

A Further Minute Analysis by Electric Stimulation of the So-Called Motor Region (Facial Area) of the Cortex Cerebri in the Monkey (Macacus sinicus)

Charles E. Beevor and Victor Horsley

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- III. A Further Minute Analysis by Electric Stimulation of the So-called Motor Region (Facial Area) of the Cortex Cerebri in the Monkey (Macacus sinicus).*
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[Plates 8, 9.]

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Introduction.

In continuation of our former minute analysis of the excitable region of the cerebral cortex, we have explored the so-called centres for the facial, lingual, and pharyngeal movements, or as we prefer to speak of them collectively, the facial area. This district, as will presently be seen, has been mapped out by numerous investigators, and its general limits are fairly well understood; but as we have found in the course of our investigations several points untouched, especially relating to the

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representation of the movements of the tongue, we think it better to arrange the facts previously determined in an historical introduction and to subjoin our own observations. In this, as in our second paper on the minuter representation of movements in the cerebral cortex, we have, in order to avoid discrepancies in the arrangement of the sulci, employed only the same variety of Monkey, viz., Macacus sinicus. In all we have performed twenty experiments.

HISTORICAL INTRODUCTION.

FRITSCH[†] and HITZIG, in the original memoir which forms the basis of all modern research on the subject, contented themselves with defining the foci of representation of movements of the face in the Carnivora.

HITZIG‡ later investigated the point in the Monkey. In his paper on equivalent regions of the brain in Dogs, Monkeys, and Men, HITZIG describes an excitation experiment on a Monkey (Inuus rhesus). The representation of facial movements he obtained in this case was as follows:—The highest point of the facial "region" was "centre 3" and is figured by him as just above the genu of the fissure of Rolando and in the ascending frontal gyrus. At this point he obtained closure of the eye and retraction of the ear. Below this point, excitation elicited, in addition to the ear movement, contraction of the masseters, then movement of the lips, and finally, at a point just above the fissure of Sylvius, the current produced opening (aufsperren) of the mouth. Just above this latter place he obtained retraction of the angle of the mouth, and in neighbouring parts movements of the tongue muscles, depressors of the jaw, elevators and depressors of the hyoid bone. All these latternamed movements were bilateral.

FERRIER. FERRIER, in the Monkey, determined four points in which are represented movements of the facial muscles and tongue, as follows:—

- No. 7. (Situated on the ascending frontal gyrus apparently just opposite and below the genu of the fissure of Rolando, see further, "Anatomy," p. 4), "Retraction and Elevation of the Angle of the Mouth and the Action of the Zygomatic Muscles."
- No. 8. (Situated just below and above sulcus v, see further, "Anatomy," p. 4), "Elevation of the Ala of the Nose and Upper Lip, Associated with Depression of the Lower Lip so as Fully to Expose the Canine Teeth."
- No. 9. (Situated on the lower extremity of the ascending frontal gyrus immediately in front of the sulcus v, see further, "Anatomy," p. 4), "Opening of the Mouth with Protrusion of the Tongue."
 - No. 10. (Situated on the lower end of the ascending frontal gyrus between the

^{* &#}x27;Phil. Trans.,' B, 1888.

^{† &#}x27;Archiv für Anat. und Phys.' (DU BOIS-REYMOND), 1870, p. 300.

^{‡ &#}x27;Untersuchungen über das Gehirn,' Berlin, 1874, p. 132.

^{§ &#}x27;The Functions of the Brain,' 1st ed., 1876, 2nd ed., 1886.

lower end of the fissure of Rolando and v, see further, "Anatomy," p. 4), "Opening of the Mouth with Retraction of the Tongue." "These movements" (described under Nos. 9 and 10) "are occasionally repeated for some time after the electrodes are withdrawn. The movements are bilateral."

No. 11. (Situated on the lower extremity of the ascending parietal gyrus covering the space between the hinder end of the fissure of Rolando and the lower end of the intraparietal sulcus,) "Retraction of the Angle of the Mouth." "The action is that of the platysma myoides, and when this is strong the head is drawn slightly to the side."

H. Munk* confirmed the fact that the movements of the face and tongue were represented in the Monkey in the area delineated by HITZIG and by FERRIER, but did not record minuter details of the localisation.

Schäfer and Horsley.†—These investigators found on sub-dividing the facial area, as marked out by Ferrier, that the broad facts described by him were correct, except that the *upper* part of the area was the seat of elevation of the angle of the mouth, and that the lower half was the region of retraction of the same. (It may be noted that Ferrier, in the last chapter of his book, when he transfers the excitation results from the Monkey's brain to that of Man, places these areas of representation in the reverse order, i.e., the same as Schäfer and Horsley, and, as will presently be seen, the same as we have found it, namely, "Elevation" above "Retraction.) They further observed that just below the upper border of the so-called face region, i.e., just opposite to the lower end of the intraparietal sulcus, the movements of winking and of closure (synchronous) of both pairs of eyelids were therein represented; also that half-way down the vertical limit of the præcentral sulcus and just below it, the movement of drawing in and out of both cheeks was elicited on excitation; also that pouting and pursing of the lips were evoked from the horizontal strip of cortex running forwards from the lower end of the fissure of Rolando towards the præcentral sulcus; finally, from above the Sylvian fissure and between the lower end of the fissure of ROLANDO and "v," it was found that the tongue was actively retracted and also directed towards the side of excitation.

ANATOMY.

The excitable region of the cortex which we have investigated in this research comprises about the lower third of the ascending frontal and parietal convolutions and the commencement of the supramarginal gyrus. More exactly, the area now under consideration is bounded below by the fissure of Sylvius, in front by the

^{* &#}x27;Ueber die Funktionen der Grosshirnrinde. Gesammelte Mittheilungen,' 2te Auflage, 1890, p. 53, also 'Real-Encyclopädie d. Gesammten Heilkunde.'

^{† &#}x27;Phil. Trans.,' 1888 (paper read February, 1887). For certain minute details see also Schäfer, 'Ueber die Motorischen Rinden-Centren des Affen-Gehirns,' Festgabe z. CARL LUDWIG gewidmet, 1887. MDCCCXCIV.-B.

vertical limb of the præcentral sulcus, and by a line drawn from the inferior end of this latter vertically down to the Sylvian fissure, behind by a line drawn from a point just behind the anterior end of the intraparietal sulcus vertically downwards to the Sylvian fissure; and superiorly by a line drawn horizontally across the ascending frontal convolution on a level with the upper extremity of the præcentral sulcus above the bend in the fissure of Rolando, called the genu (inferior genu), and by a line drawn across the ascending parietal convolution from the genu of the fissure of Rolando to the anterior end of the intraparietal sulcus.

In our paper ('Phil. Trans.,' B., 28, 1888) on the minuter representation of the movements of the limbs, we have described and figured the anatomy of the excitable region, with a minor exception, which we must now notice. It will at the same time, perhaps, be useful to enumerate the chief points before described. Reference, moreover, to fig. 1 (Plate 8) will render this more easy.

The mode of termination and form of the fissure of Rolando we have elsewhere* fully described, and need, therefore, only allude to the inferior genu, as showing the position of the borderland between the areas for representation of the upper limb and of the face.

The præcentral sulcus we have fully described in our first paper in the 'Philosophical Transactions,'* but we would here refer to two small sulci in the ascending frontal and parietal convolutions respectively. In the ascending frontal convolution, at its lower part, there is a small vertical sulcus, st in fig. 1, about 3 millims. long, the lower end of which is about 4 millims. from the fissure of Sylvius, and it is situated about 8 millims. behind the præcentral sulcus and 5 millims. in front of the fissure of Rolando. This sulcus, which is very constant in Macacus sinicus, was figured in a previous paper† of ours as "v," and was described by Semon and Horsley‡ as forming the posterior border of the area for the more absolute representation of the vocal cords. In the ascending parietal convolutions there is also a slightly marked sulcus, ret in fig. 1, about 2 millims. long, situated vertically about 2 millims. behind the fissure of Rolando, and the same distance above the fissure of Sylvius and below the anterior end of the intraparietal sulcus. This small sulcus, which is not so constant as the sulcus "v," we propose to call "u."

These two small subordinate sulci are termed by EBERSTALLER, in Man, the sulcus transversus frontalis inferior and the sulcus retrocentralis transversus respectively.

We are inclined to adopt this nomenclature for the lower Monkey also. The point is specially discussed by Professor Cunningham in his memoir "A Contribution to the Surface Anatomy of the Cerebral Hemispheres" (Royal Irish Academy, Dublin, 1892).

^{* &#}x27;Phil. Trans.,' vol. 178 (1887), B, 6, p. 154.

^{† &#}x27;Phil. Trans.,' vol. 179 (1888), B, p. 206.

^{‡ &#}x27;Phil, Trans.,' vol. 181 (1890), B, p. 197.

METHOD OF INVESTIGATION, INCLUDING NOTATION.

Operation and Method of Recording.—In all cases we have exposed the cortex cerebri, with the precautions against cooling, drying, &c., described in our previous papers. After the opening of the dura mater the sulci were, as before, carefully plotted out with fine compasses on paper, ruled mathematically with squares whose sides measured 2 millims. In this way, as before said, we obtained a projection of the configuration of the cortex, the surface of which was thus already divided into squares of 4 square millims. in extent (see Plate 8, fig. 2), an arbitrary number being given to denote each square; these were successively stimulated, and the result recorded. Throughout this paper we shall refer, as before, to these units of localisation as "squares."

In every case the anæsthetic employed was ether, and the animal was killed before it recovered from the narcosis.

Method of Excitation.—The excitation, as before, was applied by fine platinum electrodes 2 millims, apart and furnished from the secondary coil of a Du Bois-Reymond inductorium served by a one-litre bichromate cell. The strength of the faradic current used was very weak, the distance of the secondary coil varying from 12 to a maximum of 9 centims. Momentary application of the electrodes was also resorted to for the detection of the initial contraction. For the complete development of any movement, and at the same time ensuring against the incidence of epilepsy, we found that usually 2 seconds was a sufficient duration for the stimulus.

Arrangement of the Results Obtained.—Even with every effort to obtain an animal of the same size and age and of the same variety, it is nevertheless impossible to avoid certain minute differences which render difficult the direct transference of the facts relating to one square in one animal to another square in another experiment.

We combined the results of our twenty experiments in the following manner, and from control observations subsequently carried out are sure that our procedure has not involved any serious error.

Mode of Notation.—As in each experiment we had made exact drawings of the sulci on the ruled paper (see fig. 2), it was easy to denominate the horizontal lines of squares in successive order from the fissure of Sylvius by capital letters, viz. :— A, B, C, D, E, &c. (see fig. 2), whereas the vertical rows were designated by italic letters a, b, c, d, e, &c., commencing opposite the precentral sulcus and proceeding from front to back.

In this way any given square could be at once fixed and spoken of, for example, as Ad, Fe, &c. When thus in possession of a general classification the average position and inclination of the sulci could be discovered and pricked off.

By this means we constructed fig. 2, in which is correctly given the average position of the sulci and size of the gyri in all the cases observed by us.

Having therefore before us the average configuration of the area under discussion

and having denominated the squares subdividing it as above stated, the aggregation and collocation of the individual observations in each experiment became a very easy matter, since for any given portion of the surface explored the result of excitation in each animal was placed under the same heading.

To guard against the fallacy of producing a state of hyper-excitability in any one direction and to check our results containing the arrangement of representation, *i.e.*, whether vertical, or lateral, we moved the electrodes in different experiments sometimes vertically from square to square, at other times horizontally.

PRELIMINARY CONSIDERATIONS.

Before giving a detailed account of the results obtained in these experiments, it will be advisable to say a few words about the phenomenon of bilateral representation.

Bilateral Representation.—In a previous paper* by us on the excitable fibres of the internal capsule the question of bilateral representation was discussed. The views of Broadbent were there referred to, viz.:—that bilateral movement was effected by impulses passing from the sound hemisphere across commissural fibres postulated to exist between the lower (i.e., bulbo-spinal) centres of the two sides; we gave also a list of movements credited as being bilaterally represented. As this question is so important, we have reproduced this list (see Table), and desire to comment further upon it.

Table 1.—Credited as Bilateral.

Movements of trunk muscles,	$i.\epsilon$	2., 1	ect	us	ab	dor	nin	is
Certain movements of tongue			•					Class I. Not bilaterally represented.
Conjugate deviation of eyes Turning of head	•	:	:	•	:	•	•	Class I. Not bilaterally represented.
								Class II. Imperfectly bilaterally represented.
Pursing of lips							•	Class II
Opening of eyelids			•				•	Imperfectly bilaterally re-
Closing of eyelids	٠	•	. •	٠	•	•	•	presented.
Opening mouth	٠	•	•	•	•	•	•	• •
Elevation of soft palate	٠	٠	•	•	•	٠	٠	•)
Pouting of lips								Class III. Truly bilaterally represented.
Mastication					٠		٠	Truly hilaterally renre-
Swallowing	•	•	٠	• *	•	•	•	sented.
Adduction of vocal cords .								.]

In our previous paper on the Internal Capsule we showed that movements of a special character and which we have placed in Class I. being elicited from only a definite part of the cortex, could not be regarded as being bilaterally represented, *i.e.*, as being represented in both hemispheres, and being evoked by excitation of either hemisphere. Consequently, for these movements, no substitution of function by the opposite side of the brain is conceivable.

^{* &#}x27;Phil. Trans.,' vol. 181 (1890), B, p. 73.

