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BASAL CEREBRAL CORTEX. II. MONKEY

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NEURONOGRAPHIC ANALYSIS OF MEDIAL AND BASAL CEREBRAL CORTEX. II. MONKEY¹

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ATTEMPTS TO ANALYZE the highly complex behavioral effects of large cerebral lesions of the frontal and temporal lobes have emphasized the need for more information regarding the functional organization of the cortex on the medial and basal aspects of the hemispheres. Comparative, ontogenetic, and cytoarchitectural studies have drawn a distinction between the cortex surrounding the hilus of each hemisphere, known as the great limbic lobe (6), and the rest of the cerebral mantle. It has consequently been postulated that lesions limited to the limbic system and the adjacent related cortex would result in behavioral changes distinctive from those restricted to the phylogenetically newer part of the forebrain. In order to test this hypothesis and to have a guide for making lesions, knowledge was required concerning the related areas of limbic and extralimbic cortex. The method of physiological neuronography was applied in this study for obtaining such information. In both cat and monkey five corresponding large regions, each including limbic and extralimbic cortex, were delineated. The experiments on cat were reported in the preceding communication. This paper deals with the findings in monkey.

MATERIALS, METHODS, AND PROCEDURES

Twenty *Rhesus macacus* monkeys were used. Anesthesia was produced with Dial with urethane,³ half given intravenously and half intraperitoneally, in a dosage of 0.4 cc./kg. of body weight.

Surgical procedures. A combined exposure of the frontal, insular, and temporal regions was obtained as follows: a linear scalp incision was made extending from the vertex and across the temporal region to a point well below the zygoma. The entire temporal muscle and the zygoma were resected. A burr hole in the temporal bone was enlarged to expose the frontal, temporal, and anterior parietal areas. For access to the medial surface of the hemisphere the exposure was extended well past the midline. Adequate exploration of inferior frontal and temporal regions required excision of both the roof and contents of the orbit. The insula was usually exposed by blunt dissection of the pial layers and temporary packing with cotton patties for separating the supratemporal plane from the frontoparietal operculum. After the packing was removed, only intermittent gentle retraction was required to maintain the exposure of the insula. As a control to such manipulation, three animals were prepared in which access to the insula was obtained by resection either of the frontoparietal operculum or the supratemporal plane. A combined exposure of the parietal, occipital, and temporal regions was performed as follows: a semicircular scalp incision which passed through the vertex was made from the zygoma to the cervical region. The temporal and occipital muscles were resected. A burr hole in the temporal bone was enlarged to expose the posterior three-quarters of the hemisphere on that side as well as the contiguous part

¹ Supported by grant from Contract VAM 23379 of the Veterans Administration.

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³ Each cc. contains: Diallylbarbituric acid, 0.1 g.; urethane, 0.4 g.; Monoethylurea, 0.4 g.

FIG. 1A *Posterior orbital area*. Fires precallosal, subcallosal and medial orbital areas; anterior frontal operculum; limen insulae and anterior insula; anterior supratemporal plane, temporal pole, pyriform (periamygdaloid) area; amygdala and anterior hippocampus. In one preparation there was questionable spotted firing just posterior to arcuate sulcus. The connections with the frontal operculum have not been previously described. Otherwise, the findings are consistent with those of Bailey *et al.* (2) and Pribram *et al.* (22). This firing pattern should be compared with those illustrated in remainder of this figure and those in Fig. 2.

FIG. 1B *Anterior insula*. Fires frontal operculum, posterior and posterolateral orbital areas, limen insulae, pyriform (periamygdaloid) area, temporal pole. The reciprocal relationships among areas shown in Fig. 1 form basis for demarcating frontotemporal region. Also fired are amygdala and anterior hippocampus. There are no previous reports on strychninization of this area.

FIG. 1C *Pyriform (periamygdaloid) area (anterior hippocampal gyrus)*. Fires posterior orbital area, limen insulae, anterior insula, rest of hippocampal gyrus, temporal pole, amygdala, and anterior hippocampus. [No firing was obtained from opposite pyriform (periamygdaloid) cortex.] Findings are consistent with those of Petr *et al.* (20) and Pribram *et al.* (22). Compare similarity of this firing pattern with those in other illustrations in Fig. 1.

FIG. 1D *Temporal polar area*. Temporal polar cortex adjacent to rhinal fissure fires entire temporal pole, posterior orbital area, anterior insula, pyriform (periamygdaloid) area, anterior fusiform gyrus, amygdala, and anterior hippocampus. These findings confirm observations of Bailey *et al.* (2), Petr *et al.* (20) and Pribram *et al.* (22). As can be seen, all of the areas illustrated in Fig. 1 fire each other reciprocally. As stated above, this relationship forms basis for delineating frontotemporal region. For demarcation of limits of this region see Fig. 2.

of the opposite hemisphere across the midline. After the bridging veins in the posterior parasagittal and occipitotemporal regions were sacrificed, the hemisphere could be easily retracted for exploring the entire medial parieto-occipito-temporal cortex. The parasplenic and hippocampal gyri were dissected out by freeing the arachnoidal tissue binding them to the brain stem. Oozing of the subarachnoid fluid was controlled by the use of cotton packs and wicks. The hippocampus was approached intraventricularly through an incision in the inferotemporal convolution. In all the foregoing procedures the head of the animal was placed in whatever position afforded maximum exposure of the region to be investigated.

