*Motor Localisation in the Brain of the Gibbon, correlated with a Histological Examination.**

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Motor localisation in the Gibbon has not been hitherto determined experimentally, probably owing to the difficulty of obtaining a suitable animal. It appeared to be desirable, therefore, to see whether the habits and mode of life of this animal could be correlated with an increased development of the motor cortex. One of us (F. W. M.) had some years ago, by a comparative study of the convolutional pattern of the brains of Lemurs and Apes, made the following deduction:† "The remarkable use this animal makes of its arms and hands can be correlated with a remarkable expansion of the cortex in the precentral region, as shown by the development of a broad gyrus extending from the middle of the precentral region to form the second frontal convolution. Now if we turn to the Ape's brain (Macacus), and see what the effect of this development would be, we observe that it would push forwards and downwards that portion of the cortex which on stimulation gives rise to movement of the head and eyes, particularly that which gives rise to eye movements, etc." Figures were shown to indicate that the sulcus arcuatus would be pushed down to join the sulcus rectus. The following experiments by stimulation, correlated with a complete histological examination of the cortex in front of the central sulcus, have confirmed this deduction.

The animal used for the experiments was a male and black in colour; it was remarkably agile; when standing or running on the ground it maintained almost an erect posture, using its long arms to balance itself very much as a man would walk on a tight rope with a balancing-pole. It was kept for some days before the experiment in the animal room of the Physiological Laboratory, Liverpool, and it was frequently heard to utter vocal sounds of very varying pitch and quality. Thus it could imitate the shrill high-pitched whistles of the guinea-pig and the relatively low-pitched bark of the dog. A short account of the larynx of this animal will be made the subject of a future publication.

* A portion of the expense of this research has been defrayed by a Government Grant from the Royal Society.

† "On the Physiological Significance of the Convolutional Pattern in the Primates," 'Brit. Med. Journ.,' 1906.

Details of the Experiments.

The animal was anæsthetised with chloroform and ether, and a light degree of anæsthesia maintained after the brain had been exposed.

The accompanying protocol describes the results obtained, and fig. 1 L and R indicate the points of stimulation.

Protocol of Experiments.

Left Hemisphere.

Unipolar stimulation: diffuse electrode on R. foot; small electrode (ball-pointed, ball about 0·5 mm. diameter); stimulus in Kronecker units (K.U.):—

500 K.U.—

1. Movements of nostril.
2. Retraction of lip, opening of jaw.
3. Turning of head to opposite side.
4. Extension of elbow.
5. Ditto and movement of thumb.

600 K.U. (large electrode with ring loop for application, 4 mm. in diameter)—

6. Flexion of elbow, some retraction of shoulder.
7. Closure of eyelids.
8. Inward rotation of wrist, reaching forward movement from shoulder.

8 (again). Drawing-back movement.

6 (again). Flexion of elbow, drawing-to of shoulder.

8 (again). Drop (flexion) of wrist.

9. Extension of shoulder.
10. Extension of shoulder, accompanied by abduction of wrist, extension of fingers, with a little abduction of thumb (also relaxation of biceps).
11. Elevation of shoulder.
12. Slight flexion of knee.

Bipolar stimulation (stimulus value in centimetres):—

9 cm.—

13. Wrinkling of forehead.
14. Closure of lower and upper eyelids.
15. Forehead and nostril.

Unipolar stimulation: diffuse electrode on L. foot; loop electrode as before:—

600 K.U.—

16. Flexion of hip.
17. Flexion of knee and extension of toes and hallux (succeeded by flexion).

17 (again). Flexion of knee, extension of ankle and toes, going back into flexion.

17 (again). Flexion of hip and knee, extension of foot and toes.

18. Slight flexion of toes (without hallux), extension of ankle with some opening (*i.e.* separation) of toes.

Bipolar stimulation as before:—

18. (again). Slight contraction of toes.

Unipolar stimulation with fine ball-pointed electrode:—

17 (again). Extension of hip and knee, abduction of leg.

17 (again). Abduction.

19. Extension of foot (very slight).

20. Distinct flexion of hip and knee, flexion of toes.
20 (again). Flexion of knee, flexion of hip.
21. Mouth.
22. Retraction of tongue.
22 (repeated). Same results. ($\frac{1}{2}$ cm. of cortex for tongue.)

1000 K.U.—
23. Eyeballs turned inwards and downwards.
24. Upward movement of eyeball.
23 (again). Eyeballs turned downwards and slightly inwards.
23 (repeated). Same results.