We desire now to say a few words respecting the present use of the term, bilateral movement, and also the term, bilaterally associated movement. As regards bilateral movement we believe we are right in stating that the general use of this term at the present time is partly the same as that of bilaterally associated movement, but this second term premises that there is an association between the representations in the nervous system of so-called bilaterally associated movements. We venture to think that the term bilateral movement should be strictly confined to its simplest meaning, viz., that in the execution of any definite muscular action or movement the muscles of both sides of the body are involved, though not necessarily to the same extent, or that the muscles acting are of the same name. We would urge that, physiologically speaking, the term bilateral movement can only mean simultaneous action of muscles on both sides of the body, and ought not to be used for the representation of those muscles in the nerve centres. We believe that a certain degree of laxity in the use of this expression has crept in by the employment of the word "associated." term association connotes physiological co-operation and arrangement in the nervous system, i.e., motor representation when the term is applied to movements. With this view the expression "bilaterally associated movement" has been frequently used to characterise the activity of the trunk muscles. We showed in our Internal Capsule paper that this was not justified by the facts, since the somatic or trunk muscles are as unilaterally represented, with the exceptions denoted in Table I., as are the This point has been treated of late by Sherrington,* who has since limb muscles. shown that even the sphincter ani is unilaterally represented. Whatever may be the physical condition, i.e., movements of different muscles for the performance of definite acts, there does not seem to be any ground for assuming, as has been so frequently done, that certain muscles, e.g., those of the trunk, act in association, or that they are, therefore, bilaterally represented.

Apart from the special physiological interest attaching to this question of bilaterality, it is impossible for neurologists to correctly appreciate the pathology of epilepsy or the restoration of function when certain districts of the cerebral hemisphere have been destroyed until this question has been settled.

ANALYSIS OF RESULTS.

We have arranged the movements elicited by excitation of the region observed according to the following classification.

I. Orifacial Movements.

$ \begin{pmatrix} (a) & \text{Upper face} & \cdot \\ (2) & \\ (3) \end{pmatrix} $	
A. Face $\begin{cases} (b) \text{ Lips.} & . & . & . \begin{cases} \binom{1}{2} \\ 2 \end{pmatrix} \end{cases}$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
	Angle of mouth . Retraction of Opposite side Same side Bilateral
$ \begin{array}{c} (c) \text{ Lower face} \\ (3) \\ (4) \\ (5) \\ (6) \end{array} $	Angle of mouth . Retraction of
B. Tongue $\binom{(1)}{(2)}$	Movements towards the opposite side Movements towards the same side Bilateral movements
	$\begin{array}{cccc} \text{Single movements} & \cdot & \cdot \begin{cases} \text{Lateral} \\ \text{Vertical} \end{cases} \\ \text{Rhythmical movements} & \cdot & \text{Mastication} \end{array}$
D. Pharynx	$egin{array}{ll} ext{Soft palate (elevation of)} & egin{array}{ll} ext{Opposite side} \ ext{Same side} \ ext{Bilateral} \ ext{Swallowing} \end{array}$

II. Movements otherwise than Orifacial.

A. Head.

B. Upper Limb.

We will now take the movements observed in the present research, seriatim, and give in detail first the squares in which they are represented, arranging these in the order of greatest frequency of occurrence of the movement. Under the same heading we shall treat of the individual points of importance and interest observed for each movement.

I. ORIFACIAL MOVEMENTS.

A. Face.

(a.) Upper Face.

(1.) Representation of the Movements of the Eyelids.

(a.) Closure . . . $\left\{ \begin{array}{ll} \text{Opposite eyelids.} \\ \text{Eyelids of both sides.} \end{array} \right.$

(b.) Opening . . . Eyelids of both sides.

(a.) Closure of Opposite Eyelids (fig. 3).—This movement, which possesses a well-defined focus of representation in the Monkey's cortex, corresponds to that seen in the cortex of the Dog (vide Fritsch and Hitzig, Ferrier, Luciani, Paneth, and others).

Closure of the opposite eyelids was noted by us to occur at the following squares in the order of greatest frequency, as shown by the numbers:—

6.	5.	5. 4.		2.	1.					
$_{ m Hj}$	Fj Gj	$egin{array}{c} \mathbf{F}i \ \mathbf{G}i \ \mathbf{I}g \end{array}$	$egin{array}{c} \mathbf{F}k \ \mathbf{F}l \ \mathbf{I}i \end{array}$	Ih	$egin{array}{cccccccccccccccccccccccccccccccccccc$					

It will be understood that excitation of these points elicited only closure of the pair of eyelids of the opposite side to that of the hemisphere stimulated. It is very well shown to be unilateral in instantaneous (flash) photographs taken during excitation. We only once observed bilateral action, viz., closure of both pairs of eyelids at Gj.

There is in addition a very characteristic bilateral movement of the eyelids (i.e., both pairs), popularly termed blinking, which requires description. This consists of a rhythmical closure, or opening of both pairs of eyelids. This is, of course, quite different to the movement just mentioned. We observed it to occur in three separate experiments upon excitation of the square F_j .

- (b.) Opening of the Eyelids of Both Sides.—This movement we do not regard as being specially represented in the area under discussion (i.e., posterior to the sulcus præcentralis, inferior and anterior to the lower end of the intraparietal sulcus), because, as has been shown by other investigators besides ourselves, the focus of this movement is situated in front of the præcentral sulcus. We noted it, however, to occur once at Ie in an animal in which the ascending frontal gyrus was exceptionally broad.
 - (2.) Representation of the Movements of the Eyes.
- (a.) Conjugate Deviation of the Eyeballs to the Opposite Side to that of Excitation.

 —This well-known movement, the chief focus of which is situated in front of the præcentral sulcus, we elicited from the squares—

2.	1.
Gĺ	$rac{\mathbf{E}l}{\mathbf{F}m}$

These squares, it will be seen, are situated at the commencement of the supramarginal gyrus, or, as it is often improperly termed, the anterior limb of the angular

gyrus, wherein this movement has previously so often been observed to be represented (vide Ferrier, Luciani, Schäfer).

We observed no other movements of the eyeballs.

(3.) Angle of Mouth, Elevation of.

We subdivide the representation of the movement of elevation of the angle of the mouth under the following headings:—

- (a.) Elevation of the opposite angle of the mouth.
- (b.) Elevation of the angle of the same side.
- (c.) Elevation of both the angles of the mouth.
- (a.) Elevation of the Angle of the Opposite Side (fig. 4).—This, by far the most frequent movement of elevation, was observed at the following large number of squares:—

7.	6.	5.	4.	3.	2.	1.
$rac{\mathrm{G}g}{\mathrm{G}h}$	$egin{array}{c} \mathrm{E}j \ \mathrm{G}f \ \mathrm{G}i \ \mathrm{H}h \ \mathrm{I}g \end{array}$	$egin{array}{c} \mathbf{E}k \ \mathbf{F}g \ \mathbf{H}g \end{array}$	$egin{array}{cccc} \mathrm{D}k & \mathrm{H}f \ \mathrm{E}i & \mathrm{I}h \ \mathrm{F}h \ \mathrm{F}j \ \mathrm{F}k \end{array}$	$egin{array}{c} \mathbf{E}g \\ \mathbf{F}f \\ \mathbf{F}i \\ \mathbf{G}j \\ \mathbf{H}j \\ \mathbf{I}f \end{array}$	$egin{array}{c} \mathrm{D}i \ \mathrm{D}j \ \mathrm{E}h \ \mathrm{E}l \ \mathrm{F}l \ \mathrm{G}e \ \end{array}$	$\begin{array}{cccc} \mathbf{C}h & \mathbf{E}e & \mathbf{J}f \\ \mathbf{C}i & \mathbf{E}f & \mathbf{J}g \\ \mathbf{C}j & \mathbf{F}d & \mathbf{J}h \\ \mathbf{C}k & \mathbf{G}d \\ \mathbf{D}e & \mathbf{H}k \\ \mathbf{D}l & \mathbf{I}i \end{array}$

As is seen in fig. 4 the focus of greatest representation is at Gg, Gh.

(b.) Elevation of the Angle of the Same Side.—The representation of this movement, which from à priori considerations we did not anticipate finding, was observed in single instances at squares:—

$$Af$$
 Bi Ci Di Fh .

(c.) Elevation of both the Angles of the Mouth.—As a corollary to the facts just related, the actual observation of bilateral representation of this movement of elevation of the angle of the mouth was seen on two single occasions, viz., at squares—

This bilaterality is therefore very rare.

(b.) Lips.

In describing the movements of the lips we have observed occasionally such unilaterality of representation as to lead us to regard the lips, e.g., the upper and the lower, as divisible into two halves, viz., the right and the left. We have, therefore, subdivided the lips into four regions, a right and left upper and lower lip. We thus classify the movements noted, according as to whether they affect the upper or lower

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lip individually, and further whether it is of the opposite or of the same side, or whether both sides move at once. The movements observed are as follows:—

- (a.) Elevation of the upper lip of the opposite side.
- (b.) Depression of the lower lip of the opposite side.
- (c.) Inversion of the lower lip of the opposite side.
- (d.) Inversion of both lips of the same side.
- (e.) Inversion of both lips of both sides, but especially of the opposite side.
- (f.) Inversion of both lips.
- (a.) Elevation of the Upper Lip of the Opposite Side.—This is a rare movement of remarkably unilateral character which differs from simple elevation of the angle of the mouth in that the ala of the nose is not moved. It was observed to occur only once at squares Bj, Cf, and Cg.
- (b.) Depression of the Lower Lip of the Opposite Side (fig. 5).—This movement is represented at the following squares:—

3.	2.	, 1.
\mathbf{F}_g \mathbf{I}_g	$\begin{array}{c} \mathbf{F}e \\ \mathbf{G}g \\ \mathbf{H}g \\ \mathbf{I}f \\ \mathbf{I}h \end{array}$	$egin{array}{cccc} \mathbf{F}h & \mathbf{I}i & \\ \mathbf{G}d & \mathbf{J}f & \\ \mathbf{G}e & \mathbf{J}g & \\ \mathbf{G}f & \end{array}$

- (c.) Inversion of the Opposite Lower Lip.—This, as a solitary movement, occurred only once at Gl.
 - (d.) Inversion of both Lips of the Same Side.—This occurred twice at Eh.
- (e.) Inversion of both Lips of Both Sides, but especially the Halves of the Opposite Side.—In this case the whole length of the upper and lower lips was inverted, but the opposite halves were affected notably more than those of the same side. The movement was found at squares—

2.	1.
$egin{array}{c} \mathbf{F}e \ \mathbf{F}j \ \mathbf{G}i \ \mathbf{G}j \ \mathbf{G}k \ \mathbf{I}f \end{array}$	$\begin{array}{ccccc} \mathbf{A}f & \mathbf{E}c & \mathbf{F}f & \mathbf{H}e \\ & \mathbf{E}d & \mathbf{F}k & \mathbf{H}f \\ & \mathbf{E}e & \mathbf{G}e & \mathbf{H}j \\ & \mathbf{E}i & \mathbf{H}k \\ & \mathbf{E}j & \mathbf{H}l \\ & \mathbf{E}k \end{array}$

(f.) Inversion of Upper and Lower Lip of Both Sides.—This movement is similar to the one just described, except that it was completely bilateral, no difference being found between the two sides. It occurred once at Ag, Bf, Bg, Bh, Bi, Bj, Di, Dk, Eh.

(c.) Lower Face.

We now come to the movements of the lower part of the face and commence with those of the angle of the mouth. These may be suitably arranged as follows:—

- (a.) Retraction of the angle of the Mouth of the opposite side.
- (b.) ,, ,, ,, same side.
- (c.) ,, ,, ,, both sides.
- (d.) Advancing ", ", the opposite side.
- (e.) ,, ,, ,, same side alone.
- (f.) ,, ,, ,, both sides.
- (g.) ,, ,, ,, the same side together with the cheek.
- (a.) Retraction of the Angle of the Mouth of the Opposite Side (Plate 8, fig. 6).— This, with that of elevation of the angle of the mouth, is the most important movement of the face, and has long been recognized to be so. In the movement of retraction, the angle of the mouth is drawn horizontally backwards without necessarily parting the lips. It occurred at squares—

12.	9.	8.	7.	6.	5.	4.	3.	2.	1.
$\mathrm{D}j$	$^{\mathrm{E}j}_{\mathrm{H}g}$	$rac{\mathrm{E}k}{\mathrm{H}h}$	$egin{array}{c} \mathbf{E}g \\ \mathbf{E}i \\ \mathbf{F}i \end{array}$	$egin{array}{c} \mathrm{D}k \ \mathrm{F}g \ \mathrm{H}f \end{array}$	$egin{array}{c} \mathrm{C}j \ \mathrm{D}i \ \mathrm{G}f \ \mathrm{H}j \end{array}$	$\begin{array}{c} \mathrm{D}f \\ \mathrm{F}e \\ \mathrm{F}f \end{array}$	$egin{array}{c} \mathrm{C}h \\ \mathrm{C}k \\ \mathrm{D}l \end{array}$	$egin{array}{c} \mathrm{B}g \ \mathrm{B}i \ \mathrm{B}j \end{array}$	$egin{array}{c} \mathbf{B}h \\ \mathbf{C}f \\ \mathbf{C}g \\ \mathbf{C}h \end{array}$
			$rac{{ m F}j}{{ m G}g}$,	$\mathbf{H}j$	$egin{array}{c} \mathbf{F}h \ \mathbf{G}h \ \mathbf{G}j \ \mathbf{I}e \end{array}$	$egin{array}{c} \mathbf{E}h \ \mathbf{F}k \ \mathbf{G}i \ \mathbf{G}k \end{array}$	$egin{array}{c} \mathbf{D}h \ \mathbf{E}e \ \mathbf{E}f \ \mathbf{F}m \end{array}$	$egin{array}{c} \operatorname{C}h \ \operatorname{D}g \ \operatorname{E}d \ \operatorname{E}l \end{array}$
						$egin{array}{c} \operatorname{I} \overset{oldsymbol{e}}{e} \ \operatorname{I} g \end{array}$	Gl Ih	$egin{array}{c} \mathbf{H}l \ \mathbf{J}f \ \mathbf{J}g \end{array}$	$egin{array}{c} \mathbf{F}l \ \mathbf{G}d \ \mathbf{G}e \end{array}$
			,	٠,		. *.			$egin{array}{c} \mathbf{H}k \ \mathbf{J}h \end{array}$

(b.) Retraction of the Angle of the Mouth of the Same Side.—Particular notice must be taken of this movement as it occurs on the same side as that of the hemisphere excited. It was found in squares—

2.		1.		
$egin{array}{c} \mathbf{A}f \ \mathbf{B}f \ \mathbf{B}g \end{array}$	$egin{array}{c} \mathbf{A}g \ \mathbf{A}i \end{array}$	$egin{array}{c} \mathrm{B}i \ \mathrm{C}b \ \mathrm{D}f \end{array}$	$egin{array}{c} \mathbf{E}g \ \mathbf{G}h \end{array}$	

Its relative infrequency is very obvious.