Neuronographic methods. These were described in detail in the previous paper (16).

Experimental procedure and analysis of data. Strychnine patties were successively applied to accessible points of limbic cortex. A map was made of the cortical extent of the propagation of abrupt potential changes (spikes) induced by each strychninization. Negative findings were also plotted. Those extralimbic points shown to be "fired" in these experiments were then strychninized and the findings similarly recorded. Analysis of the data upon completion of all experiments showed limbic and extralimbic points either to be related reciprocally, related unidirectionally, or not related. All points on the limbic and extralimbic cortex that showed reciprocal connections were subsumed under a regional name. Boundaries of regions were demarcated by points showing unidirectional or no connections between the limbic and extralimbic cortex.⁴

RESULTS

Figures and legends summarize the results of 60 strychninizations (not including the repetition of a strychninization of the same area in the same animal, which was occasionally done to check consistency of "firing" pattern). The figures show lateral and mediobasal views of the monkey's cerebral hemisphere. Broken lines indicate externalized hippocampus and amygdaloid formations. The extent and distribution of the "firing" is described on an external morphological basis. The terminology used to designate gyri,

Table 1. Areas included in limbic cortex

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| 1. The cortex surrounding the medial and lateral olfactory striae; the anterior perforate substance and the olfactory tubercle; the subcallosal field of Broca; the limen insulae; the pyriform (periamygdaloid) area. |
| 2. Dentate gyrus, hippocampus (cornu ammonis); subicular formation. |
| 3. The hilar portions of the hippocampal gyrus. |
| 4. The parasplenic gyrus and the supracallosal part of the cingulate gyrus. |
| 5. Cortex of the subcallosal gyrus and hilar part of the medial orbital gyrus. |

sulci, as well as specific areas, is taken from Papez (18). The areas considered to be limbic cortex are listed in Table 1. In the subsequent figures a positive sign indicates "firing"; a zero, "no firing"; \pm designates "minimal firing"; and \oplus signifies "firing" in some preparations but not in others. Unexplored areas are left blank. In the legends of the figures the results of a par-

(Continued on page 334)

⁴There has been some doubt expressed as to whether or not the activity induced in a neurone by strychnine application is stopped at a synapse, and whether all possible connections of that neurone are activated. These problems, though significant in themselves, are irrelevant to the purpose of the present experiments. By describing the limits of the extent of propagation of abrupt potential changes induced by strychninization of a cortical point, this study aimed only at the possible delineation of cortical subdivisions which in subsequent experiments might prove to have functional significance. Cf. also *Methods* described in the preceding paper (16).

