PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

A Record of the Results Obtained by Electrical Excitation of the So-Called Motor Cortex and Internal Capsule in an Orang-Outang (Simia satyrus)

Charles E. Beevor and Victor Horsley

Phil. Trans. R. Soc. Lond. B 1890 **181**, 129-158
doi: 10.1098/rstb.1890.0006

VI. *A Record of the Results obtained by Electrical Excitation of the so-called Motor Cortex and Internal Capsule in an Orang-Outang* (Simia satyrus).

By Charles E. Beevor, *M.D., F.R.C.P., and* Victor Horsley, *B.S., F.R.S.*
(*From the Laboratory of the Brown Institution.*)

Received June 5,—Read June 12, 1890.

[Plates 16–21.]

Contents.

Introduction.

Having been occupied with the study of the minute representation of motor function in the cortex of the Bonnet Monkey (*Macacus sinicus*), it seemed to us extremely necessary to investigate the character of such representation in the cortex of an anthropoid Ape, in order that we might form a more correct estimate of the mode of localisation in Man. A comparative study of the brains and habits of the more easily obtainable anthropoids showed clearly that for our object the Orang was more suitable than the Chimpanzee, in being likely to afford results nearer to those presumed to exist in Man. We therefore procured a young Orang which, in the opinion of Professor D. J. Cunningham, of Trinity College, Dublin, was about $2\frac{1}{2}$ years old.

In addition to excitation of the cortex, we also investigated the movements obtained by stimulating the fibres of the internal capsule.

We shall therefore arrange the facts as follows :—

Anatomy.

Method of Investigation.

Results of Excitation—
A. Cortex.
B. Internal Capsule.
Summary and Review of the Character of Localisation in this Animal.

ANATOMY.

We say nothing here respecting the general anatomy of the animal, having deposited the carcass in the Hunterian Museum.

The area of cortex which we explored comprises the so-called motor region. This area is bounded below by the Sylvian fissure, above by the longitudinal fissure, posteriorly by the intra-parietal sulcus, and anteriorly by a line drawn vertically through about the middle of the three frontal convolutions. It includes the fissure of ROLANDO, the posterior half of the superior frontal sulcus (corresponding to the sulcus x in the Bonnet Monkey: *vide* 'Phil. Trans.,' B, 1887), the præcentral sulcus, and the postcentral sulcus in the parietal lobule (corresponding to sulcus z in the Bonnet Monkey). Of the two small sulci which are so commonly seen in the Bonnet Monkey and in Man at the foot of the ascending or central convolutions, the one which is usually situated at the foot of the ascending frontal (v in the Bonnet Monkey*) was absent, while that at the foot of the ascending parietal was not only strongly developed, but there was also another small indentation in front of it, in the foot of the gyrus.

We will now proceed to make a few remarks in detail on these fissures and sulci, as we believe that there are certain features in their conformation which are of practical importance for the purposes of localisation.

Fissure of ROLANDO.

We have already drawn attention to the shape of this fissure in the Bonnet Monkey ('Phil. Trans.,' *loc. cit.*), and we have shown that in that animal it presents a well marked genu at the junction of its middle and lower thirds, and we have further shown that this genu indicates the lower border of the upper limb area of representation.

In the Orang this genu is extremely well marked, so that in tracing the fissure from below upwards it makes almost a right angle as it turns backward, and then, as a necessary consequence to reach the upper margin of the hemisphere, it has to turn again upwards almost at a right angle, see figs. 1, 2, 3, Plates 16, 17. It follows from this that the principal axes of the ascending or central convolutions being parallel to the Fissure of ROLANDO are very flexuous, instead of being merely oblique as in the Bonnet Monkey. This extreme angularity seems to be a very characteristic feature of the anthropoid Apes, as contrasted with the brain of Man, in whom, however, it is sometimes seen.

* See forthcoming paper by the authors on the facial region of representation.

It will now be important to note the position of the genu of this fissure in the Orang and Man, as compared with the Bonnet Monkey. In the last, it is situated at the junction of the middle and lower thirds of the fissure, in the Orang and in Man it is found at about the mid-point between the upper margin of the hemisphere and the Fissure of SYLVIUS, or higher. We would suggest that this is due to the greater development in the higher animals of the convolutions about the lower end of the Fissure of ROLANDO, including the third frontal gyrus. We think this is borne out by the fact that it is the lower part of the Fissure of ROLANDO, *i.e.*, that part below the genu, which is so much lengthened.

Of further curvation, the Fissure of ROLANDO often exhibits at its upper end a slight bend forwards which, in man, is surmounted by a small curve in the opposite direction.