(c.) Retraction of the Angle of the Mouth of Both Sides (fig. 7).—This truly bilateral movement was seen at squares—

3.	2.	1.							
Cj Ck	$egin{array}{c} { m C}i \ { m E}f \ { m E}g \end{array}$	$egin{array}{c} \mathbf{C}g \\ \mathbf{C}h \\ \mathbf{D}c \end{array}$	$egin{array}{c} \mathrm{D}g \ \mathrm{D}i \ \mathrm{D}j \end{array}$	$egin{array}{c} \mathrm{D}k \ \mathrm{D}l \ \mathrm{F}f \end{array}$					

The next kind of movement which we noticed to affect the angle of the mouth was in the opposite direction to that just mentioned of retraction, and may properly be described as advancing. In this the angle of the mouth is drawn or pushed forward, and the movement may occur on either the side opposite to that of the hemisphere excited, or on the same side, or bilaterally, *i.e.*, both angles of the mouth are advanced simultaneously, and, as will be subsequently seen, also accompanied by movement of the cheek.

(d.) Advancing of the Angle of the Mouth of the Opposite Side.—This, the crossed unilateral action as generally understood, we only noted to occur in single instances at

Dh Ge Gg Gh H
$$f$$
 H g .

- (e.) Advancing of the Angle of the Mouth of the Same Side Alone.—This rare movement was observed only once at Dh.
- (f.) Advancing of the Angle of the Mouth of Both Sides.—This, which is a well-marked bilateral movement, is in our opinion the forerunner to the important movements of pouting and pursing of the mouth. We observed it repeatedly at squares, viz.:—

3.	2.	1.							
$\mathbf{F}g$	$egin{array}{c} \mathrm{D}h \ \mathrm{G}f \end{array}$	$egin{array}{c} \mathbf{B}e \ \mathbf{C}f \end{array}$	$egin{array}{c} \mathrm{D}d \ \mathrm{D}e \end{array}$	$\mathop{\mathrm{D}f}_{\mathop{\mathrm{D}g}}$	$egin{array}{c} \mathrm{D}k \ \mathrm{G}h \end{array}$				

- (g.) Advancing of the Angle of the Mouth of the Same Side together with the Cheek. This combined action of the forward movement of the angle of the mouth and cheek was only observed twice at Ch, and must be looked upon as an exceptional development of the advancing of the angle of the mouth.
- (h.) Depression of the Angle of the Mouth (i.e., Platysma Action).—We only observed this movement to occur twice, viz., at centres Cg and Ch.
 - (3) and (4). Pursing and Pouting.*

There remain for consideration certain combined actions of the lips and orifice of the

mouth which are easily recognized under the quasi-popular expressions of pursing and pouting, but which cannot be described sufficiently accurately except by long periphrasis. To avoid this we employ the former expressions under the following meanings.

Pursing.—By this term, as we have already described in our paper on the motor cortex of the Orang,* we mean the drawing together of the lips, together with slight protrusion, both parts of the orbicularis being contracted, whilst in *Pouting* the lips are strongly protruded, and at the same time they are much everted.

We may subdivide this subject in the following manner:-

- (a.) Pursing of the opposite side of the mouth.
- (b.) Pursing of both sides of the mouth (bilateral).
- (c.) Pouting of the opposite side of the mouth.
- (d.) Pouting of the same side of the mouth.
- (e.) Pouting of both sides of the mouth.
- (a.) Pursing of the opposite side of the mouth was only observed once at the squares Ec, Ed, Ee, Ig.
 - (b.) Pursing of both sides of the mouth occurred at—

2.		1.	
$egin{array}{c} \mathbf{E}g \\ \mathbf{F}g \\ \mathbf{H}f \end{array}$	$egin{array}{c} \mathbf{E}h \ \mathbf{F}e \ \mathbf{F}f \end{array}$	Fh Fk Ge	$egin{array}{c} \mathrm{G}f \ \mathrm{H}e \ \mathrm{H}g \end{array}$

(c.) Pouting of the opposite side occurred at-

3.	2.	1.			
$oxed{ egin{array}{cccccccccccccccccccccccccccccccccccc$	Ee	$\mathbf{E}c$ $\mathbf{F}d$			

- (d.) Pouting of the same side of the mouth occurred only once at Dh
- (e.) Pouting of both sides of the mouth was seen at-

3.	2.				1.		
Fh.	Be Ce Di	$egin{array}{c} \mathbf{E}f \\ \mathbf{F}f \\ \mathbf{G}g \end{array}$	$egin{array}{c} \mathbf{A}d \\ \mathbf{B}b \\ \mathbf{B}d \end{array}$	$egin{array}{c} \mathbf{B}f \\ \mathbf{C}b \\ \mathbf{C}c \end{array}$	$egin{array}{c} \mathbf{C}h \ \mathbf{E}g \ \mathbf{E}h \end{array}$	$\operatorname*{\mathbf{F}g}\mathbf{G}f$	

^{* &#}x27;Phil. Trans.,' B, 1890, p. 136.

(5.) Movements of the Cheek.

In close relation with the movements of the angle of the mouth are those of the cheek, which may be divided into the two following groups:—

MOTOR REGION OF THE CORTEX CEREBRI IN THE MONKEY.

- (a.) Flattening of the cheek on the same side.
- (b.) Flattening of both cheeks.
- (a.) Flattening of the Cheek on the Same Side (fig. 8).—This movement was found at the following squares:—

4.	3.	2.	1.
Dg Cf	Dh	$egin{array}{c} \mathbf{B}g \\ \mathbf{C}g \\ \mathbf{E}h \\ \mathbf{G}h \\ \mathbf{E}f \\ \mathbf{E}g \end{array}$	$egin{array}{lll} \mathbf{B}d & \mathbf{E}d \ \mathbf{B}f & \\ \mathbf{D}f & \mathbf{G}g \end{array}$

And it was seen to be almost invariably associated with a special movement of the tongue, viz.: rolling over of the dorsum to the cheek of the same side (p. 55), so that the cheek moved to meet the dorsum of the tongue, and would thus force, and keep the bolus of food between the molar teeth.

It is interesting to note that this movement occurred as a unilateral action and only on the same side as that of the cortex stimulated,

- (b.) Bilateral flattening of the cheeks occurred only as a single instance at Eh. It is, therefore, very exceptional.
 - (6.) Movements of the Chin.

The movements of the chin are the last we have to note, of those observed in the lower face.

They may be considered under the heads of-

- (a.) Elevation of the chin on the opposite side.
- (b.) Elevation of the chin on the same side.
- (c.) Bilateral elevation of the chin.
- (a.) Elevation of the Chin on the Opposite Side.—This is by far the commonest movement of the chin met with, and is probably caused by the levator menti muscle. It occurred at—

2.	1.				
$egin{array}{c} \mathrm{D}i \ \mathrm{E}j \ \mathrm{E}k \end{array}$	$egin{array}{c} \mathbf{C}h \ \mathbf{C}i \ \mathbf{C}j \end{array}$	$egin{array}{c} \mathrm{D}g \ \mathrm{D}h \ \mathrm{D}j \end{array}$	$egin{array}{c} \mathrm{D}k \ \mathrm{E}i \ \mathrm{E}l \end{array}$	$egin{array}{c} \mathbf{F}h \ \mathbf{F}k \end{array}$	

- (b.) Elevation of the Chin on the Same Side.—This was very rare and occurred as a single observation at Eg.
 - (c.) Bilateral Elevation of the Chin.—This occurred only once at squares Ch, Eh.

B. Movements of the Tongue (Plate 9, fig. 9).

The question of the manner in which the various movements of the tongue should be grouped was alluded to in the consideration of bilateral representation on p. 44. We have decided to divide the movements of the tongue into—

- 1. Movements bilaterally represented.
- 2. Movements not bilaterally represented.

They may therefore be arranged in the following order:-

- 1. Movements bilaterally represented.
 - (1.) Tongue protruded straight.
 - (2.) Tongue retracted straight.
- 2. Movements not bilaterally represented.
 - (1.) Tongue protruded, tip to the opposite side.
 - (2.) Tongue protruded to the same side.
 - (3.) Tongue retracted on the same side.
 - (4.) Tongue rolled over with the dorsum to the cheek of the same side.

1. Movements Bilaterally Represented.

(1.) Tongue Protruded Straight (Plate 9, fig. 10).—This simple bilaterally represented movement, i.e., which can be evoked equally well from the cortex of either hemisphere, was found at the following squares:—

6.	5.	4.	3.	2.	1.
Ae Bf Ce	$egin{array}{c} \mathbf{Be} \ \mathbf{Cd} \end{array}$	$\mathbf{A}b$	$egin{array}{c} \mathbf{A}c \\ \mathbf{A}d \\ \mathbf{A}f \\ \mathbf{A}g \\ \mathbf{C}f \\ \mathbf{D}d \\ \mathbf{D}e \\ \end{array}$	$egin{array}{c} \mathbf{B}g \\ \mathbf{C}c \\ \mathbf{C}g \\ \mathbf{C}j \\ \mathbf{D}g \\ \end{array}$	$egin{array}{c} \mathbf{A}b \\ \mathbf{B}d \\ \mathbf{B}c \\ \mathbf{B}d \\ \mathbf{C}b \\ \mathbf{C}i \\ \mathbf{C}k \\ \mathbf{D}c \\ \mathbf{D}f \\ \mathbf{E}i \\ \mathbf{F}i \\ \end{array}$
		, , , , , , , , , , , , , , , , , , , ,		and the second s	

In this movement the tongue is protruded quite flatly and without any deviation of the tip to one side, and without any heaping up posteriorly.

(2.) Tongue Retracted Straight.—This was less widely represented than the former, and was found at—

3.	2.	1.
Bh Ce	$rac{\mathrm{B}g}{\mathrm{B}i}$	$egin{array}{ccc} \mathbf{C}c & \mathbf{D}e & \mathbf{G}h \ \mathbf{C}h & \mathbf{D}h \ \mathbf{C}j & \mathbf{D}j \end{array}$

2. Movements not Bilaterally Represented.

(1.) Tongue Protruded with the Tip to the Opposite Side (fig. 11).—This is the movement upon which so much stress has been laid in clinical observation, and the real nature of which will further on be more minutely discussed. It was found to be represented at squares—

4.	3.	2.	. 1.
Df Eg .	$egin{array}{c} \mathrm{B}i \ \mathrm{C}i \ \mathrm{D}j \ \mathrm{E}i \ \mathrm{H}g \end{array}$	$egin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$

- (2.) Tongue Protruded with the Tip to the Same Side.—This movement, in marked contrast to the former one, was obtained three times at only one square, Af.
- (3.) Tongue Retracted on the Same Side.—This movement, which is very slightly represented, was found once at Gg.
- (4.) Tongue Rolled over so that the Borsum comes into contact with the Cheek of the Same Side (fig. 12, cf. fig. 8).—This movement is one in which there is no protrusion of the organ, but in which it is so rotated on its longitudinal axis that the dorsum of the tongue is closely applied to the mucous membrane of the cheek of the same side as that of the cortex stimulated. As previously stated, the cheek of the same side is flattened to meet the convexity of the approaching tongue. It occurred at—

5.	4.	3.	2.	1.
$\mathrm{B}g$	$egin{array}{c} \mathrm{C}g \\ \mathrm{C}h \\ \mathrm{D}h \end{array}$	$\mathop{ m Df}_{{ m D}g}$	$egin{array}{c} \mathbf{A}h \ \mathbf{B}h \ \mathbf{C}e \ \mathbf{E}f \ \mathbf{F}h \end{array}$	$egin{array}{cccc} \mathbf{B}f & \mathbf{D}e & \mathbf{E}k \ \mathbf{C}b & \mathbf{E}g & \mathbf{F}g \ \mathbf{C}f & \mathbf{E}h & \mathbf{C}i & \mathbf{E}i \ \mathbf{C}j & \mathbf{E}j & \end{array}$

Consideration of the foregoing Facts with especial Reference to Movements of the Individual Halves of the Tongue after Separation along the Median Plane.

We have already described the movements of the tongue as a whole, and we have alluded to the questions of unilaterality and bilaterality of movement of this organ. A new and unexpected light was thrown on this subject by the following attempt to differentiate the complex movements of the entire tongue, and to determine what share is taken by each half in the production of any given action.

It occurred to us that much might be learnt by regarding the tongue, at least for the longitudinal muscles, as constructed of two similar halves; further, that these might be separated from each other by a vertical incision in the middle line, and this without injury to the nerve supply of each half.

Of course we recognize that this procedure involves the median* division of the septal origin of the transverse muscular fibres and also the division of any hypothetical nerve fibres crossing the raphe, but this does not invalidate the results we obtained, and which show most definitely that the movements of both halves of the tongue are represented in the hemisphere of each side respectively. For illustration of our meaning, and for the better comprehension of the facts about to be related, we may compare the question of this bilateral representation of the movements of the respective halves of the tongue with those of the conjugate movements of the eyes, and it will be seen presently that the common, and in hemiplegia previously supposed unilateral, movement of the tongue is really a conjugate movement.

The operation of separation was performed by dividing the tongue along the median plane from the hyoid bone and root of the epiglottis forward to the genial tubercles. As a rule there was exceedingly little hæmorrhage, and this was easily arrested by pressure. The reflex movements of the tongue were as complete as before, showing that the functions of the organ were not interfered with.

We will now take the movements of the torgue as a whole (see p. 54), and discuss in the light obtained by this method how far the change of form of the whole organ is dependent on each of the halves respectively; we will therefore take the movements in the same order in which they have just been considered.

Movements Bilaterally Represented.

- (1.) and (2.) Advancing and Retraction of the Tongue.—We observed that in these movements executed symmetrically forwards or backwards, each half of the tongue performed exactly the same evolution, and in no case could preponderance of action be shown to take place on either side. It follows therefore that these movements are truly bilaterally represented.
- * Practically the line of separation frequently passed close to the side of the septum, this, of course, not interfering with the power of the transverse fibres to contract, and so narrow the half of the tongue.