1250 K.U.—
Eyes. No result.

Bipolar stimulation :—
9 cm. No result.
8 cm. Mouth moves.

Unipolar stimulation as before :—

1250 K.U.—
22*a*. Movement of tongue (protrusion of opposite side).
22*b* (at lowest point). Movement of tip of tongue.
25. Here a very slight movement of tongue tip was obtained from just behind inferior extremity of central fissure, tip of tongue deviated to opposite side (but see below).

Unipolar stimulation: small electrode :—

800 K.U.—
22*a*. In front of fissure, deviations of tongue as before.
25. And various other points behind fissure, nothing.

1250 K.U.—
22*a*-*b*. Well-marked protrusion and deviation to opposite side.
22*a*–*b* (again). Protrusion, obtained repeatedly.
22*a*–*b* (again). Retraction.
25. Nothing.
25 (again). Nothing (repeated).
(Results obtained above from 25 with large electrode attributed to diffusion.)

Right Hemisphere.

Unipolar stimulation: coarser electrode :—

800 K.U.—
1. Extension of wrist, opening of fingers.
2. Extension of elbow and wrist, flexion of fingers.
3. Flexion of fingers, chiefly index, abduction of thumb.
4. Movements of wrist, tendency to pronation.
5. Extension of fingers, hallux, wrist; some abduction and tendency to pronation.
6. Eye-movements, outward and upward.

900 K.U.—
7. Extension of wrist.

1000 K.U.—
3 (again). Flexion of fingers and wrist (clenching of hand).

(*Interval of* 20 *minutes; stimulation then resumed.*)

As before, but with fine electrode :—

900 K.U.—

8. Primary eversion of foot, followed by inversion ; movements of hip and knee.

8 (again). Slight eversion, then inversion.

9. Slight flexion of hip and knee, movements of trunk (pelvis raised).

8 (again). Movements of trunk, flexion of hip and knee, dorsal flexion of foot.

8 (again). Extension of foot.

9 (again). Marked extension of foot and extension of knee.

Left Hemisphere.

1000 K.U.—

19*a*. Dorsal flexion of (right) foot, flexion of (right) hip and knee (walking movements).

19*b*. As before ; more definite.

Calcarine Region. (*Both Hemispheres.*)

Bipolar stimulation : distance between points widened to 6 mm. :—

8 cm.—

1. Left hemisphere, just above polar end of calcarine ; slight movement of eyeball upwards and to left.

2 (repeated). Movement of eyeball upwards and a little inwards.

3. Right hemisphere, corresponding point to 1 ; movement of eyeball over to left in wavering manner.

6 cm.—

4. Right hemisphere, mesial surface of pole ; movement of eyeball over to left, and somewhat downwards, dilation.

5. Right hemisphere, outer surface (polar region) ; same result.

6. Left hemisphere, similar point to 5 ; eyes move to right.

7. Left hemisphere, at anterior extremity of external calcarine ; same result.

Larynx.

Left Hemisphere.—Bipolar stimulation : wide electrodes :—

6 cm.—

26. Adduction of chords.

26 (repeated). Same results.

26 (again). Adduction of both chords, but chiefly same side.

Bipolar stimulation (C. S. S. stimulating) :—

5 cm.—

26. Slight adduction.

26*a*. Same as 26.

The stimulation of the calcarine region of the occipital lobe was not performed until the motor area had been mapped out, consequently the cortex may not have been in such a favourable condition for excitation. Unipolar excitation gave no definite results; the stimulation so given may not have been diffuse enough. Bipolar excitation invariably produced deviation of the eyes away from the hemisphere stimulated when one pole was placed above and the other below the calcarine fissure; the regions stimulated extended from the mesial surface of the pole of the occipital

lobe along the external surface to the anterior extremity. The electrodes placed elsewhere on the occipital lobe gave no movements. It may therefore be inferred that owing to the infolding of the cortex to form the fissure stimulation of this region by bipolar excitation extended to a sufficient number of motor neurones, or that it is in this region indicated in fig. 1 R by area 28 that the optic radiations terminate in greater numbers than elsewhere in the occipital lobe.

Again, it is probable that unilateral stimulation was inefficient in the production of adduction of the vocal chord, because this experiment was the last performed. Definite movements were obtained for a short time, however, by bipolar stimulation of the region 26 indicated; later on, however, the same strength of stimulus failed to give any response, and the animal was killed.

It is of interest to note that unipolar stimulation gave no result when applied to the ascending parietal convolution; this fact, as we shall see, accords completely with the histological observations.

