[*Reprinted from the* PROCEEDINGS OF THE ROYAL SOCIETY, B. Vol. 82]

Cortical Lamination and Localisation in the Brain of the Marmoset.

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(Received October 20,—Read December 9, 1909.)

[PLATES 6 AND 7.]

The following research is one which has been carried out on lines similar to that previously published by two of us* in relation to the brain of the Lemur. A series of sections of the cerebral cortex has been examined in order to map out the extent and boundaries of the types of cell-lamination observed. It is now well known that these differences are correlated with differences in function, and this method of histological localisation of function (as it may be termed) has been controlled by the physiological method of stimulation. The histological portion of the work has been carried out by two of us (M. and S.), and the physiological experiments were performed at King's College, London, by the third (H.).

Brief Introductory Remarks upon Correlation of Structure and Function.—The smooth brain of the Marmoset stands in structural development in some respects midway between the smooth brain of the Lemur and the convoluted brain of platyrrhine Apes higher in the zoological scale, *e.g.* Macacus. There are certain facts in the morphology, mode of life, and habits of these three types of animals which may be correlated with the differences in structure of their brains. The Lemur is an arboreal animal, and being nocturnal and insectivorous, it depends largely upon smell as a guiding sense. It is not surprising, therefore, to find large olfactory nerves and a relatively large area of archi-cortex. In the Lemur (half ape) the neo-cortex has not developed sufficiently to push the rhinal fissure downwards to the under surface of the temporal lobe as is found to be the case in the Ape.

The eyes in the Marmoset are set so that the visual axes are parallel. The optic nerves are well developed, and, according to Lindsay Johnston, there is a macula; it may, therefore, be assumed that this animal possesses binocular vision, which enables it to employ this sense for obtaining food by seizing with its mouth the insects and fruits upon which it lives.

In contrast with the Lemur, the sense of smell plays a subordinate part

* Mott and Halliburton, 'Roy. Soc. Proc.,' B, vol. 80, p. 136. See also Mott and Kelley, *ibid.*, p. 488, 1907.

in the preservation of the animal, consequently the olfactory nerves and the archicortex are relatively less developed, but the occipital cortex is more developed, and forms a definite occipital lobe covering the cerebellum. The relative extent of the motor area and tactile motor or kinæsthetic area of the neo-cortex of the Marmoset, compared respectively with that of the Lemur and with that of the *Macacus rhesus*, shows that it corresponds more with the former than with the latter. This fact may be correlated with the following statement by Bates concerning the habits of the Marmoset: "they are arboreal animals, but their manner of climbing resembles that of squirrels rather than monkeys; this is due to the fact that they have no means of gripping a bough since the pollex is not opposable, neither is the tail prehensile. They therefore confine themselves to the larger branches, where their long claws are of assistance in enabling them to cling securely to the bark." The Marmosets, owing to their claws and non-opposable pollex, are unable to use their limbs for prehension with anything like the delicacy and refinement of the higher Apes. Although the Marmoset possesses stereoscopic vision, it is unable to translate all visual into tactile-motor impressions to the same degree of perfection as the Macacus, consequently the stereognostic sense must be comparatively rudimentary. This fact may account for the existence of a convoluted parietal lobe which indicates a considerable extension of surface lying between the occipital lobe and the post-central convolutions in the Macacus, which is not found either in the Lemur or in the Marmoset.

General Description of the Brain.

The Marmoset has a small brain, and the surface is broken by unusually few fissures. On the external surface the Sylvian fissure (F. S., fig. 2) is the most conspicuous, and there is also an indication of a lateral sulcus (f. pa.) on the temporal lobe. On the under side of the temporal lobe the rhinal fissure (f. rh.) is found, and it may be noticed that it does not come so far around as in the Lemur, where it is seen on the external surface. Thus in the Lemur there is a larger space between the hippocampal and the rhinal fissures, and, therefore, a more extensive olfactory area than in this animal. On the orbital surface a small orbital sulcus appears. An unbranched calcarine fissure (f. cal.) is seen on the mesial surface extending from the hippocampal nearly to the extremity of the pole. A small hippocampal tubercle lies in front of this hippocampal fissure, and a short intercalary sulcus appears above the corpus callosum, while in the frontal region there is an indication of a small fissure. These sulci, however, are only faintly indicated on the surface of the brain, and only the Sylvian, the hippocampal, and the calcarine fissures show any considerable depth in section. It will also be observed that there is a definite occipital lobe which covers the cerebellum.