Movements not Bilaterally Represented.

(1.) Protrusion of the Tongue to the opposite side.—From the time of Aberchambie* it has been noticed in clinical medicine that in hemiplegia the tongue was protruded towards the paralyzed side, i.e., opposite to the lesion, and this was assumed to be due to the genio-hyo-glossus muscle of the healthy side (i.e., the same as the lesion) pressing the tongue towards the paralyzed side, i.e., away from the lesion.

In Carpenter's Physiology[†] it is stated that the deviation is due to the want of action of the lingual muscles of the paralyzed side, the tip being directed by the muscles of the other (*i.e.*, healthy) side, "which will not act in a straight direction when not antagonized by their fellows."

In short, it is evident that a general belief exists to the effect that if one side of the tongue is being actively protruded, the other half remaining passive the resulting position of the tongue is a deviation towards the paralyzed side owing to the passive flaccid condition of the non-acting muscles. The first point which we think requires to be definitely ascertained in treating this subject is the determination as to whether excitation of one hypo-glossal nerve produces any movement of the tongue across the median plane, as is evidently generally supposed. We ourselves having foreseen the complex problems involved in the movements of this part especially re-investigated, by excitation experiments at the base of the skull, the functions of several cranial nerves separated from the medulla. We found ('Roy. Soc. Proc.,' vol. 44, June 7, 1888) that excitation of the hypo-glossal nerve of one side produced in the whole tongue "flattening posteriorly on the same side and the tip protruded also on the same side." The purely unilateral character of the movement was further established by experiments in which the tongue was divided longitudinally to the hyoid bone when the movements were seen to be entirely confined to the side stimulated.

It will therefore be seen that stimulation of the hypo-glossal nerve of one side does not protrude the tongue towards the opposite side.

We will now proceed to describe what happens to the individual parts of the tongue when in the left cortex the squares for the representation of protrusion of the tongue to the opposite side are excited. Instead of the right half of the tongue remaining passive as has always been presupposed by anatomists and clinicians, we discovered that when the left cortex was stimulated the following remarkable conjugate movement occurred:—the left half of the tongue was advanced beyond the teeth, whereas the right half was actively retracted into the mouth. It is perfectly obvious therefore, that this movement of protrusion of the tongue to the opposite

^{* &#}x27;Pathological and Practical Researches on Diseases of the Brain and Spinal Cord,' Edinburgh, 1834, p. 271.

[†] Carpenter's 'Physiology' edited by Power, 7th edition, 1869. Compare also Ross' 'Treatise on Diseases of the Nervous System,' 1883, and Gower's 'Diseases of the Nervous System,' 1888.

fact and will have to be altered.

side from stimulation of the cortex is exactly comparable to the conjugate movement of the eyes to the opposite side when the same hemisphere is excited. In this way the right half of the tongue would correspond to the right external rectus, and the left half of the tongue to the left internal rectus. In each case we have the combination of two opposite movements for the production of one resultant action. The opposite character of the movements of the two halves of the tongue was emphasized in a very remarkable degree when there was epileptic disturbance of the cortical focus in question. In the clonic spasm of the epileptic fit the two halves performed remarkable "see-saw" contractions, that of the same side being shot forwards at the same time as the opposite half was retracted. On several occasions we observed that retraction of the opposite side not only began before the protrusion of the same side, but actually in a few instances it occurred alone, thus showing that it is probably the more important movement of the two. We are now in a position to examine into the condition of the tongue as observed in hemiplegia. Unfortunately the clinical examination of the tongue has hitherto not been conducted so thoroughly as its importance warrants; and in fact, clinical observation is usually limited to noticing whether the tongue is deviated to one side when protruded, without further exploration of other movements. This is doubtless due to the fact that the movements of the tongue generally have hitherto not been completely ascertained. Although this makes the task of explanation very difficult and for the present impossible, we take leave to point out that the accepted views are plainly contrary to

(2.) Rolling over with the Dorsum directed towards the Cheek of the Same Side.—
This movement we found to be distinctly compound in character, both separated halves of the tongue rolling to the same side. In the execution of this movement the mucous membrane of each half of the tongue was turned so as to be directed towards the left cheek, as a result the cut surfaces glided upon each other so that the two halves were arranged en échelon in place of being in line; the cut surface of the same side being directed upwards and that of the opposite side downwards.

Each half of the tongue therefore executes a rotation around its longitudinal axis.

Vertical Arrangement of the Representation of the Movements of the Tongue.

Reference to the diagrams (Plate 9, fig. 9, &c.) will show that a very definite differentiation of the representation of the tongue movements can be made as follows. In the upper part of the area, i.e., just below a line drawn between the upper end of the præcentral vertical stem and the genu of the fissure of Rolando, the action of protrusion of the tongue with the tip directed to the opposite side is elicited on excitation. On the contrary, the movement of retraction is represented at the lowest portion of the area, i.e., around the lower end of the fissure of Rolando. Intermediately, i.e., opposite the upper end of the sulcus transversus frontalis inferior (see p. 42) we find the movement of rotation of the tongue towards the same side.

C. Movements of the Lower Jaw.

The movements of the lower jaw may be divided into:—

- 1. Single movements.
 - (1.) Opening the mouth straight.
 - (2.) Opening of the mouth with the lower jaw directed towards the same side.
 - (3.) Opening of the mouth with the lower jaw directed towards the opposite side.
 - (4.) Shutting the mouth.
- 2. Rhythmical.
 - (1.) Mastication.

1. Single Movements.

By the term "opening the mouth" we understand that the lower jaw is depressed. This movement we have observed to occur without necessarily separating the lips, which additional passive action, however, nearly always happens concurrently. We therefore consider these two cases.

We look upon the movement as being accomplished by the muscles of both sides, but we have no evidence to show whether they act concurrently and whether the movement, if it does not deviate from the middle line, is capable of being produced by the muscles of one side only. It is known that if one external pterygoid muscle act alone, the jaw on being depressed is carried towards the opposite side, and we therefore assume that this occurs when the jaw deviates towards one side or the other.

(1.) Opening the Mouth Straight (fig. 13).—In this movement the jaw is depressed exactly straight along the line between the two central incisors. It was found at—

10.	9.	8.	7.	6.	5.	4.	3.	2.	1.
$\mathrm{D}g$	$egin{array}{c} \mathbf{A}f \\ \mathbf{A}g \\ \mathbf{B}f \end{array}$	Cg Ci	Bg Bi Ce Ch	$\begin{array}{c} \mathbf{A}c \\ \mathbf{A}h \\ \mathbf{B}e \\ \mathbf{B}h \\ \mathbf{C}f \\ \mathbf{D}f \\ \mathbf{D}h \end{array}$	Cj	$egin{array}{c} \mathrm{C}d & \\ \mathrm{C}k & \\ \mathrm{D}e & \\ \mathrm{E}g & \end{array}$	$egin{array}{l} \mathbf{A}b \\ \mathbf{A}d \\ \mathbf{A}i \\ \mathbf{B}d \\ \mathbf{B}j \\ \mathbf{C}c \\ \mathbf{D}d \\ \mathbf{G}g \end{array}$	$egin{array}{c} \mathbf{A}c \\ \mathbf{B}d \\ \mathbf{D}c \\ \mathbf{D}i \\ \mathbf{E}h \\ \mathbf{E}i \\ \mathbf{E}k \\ \mathbf{F}h \\ \mathbf{G}h \\ \end{array}$	$\begin{array}{c} \operatorname{B} c \\ \operatorname{C} l \\ \operatorname{D} j \\ \operatorname{D} k \\ \operatorname{E} f \\ \operatorname{E} j \\ \operatorname{H} g \\ \operatorname{H} l \end{array}$

(2.) Opening the Mouth with the Lower Jaw Carried to the Same Side (fig. 14).— In this movement, with stimulation of the left hemisphere, the lower jaw as it descended moved markedly towards the left side; this we take to be due to the fact that either the right pterygoid muscle alone was in action, or that it overpowered that of the left side. While as just seen the commonest movement of depressing the lower jaw in opening the mouth is the bilateral or straight movement, where any

deviation was noticed, it was this one of the lower jaw passing to the same side as that of the cortex excited. This might have been anticipated from what has been stated, as it is obviously an instance of the ordinary crossed effect of stimulation. This movement occurred at—

4.	3.				
$egin{array}{c} \mathrm{B} g \ \mathrm{D} g \end{array}$	Cg	$egin{array}{cccc} { m A}e & { m D}h \ { m A}f & { m E}h \ { m B}d & { m E}j \ { m C}d \end{array}$	$egin{array}{ccccc} \mathbf{A}d & \mathbf{B}h & \mathbf{D}d \\ \mathbf{B}c & \mathbf{C}b & \mathbf{D}f \\ \mathbf{B}e & \mathbf{C}f & \mathbf{E}g \\ \mathbf{B}j & \mathbf{C}h \\ \end{array}$		

(3.) Opening of the Mouth with the Lower Jaw carried to the Opposite Side.—This, which is the converse of that described, and was very rarely observed, is conceivably due to the action of the external pterygoid muscle of the same side, and was obtained only once at two squares, Ad, Ae.

On looking at the previous Table it will be seen that the movement of the jaw towards the same side was also obtained twice at Ae and once at Ad, thus showing that there are squares where the differentiation of the movement of the lower jaw towards the opposite side was incomplete, its production being due, therefore, more or less to an accidental causation.

(4.) Shutting of the Mouth.—This well recognized movement of closing the mouth was, to our surprise, obtained at only one square, viz., Dh. By this movement we mean simply raising up the depressed lower jaw, without any further action, and the very small representation of this deliberate act is in marked contrast to that of the rhythmical movements to be next described.

2. Rhythmical Movements.

(1) Movements of Mastication (fig. 15).—By the term "mastication" we mean that on the application of the electrodes to the cortex, the lower jaw begins to execute a series of rhythmical movements of grinding of the teeth. To describe the movement in detail:—the mouth is opened, the lower jaw depressed and carried towards the same side, and then the mouth is closed by raising the lower jaw; directly the teeth are separated the tongue is advanced, and it is retracted immediately before the teeth come together again; this latter movement of the tongue is thus dependent on and coincident with the action of the lower jaw. This complex act of mastication begins immediately the electrodes are applied, and continues until the electrodes are removed, when it ceases. The movement is what would generally be termed that of mastication of a very pronounced type, and as such it differs somewhat from the description given by Professor Ferrier, in that he does not seem to have observed the grinding movements of the lower jaw. The most important point concerning it is

that it is an instance of rhythmical discharge of the cortex evoked by a constant stimulus, and lasts only during the duration of the excitation. So far as we know, it is the only truly rhythmical action following on stimulation of the cortex.*

With a view to seeing what this rhythmical rate might be we observed the time of it in seventeen cases, and found it to be on an average 135 movements per second, the most rapid rate observed being nine times in five seconds, and the slowest being one in one second, and each of these extreme cases was noted three times.

This compound act was observed at—

8.	7	6.	5.	4.	3.	2.	1.
${ m Be}$	$\mathbf{B}d$	Cd	Ae Bc Ce	$egin{array}{c} \mathbf{A}b \\ \mathbf{A}d \\ \mathbf{B}f \\ \mathbf{C}f \\ \mathbf{D}d \end{array}$	$egin{array}{c} \mathbf{A}c \\ \mathbf{A}f \\ \mathbf{B}g \\ \mathbf{C}c \\ \mathbf{C}h \\ \mathbf{D}e \\ \mathbf{D}f \\ \end{array}$	$egin{array}{c} \mathbf{A}g \\ \mathbf{C}g \\ \mathbf{D}c \\ \mathbf{D}g \\ \mathbf{E}f \\ \mathbf{E}g \end{array}$	$egin{array}{c} \mathbf{B}b \\ \mathbf{C}b \\ \mathbf{C}i \\ \mathbf{C}j \\ \mathbf{D}h \\ \mathbf{E}d \\ \mathbf{E}h \\ \mathbf{F}e \\ \mathbf{F}f \\ \mathbf{F}h \end{array}$

Grinding of the Teeth.—On three occasions the teeth were observed to grind during the act of mastication, and in two of these the movement of the jaw was traced and found to pass from the opposite side to the same side. The squares where it was observed were Ad, Ae, Af.

Movements of the Pharynx.

In observing these movements, we kept the mouth forcibly opened, and recorded, as far as possible, the movement of, 1, the soft palate; and 2, that of swallowing.

1. Movements of the Soft Palate (fig. 16).

We may arrange the movements of the soft palate as follows:-

- (1.) Elevation of the soft palate on the opposite side.
- (2.) Bilateral elevation of the soft palate.
- (3.) Bilateral elevation of the soft palate, commencing with elevation of the opposite side, followed later by that of the same side.
- (1.) Elevation of the Soft Palate on the Opposite Side.—This movement of the soft palate, when viewed in the manner described, is quite unmistakable when it occurs; but it has to be carefully distinguished from the irregular movements of the arches of the fauces, when these are drawn forward by the tongue and by the movements of this organ itself. The movement was only observed once, at Bd; and at the same
 - * Compare as an imperfect rhythm the act of blinking, see p. 47.

place slight opening of the mouth and protrusion of the tongue to the opposite side were noted.

(2.) Bilateral Elevation of the Soft Palate.—This movement, which is the commonly understood effect—viz., the raising of the whole soft palate—was seen only four times, viz., once at squares Ad, Ae, Bd, Cd. Of these at Ad, Bd, Cd, this was the only movement obtained; while at Ae there was also the movement of mastication.

The foregoing refers to experiments in which the observation of the soft palate was made at the end of the exploration. It occurred to us that possibly the paucity of these results was due to exhaustion of the cortex. We therefore devoted two experiments to examine this point first, with the effect that we obtained very definite localisation of the palate movements.

(1.) ELEVATION of the Soft Palate on the opposite side.

2.	1.
$_{\mathrm{C}f}^{\mathrm{B}f}$	$egin{array}{ccc} \mathbf{A}d & & & & \\ \mathbf{A}e & & & & \\ \mathbf{A}f & & & & \\ \mathbf{B}d & & & & \\ \mathbf{B}e & & & & \\ \mathbf{C}d & & & & \\ \mathbf{C}e & & & & \\ \end{array}$

(2.) BILATERAL Elevation of the Soft Palate.