The Præcentral Sulcus

Consists of a vertical arm, which springs from close above the Fissure of SYLVIUS, and ascends till it bifurcates just below the horizontal level of the genu of the Fissure of ROLANDO, into a posterior ascending branch and an anterior horizontal. Where this latter joins the vertical limb, it forms a right angle anteriorly, which, as will be subsequently seen, is just as in the Bonnet Monkey, the focus for the representation of the movement of turning the head and eyes to the opposite side.

In this angle, formed by the limbs of the præcentral sulcus, there is another sulcus, directed downwards and forwards, and which we believe to be the homologue of the sulcus which we have temporarily called "*w*" in the Bonnet Monkey.* In the anthropoids, its anterior end seems to extend down to the orbital surface of the lobe, and to wind round in front of the anterior extremity of the Fissure of SYLVIUS.

(We believe that this sulcus corresponds to the inferior frontal sulcus of Man.)

We have pointed out in a previous communication ('Phil. Trans.,' B, 1887) that the sulcus in the Bonnet Monkey, which Professor SCHÄFER provisionally termed x, is the superior frontal sulcus of human nomenclature. We also showed that it consisted in its simplest condition of a vertical and a longitudinal limb. Now it has been proposed by JENSEN to call the vertical limb the superior præcentral sulcus; without giving our support to this step, we wish to emphasize the correctness of the description, and to point out that in the Orang this limb is well marked. As a rule, we believe that it will be found that this limb, or its secondary continuation, reaches down to the horizontal level of the genu of the Fissure of ROLANDO. For localising purposes, however, as we have shown in the Bonnet, the important feature of the superior frontal sulcus is not so much the vertical as the horizontal limb; for, on continuing the direction of the latter limb backwards across the ascending frontal and parietal convolutions it constitutes, according to our observation, the boundary

* 'Phil. Trans.,' B, 1888.

between the representation of the upper and the lower limbs respectively; this we similarly find to be the case in the Orang (see fig. 4, p. 150).

The Intraparietal Sulcus

In the present brain runs a characteristic course, viz., from near the lower end of the ascending parietal gyrus (where it bifurcates) upwards and backwards. At the bifurcation one limb runs forwards and upwards towards the genu of the Fissure of ROLANDO, and the other downwards towards the Fissure of SYLVIUS. As it courses across the parietal lobe it follows in a fairly parallel manner the direction of the Fissure of ROLANDO.

The post-central sulcus (Ramus Superior of the intraparietal sulcus, according to CUNNINGHAM, 'Journ. of Anat. and Physiol.,' 1889) is well marked, and begins near the longitudinal fissure at the upper margin of the hemisphere, and follows close round, strictly parallel to the Fissure of ROLANDO, reaching down the ascending parietal convolution almost as far as the genu of the Fissure of ROLANDO, *vide* figs. 2 and 3.

Convolutions.

The ascending frontal and parietal convolutions have the same position and relations as in Man and are bound by the same fissures and sulci.

The *three frontal convolutions* present more difficulty, as their boundaries are not so evident. The division between the superior and middle convolutions is sufficiently indicated by the superior frontal sulcus; but the line of separation between the middle and inferior convolutions is not so evident; we think, however, that the sulcus "*w*," *i.e.*, the inferior frontal sulcus, marks the boundary between the two. Around the posterior end of this sulcus, as will be subsequently seen, is situated the focus of the representation of the movement of turning the eyes to the opposite side; and since this particular focus of representation in the Bonnet surrounds the posterior end of the sulcus *w*, we think we are justified in regarding the sulcus marked I.F.S., in figs. 1, 2, and 3, as homologous to the *w* or inferior frontal sulcus of the Bonnet, and, consequently, as the dividing line between the middle and inferior *frontal convolutions.*

For topographical purposes, as was shown many years ago, the sulci are of very much more importance than the convolutions which they fashion, consequently, we need not prolong the description of the latter. We must, however, recall attention to the determination by the sulci of representation or its absence, a point which we first observed in the Bonnet. To repeat, representation of movement in the cortex is found only on the summits of the gyri of the convoluted surface, and the approach of a sulcus dimpling the cortex at all makes it at once inexcitable. This, true of the Bonnet, is still more marked in the Orang, where, in addition, as will be seen, we have slands of smooth cortex, even between foci, which are inexcitable.

In the yet more highly divided human cortex this principle naturally must be held to prevail with still more force, as seems, in fact, to be the case, see p. 152, *et seq.*

METHOD OF INVESTIGATION.

In accordance with our present mode of recording the results of excitation of the cortex cerebri, we proceeded to expose and explore the surface of the so-called motor region in the left hemisphere in the following manner :—

1. *Anæsthetisation.*—The animal was thoroughly narcotised with ether. It was interesting to note that, in harmony with the greater size and the more highly evolved intelligence of the animal, it required, relatively, as well as of course absolutely, more ether than the lower Macacque Monkeys do.