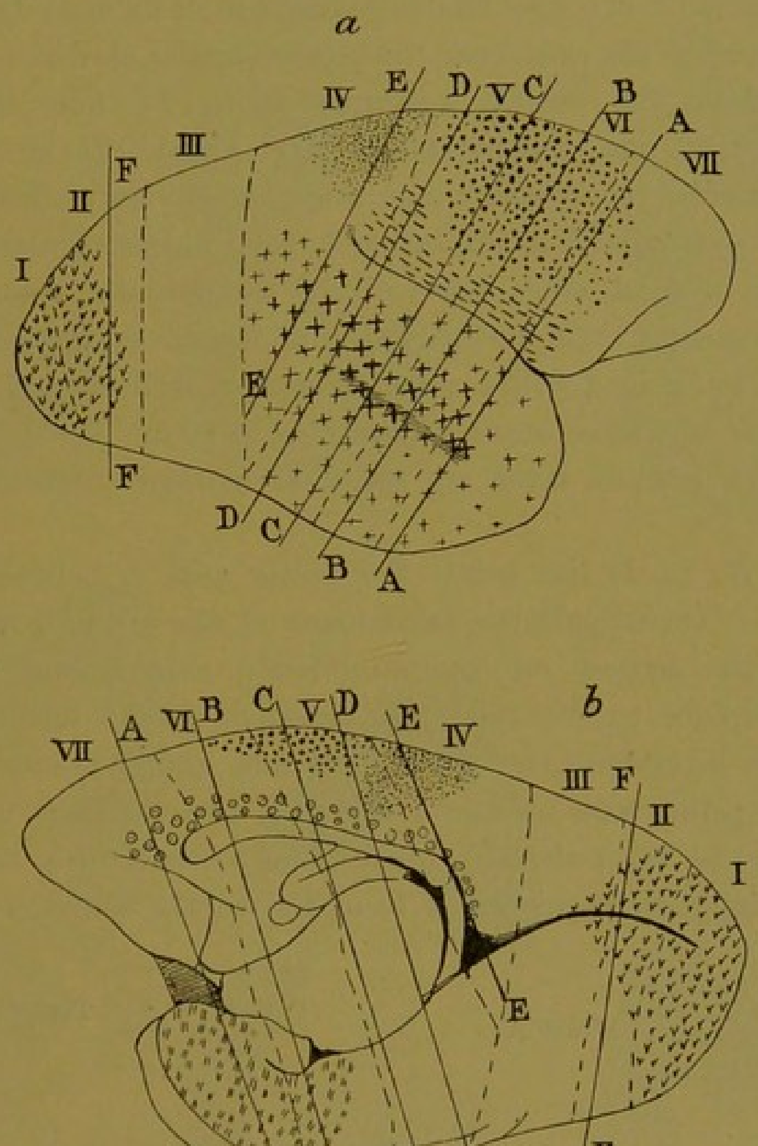


FIG. 1.—Right hemisphere of Marmoset's brain, seen (*a*) from the outer and (*b*) from the mesial surface, × 2. The extent of the different types of cortex described is shown diagrammatically (see key). The lines AA, BB, etc., show the planes of the sections represented in fig. 2. The Roman figures refer to the paraffin blocks made, and have no significance except to the authors.

