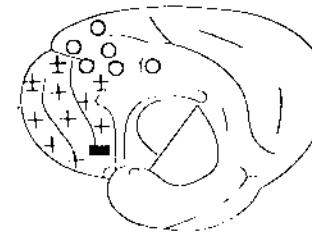
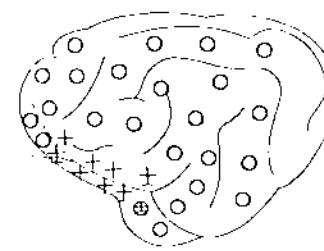
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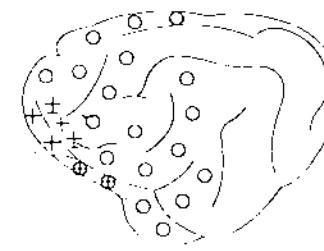
5 B

FIG. 5

FIG. 5. MEDIAL FRONTOPARATEL REGION.



6 A



6 B

FIG. 6

FIG. 6. MEDIAL FRONTAL REGION.

brain. The terminology used to designate the sulci and gyri is taken from Papez's *Comparative neurology* (9) with the exception that Winkler and Potter's (14) term, "orbital gyrus," will be applied to the cortex lying between the diagonal (orbital) and rhinal sulci.

The results of the respective strychninizations are diagrammatically summarized in figures showing the lateral and medial aspects of the cat's brain. In each figure the black rectangle identifies the area strychninized. A positive sign indicates easily identifiable firing; a plus-minus sign, barely detectable firing; and a zero sign, no firing. A plus mark within a zero signifies that a firing of the respective cortex was found in some preparations, but not in others. Unexplored areas are left blank. Except for the superior frontal gyrus all the figures are based on the results obtained in two or more cats. Strychninization of extralimbic areas that did not result in firing of the limbic cortex will not be represented by figures.

### RESULTS

As previously stated, it was not practicable in this study to explore the cortex in the depths of the sulci and fissures. In regard to the superficial cortex, however, it will be seen that almost every portion of the limbic lobe was related to a greater or lesser extent to neighboring parts of extralimbic cortex. Where the relationship was of a reciprocal nature, it was presumed that these respective areas of limbic and extralimbic cortex could usefully be grouped to the exclusion of those with unidirectional connections or no connections. An analysis of all the strychninizations showed that there were five regions comprised of contiguous areas of limbic and extralimbic cortex that could be distinguished on the basis of their reciprocal connections. Together these regions surround the hilus of the hemisphere. Their respective locations, and the strychninizations on which they were differentiated, will now be considered.

To facilitate comparative examination of the data as well as to avoid repetition, the greater part of the textural description of the results will be given in the legends which appear on the page opposite the figures. The legends therefore should be read in continuation as though they were part of the body of the text.

### DISCUSSION

In presenting the results of the individual strychninizations it was indicated how five regions of limbic-extralimbic cortex can be differentiated if one allocates to a region all those areas of cortex that are reciprocally connected. In summary, the five regions and the limbic and extralimbic areas comprising them are tabulated below (Table 1).

The existence of reciprocal connections among cortical areas is indicative that the latter may function together as a unit. In regard to the frontotemporal region, physiological and psychological studies have been performed that support this assumption. Briefly, this work indicates that the frontotemporal region is concerned with organizing the oral and affective behavior of animals as it pertains to feeding, vocalizing, approach and avoidance situations (8, 11). Details of these studies are reported in other communications, as well as investigations on the functions of the other regions.

A number of other findings come out of the present study. If one super-

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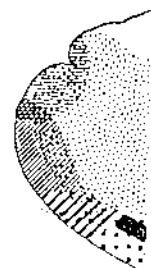


FIG. 7. Diagrammatically divided into five regions of the limbic cortex. (i) The entire limbic cortex is shown. (ii) The five regions are shown to be separated from each other. (iii) Within each region, the various areas are shown to be interconnected. Total area is referred to as the limbic cortex. (iv) The exception of the temporal; (v) the parietal; (vi) the frontal.

Table 1

Region	Limbic Area	Extralimbic Area
1. Frontotemporal	Pyriform area	Orbital gyrus, inferior portion of anterior sylvian gyrus, temporal polar gyrus
2. Medial occipitotemporal	Hippocampal gyrus	Fusiform and hippocampal fusiform gyri
3. Medial parieto-occipital	Parasplenial gyrus	Portion of suprasplenial gyrus contiguous with parasplenial gyrus
4. Medial frontoparietal	Anterior portion of cingulate gyrus	Superior frontal gyrus
5. Medial frontal	Subcallosal gyrus	Ventromedial frontal polar cortex

imposes the firing patterns produced by the areas comprising one of the limbic-extralimbic regions, one finds they form a large cortical segment, e.g., the segment formed by the total area fired by the frontotemporal region and represented in Figure 7 by the bold and fine stippling. Further analysis shows that the extralimbic portion of each region accounts for the firing of the greater part of the extralimbic cortex within respective segments, whereas the limbic portion fires the bulk of the limbic cortex.