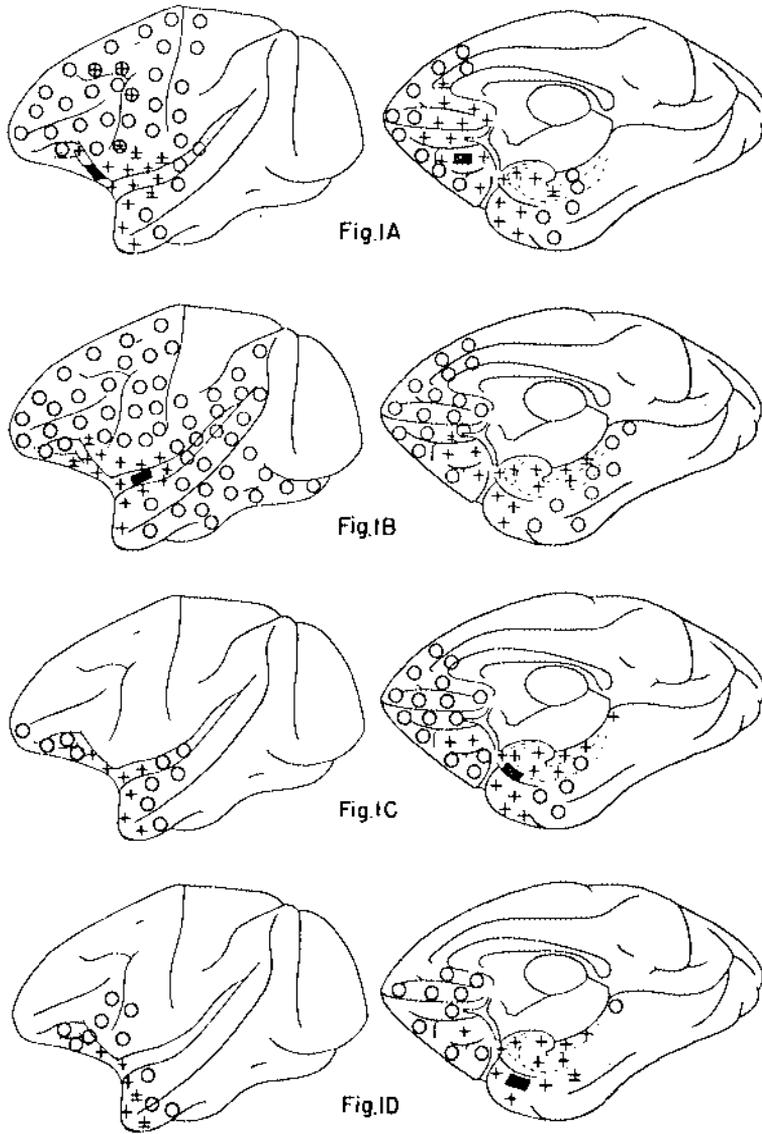


FIG. 1

FIG. 2A *Frontal operculum*. Fires cortex posterior and immediately adjacent to inferior ramus of arcuate sulcus; posterior and lateral orbital areas; limen insulae; and anterior insula. French *et al.* (10) in their investigation of this region reported connections with cortex posterior to inferior limb of arcuate sulcus. This area was found to have reciprocal connections with part of limbic portion of frontotemporal region. Due to technical difficulties, relationship of frontal operculum to temporal polar and pyriform cortex was not ascertained. Inclusion of frontal operculum in the region must therefore be tentative.

FIG. 2B *Anterior supratemporal plane*. Fires adjacent cortex of anterior insula; anterior half of supratemporal plane; superior temporal gyrus and cortex immediately adjacent to it on middle temporal gyrus. Firing of insula has not been previously reported. Other findings are similar to those of Sugar *et al.* (26). This area is outside the borders of frontotemporal region since connections from limbic cortex of temporal lobe to supratemporal plane are not reciprocated.

FIG. 2C *Middle supratemporal plane*. Fires adjacent insula for a short distance anteriorly and posteriorly. Laterally, firing extends across superior temporal gyrus and onto cortex of middle temporal gyrus adjacent to sulcus. Posteriorly greater part of superior temporal gyrus is involved. Firing of insula has not previously been reported; other findings are compatible with those of Sugar *et al.* (26). This area is outside frontotemporal region for the reasons noted above.

FIG. 2D *Posterior insula*. Fires itself and adjacent cortex of parietal operculum and supratemporal plane. In one of four preparations, firing extended forward onto anterior insula. In the latter respect findings are comparable to those of Bailey *et al.* (4) in chimpanzee. Perhaps failure to demonstrate connections with anterior insula in the other three cases resulted from trauma associated with making exposure. There are no other reports of strychninization of this area. Lack of reciprocal connections with limbic cortex of frontotemporal region places posterior insular cortex beyond regional border. *In a similar manner a series of strychninizations of lateral frontal cortex (not pictured) also failed to reciprocate connections with limbic portions of frontotemporal region, thus further delineating regional boundaries.*

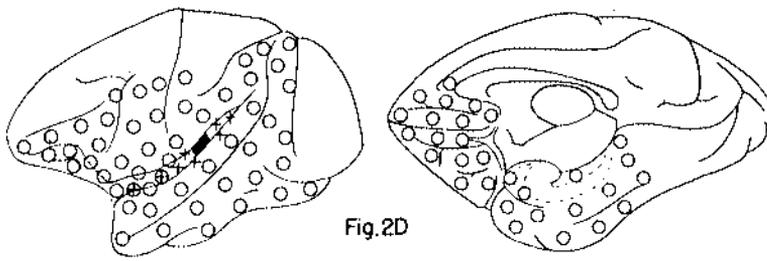
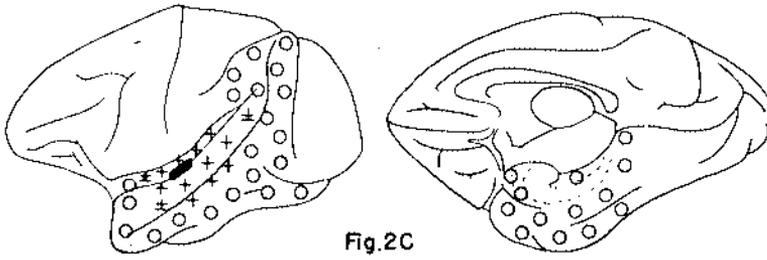
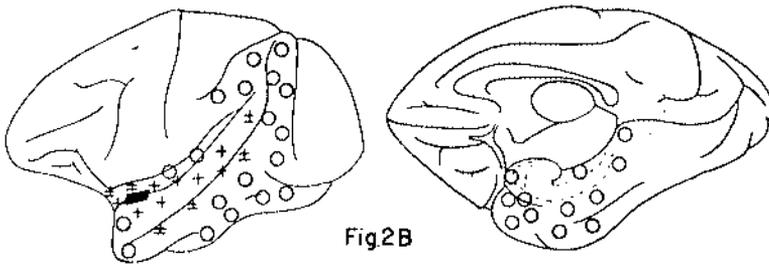
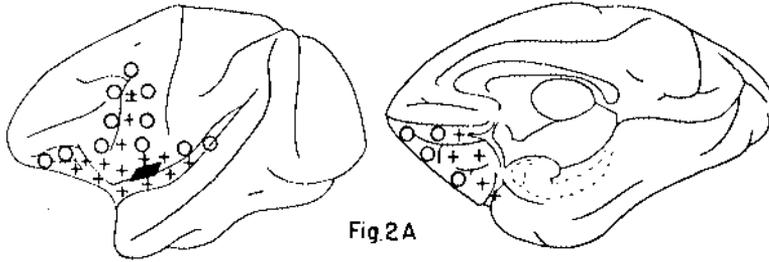


FIG. 2

FIG. 3A *Hippocampal gyrus (Entorhinal area)*. Fires entire hippocampal and fusiform gyri, all but most caudal part of lingual gyrus, parasplenic area and most rostral portion of cuneal gyrus. Sometimes firing does not extend all the way forward on hippocampal gyrus to include pyriform (periamygdaloid) area. In one preparation firing spread laterally just across occipitotemporal sulcus. Firing of lingual, parasplenic, and cuneal cortex has not been previously reported. Rest of the observations are consistent with findings described by Pribram *et al.* (22). Although reciprocal connections exist between this area and some of limbic cortex of frontotemporal region, cortex of hippocampal gyrus must be considered separately since no such connections exist with extralimbic portions of frontotemporal region.