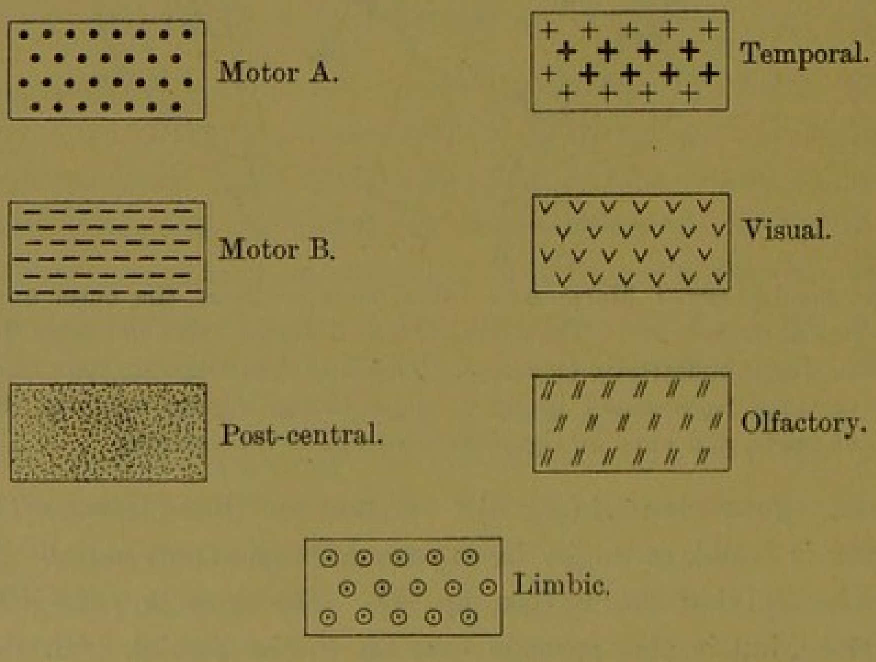
Neopallium. Motor Area A (*fig.* 3).* Extent and Boundaries.—The motor type of cortex is found, as might be expected, on the front half of the brain, and above the Sylvian fissure (see fig. 1). The greater part lies on the external surface, but it also spreads over on to the mesial. On the mesial

* For figs. 3 to 6 see accompanying plates (Plates 6 and 7).

surface, where the post central and limbic types adjoin it, it is not difficult to determine the border line, but anteriorly and posteriorly, and inferiorly on the dorsal surface, the type becomes less characteristic, and gradually its distinctive character is lost as it merges into the intermediate indefinite areas which surround it. The lamination is seen in its most typical form in the posterior part of the area, near the postero-mesial border.

Characteristics.—The cortex measures about 1·5 mm. in depth, the molecular layer 0·1 mm., the pyramidal layer about 0·75 mm., the zone in which the Betz cells lie about 0·2 mm., and the polymorph layer 0·3 mm. to 0·4 mm. The pyramidal cells are rather larger and less regularly and closely arranged than in most other parts of the neopallium. Scattered granule cells are found among them, but they do not form a separate layer. Below the pyramids, lying in a pallid zone, there is a well-marked line of Betz cells, the largest of which measure from 50 μ to 60 μ. These Betz cells, and the absence of a granule layer, are the most marked characteristics of this area.

Motor Area B (*fig.* 4) lies below the motor area A between it and the Sylvian fissure. On stimulation, movements of the jaw and mouth occur as described in the account of the stimulation experiments, but it shows a marked difference to the type just described in its histological details. The molecular layer measures 0·1 to 0·15 mm., the pyramidal layer about 0·75 mm., the pallid zone about 0·1 mm., the granule layer 0·3 to 0·4 mm., and the polymorph layer about 0·3 mm. The presence of a distinct band of granules specially distinguishes it from the cortex above. There is also



Key to diagrammatic representation of different types of cortex in figs. 1 and 2.