1.	*
$egin{array}{c} \mathbf{A}e \ \mathbf{B}c \ \mathbf{B}e \ \mathbf{C}e \end{array}$	-

(3.) BILATERAL Elevation commencing with elevation of the opposite side, followed later by that of the same side.

1.	
$egin{array}{c} \mathrm{B}d \ \mathrm{C}d \end{array}$	

These further observations showed clearly the real degree of representation of the palate, and in addition, what we did not anticipate, namely, a considerable degree of unilaterality of representation.

2. Movement of Swallowing.

This movement was observed once at four squares, viz.:—

The paucity of representation is perhaps accounted for by the movement of swallowing in the Monkey being more automatic than is generally considered to be the case, but it is possible that the effect of exposure may influence the result.

In relation to this question, the recent observations of Goltz,* in which he successfully removed both cerebral hemispheres in the Dog, leaving only the cerebellum, pons, bulb, and posterior corpora quadrigemina intact (the anterior partially so), and kept the animal alive for many months, must be specially mentioned. The animal had to have milk poured down its throat through a tube, because the act of swallowing was so far interfered with that fluid almost always escaped into the larynx. In two months after the operation, it would, when its nose was touched with a piece of meat, seize it, masticate it, and swallow it without any assistance. There seems, therefore, on the whole, to be no real reason why in the Monkey the cortical representation of swallowing should be more extensive than such as we find it to be.

II. MOVEMENTS OTHERWISE THAN ORIFACIAL.

In exciting the area under examination, since we were devoting ourselves especially to the orifacial movements, we only noted the concurrence of movements of other parts of the body when those appeared to us anomalous, and in order to satisfy ourselves of the extent of such extra movements, and to control the observations which we made in 1886, and also to ascertain to what extent the orifacial area overlapped the neighbouring areas.

The movements thus noted comprised those of the head and of the upper limb.

A. Movements of the Head.

Since the region which we have explored in the present research is in direct continuity with the supramarginal gyrus, and this with the anterior limit of the angular gyrus, it was to be anticipated that we should observe movements of the head and eyes to the opposite side, inasmuch as Ferrier, Schäfer, and others, observed these movements to occur from excitation of this region. The movements of the head which we noticed were (1) the turning of the head to the opposite side, and (2) retraction of the head.

^{* &#}x27;Archiv für d. Gesammte Physiologie' (Pflüger), vol. 51, p. 570, 1892.

(1.) Turning of the Head to the Opposite Side.—This movement, where the head is turned away from the side of the cortex stimulated, was found at the following squares:—

4.	3.	2.	1.
$rac{\mathrm{D}l}{\mathrm{D}m}$	Cl	$egin{array}{ll} ext{E}j & ext{G}k \ ext{F}k & ext{I}f \ ext{F}l \ ext{F}m \end{array}$	$egin{array}{cccccccccccccccccccccccccccccccccccc$

The representation of this act is, therefore, round the fringe of the orifacial representation, especially at the posterior part near to the supramarginal gyrus, and also at the upper part of the region where it borders on the area representative of this movement in front of the precentral sulcus.

(2.) Retraction of the Head.—Similarly the rarer movement of retraction of the head was noted to occur once at each of the following squares:—Cj, Ck, Dh, Di, Ej, Fh, Fi, Fk, Ig.

B. Movements of the Upper Limbs.

Although we noted the various movements of the segments of the upper limb we did not record the occurrence of the same in the present work with detail, but we have made a considerable series of observations to re-investigate the question of overlapping, and the extent of border centres, and recorded also certain anomalies of representation. In the present instance we have specially noted the lowest points at which movements of the upper limb could be elicited. These when arranged give the following results, commencing with the thumb and fingers, which according to our observations, both in 1886 and in the recent experiments, are the lowest segments represented.

	In front of Rolando.	Behind Rolando, anomalous.
Thumb Fingers	$egin{array}{ccccc} \mathrm{D}d & \mathrm{D}e & \mathrm{E}f & \mathrm{E}g & \mathrm{G}h \ \mathrm{D}c & \mathrm{D}d & \mathrm{D}e & \mathrm{E}f & \mathrm{F}g & \mathrm{G}h \end{array}$	$egin{array}{cccc} \mathbf{H}j & \mathbf{C}j & \mathbf{C}k \ \mathbf{G}j & \mathbf{E}k & \mathbf{D}l & \mathbf{D}m \end{array}$

In contrast to these segments we give the lower limits of the representation of the elbow and shoulder, as found in the present experiments.

MOTOR REGION OF THE CORTEX CEREBRI IN THE MONKEY. In front of Rolando. Behind Rolando, anomalous

	In front of Rolando.	Behind Rolando, anomalous.
Elbow Shoulder	$\mathbf{I}f \qquad \mathbf{E}d \ \mathbf{I}i$	$egin{array}{cccccccccccccccccccccccccccccccccccc$

These lower borders of the upper limb area of representation correspond absolutely closely to the levels given in the paper in 'Philosophical Transactions,' 1887.

In addition, however, we observed, to our surprise, that we occasionally obtained from the cortex of the foot of the ascending parietal gyrus movements of the upper limb, and not merely of the lowest segments, but also of the shoulder. Of fifteen experiments we noted at Ck that the thumb was flexed twice, the fingers flexed twice in the interesseal position, and the shoulder adducted once at Cl. The great rarity of this representation of the shoulder so low down on the outer or convex surface of the hemisphere, shows that it is quite exceptional, and no explanation of its occurrence in the evolution of the function of this part presents itself to us.

SOCIETY

TABLE I.—Giving Absolute Number of Movements noted at any given Square, arranged in Order according to Frequency See Table II. of "Marches." of Occurrence and not according to their Relative Sequence.

Abbreviations to Table I.

pron. $=$ pronate.	rot. = rotate.				
			fex. = fexion.		
elev. = elevate.	inteross. = interosseal.	mastic. $=$ mastication.	adv. = advance.	dors. = dorsum.	abd. = abduct.
retr. = retraction.		opp. = opposite.	str. = straight.	protr. = protrude.	add. = adduct.
Th. = thumb.					
T = tongue.	M. = mouth.	M. \angle = angle of mouth.	U.L. = upper lip.	H^{a} . = head.	F = fingers.

of observations.	15 10	15 11	15 5	15	15	15 4	15 9	15 10
Number of observations.			Pouting bilat., 1. Grinding teeth, 1. Swallowing, 1.	M. open, jaw to opp. side, 1. S.P. elevated bilat., 1. Teeth grind from opp. to same side, 1.	M. 2, same side elev., 1. Grind teeth, 1. Lips invert. (espec. opp. side), 1.			
			M. open, jaw to same side, 1. M. open, jaw to opp. side, 1. S.P. elevated bilaterally, 1.	M. open, jaw to same side, 2.	M. open, jaw to same side, 2. M. Z, same side retract., 2.	M. 2, same side retr., 1. Lips invert., 1.	T. protr. str., 1.	M. 2, same side retr., 1.
	M. open, 3.	M. open, 2.		Mastic., 5.	Mastic., 3. side, 3.	Mastic., 2.	side, dors. to	p. side, 2.
	T. protr. str., 4.	T. protr. str., 3.	T. protr. str., 3. M. open, 3.	T. protr. str., 6.	T. protr. str., 3. T. protr. to same	T. protr. str., 3.	T. rolled to same side, dors. to cheek, 2.	T. protr. tip to opp. side, 2.
	Mastic., 4.	Mastic., 3.	Mastic., 4.	M. open, 6.	M. open, 9.	M. open, 9.	M. open, 6.	M. open, 3.
Square.	A.b.	A.c.	A.d.	A.e.	A.f.	A.g.	A.ħ.	A.i.

1-	1						
	Nil.	13	∞	41	ಣ	4.	¢J
	Number of observations.	15	15	15	15	70	12
			Į,	T. protr. str., 1. Cheek flattened, 1. T. protr. tip to Pouting, 1. Opp. side, 1. S.P. elev. bilat., 1. S.P. elev. opp. side, 1.	M. open, jaw same side, 1. M. 2 adv., 1.	M. open, jaw same Pouting, 1. side, 1. T. rolled dors. to Lips inverted, 1. same cheek, 1. Cheek flattened, 1.	T. tip to opp. side, 2. Lips inverted, 1. T. protr. str., 2. T. refracted, 2. M. \(\times \) opp. retr., 2. M. \(\times \) same retr., 2. Cheek flattened, 2.
	•		M. open, jaw to same side, l. M. open, l. T. protr. str., l. T. tip to opp. side, l.	me side, 2.	T. tip to opp. side, 2.	M. z (same) retract., 2.	Mastic., 3.
		p. side, 1.		M. open, jaw to same side, 2.	T. protr. str., 5.	Mastic., 4.	M. open, jaw to same side, 4.
-		Mastic., 1. T. protr. str., 1. T. protr. tip to opp. side, 1. Pouting, 1.	Pouting, 2.	M. open str., 3.	M. open str., 6.	T. protr. str., 6.	T. dors. rolled to same cheek, 5.
		M. open, 2.	Mastic., 5.	Mastic., 7.	Mastic., 8.	M. open str., 9.	M. open str., 7.
	Square.	B.b.	B.c.	B.d.	B.e.	$\mathrm{B}f$	B.g.
مييهدا		-		к 2			

	_	٠	
•	Continuitado,	מסוד הדו מסמ	
	/ alay.	or anger	

Nil.	זכ	9	4	10	12	6	ಸಂ	ಸರ	λO
Number of obser- vations.	15.	15	15	15	15	15	15	15	ng ng
	. side, 1. ne side, 1. 1.	M. \(\text{\chi} \), same retr., 1. Lips invert., 1.	•		T.dors.rolledto M. 2 same Pouting, 1. same cheek, 1. sideretr., 1.	Pouting, 1.	S.P. elev. bilat., 1.	T.dors.rolled to Swallowing, 1. same cheek, 2. Pouting, 2.	M. open, jaw to Swallowing, l. same side, l. T. protr. tip to M. opp. \angle retr., l. opp. side, l. T. dors. to same Puckering, advancing both cheek, l. U.L. opp. elev., l.
	T. protr. tip to opp. side, 1. M. open, jaw to same side, 1. M. 2 opp. retract., 1. Lips invert., 1.	M. 2 opp. retr., 2.	U.L. opp. elev., 1. Hd. turn, 1.		T. protr. str., 1.	T. retr., 1.	M. open, jaw same side, 2.	T. retr., 3.	Cheek flattened, 3.
	T. rolled, dors. to same cheek, 2.	T. retr., 2.	M. same z retr., l. Lips invert., l.	U.L. opp. elev., 1.	Mastic., 1.	T. protr., 2.	M. open str., 4.	Mastic., 5.	T. protr. str., 3.
	M. open str., 6. T. retr., 3.	M. open str., 7. T. protr. opp. side, 3.	M. open str., 3. M. opp. z retr., 2.	M. opp. 2 retr., 1. Lips invert., 1.	M. open, jaw to same side, 1.	, 3. M. open str., 3.	, 6. T. protr. str., 5.	M. open str., 7. T. protr. str., 6.	M. open str., 6. Mastic., 4.
	M. oper	M. oper	M. oper	M.opp.	M. oper	Mastic., 3.	Mastic., 6.	M. oper	M. oper
Square.	В.ћ.	B <i>i</i> .	B.j.	B.k.	C.b.	C.c.	C.d.	C.e.	C.f.

Square.						Number of observations.	Nil.
C.g.	M. open str., 8.	T. dors. to same cheek, 2.	M. open, jaw to same side, 3.	Mastic., 2. T. protr. str., 2.	 T. protr. to opp. Cheek flattened, 1. side, 1. M. both 2 retr., 1. U.L. same side elev., 1. M. opp. 2 retr., 1. 	15	က
G.h	M. open str., 7.	T. dors. to same cheek, 4.	Mastic., 3.	Cheek same side adv., 2.	 M. open, jaw to M. opp. elev., 1. same side, 1. T. protr. to opp. Chin elev. bilat., 1. side, 1. T. retr., 1. M. both Z retr., 1. Pouting, 1. M. opp. Z retr., 1. 	7.5	Ø
C.i.	M. open str., 8.	M. opp. 2 retr., 3.	M. both 2 retr., 2.	M. both 2 retr., 2. T. protr. to opp. side, 2.	 T. protr. str., 1. M. opp. 2 elev., 1. T. dors. to same Chin opp. elev., 1. cheek, 1. M. both 2 elev., 1. Mastic., 1. 	15	ಸರೆ
C_{J}	M. open str., 5.	M. opp. 2 retr., 5.	M. both 2 retr., 3.	M. both 2 retr., 3. T. protr. to opp. side, 2.	T. protr. str., 2. Mastic., 1. M. same 2. elev., 1. T. dors. to M. opp. 2. samecheek, 1. elev., 1. T. retr., 1. Chinopp. side elev., 1. F. inteross. Hd. retr., 1. fax., 1. Th. flexed, 1.		9
C.k.	M. open str., 4. Hd. to opp. side, 3.	M. both 2 retr., 3. Sh. add., 1.	M. opp. 2 retr., 3. M. open, 1.	T. protr. to opp. side, 2. F. inteross. flex., 2. Th. flexed, 2.	T. protr. str., 1. Hd. retr., 1. M. opp. 2 elev., 1. Hd. to opp. side, 1. Sh. add., 1.	15	9

Nil.	日	o	4	ന .	Н	4
Number of obser- vations.	15	15	10 10	15	15	1.0 1.0
			Th. flex., 1.	Pouting, 1. Both cheeks adv., 1.	M. both 2 adv., 1.	T. retr., 1. Opp. chin elev., 1. Pouting same side, 1. M. opp. 2 adv., 1. M. same 2 adv., 1.
		Th. flex., 1. 1.	M. both z adv., 1. F. inteross. flex., 1.	Swallowing, 1. K. same 2 retr., 1.	M. both 2 retr., 1.M. opp. 2 retr., 1.	Mastic., 1. M. closes, 1. T. protr. to opp. side, 1. Hd. retr., 1.
	1.	M. both angles 7 adv., 1. F. inteross. flex., 1.	T. retr., 1. M. opp. 2 elev., 1.	M. open, jaw to same side, 1. M. protr. str., 1.	Mastic., 2. T. protr. to opp. side, 2. T. protr. str., 2.	M. open, jaw to same side, 2. M. opp. 2 retr., 2. M. both angles adv., 2.
	W. flex., 1. F. inteross. flex., 1.	M. open, jaw to same side, 1.T. protr. to opp. side, 1.	T. protr. to opp. side, 1. T. drawnto same cheek, 1.	Mastic., 3. T. dors. to same cheek, 3.	T. dors. to same cheek, 3. Same cheek puckered, 3.	Same cheek puckered, 3.
	T. protr. str., 1. M. both 2 retr., 1.	M. open str., 3. T. protr. str., 3.	Mastic., 3. T. protr. str., 3.	T. protr. to opp. side, 4. M. opp. Z retr., 4.	M. open str., 10. M. open, jaw to same side, 4.	T. dors. to same cheek, 4.
	M. open str., 2. Mastic., 2.	Mastic., 4.	M. open str., 4.	M. open str., 6.	M. open str., 10.	M. open str., 6.
Square.	D.c.	D.d.	D.e.	D.f.	D.g.	D.ħ.