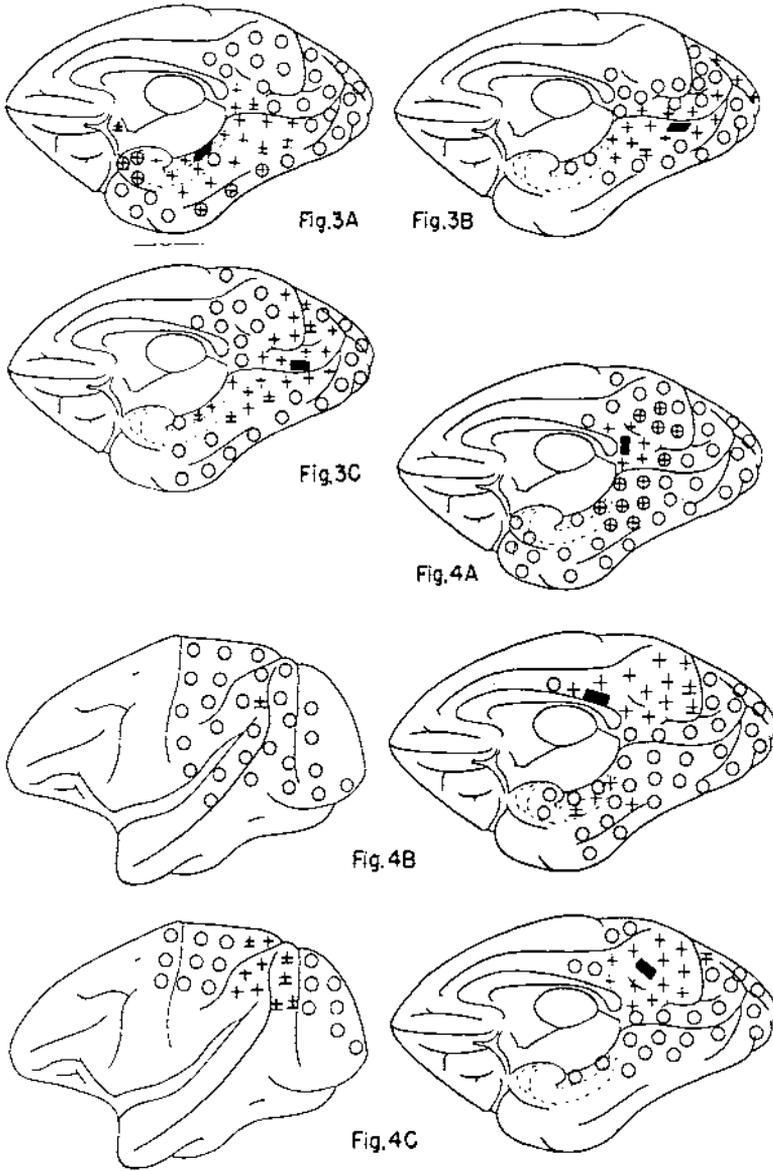
FIG. 3B *Mid-lingual area*. This portion of lingual gyrus immediately below calcarine fissure and about midway between occipital pole and corpus callosum fires medial occipital polar cortex, lingual gyrus, posterior parts of fusiform and hippocampal gyri, and cortex of cuneal gyrus immediately adjacent to calcarine fissure. This is in agreement with the study of functional organization of occipital lobe reported by von Bonin *et al.* (4), with the addition that posterior hippocampal gyrus is brought into firing pattern. Petr *et al.* (20) have shown that strychninization of fusiform gyrus results in firing of hippocampal gyrus. Reciprocal connections between mid-lingual area, fusiform and hippocampal gyri are the basis for region designated as medial occipitotemporal.

FIG. 3C *Mid-cuneal area*. This region of cuneal gyrus immediately above calcarine fissure, and about midway between occipital pole and corpus callosum, fires into posterior parts of hippocampal and fusiform gyri but not into parasplenic area. It fires lingual gyrus along calcarine fissure, entire cuneal gyrus, and cortex along both sides of parieto-occipital fissure. Firing extends over into dorsal margins of posterior marginal and angular gyri but nowhere else on the lateral surface. As noted in 3A, this area is not fired by strychninization of hippocampal gyrus, thus giving boundary of occipitotemporal region. In summary, boundaries of occipitotemporal region are indicated by the unidirectional connection between this area and hippocampal gyrus and parasplenic cortex (4A); absence of connections between precuneal (4C) cortex and limbic portions of region; and, as has already been noted, absence of connections between limbic portions of this region and extralimbic portions of frontotemporal region.