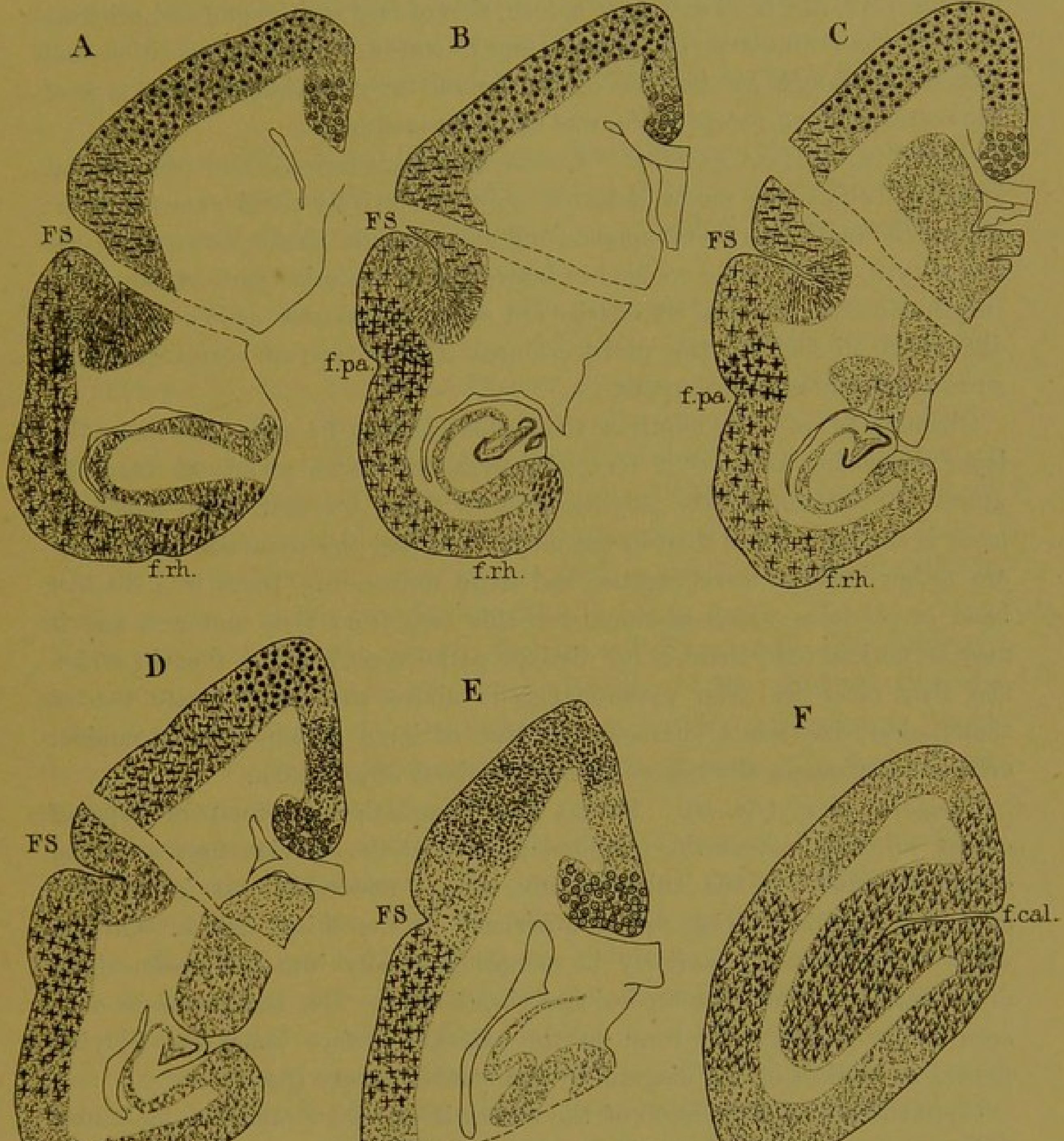


FIG. 2.—Diagrams of six sections, the position of which are shown in fig. 1. FS, Sylvian fissure ; f.pa., lateral fissure ; f.rh., rhinal fissure ; f.cal., calcarine fissure.

a disappearance of the large Betz cells, the largest cells in this area measuring from 25 to 30 μ. It has indeed the appearance of a sensory area, and it is possible that it is a continuation of the post central area. The fact, however, that it was from this part of the hemisphere that movements of the face, jaw, mouth, and tongue were obtained, renders it probable that this is a sensori-motor area. Experiments on the Lemur also showed that movements of the head and eyes, mouth, side of face and tongue and pricking of ears were obtained by stimulating a cortex similar in position and structure; though in the case of the Lemur the essentially sensory type of the cortex, though recognisable, was not so pronounced.