Nil.	4	H	λΟ	-	Ħ	12	6	ಸಂ	ಸು
Number of obser- vations.	15	15	15	35 15	Æ.	15	15.	12	15
		T. retr., 1.	M. both z adv., 1. Hd. to opp. side, 1.				Cheek of same side flattened, 1.		Cheek same side flat, 1. Th. add., 1.
		M. open str., 1. M both 2 retr., 1.	Opp. chin elev., 1. Invert. lips, 1.	F. ext., 1.			M. opp. side rolled in, 1.	M. opp. side pout., 1. M. opp. side purs., 1.	M. opp. 2 elev., 1.
	M. both z retr., 1. M. same z elev., 1. Lips inverted, 1 Hd. retr., 1.	Chin opp. side elev., 1. Hd. to opp. side elev., 1.	M. open, 1. M. both 2 retr., 1.	M.opp. 2 elev.,1.	•	in, 1.	. M. opp. 2 pursed, 1. Th. ext., 1.	. M. both 2 elev., 1 M. opp. 2 elev., 1.	M. bilat. pout., 2.
	, 2. Pouting, 2. opp. side, 2. v., 2. v., 2. v., 2.	T. protr. to opp. side, 2. M. opp. z elev., 2.	T. protr. to opp. side, 2.	M. both / retr., 1.		M. opp. side rolled in, 1.	M. opp. z retr., 1. M. opp. z elev., 1. Wrist, 1. Fingers, 1.	M. opp. 2 retr., 2. Th. abd. and flex., 2.	M. both 2 retr., 2. M. opp. 2 retr., 2.
	M. open str., T. protr. to M. opp. z ele Opp. chin ele	". Pouting opp. side, 3.	M. opp. 2 retr., 6. M. opp. 2 elev., 4.	o. M. opp. 2 retr., 3.	e, 4.). side, 2.	M. opp. 2 retr., 1 Wrist, 1.	lled in, 3.	side, 2.
	M. opp. 2 retr., 5.	M. opp. 2 retr., 12.	M. opp. 2 retr.,	Hd. to opp. side, 4.	Hd. to opp. side, 4.	M. pouting opp. side, 2.	Mastic., 1. Elb. flexed, 1.	M. opp. side rolled in, 3.	Mastic., 2. T. dors. to same side, 2.
Square.	D.i.	D.j.	D.k.	D.Z.	D.m.	因.6.	E.d.	E.e.	E.f.

Square.						Number of observations.	Nil.
E.9.	M. opp. 2 retr., 7. M. open, 4.	M. opp. z elev., 3. Mastic., 2. T. tip to opp. side, 3. M. both z retr., 2. M. pursing, 2.	Mastic., 2. M. both 2 retr., 2. M. pursing, 2.	M. open, jaw to same side, l. T. dors. to same side, l. side, l. M. \(\alpha \) same side retr., l.	Cheek of same side elev., 1. M. bilat. pout., 1. Cheek of same side flat, 1. Th. add., 1.	15	Н
E.h.	 M. opp. 2 retr., 3. M. open str., 2. M. open jaw to same side, 2. Lips same side rolled in, 2. 	T. protr. tip to opp. side, 2. M. opp. \angle elev., 2. Cheek same side flat, 2.	Mastic., 1. T. rolled over dors. to same side, 1. Chin bilat. elev., 1.	M. bilat. pout., 1. Cl M. bilat. purs., 1. Lips bilat. rolled in, 1.	Cheeks bilat.flat., 1. 1.	ಸ	yO.
E.i.	M. opp. 2 retr., 7. M. opp. 2 elev., 4. M. open 2. T. protr. til side, 2. Lips opp. s.	p to opp. ide rolled	T. protr. str., 1. T. dors. rolled to same side, 1.		Opp. chin elev., 1. Elb. flex., 1.	15	CJ
E.g.	M. opp. 2 retr., 9. M. opp. 2 elev., 6.	m, 2. M. open, jaw to same side, 2. T. protr. tip to opp. side, 2.	Chin opp. elev., 2. Hd. to opp. side, 2.	M. open str., 1.T. dors. rolled to same side, 1.Lips. opp. side rolled in, 1.	Elb. flex., 1. W.ext. and pron., 1. Hd. retr., 1.	ΙΩ	—
E.k.	M. opp. z retr., 8. M. opp. z elev., 5.	M. open str., 2. T. protr. tip to opp. side, 2. Chin opp. side elev., 2.	Elb. flex., 2. F. flex., 2.	 T. dors. rolled to same side, 1. Lips opp. side rolled in, 1. Th. flex., 1. 	Opp. eyelids closed, 1. W.sup.andpron.,1. Hd. to opp. side, 1.	10 10	ಣ

Table I. (continued).

Nil.	∞	12	11	4	4	0		4	C 3
Number of obser- vations.	TG.	L	15	TG.	15	15		15	15
	Elb. flex., 3. M. opp. 2 elev., 2. M. opp. 2 retr., 1. Opp. eyelids close, 1. Eyes to opp. side, 1. F. ext. 1. Chin opp. side elev., 1. W. sup., 1.	Opp. eyelids Sh., rot. in., l. Fingers, l. Hd. to opp. side, l. close., l.	M. opp. 2 M. opp. side F. ext., 1. Th. ext., 1. elev., 1. pout., 1.		M. opp. 2 M. opp. 2 M. bilat. Th. opp., l. F. ext., l. Mastic., l. Opp. lower Opp. lips retr., 4. elev., 3. pout., 2. Elb. flex., 1. W. ext., l. M. bothangles M. bilat. purs., l. retr., l. retr., l.	T. protr. tip to opp. side, 1.	Bilat, drawing forward of T. dors. to F. ext., 1. lips, 3. same side, 1.	M. opp. 2 M. bilat. M. open str., 2. Mastic., 1. M. same 2 Opp. chin Hd. retr., 1. retr., 4. pout., 3. T. dors. to same T. protr. tip to opp. side, 1. Opp. lower lip M. bilat. purs., 1. elev., 4. side, 2.	M. opp. 2 Opp. eyelids M. opp. 2 Elb. flex., 1. Hd. retr., 1. T. protr. tip to T. protr. str., 1. retr., 7. closed, 4. elev., 3.
	Eib.	lo Opp	M. ele	M. opp retr., 4.	M.	$_{ m ret}$		M. ret M. ele	M. ret
Square.	E.L.	E.m.	F.d.	F.e.	F.f.	F.g.		F. <i>h</i> .	F.i.

DR. C. E. BEEVOR AND PROFESSOR V. HORSLEY ON THE

TABLE I. (continued).

Nil.	0	9	7 .	12	13	6.	ಣ	0
Number of obser- vations.	15	15	15	15	15	T.	٠ ت	15
	Hd. to opp. side, 1.							
. •		•				W. sup., 1. W. ext., 1.	Th. flex., 1.	F. ext., 1.
	Opp. lower lip roll in, 2.	Opp. lower lip roll in, 1.				op. 2.	Lower lip de- Ti press., l. W. flex., l.	W. ext., 1. F. Th. ext., 1.
	Eyelids bilat., Elb. flex., 2. Oppleblink, 3.	Opp. chin, Oppelev., 1. M. purs., 1.			ss., 1.	M. bilat. purs., 1. M. oj adv Opp. lower lip depress., 1.	M. bilat. pout., 1. M. bilat. purs., 1.	T. same side retr., 1. Cheek on same side puckered, 1.
	No.	Hd. retr., 1.	retr., 1.	. flex., 1.	Opp. lower lip depress., 1.	M. opp. 2 retr., 1.Opp. lips roll in, 1.	M. 2 bilat. adv., 2.Th. ext., 2.	M. bilat. pout., 2. Opp. lower lip de- press., 2.
	M. opp. 2	Elbow, 2. Hd. to opp. side, 2.	M. opp. 2 retr., 1. de, 2.	F. inteross. flex., 1. side, 1.				
	Opp. eyelids closed, 5.	M. opp. 2 retr., 4. Opp. eyelids close, 3.	 M. opp. 2 elev., 2. Hd. to opp. side 	Opp. eyelids F. in: close, 1. Eyes to opp. side, 1.	M. opp. 2 retr., l. M. opp. 2 elev., l.	M. opp. 2 elev., 2.	. M. opp. 2 retr., 5.	. M. opp. 2 adv., 3. M. opens, 3.
	M. opp. 2 Opretr., 7.	$egin{array}{ll} M. & \mathrm{opp.} & Z & M. \\ \mathrm{elev., 4.} & \mathrm{re} \\ O_\mathrm{p} & \mathrm{obs.} \\ O_\mathrm{p} & \mathrm{obs.} \end{array}$	Opp. eyelids M. close, 3. Hc	M. opp. 2 Orretr., 2. cl Hd. to opp. Ey side, 2.	F. opp., 2. Th. opp., 2.	F. ext., 4. Th. ext., 4.	M. opp. 2 elev., 6.	M. opp. 2 elev., 7. M. opp. 2 retr., 7.
Square.	F.j.	F. <i>R</i> .	F.7.	F.m.	G.d.	G.e.	G.f.	G.g.

Table I. (continued).

Nil.	62	4	70	∞ .	11	7	4	က်
Number of observations.	10 10	15	15	15	15	15	15	15
	M. opp. 2 elev., 7. M. opp. 2 retr., 4. M. opens, 2. Th. ext., 2. T. retr., 1. M. bilat. pout., 1. T. protr. tip to Opp. cheek puck- M. same 2 M. 2 bilat. adv., 1. opp. side, 2. ered, 2. M. opp. 2 W. ext., 1. F. ext., 1. adv., 1.	M. opp. 2 elev., 6. Opp. eyelids M. opp. 2 retr., 3. Opp. lips roll in, 2. W. pron., 1.	elids M. opp. 2 retr., 4. M. opp. 2 elev., 3. Opp. lower lip roll T. protr. tip F. ext., 1. 5. Eyelids bilat. Th. ext., 1. closed, 1.	M. opp. 2 retr., 3. Opp. lips roll in, 2. Opp. eyelids Elb. flex., 1. close, 1. F. ext., 1.	r., 3. Eyes to opp. Opp. lower lip roll W. sup., 1. F. ext., 1. Hd. to opp. side, 1. side, 2. in, 1.	M. opp. 2 refr., 3. M. bilat. purs., 1. Opp. lips roll in, 1.	 M. opp. Z retr., 6. M. opp. Z elev., 4. M. bilat. purs., 2. Opp. lips roll Elb. flex., 1. W. ext., 1. in, 1. Th. flex., 4. F. flex., 2. M. opp. Z adv., 1. W. sup., 1. Th. add., 1. 	M. opp. 2 retr., 9. M. opp. 2 elev., 5. Th. flex., 3. Opp. lower lip M. open, 1. M. opp. 2 Elb. flex., 1. depress, 2. adv., 1. F. flex., 2. M. bilat. purs., 1. Opp. eyelids W. sup., 1. closed, 1.
	M. opp.	M. opp.	Opp. eyelids close, 5.	M. opp.	M. 2 retr., 3.	M. opp.	M. opp.	M. opp.
Square.	G.h.	G.i.	G.j.	G.k.	G. <i>l</i> .	Н.е.	$\mathrm{H.}f.$	Н.д.

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BIOLOGICAL

PHILOSOPHICAL THE ROYAL TRANSACTIONS

DR. C. E. BEEVOR AND PROFESSOR V. HORSLEY ON THE

TABLE I. (continued).

Square.							Number of observations.	Nil.
Н.ћ.	M. opp. 2 retr., 8.	M. opp. 2 elev.,6. Th. flex., 6.	Index finger ext., 3.	Opp. eyelids close, 1.	Elb. flex., 1.		15	0
H.j.	Opp. eyelids close, 6.	M. opp. 2 retr.,5.	M. opp. 2 elev.,3.	Th. flex., 2.	Opp. lips roll in, 1.	F. flex., 1.	JŠ	ಸ್
Н.К.	M. opp. 2 retr., 1.	M.opp. 2 elev.,1.	Opp. lips roll in, 1.	Opp. eyelids close, 1.	1.		15	12
Н.7.	M. opp. 2 retr., 2. M. open, 1.	M. open, 1.	Opp. lips roll in, 1.	• • • • • • • • • • • • • • • • • • • •			15	13
H.m.	Hd. to opp. side, 1.			9			15	14
***************************************							-	-
Le.	M. opp. z retr., 4.	Eyes open, 1	Elbow flex., 1.	W. sup., 1.	Fingers, 1.	Hd. to opp. side, 1.	15	П
I.f.	M. opp. 2 retr., 3. M. opp. 2 elev., 3.	Opp. lower lip de Thumb, 2.	ip depress., 2.	Hd. to opp. side, 2.	Opp. lips roll in, 1. Opp. eyelids close, 1	Fingers, 1.	15	4
$\Gamma.g.$	M. opp. 2 elev., 6.	Fingers, 5. Thumb, 5.	Opp. eyelids close, 4. M. opp. 2 retr., 4.	M. opp. ∠ retr., 4.	Opp. lower lip de- press., 3.	M. opp. pursed, 1. Hd. retract., 1. Hd. to opp. side, 1.	L	က
I.h.	Thumb, 6.	M. opp. 2 elev., Fingers, 4.	M. opp. 2 elev., 4. M. opp. 2 retr., 3. Fingers, 4.	Opp. lower lip de- press, 2. Opp. eyelids close, 2.	Hd. to opp. side, 1.		15	9
L.i.	Thumb, 6.	Opp. eyelids close, 3.	M. opp. 2 retr., 1.	M. opp. 2 elev., 1.	Opp. lip depress., 1. Sh. 1. Elbow, 1. Wrist,	Sh. 1. Fingers, 1. Wrist, 1.	15	∞

TABLE I. (continued).