FIG. 4A *Parasplenic area*. Fires into immediately adjacent posterior cingulate cortex and posterior part of hippocampal gyrus. The more extensive firing indicated in some preparations may have resulted from spread of strychnine by seepage of cerebrospinal fluid onto cortex adjacent to parasplenic area. Cf. previous reports by Bailey *et al.* (3) and Pribram *et al.* (22). The more extensive firing pattern suggests that the only extralimbic cortex with which this area reciprocates connections is precuneus. (See Figs. 3B, 3C, 4C). Thus, these areas must be considered separately from medial occipitotemporal region.

FIG. 4B *Posterior cingulate area*. Fires parasplenic, posterior part of cingulate gyrus, precuneus, and posterior part of hippocampus. Firing of hippocampus has not been previously reported, but would be in keeping with anatomical findings of Gardner and Fox (11) in monkey. The other findings are in accord with those of Bailey *et al.* (3). This area also reciprocates connections with precuneal cortex. These relationships among limbic parasplenic, posterior cingulate and extralimbic precuneal areas form basis for demarcating medial parieto-occipital region.

FIG. 4C *Precuneal area*. Strychninization of precuneus at site indicated in figure results in firing parasplenic area, posterior part of cingulate gyrus, entire precuneus, posterior superior parietal gyrus, and posterior marginal and angular gyri. In regard to areas explored, results are in partial agreement with those of Ward *et al.* (27). Inclusion of this cortex in medial parieto-occipital region has been described. Boundaries of this region are delimited by lack of reciprocal connections of limbic cortex of medial parieto-occipital region with extralimbic cortex of medial occipitotemporal region (Fig. 3) and medial frontoparietal region (Fig. 5).



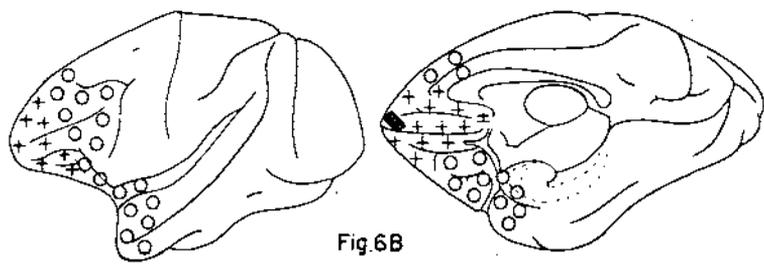
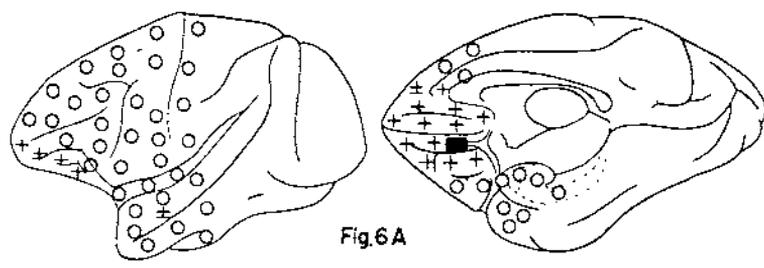
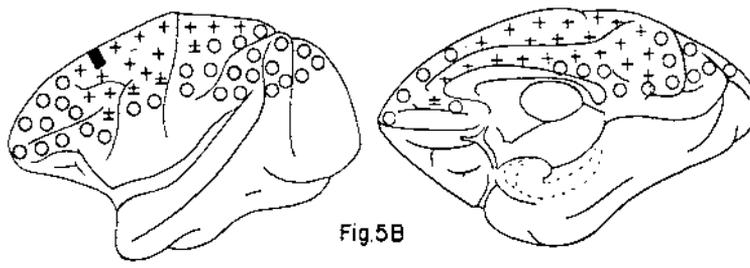
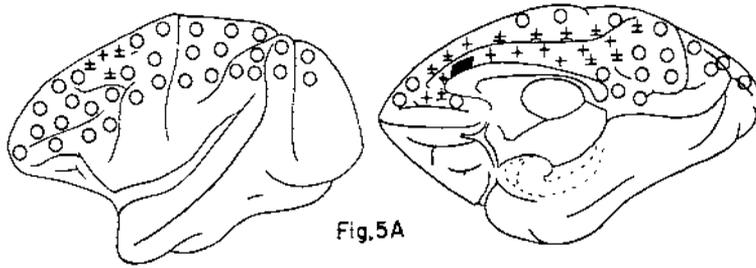
FIGS. 3 AND 4

FIG. 5A *Rostral cingulate area*. Fires superior frontal area and supracallosal cingulate gyrus, together with so-called "cingular belt" bordering callosomarginal sulcus that Bailey *et al.* (3) first described. The connections with lateral surface are in part consistent with the reports of Ward *et al.* (27) and Dunsmore and Lennox (8). Medially, more restricted firing has previously been reported from strychninization of the anterior cingulate in the monkey (3, 22, 27). In the present experiments such results were obtained from strychninization of more caudal portions of cingulate gyrus. Strychninization of rostral cingulate area fails to fire extralimbic cortex of either medial parieto-occipital or medial frontal regions.