Post Central Area (*fig.* 5). Extent and Boundaries.—The post central type lies behind the motor, covering only a relatively small external area; but on the mesial surface it spreads out and extends farther down than the motor type, and is found wedged in between the posterior part of the motor and limbic areas. These boundaries are only approximate, as it is extremely difficult to distinguish the peri-focal area of this type of cortex from the surrounding intermediate types.

Characteristics.—The depth of the cortex is about 1·4 mm.; the molecular layer measuring about 0·12 mm., the pyramidal layer about 0·6 mm., the granules 0·15 mm., and the polymorph layer about 0·4 mm. The molecular layer is slightly deeper than in the motor area, and the pyramids as a whole are rather smaller, more regular, and more numerous. There is a distinct band of granules which distinguishes this area from type motor A, and it may be noticed that there is no distinct pallid zone, such as that in which the Betz cells lie. The pyramidal cells above the granules are not of remarkable size, but a characteristic line of large plump infra-pyramidal cells is conspicuous, the largest measuring about 35 μ to 20 μ.

Temporal Area (*fig.* 6). Extent and Boundaries.—A temporal type of cortex probably covers the temporal lobe from the Sylvian fissure on the external surface to the rhinal fissure on the underside. It is bounded superiorly by the Sylvian fissure, anteriorly by the rhinal fissure. On the under surface and posteriorly it merges gradually into the intermediate areas lying between the temporal and visual types. But the cortex is only seen in its most typical form on the external surface below the Sylvian fissure, as marked on the diagram by the blacker crosses (fig. 1).

Characteristics.—The depth of the cortex is about 1·5 mm., the molecular layer measuring 0·12 mm., the pyramidal 0·6 to 0·7 mm., the granules about 0·25 mm., and the polymorph layer about 0·5 mm.

In the most typical region the cells of the pyramidal layer, like those in the motor area, are of relatively good size, and are neither very numerous nor regular in arrangement as compared with other regions. The most conspicuous feature of this area is the presence of large, attenuated, deeply staining pyramidal cells, the biggest measuring about 40 μ by 10 μ. These are found both above and below the granules, but are more numerous above. The granule layer is deep and very rich in cells. In its peri-focal area the cortex becomes less typical. As it approaches the anterior extremity of the temporal lobe a comparative poverty of cells is noticeable, both in the pyramidal and granule layers. Posteriorly the pyramids are smaller and more crowded, and in both regions the large pyramids are greatly diminished in size.

Visual Area. Extent and Boundaries.—The visual area covers the posterior pole of the hemisphere. It extends forward on the external surface for about 3 or 4 mm., and on the mesial surface to about halfway between the pole and the corpus callosum, as shown in fig. 1.

Characteristics.—The depth of the cortex is about 1·5 mm., the molecular layer measuring about 0·1 mm., the pyramidal layer about 0·6 mm., the granule layer 0·3 mm., the line of Gennari 0·1 mm., and the polymorph layer 0·3 to 0·4 mm. The pyramidal cells are rather smaller than those of the motor and temporal types, and more numerous, and the granules also are smaller and more crowded. Large solitary cells of Meynert, measuring about 20 μ by 15 μ, are scattered above and below the granules.

In the Lemur the visual cortex is more shallow, and the individual cells are smaller and more closely crowded together.

Archipallium. Olfactory Area. Extent and Boundaries.—The olfactory area lies on the under side of the anterior portion of the temporal lobe, the rhinal fissure forming its inferior and anterior, and the hippocampal fissure its superior boundary. Posteriorly it extends to about the level of the extremity of the rhinal fissure.

Characteristics.—This cortex measures about 1 mm. in depth, the molecular layer measuring about 0·2 mm., the pyramidal layer about 0·4 mm., the pallid zone about 0·1 mm., and the polymorph layer 0·3 to 0·4 mm. Thus, though the cortex as a whole, and the pyramidal layer particularly, are more shallow than in the neopallium, the molecular layer is deeper. A line of characteristic cells lies at the top of the pyramidal layer, larger than the adjacent pyramids, they are more closely crowded together, and form a characteristic darkly staining line under a low power of the microscope. They are angular, and generally quadrilateral in shape, and have several clearly staining branched processes, of which two generally pass upwards into the molecular layer. The pyramidal cells as a whole are comparatively large, though they are not numerous; but there is no line of specially large supra- or infra-granular pyramids. Scattered granules are seen among the pyramids, but do not form a distinct granule layer. A conspicuous pallid zone lies below the pyramids. The polymorph layer is composed of blunt roundish cells, similar to those found in the limbic area.