Square.						Number of observations.	Nil.
J.f.	Thumb, 3.	M. opp. 2 retr., 2.		M. opp. 2 elev., 1.	Opp. eyelids close, 1.	15	6
	Wrist, 3. Shoulder, 3. Fingers, 3.			Opp. lower lip depress., 1.	Hd. to opp. side, 1.		
J.g.	M. opp. 2 retr. 2.	M. opp. 2 elev., 1. Opp. lower lip depress., 1.	Opp. lower lip depress., 1.	Wrist flex., 1.		15	13
J.h.	M. opp. z retract, 1. M. opp. z elev., 1.	Hd. to opp. side, 1.	•			15	13
J.i. J.j.							
K.f. $K.g.$	Opp. eyelids closed, 1. (Face only observed).	face only observed).				15	14
K.h.						,	eer-descension - general value v
D.%.	_						

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DR. C. E. BEEVOR! AND PROFESSOR V. HORSLEY ON THE

MARCHES.

Under this heading we wish to describe, in the meaning of the word as originally used by Dr. Hughlings Jackson, such sequences by movements as we occasionally observed to take place.

At the outset we would state that a great difference characterises the area of representation for the face as contrasted with that for the limbs. Whereas it was possible in the case of the limbs to make out a definite march for individual parts of the cortex, we have not been able to find sufficient examples of such similarity as to justify us in attributing a definite march to the different parts of the area of representation for the face, but although this exact localisation is not possible the representation of the primary movement, as given in the accompanying list, is such as we have already described in each case.

We have therefore simply appended a list of the sequences of movements or marches arranged in the order in which they most frequently occurred.

MOTOR REGION OF THE CORTEX CEREBRI IN THE MONKEY.

TABLE II.

Marches.		Number of squares at which observed.
Primary Secondary	Mouth opens	7
Primary Secondary Tertiary	Bilateral pouting	5
Primary Secondary	Opposite angle retracted or elevated	5
Primary Secondary	Both angles bilaterally retracted	4
Primary Secondary	Mouth retracted to opposite side, opposite lower lip inverted	4
Primary Secondary	Mouth opens	3
Primary Secondary	Mouth opens	3
Primary Secondary Tertiary	$egin{array}{lll} ext{Pouting or pursing of lips} & . & . & . & . & . & . \\ ext{Opposite angle retracted} & . & . & . & . & . & . \\ ext{Tongue rolled to same side} & . & . & . & . & . & . & . \\ \end{array}$	3
Primary Secondary Tertiary	Pouting or pursing	3
Primary Secondary Tertiary	Angle of mouth retracted on same side	2
Primary	$egin{array}{llll} ext{Mouth opens straight} & . & . & . & . & . & . & . & . & . & $	2
Primary Secondary	Mouth opens wide	2
Primary Secondary	Opposite lower lip rolled in	2
Primary	Pouting and pursing, especially of opposite side . Opposite lower lip everted and depressed	2
Primary Secondary	Mouth opens	1
Primary Secondary Tertiary	Mouth pursed up	1 .
Primary Secondary	Pursing of mouth	1
Primary Secondary	Opposite eyelids closed, opposite side of mouth retracted	1

DR. C. E. BEEVOR AND PROFESSOR V. HORSLEY ON THE

DESCRIPTION OF PLATES.

Note.—In constructing the figures, the actual number of dots represents the precise number of cases in which the movement was elicited at that particular square.

PLATE 8.

Fig. 1. Photograph of the outer surface of the right cerebral hemisphere of the Bonnet Monkey (*Macacus sinicus*). The shaded lines indicate the area which is the object of the present investigation.

Sy. = Fissure of Sylvius.

R. = Fissure of Rolando.

I.P. = Intraparietal sulcus.

Pc. = Præcentral sulcus.

S.F.S. = Superior frontal sulcus.

S.T. = Sulcus frontalis transversus inferior.

Rc.t. = Sulcus retrocentralis transversus.

- Fig. 2. Drawing of the portion of the left cerebral cortex under observation on the paper ruled in squares of 2 millim. side, similar to that used in each experiment. The fissures and sulci indicated are the average of all the twenty experiments, as described in the text. The squares are, as shown, denoted by the double enumeration of capital letters and italics. The lettering for the fissures and sulci are the same as in fig. 1, except F.t., which is the same as S.t.
- Fig. 3 shows the localisation of the representation of the movement of the closure of the opposite eyelids.
- Fig. 4 shows the localisation of the representation of the angle of the mouth of the opposite lip.
- Fig. 5 shows the localisation of the depression of the lower lip of the opposite side.
- Fig. 6 shows the localisation of the retraction of the angle of the mouth of the opposite side.
- Fig. 7 shows the localisation of the retraction of the angle of the mouth of both sides. Fig. 8 shows the localisation of the flattening of the cheek on the same side.

PLATE 9.

Fig. 9 shows the localisation of the representation of all the movements of the whole tongue. General view. The horizontal lines denote the representation of protrusion of the tongue, with deviation of the tip to the opposite

MOTOR REGION OF THE CORTEX CEREBRI IN THE MONKEY.

side; the vertical lines denote that of rolling over of the tongue on its longitudinal axis with the dorsum directed towards the cheek of the same side; the lines sloping forwards and downwards denote that of protrusion of the tongue straight; the lines directed downwards and backwards denote that of retraction of the tongue.

- Fig. 10 shows the localisation of the representation of the movement of protrusion of the tongue straight.
- Fig. 11 shows the localisation of the protrusion of the tongue with the tip to the opposite side.
- Fig. 12 shows the localisation of the rolling over of the tongue with its dorsum to the cheek of the same side.
- Fig. 13 shows the localisation of the opening of the mouth straight.
- Fig. 14 shows the localisation of the opening of the mouth in which the lower jaw is carried towards the same side.
- Fig. 15 shows the localisation of the rhythmical movements of mastication.
- Fig. 16 shows the localisation of the elevation of the soft palate.

Beevor and Horsley.

Fig.1.

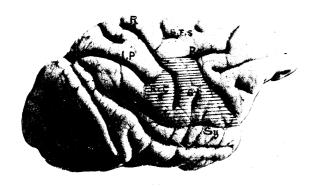


Fig. 3.



Fig. 5.

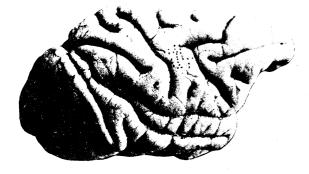


Fig. 7.



Frg. 2.

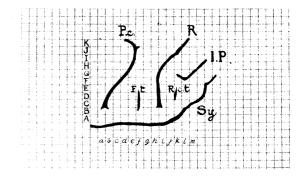


Fig.4.

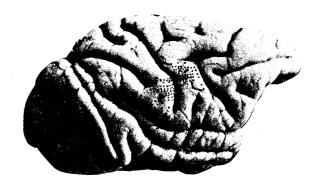


Fig. 6.

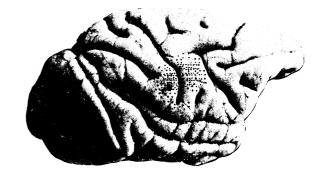
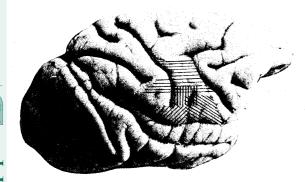


Fig.8.





Frg. 9.

Fig.11.

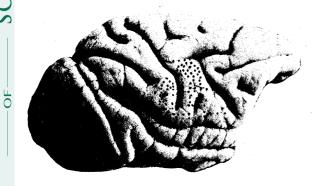


Fig. 13.



Fig.15.





Fig.12.

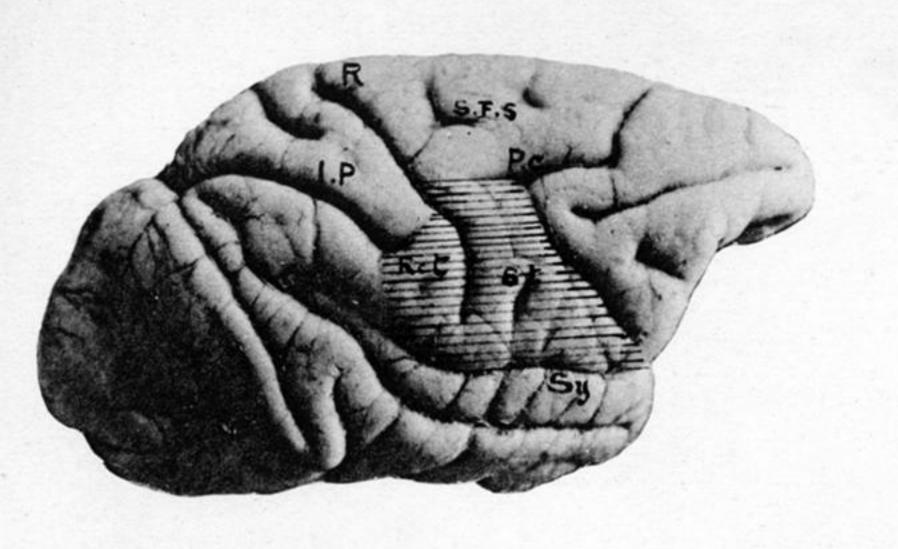


Fig. 14.



Fig.16.





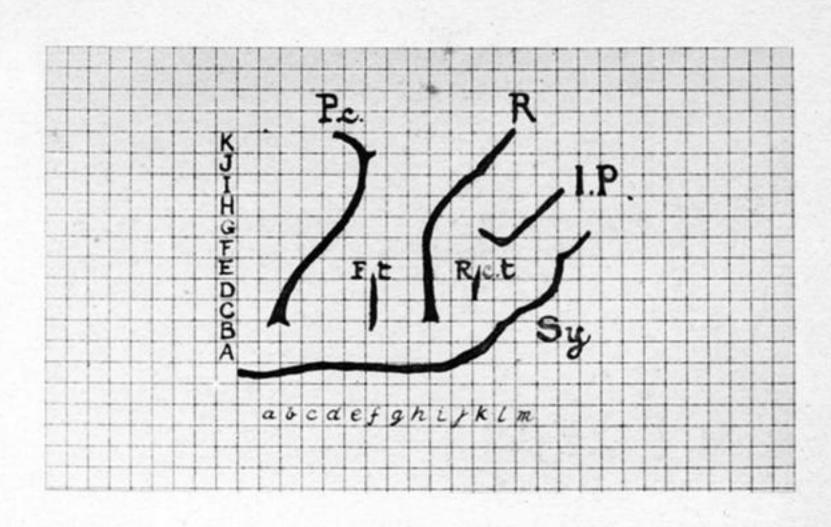


Fig. 3.

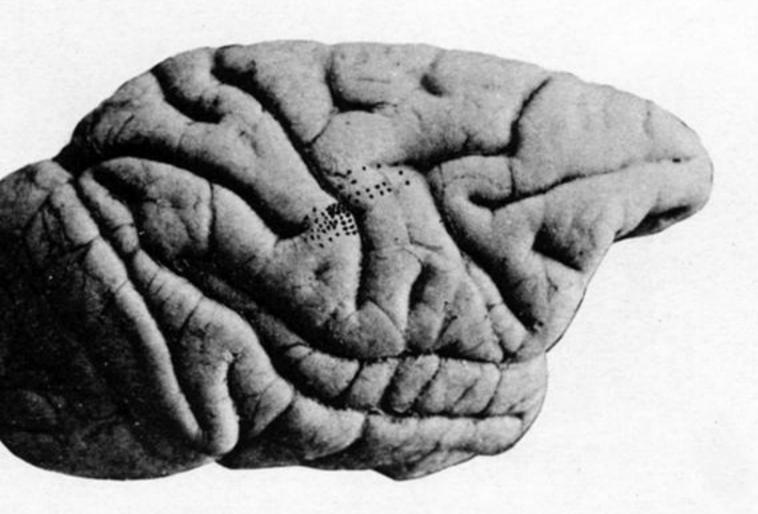


Fig.4.

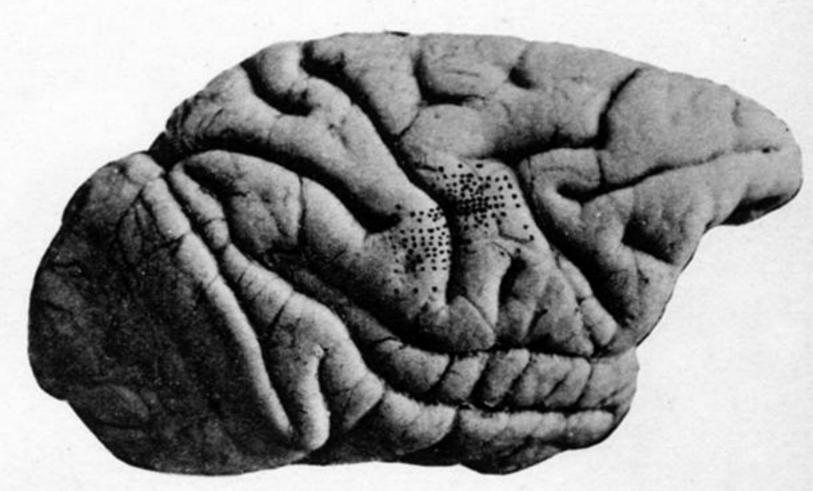


Fig. 5.