FIG. 5B *Superior frontal area*. Extensive firing represented in this figure corresponds to previous report of Dusser de Barenne and McCulloch (9) and extends their findings to medial surface. Supracallosal cingulate gyrus is included in firing pattern. Reciprocal connections between rostral cingulate gyrus and this area are the basis for delineating the medial frontoparietal region. Borders of this region are indicated by findings in Fig. 5A as well as by lack of reciprocal connections between this extralimbic area and the limbic posterior cingulate and subcallosal areas.

FIG. 6A *Medial orbital area*. Fires entire frontal pole, precallosal cingulate and subcallosal areas, and entire basal and medial extent of gyrus rectus as well as anterior lateral orbital and posterior orbital areas. *Firing pattern of this area and that of subcallosal area are identical except that latter extends only slightly beyond orbital sulcus.* These findings supplement those of Pribram *et al.* (22) and suggest that both areas be considered as part of same region. Their lack of connections with extralimbic cortex of frontotemporal region (Fig. 1) and medial frontoparietal region (Fig. 6) furnish the basis for considering the medial orbital and subcallosal areas as being apart from these regions.

FIG. 6B *Ventromedial frontal polar area*. Fires entire frontal polar cortex, precallosal cingulate and subcallosal areas, entire medial and basal extent of gyrus rectus, as well as antero-lateral orbital area. There are no previous reports of reciprocal connections between frontal polar cortex and limbic cortex. (Here is an instance where dubious findings obtained with inkwriter were checked and confirmed by means of cathode-ray oscillograph.) The reciprocal connections between this extralimbic area and limbic subcallosal and medial orbital areas is the basis for demarcating medial frontal region. Boundaries of this region are indicated by lack of connections of frontal polar cortex with limbic posterior orbital and rostral cingulate areas.



FIGS. 5 AND 6

ticular strychninization are compared with similar strychninizations previously reported. To facilitate comparative examination of the data the figures are grouped by regions and the legends can be read as a running text.

DISCUSSION OF RESULTS BY REGIONS

On the basis of reciprocal relationships between limbic and extralimbic cortex, the medial and basal cortex of the cerebral hemispheres can be divided into five large regions. Table 2 summarizes these relationships which are discussed in detail in the following text.

Table 2

Region	Limbic	Extralimbic
Frontotemporal	Cortex surrounding lateral olfactory stria Limen insulae Pyriform (periamygdaloid) area	Posterior orbital area Anterior insular area Temporal polar area Possibly the frontal opercular area
Medial occipitotemporal	Hippocampal gyrus	Fusiform area Lingual area
Medial parieto-occipital	Parasplenic area Posterior cingulate area	Precuneal area
Medial frontoparietal	Rostral cingulate area	Superior frontal area
Medial frontal	Subcallosal area Medial orbital area	Ventromedial Frontal polar area

Frontotemporal region (Figs. 1, 2). McCulloch (14), on the basis of restricted and reciprocal connections of the posterior orbital (1A) and temporal polar cortex (1D) and the absence of known thalamic projections to this cortex, proposed that the term "orbitotemporal" be applied to this division of the brain. The studies of Petr *et al.* (20) and of Pribram *et al.* (22) added the pyriform (periamygdaloid) cortex (1C), limen insulae, and anterior insula (1B) to the cortex connected with this division. The present studies have extended the foregoing findings by showing reciprocal connections to exist between the anterior insula (1B) and this entire division. Furthermore, the frontal operculum (2A) has been shown to have two-way connections with the orbito-insular (1A and 1B) portion of the division. The anterior supratemporal plane (2C) has reciprocal connections with only a very limited portion of the adjacent anterior insula (1B), none with the limbic portions of the region. The posterior insula (2B) and posterior supratemporal plane (2C) appear to be outside the limits of this region. In a similar manner, a series of strychninizations of the anterolateral orbital gyrus and the entire lateral frontal cortex failed to demonstrate connections with the limbic portions of the region. On the basis of the classification proposed above, therefore, the frontotemporal region includes the limbic cortex surrounding the

lateral olfactory striae (limen insulae and pyriform), and the extralimbic posterior orbital, anterior insular, temporal polar areas, and possibly the cortex of the frontal operculum.

Medial occipitotemporal region (Fig. 3). This region is comprised of cortex that shows reciprocal connections among the areas of the hippocampal (3A), fusiform (20), and lingual (3C) gyri. Von Bonin *et al.* (5), in their extensive study of the functional organization of the occipital lobe, presumably did not investigate possible connections of the medial occipital with the medial temporal cortex. The present study taken together with previous findings (20, 22) demonstrates such connections to exist, relating the cortex of the hippocampal and fusiform gyri to make up the medial occipitotemporal region. It clarifies details of the extensive functional relationship of the hippocampal gyrus and the hippocampus with the surrounding cortex that was indicated by Papez (19) on the basis of anatomical studies and which has recently been re-emphasized by MacLean (15). The limits of the occipitotemporal region are marked by the lack of, or unidirectional, connections between the hippocampal gyrus and the cuneal gyrus, as well as the extralimbic cortex of the frontotemporal and medial parieto-occipital regions.