Limbic Area. Extent and Boundaries.—The limbic area covers the portion of the cortex lying immediately round the corpus callosum, from its anterior to its posterior genu. Sections cut through the hippocampal fissure show a narrow strip of cortex having the same structure bordering the olfactory type, lying between it and the distinctive structures of the hippocampal fissure. It is probable that, as in the Lemur, a narrow strip of limbic cortex is to be found curving around the posterior genu of the corpus callosum, and folding in to the hippocampal fissure, thus forming a link between the upper and lower portions of the limbic lobe.

Characteristics.—The cortex measures 0·8 mm. to 1·0 mm., the depth of the molecular layer being about 0·2 mm. The remainder of the cortex cannot be separated into layers. The cells immediately beneath the molecular layer have a tendency to be pyramidal in form, but below these the mass of them are blunt, shapeless, and faintly stained, only becoming more angular at the bottom of the cortex, in the position of the polymorph layer.

Localisation of the Motor Area by Stimulation.

The animals were anæsthetised either by ether or A.C.E. mixture, and anæsthesia was maintained throughout the whole of the operation until the animals were killed at the conclusion of the experiment.

In dealing with so small a brain, the parts are so delicate that the greatest possible care has to be exercised throughout. In one experiment the animal died from hæmorrhage owing to the injury of a vessel entering the longitudinal sinus, in an attempt to separate one hemisphere from its fellow in order to stimulate the mesial surface, and further attempts to explore this portion of the cerebrum were therefore abandoned.

In the remaining two experiments, in which the greater part of the external surface of the hemisphere was exposed, we obtained concordant results by the method of stimulation. The stimulating electrodes were finely pointed and very close together; they were made of platinum and were connected to the secondary coil of a Du Bois Reymond inductorium arranged for faradisation. The strength of current employed was that which could just be felt as a faint tingling on the tongue. The accompanying illustration (fig. 7) gives the results of these experiments. It represents the left hemisphere seen partly from the side and partly from above, to show the excitable area. This will be seen to be situated wholly above and in front of the Sylvian fissure. If the various figures placed on the diagram are compared with the description beneath it, it will be seen that the head area is a large one, and above this are situated the centres for the upper limb and then those for the lower limb, which is the usual arrangement.

The larger cortical representation of the head and face region enabled one to differentiate its subdivisions much more thoroughly than was possible in the case of the limb movements. Since in catching insects a quick play of mouth and tongue must be required, this may be an explanation of the large cortical representation of the tongue, mouth, and face. Stimulation of the occipital region gave wholly negative results, although this portion of the brain was well exposed and explored as thoroughly as possible with currents of the usual strength, as well as with currents which were somewhat stronger. There is no doubt from histological examination that the

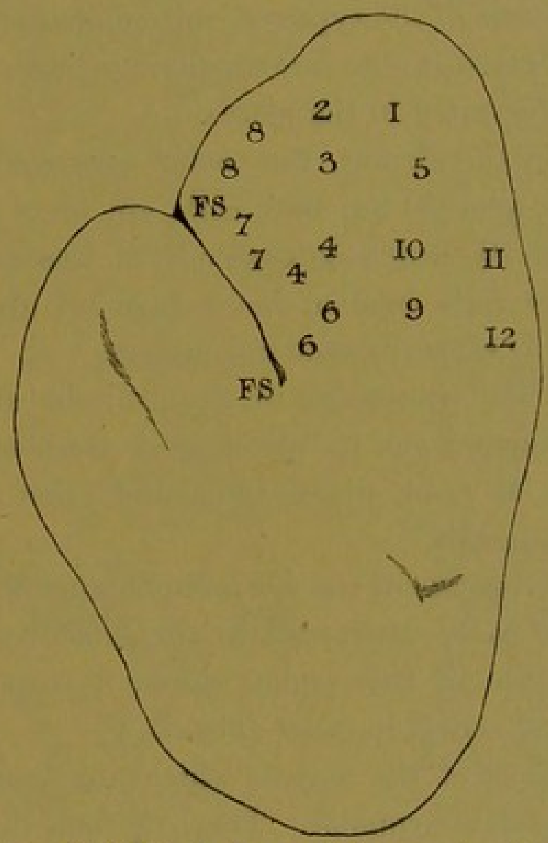


Fig. 7.—Left Hemisphere of Marmoset. Mag. 3·5.