Histological Observations.

At the close of the experiments, after the animal had been killed, the brain was hardened *in situ* by an injection of formalin solution through the carotid artery. It was thought that in this way the structure of the cells would be best preserved. Subsequent examination showed that this anticipation was not realised, for the preservation was not sufficiently good to make a complete survey of the cell lamination of the whole brain profitable. It was, however, quite adequate for the purpose of determining the extent of the principal areas in the lateral and mesial surfaces of the frontal lobe. For this purpose the brain was divided into blocks, arranged in such a way as to avoid, as far as possible, the necessity of cutting any part of the cortex obliquely or tangentially, and the planes of section were plotted carefully on outline drawings of the surface of the hemispheres. After the blocks had also been drawn, they were embedded in paraffin in the usual way, and cut into sections parallel to their faces. The sections were stained with polychrome methylene blue.

Both hemispheres were examined, but the results have been mapped only on the drawings of the right hemisphere (figs. 2 and 3). Since the types of cortex here dealt with have been often and fully described and figured, and since their structure in this case presents apparently no unusual features, special descriptions or drawings have not been given.

Figs. 2 and 3 show the distribution of two quite distinct types of cortex in the lateral surface of the Gibbon's brain. That portion which is

marked in the diagram with a number of large and small dots is covered by a type of cortex characterised by the absence of a distinct layer of "granules" or "stellate cells," and thus corresponding to Campbell's* precentral and

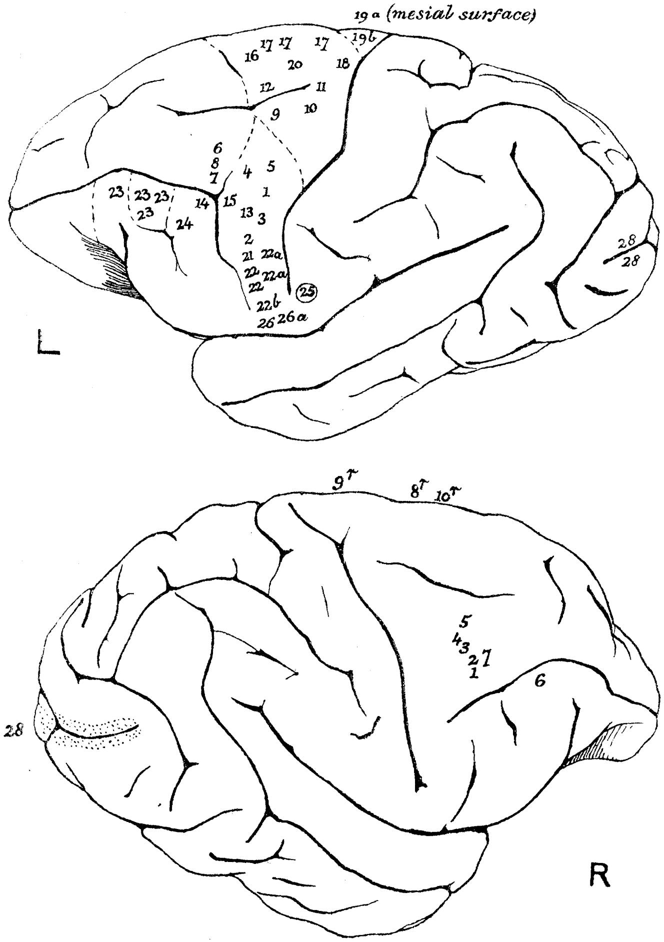

Fig. 1.

L, Lateral Surface of Right Hemisphere ; R, Mesial Surface of Right Hemisphere.

intermediate precentral types, or to Brodmann's† types 4 and 6. The size of the dots shows roughly the relative size of the largest cells in the ganglionic layer or inner layer of large pyramids. The largest of these dots indicate the presence of cells which may safely be called giant pyramids or Betz

* Campbell, 'Histological Studies on the Localisation of Cerebral Function,' Cambridge, 1905.