Medial parieto-occipital region (Fig. 4). To this limbic-extralimbic region belongs the cortex that is mutually fired by strychninization of the parasplenic (4A), posterior cingulate (4B) and the precuneal areas (4C). Connections of the parasplenic and posterior cingulate areas with the hippocampus have been demonstrated. Previously reported connections of the cingulate gyrus and of the precuneus with the lateral surface of the hemisphere (3) have been confirmed. The boundaries of the region are established by the lack of reciprocal connections of the parasplenic and posterior cingulate areas with the extralimbic portions of the medial occipitotemporal and frontoparietal regions.

Medial frontoparietal region (Fig. 5). This region comprises cortex that is reciprocally fired by strychninization of the rostral cingulate area (5A) and the superior frontal area (5B). Both the extralimbic and limbic areas strychninized fire the cortex adjacent to the callosomarginal sulcus, the "cingular belt," described by Bailey *et al.* (3). The limits of the region are established by the lack of connections between rostral cingulate cortex and the extralimbic portions of the medial parieto-occipital and medial frontal regions. More restricted firing is obtained from the more caudal portions of the cingulate gyrus (8, 22). Thus only the strychninizations of the most rostral portion of the gyrus define this region.

Medial frontal region (Fig. 6). This merits classification as a region because of the large mass of cortex that is reciprocally fired by strychninization of the medial orbital (6A), subcallosal, and ventromedial (6B) frontal polar areas. Thus, the limbic cortex surrounding the medial olfactory striae (subcallosal field of Broca) is linked with the entire ventromedial frontal extralimbic cortex. The absence of connections between the extralimbic portions of this region and the limbic portions of the frontotemporal and frontoparietal regions marks the boundaries of the medial frontal region.

GENERAL DISCUSSION

Strychnine neuronography has proved a useful method in showing a functional relationship between one part of the cerebral cortex and another. With more and more information accumulating from the application of this method, the analysis of the relevance of this information to cortical function *per se* has temporarily become more difficult. One of the principal investigators (1), utilizing the technique to clarify "problems connected with cerebral function" has recently thrown doubt as to the attainment of this goal. "Unfortunately for our hopes," he states, "these relationships prove to be so complicated as to confuse more often than enlighten." From his own laboratory, however, innovations in the method of presentation of the results of strychninization have given new impetus to an attempt at orderly interpretation. In early experiments, recordings with fixed electrode placements restricted the area of cortex which could be explored during a strychninization. More recently, recording is made with roving bipolar electrodes so that large areas of cortex can be explored during a strychninization. The bias of the early investigators that negative evidence is irrelevant has been overcome; *i.e.*, the results are recorded on charts which include the negative as well as positive findings on the areas explored. Also corrected are the misinterpretations due to presenting results only in terms of correlations with cortical topography based on cytoarchitectural classifications which have varied to a considerable extent during the years in which the neuronographic studies progressed. With these refinements it has become apparent that neuronography demonstrates larger areas of cortex to be contiguously interconnected than had at first seemed to be the case. Thus, these innovations in the method of recording results have helped in the present attempt at orderly interpretation.

Cortical parcellation on the basis of neuronographic findings can be centered around thalamocortical systems which make information from extracortical structures available to the cortex (14). Another basis for evaluation is a purely corticocortical one. It is possible that, in development, the organization of the extralimbic cortex is influenced by the adjacent phylogenetically older limbic cortex. The results of the present study indicate that for the medial and basal cortex, at least, the interrelationship between the limbic and extralimbic cortex provides one method of parcellation. It will be noted that four of the regions that have been identified bridge the grossly defined lobes of the hemisphere—namely, the frontotemporal, medial occipitotemporal, medial parieto-occipital, and medial frontoparietal regions. The medial frontal region is entirely within the confines of the frontal lobe.

The connections of the hippocampal gyrus and the hippocampus bear special mention. The extensive interrelationship of these structures with other parts of the limbic system as well as with the surrounding extralimbic cortex was indicated and given emphasis by Papez (19) and MacLean (15) in their consideration of the anatomical substratum of emotion. The present study has given clarification on a functional basis to many of the cortico-

cortical relationships that they postulated. Thus respective parts of the hippocampal gyrus have been shown to be reciprocally related to the cortex of the frontotemporal and medial occipitotemporal region, and to some of the limbic portion of the medial parieto-occipital region. In the monkey it has been demonstrated that the posterior orbital, anterior insular, pyriform, temporal polar, entorhinal, parasplenial, and posterior cingulate areas comprising parts of these regions, all fire into the hippocampus. Many of these results might have been anticipated on the basis of the anatomical findings of Déjerine (7), Ramón y Cajal (24, 25), Lorente de Nó (12, 13), Gardner