F.S. Fissure of Sylvius. 1. Deviation of head and eyes to opposite side. 2. Opening of eyes. 3. Eye movements. 4, 4. Eye and face movements. 5. Deviation of head. 6, 6. Face movements. 7, 7. Jaw and face movements, including right-sided deviation of mouth. 8, 8. Tongue movements. 9. Extension of wrist to opposite side. 10. Extension of wrist and flexion of arm. 11. Movements of opposite leg. 12. Flexion of opposite hip and knee.

visual area is situated at the occipital pole as in other animals. A similar negative result was obtained on stimulation of the corresponding region of the brain of the Lemur,* and in both cases this is probably due to the distance separating the solitary cells of Meynert in the parts stimulated.

No portion of the cerebral cortex when stimulated give any movements of the external ear; this is in striking contrast to what was found in the Lemur,

* Mott and Halliburton, *loc. cit.*, p. 140.

where the ear area is a large and important one. No experiments of the nature of extirpation were carried out.

Summary.

1. The brain of the Marmoset is small and broken by comparatively few fissures, and of these only the Sylvian, hippocampal, and calcarine fissures show any considerable depth.

2. A series of sections of the cerebral cortex were made to map out the boundaries and characters of the types of cell-lamination which occur. The result of this work is given in the accompanying diagrams, and some of the principal types are illustrated in the plates.

3. As was found in the Lemur, the motor area consists of two types; in one of these (motor area A) the Betz cells are large and conspicuous; in the other (motor area B), which corresponds to face and head movements, not only are the motor cells smaller, but a layer of granules indicates that this part of the brain is sensori-motor in function.

4. By stimulation, the boundaries of the excitable cortex were found to coincide with those mapped out by histological examination. The sequence from below upwards of head, upper limb, and lower limb is that which usually prevails in mammals.

5. Although no movements of the eye were obtainable by stimulating the occipital pole, this is to be attributed to the difficulty of the experiment. Histological examination of this region shows it to possess the structural characters of the visual cortex in other animals.

6. The other portions of the cortex, which are described in full in the text, call for no special comment. They do not differ in any marked character from those previously described in corresponding regions in related animals.

[*Additional Note.*—The cortex of the Marmoset (Hapale) has been mapped out in great detail by K. Brodmann* in a work which has come to our notice only since the completion of our paper.

As this work is rather in the nature of a general summary of the subject of cortical lamination, no special descriptions or figures are given of the numerous types of cell lamination to which he refers. To what extent his results correspond with our own may be seen by a comparison of our fig. 1 with his figs. 96 and 97 (p. 161). It will be noticed that there is a very close agreement with regard to the extent of the visual

* Dr. K. Brodmann, 'Vergleichende Lokalisationslehre der Grosshirnrinde,' Leipzig, 1909.

Fig. 3.—Motor cortex A.

Fig. 4.—Motor cortex B.

Fig. 5.—Post-central cortex.

Fig. 6.—Temporal cortex.

area. While our "Motor A" corresponds in position fairly closely with his Feldern 4 and 6 (area gigantopyramidalis and area frontalis agranularis), the larger dots which in our figures represent the region in which the largest pyramids may be found are spread over practically the same as his Feldern 4.

None of his types appears to correspond with our "Motor B." But its position at its posterior end is occupied in his figure with the lower end of his area post centralis (Feldern 1 to 3). Our post-central cortex occupies much the same position as his area præparietalis (Feldern 5), except that it does not extend so far downwards on the lateral surface. With regard to the temporal and olfactory regions we are in fair agreement.]

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