† Brodmann, "Beiträge zur histologischen Lokalisation der Grosshirnrinde," III, 'Journal für Psychologie und Neurologie,' 1905, bd. 4, heft 5—6.

cells; their position thus marks the extent of Campbell's precentral or motor area, or of Brodmann's type 4. The extent of the intermediate precentral cortex of the former, or type 6 of the latter, is shown by the smaller dots. The Betz cells are most numerous, largest, and cover a wider zone on the mesial surface of the hemisphere above the sulcus cinguli and on the lateral

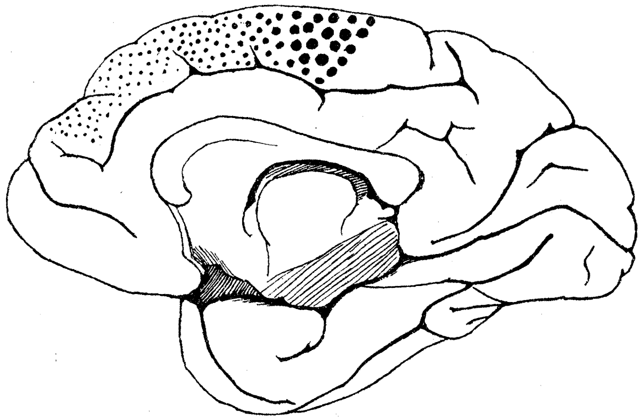

FIG. 2.

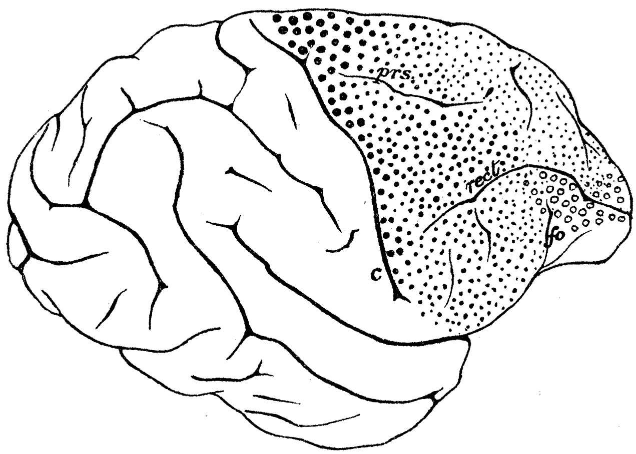

FIG. 3.

prs., Sulcus precentralis superior. *rect.*, Sulcus rectus. *fo.*, Sulcus fronto-orbitalis. *c.*, Sulcus centralis.

The black dots in the above figures indicate the area covered by the precentral (motor) and intermediate precentral types of cortex; the circles the granular frontal type of cortex.

surface in the neighbourhood of the supero-mesial border (fig. 3). On the lateral surface, below the level of the sulcus precentralis superior (*prs.*), they are confined to the anterior wall of the sulcus centralis and to a narrow strip of the ascending frontal convolution lying immediately in front of that fissure.

It will be seen on comparing these figures with Campbell's diagrams of the brains of the Orang and Chimpanzee, that the distribution of the Betz cells is very similar in all three cases. The Gibbon presents perhaps a slightly closer resemblance to the Orang in this respect than to the Chimpanzee.

It is the distribution of the intermediate precentral area which forms the most characteristic feature of the Gibbon's brain. The great forward extension of this area distinguishes it in a very striking way from the Orang and Chimpanzee, on the one hand, and Cercopithecus and the Baboon on the other. This extension is most marked in the region which may be described as the middle frontal convolution, namely, that portion of the lateral surface which lies between the sulcus precentralis superior (*prs.*) above, and the sulcus rectus (*rect.*) below. The area occupied by the granular frontal cortex (Campbell's frontal cortex and Brodmann's type 9) becomes in this way very much restricted, and above the sulcus rectus it occupies only the very small space in the neighbourhood of the frontal pole indicated in fig. 3 by small circles. Below that fissure the layer of granules or stellate cells is well developed in nearly the whole region lying in front of the fronto-orbital sulcus (*fo.*).

Probably as a result of the great development of the intermediate precentral area the sulcus arcuatus, the upper limit of which in Cercopithecus and the Baboon arches round the posterior end of the sulcus rectus, and lies just within or actually forms a boundary to this area, has been pushed downwards to such an extent that it has become continuous with that fissure. This condition can be recognised most clearly in the left hemisphere, where the sulcus rectus has posteriorly a well developed downwardly directed limb, which is clearly the homologue of the lower portion of the sulcus arcuatus; in the right hemisphere it is very difficult to recognise the latter at all.

Another point worthy of attention is that in the cortex of the posterior part of the middle frontal gyrus the large cells of the ganglionic layer, or inner layer of large pyramids, are somewhat larger than in the region lying above the anterior end of the sulcus precentralis superior, or below the sulcus rectus, but are not nearly so large as those which have previously been referred to as unquestionable giant pyramids.