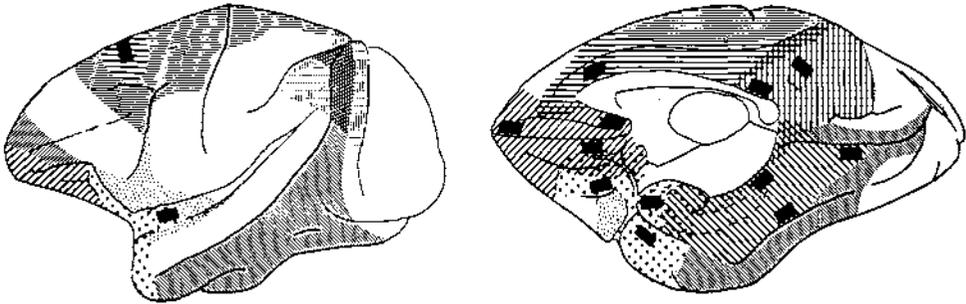


FIG. 7. This figure, depicting the lateral and inferomedial aspects of monkey's brain, shows diagrammatically the distribution of regions and segments referred to in text. It should be compared with Fig. 7 of foregoing paper which shows corresponding regions and segments found in cat's brain. Rectangles indicate representative sites of strychninizations—hilar ones of limbic cortex, more peripheral ones of extralimbic cortex. Coarse stippling or coarser ones indicate regional parcellations; finer stippling or striations (corresponding to the segments). Overlap at borders of regions and segments is shown. Stippling ::::: frontotemporal; rostroventral striations\\\\\\\\: medial occipitotemporal; vertical striations ||||: medial parieto-occipital; horizontal striations ≡: medial frontoparietal; dorsorostral striations ///: medial frontal.

and Fox (11), and others. On the other hand, application of strychnine to the hippocampus itself has been found in previous studies to elicit only local firing (20). So far, physiological neuronography has given no clue as to the functional relationship of those fibers described by Lorente de Nó (13) and assumed by him to be "a recurrent (centrifugal) path from the Ammonshorn to the Area entorhinalis." Finally it is to be noted that the entire frontotemporal region, as well as the entorhinal area of the medial occipitotemporal region, fire into the amygdala.

In both cat and monkey analysis of the data obtained from strychninizations of the medial and basal cortex has delineated five large regions⁵ (cf. Figs. 7 of this and preceding paper). On the basis of topographical loca-

⁵ The hippocampus must be classified separately because its various parts are fired by the posterior orbital, anterior insular pyriform (periamygdaloid), temporal polar, hippocampal gyrus (entorhinal), retrosplenial, and posterior cingulate areas, whereas only local firing has thus far been obtained on strychninization of the hippocampus itself (22). Thus, whereas the limbic cortex of the frontotemporal, occipitotemporal and parieto-occipital regions fires the hippocampus, these connections do not appear to be reciprocated.

tion, certain homologies may be inferred. Names for the regions in both animals were chosen in accord with such inferences. In addition, as can be seen from these figures, the total area of cortex fired by all points within a region forms a large cortical segment. It remains to be determined whether or not such parcellation of cortex into regions and segments serves a useful function in guiding experimental analysis of cerebral specialization. Already, however, with respect to the frontotemporal (21), the occipitotemporal (17), and the medial frontal regions (23), evidence is accumulating that parcellation on a neuronographic basis is superior to that based on gross or microanatomy in obtaining differential behavioral effects by making cerebral lesions.

SUMMARY AND CONCLUSIONS

The method of strychnine neuronography has been used to explore the interconnections between the limbic and extralimbic cortex of the medial and basal aspects of the cerebral hemispheres. Large regional systems can be discerned on the basis of reciprocal connections of all points within such a region. Limits of the region are demarcated by lack of, or unidirectional, connections. The following regional systems have been described.

1. *Frontotemporal*. The classification of this region is based on a firing pattern common to the strychninization of the posterior orbital, anterior insular, temporal polar and pyriform (periamygdaloid) areas. New findings include the demonstration of the firing pattern of the anterior insula as well as the reciprocal connections of the posterior orbital and insular cortex with the frontal operculum.

2. *Medial occipitotemporal*. This region is characterized by the firing pattern common to the strychninization of the cortex of the hippocampal gyrus and portions of the fusiform and lingual gyri. New findings are two-way connections relating the limbic areas of the medial temporal cortex to a variable extent of medial occipital and medial temporal extralimbic cortex.

3. *Medial parieto-occipital*. This region is delineated by the firing pattern common to the strychninization of the limbic cortex of the posterior cingulate and parasplenial gyri and the contiguous extralimbic cortex of the precuneus. Its connections with the hippocampus have been described.

4. *Medial frontoparietal*. This regional classification is based on the firing pattern common to the strychninization of the rostral cingulate gyrus (limbic cortex) and the superior frontal area (extralimbic cortex). The extent of firing of the medial cortex from the superior frontal area is surprising and has not been previously reported.

5. *Medial frontal*. This region is delineated by the firing pattern common to the strychninization of the limbic cortex of the subcallosal and medial orbital areas, and the extralimbic cortex of the ventromedial frontal polar area. The demonstration of interconnections among these areas has not previously been reported.

6. *Hippocampus*. Although no reciprocal connections between hippocampus and the other regions were established, the unidirectional firing of

these regions into Ammon's formation is of interest. The anterior hippocampus is fired by the posterior orbital, anterior insular, and temporal polar and pyriform (periamygdaloid) areas. The posterior hippocampus is fired by the cortex of the hippocampal gyrus and the parasplenial and posterior cingulate areas.

7. The largest extent of cortex fired by strychninization of all points within a region is called a "segment." Cortical segments show considerable overlap at their borders.

8. Comparison of regions and segments in cat and monkey is made.

9. The methods for establishing the relevance of this classification of neuronographic data to problems of cortical function are referred to.

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