In turn, if one were to represent the five segments by various colors and to plot them on the brain of the cat, they would be seen to fit together some-

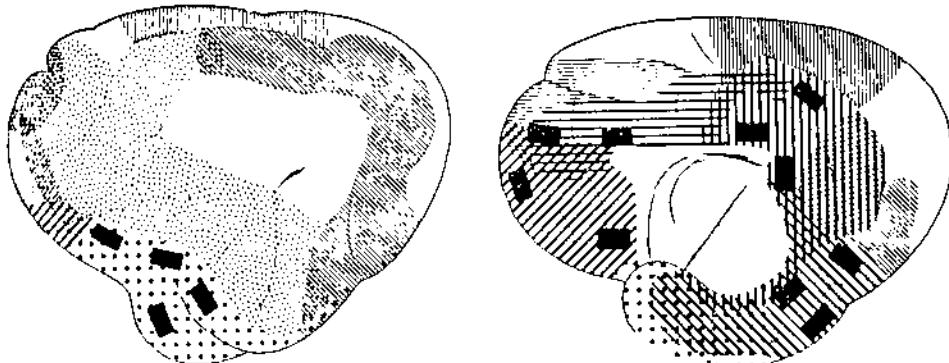


FIG. 7. This figure, depicting lateral and medial aspects of cat's brain, shows diagrammatically distribution of the regions and associated segments described in text. (i) Black rectangles next to hilus of hemisphere indicate representative points of strychninization of limbic cortex; more peripheral rectangles lie on extralimbic cortex. (ii) All rectangles within each variously heavy shaded zone correspond to areas of limbic and extralimbic cortex shown to be reciprocally connected. Such reciprocally connected cortex is referred to as a region. (iii) Heavy black stipple and lines represent extent of cortex fired by limbic portions within each region. (iv) Fine stipple and lines corresponding to that of heavy shading depicts the additional cortex which is fired by indicated extralimbic area(s) within each region. Total area covered by corresponding heavy and light shading forms what is referred to as a cortical segment. Points of overlap between contiguous segments are schematically indicated. Note that the five segments collectively cover all exposed cortex with exception of parts of visual, auditory and somatic projection areas. Regions: □□—frontotemporal; ▲▲—medial occipitotemporal; ▨▨—medial parieto-occipital; △△—medial frontoparietal; //—medial frontal.

what in the manner of a jigsaw puzzle or to resemble an imitation mosaic in which the pigments ran together at the edges. This situation is schematically indicated in Figure 7. Such a schematization also reveals that only a few parts of the cerebral cortex contained in the somatic, auditory and visual projection areas are excluded by the joint firing of the limbic-extralimbic regions (cf. Woolsey's diagrams, 15). Finally, there is to be noted the relationship of two of the limbic-extralimbic regions with those parts of the cerebral mantle that are generally classified as "association" cortex. The extralimbic portions of the occipitotemporal region (fusiform and hippocampal fusiform gyri) fires a striking extent of the arch-like span of cortex formed by the suprasylvian gyrus in which is contained the cortex encompassed by the visual, auditory and somatic areas. And in the frontal lobe the segment fired by the medial frontal region includes the entire so-called "orbitofrontal" cortex which has been distinguished by Rose and Woolsey (13) on the basis of its thalamic connections and which is inferred to correspond in part to the frontal association cortex of higher forms.

It is apparent from the foregoing descriptive material that respective portions of the entire limbic lobe are reciprocally connected to extralimbic areas which in turn relate to all parts of the cerebral mantle with the exception of parts of the visual, auditory and somatic projection areas. When, in addition, it is recalled that the *extralimbic portions* of the regions described in this paper represent the most peripheral parts of the neopallium found to fire into the limbic lobe, it emphasizes the strategic role they must play in all interassociations between the phylogenetically old and new cortex.

In the subsequent paper it will be seen that limbic-extralimbic regions have been found in the monkey which, on a topographical basis, appear to be homologous to those described for the cat. It will also be seen that the large cortical segments which have been pointed out in this discussion to be associated with these regions follow a similar pattern in the monkey.

#### SUMMARY

Phylogenetic, ontogenetic and cytoarchitectural studies, together with recent physiological and psychological investigations, suggest that the limbic system represents an early neural development involved in affectively determined processes. The limbic system comprises the cortex contained in the great limbic lobe of Broca and its associated subcortical cell stations. Further analysis of the functions of the limbic system requires a more detailed knowledge about its anatomical relationship with the rest of the nervous system. This investigation was undertaken to show on a comparative basis in the cat and the monkey the interrelationship of the limbic and extralimbic cortex. The method of physiological neuronography was employed for showing this relationship. This first paper reports the findings in the cat.

Eighteen animals were used in this study. The results indicate that five regions of limbic-extralimbic cortex can be differentiated if one allocates to a region all those areas of cortex that are reciprocally connected. Together

these regions surround the hilus of the hemisphere. They are named according to their topographical location. Further analysis shows that the total area of cortex fired by all points within a region forms a large cortical segment. The five resulting segments collectively cover the entire cerebral mantle with the exception of parts of the visual, auditory and somatic areas.

In the subsequent paper it will be seen that limbic-extralimbic regions have been found in the monkey which, on a topographical basis, appear to be homologous to those described for the cat. It will also be seen that the large cortical segments associated with these regions follow a similar pattern in the monkey. The relevance of these regions and their associated segments to cortical function is at present being investigated and will be reported in subsequent communications.

#### ACKNOWLEDGMENT

We wish to express our great appreciation to Dr. John F. Fulton for his many efforts in our behalf and for his helpful criticism. We also want to thank Dr. Leonard L. Malis for his design and construction of the electronic switch used in this study, and Dr. Hsiang-Tung Chang for his suggestions.

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