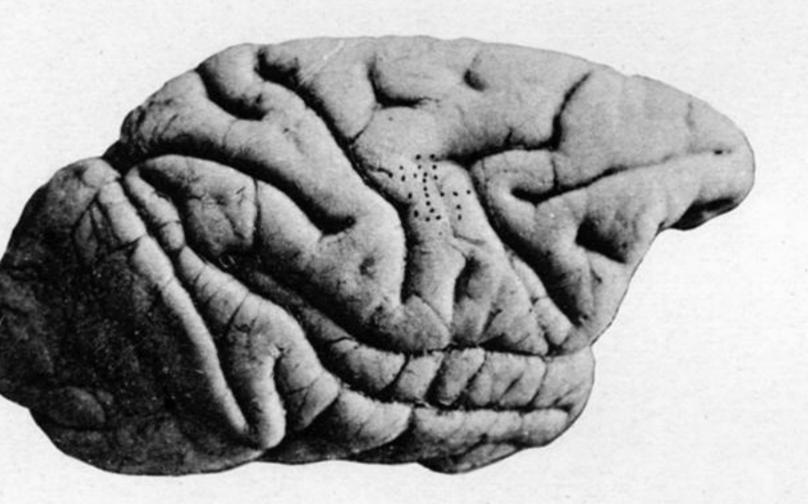


Fig. 6.

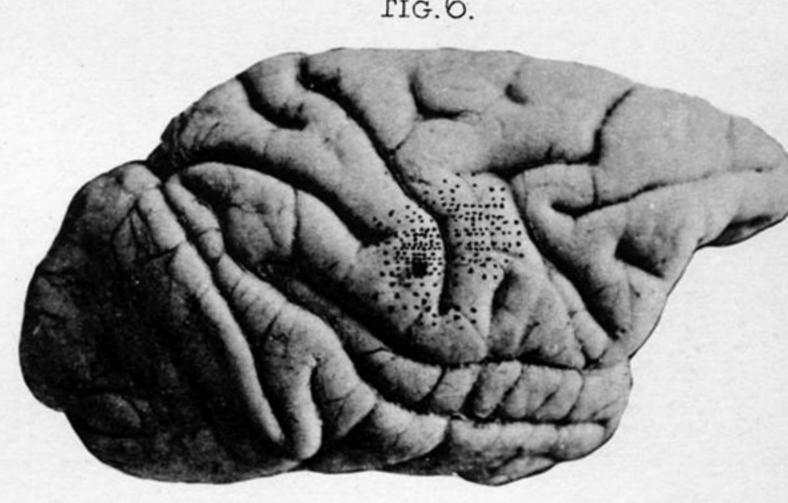
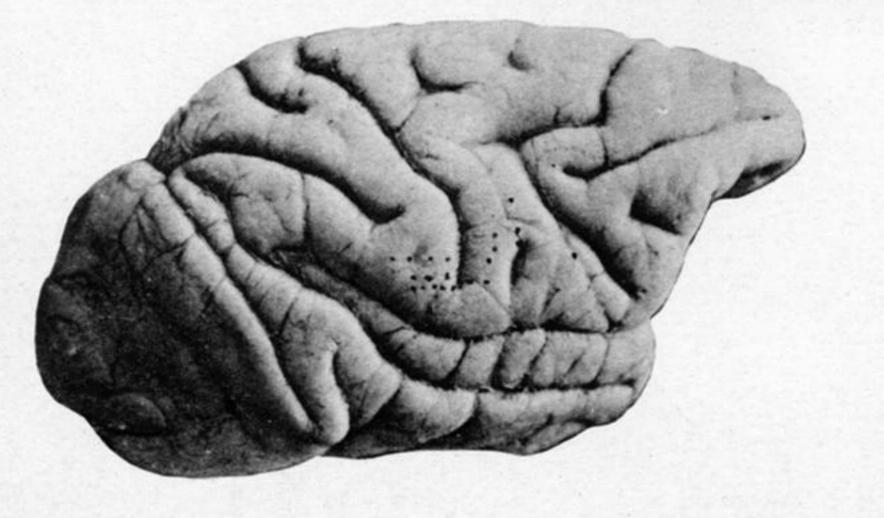


Fig. 7.



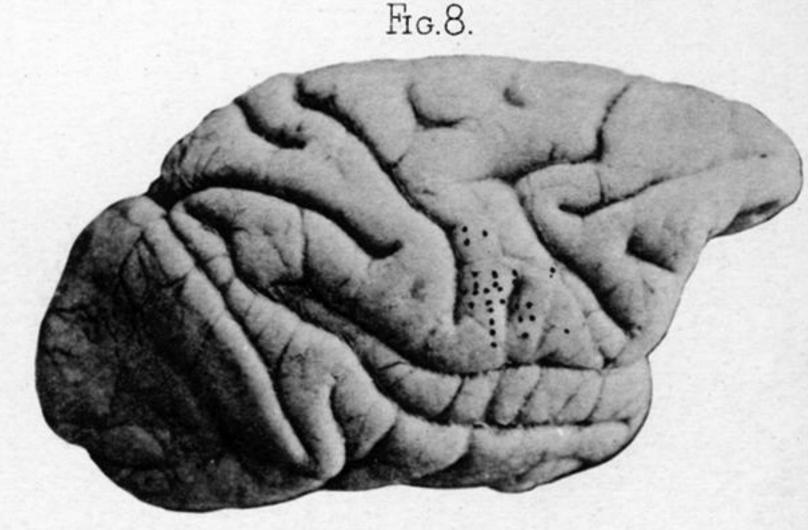


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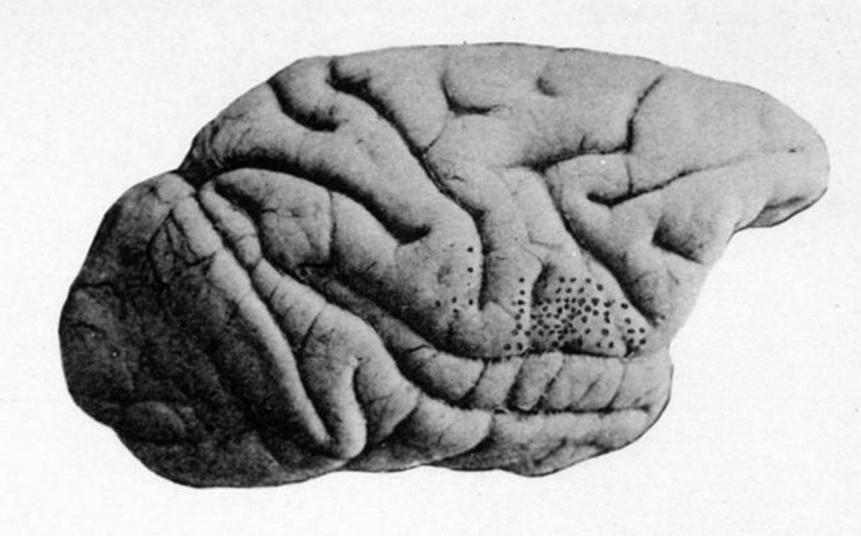
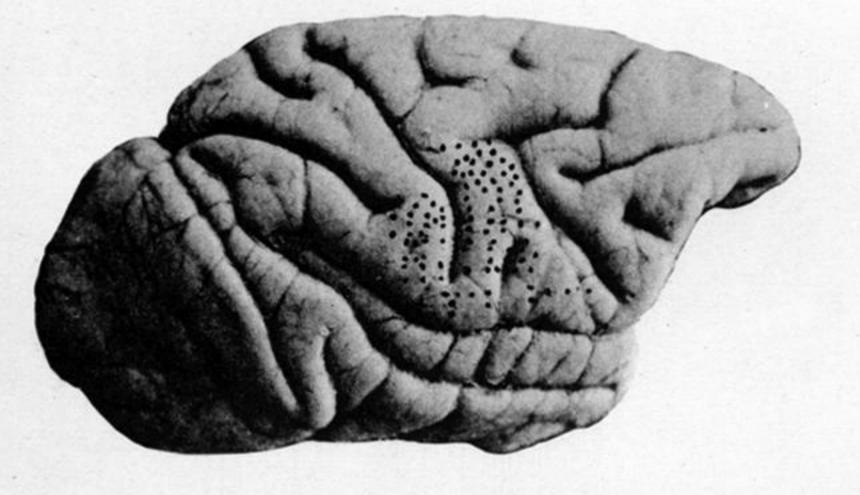


Fig.11.

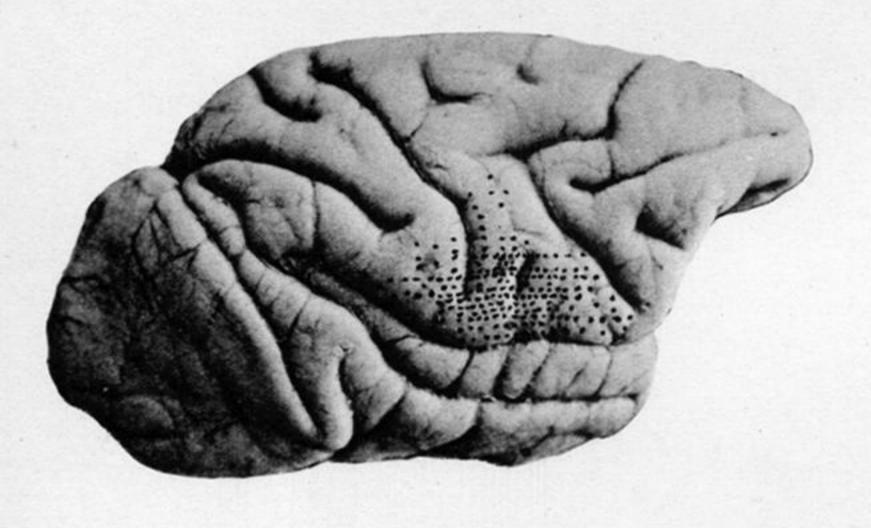
Frg. 12.





Frg. 13.

Fig. 14.



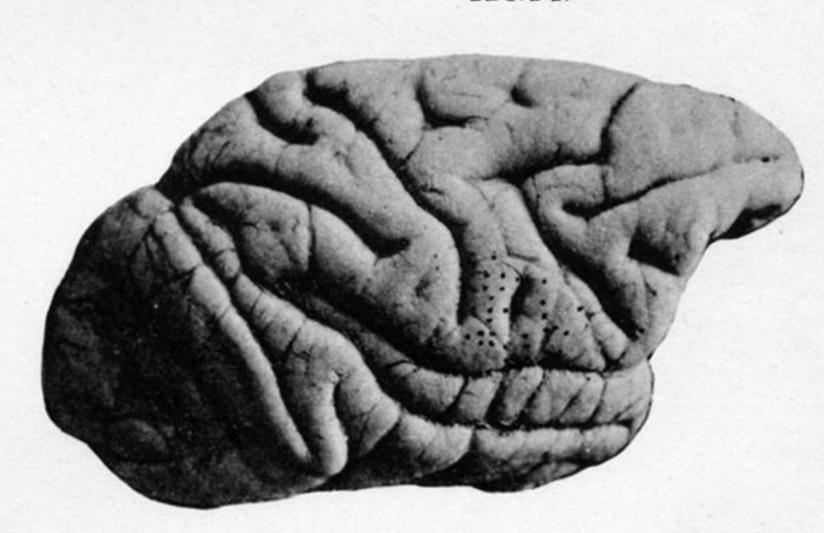
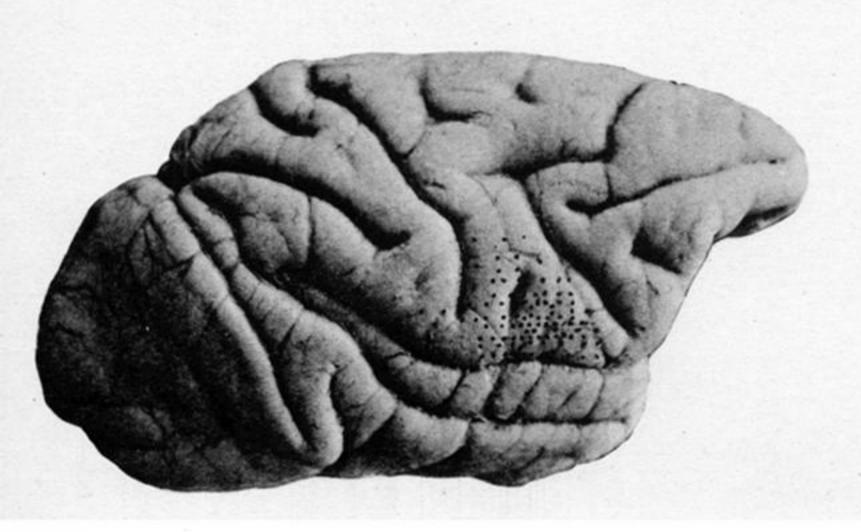


Fig.15.

Fig.16.



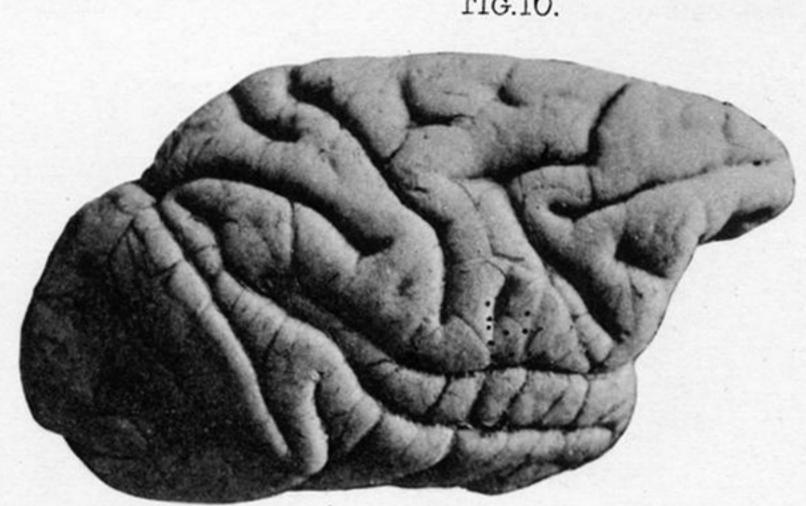


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