2. *Operation.*—The brain was exposed by the method described elsewhere ('Brit. Med. Journ.,' 1887). The large flap of scalp and segments of the dura mater were carefully replaced after each measurement of the surface (*vide infra*) or excitation, so as to entirely preclude the possibility of the cortex becoming damaged by drying and cooling. For the special prevention of the two latter sources of error, the temperature of the room was maintained at 75°–80° F., the animal was placed upon a hot tin (temperature about 100° F.) and, finally, the surface of the brain was occasionally irrigated with warm ·75 per cent. salt solution.

We found that these precautionary measures preserved the excitability of the cortex at its normal level for many hours.

3. *Method of Recording.*—The positions of the sulci of the area exposed were then transferred by means of fine compasses to paper ruled mathematically with squares, whose sides measured 2 mm. We thus obtained a projection of the configuration of the cortex, the surface of which was already divided into squares of 4 square mm.* in extent. The actual drawing made at the time of the experiment is seen in fig. 3.

Each of these squares was then excited, the strength of the minimal stimulus noted, and also the resulting movement evoked.

4. *Mode of Excitation.*—The excitation was provided by the current from the secondary coil of a DU BOIS-REYMOND inductorium, furnished with a 1 litre bichromate cell. No side wire was employed (*vide* strength required *infra*). The electrodes were fine platinum points, 2 mm. apart, and they were applied horizontally, *i.e.*, in the long axis of the brain, each electrode resting on the mid point of the two sides of each square.

The strength of current required to evoke any movement was notably in excess of that which we have found necessary to use in the Macacque. With the Orang a minimal stimulus (*i.e.*, the weakest which would produce a movement) was obtained only when the secondary coil was moved to 9·5 centims. from the zero point of completely covering the primary coil. This current was such as to cause discomfort bordering on pain when applied to the tip of the tongue of the experimenter. This (minimal) stimulus was used throughout.

The method of investigating the internal capsule is given further on; see p. 147.

* Throughout this paper we shall refer to these units of localisation as "squares."

Having now described the methods of investigation, we will now give in detail the results obtained by stimulating (A) the cortex, (B) the internal capsule.

In the description of the representation of movements obtained in the cortex we have thought it best to arrange the facts in the order in which the cortical areas were stimulated. This arrangement was similar to what we employed in the Bonnet Monkey, beginning with the foci for the smaller movements before proceeding to those for the larger, as we found by experience that the former were the first to lose their excitability. We shall therefore describe the different movements in the following order :—

Movements of the Eyes and Eyelids.
Movements of the Face and Mouth.
Movements of the Upper Limb.
Movements of the Lower Limb.

Results of Excitation.

(A.) *Cortex.—Left Hemisphere.*

Movements of Eyes and Eyelids.

(1) *Both Eyes move conjugately to the opposite side.*—The representation of this movement we found to extend in front of the præcentral sulcus, *i.e.*, to a slight extent just in front of its vertical limb, but lying principally in advance of the sulcus *w*.

The focus of the area is situated in the centre of the gyrus, at the points marked 2, 2, 2, in fig. 3. The whole representation extends as indicated by the stippling in fig. 1, Plate 18. The movement was also elicited from the centre of the gyrus, as above stated, at squares 3, 4, 5, 6 (fig. 3), but it was very slight, and at the angle formed by the two limbs of the sulcus there was no excitable point.

As compared to the same movement obtained from the Bonnet Monkey, *Macacus sinicus* (see 'Phil. Trans.,' B, 1888), this result from the Orang was characterised as being much slower in development and execution—in fact, resembling rather the movement* obtained from the angular gyrus in the Bonnet (*vide* Professor Schäfer, 'Roy. Soc. Proc.,' and confirmed by ourselves).

As indicated in the title of this section, no other movement was observed than that of both eyeballs to the opposite side, unaccompanied by the commonly-associated actions of opening the eyelids, dilatation of pupils, and turning of the head.

(2) *Combined Movement of Eyelids opening briskly, Eyeballs turning to the opposite side, and Head turning to the opposite side.*—This association of movements was obtained at squares 24, 25, 26, 27, 111, 112, 113, 114, 115, 116, 117, 118, 119, and appeared to be equably represented over the (dotted) area (see fig. 2, Plate 18), which is seen to be situated in the ascending frontal convolution. The sequence was that

* First discovered by Professor Ferrier, 'Functions of the Brain,' 2nd ed., p. 243.

indicated in the title of this section, and more closely resembled the character of the corresponding movement obtained from the angle in front of the junction of the limbs of the præcentral sulcus in the Bonnet Monkey. The head and eyes moved in the horizontal plane.

(3) *Bilateral Closure of the Eyelids, but those of the opposite side more strongly than those of the same side.*—This movement, which we have found definitely marked in the Bonnet Monkey,* situated just between the lower end of the intra-parietal sulcus and the Fissure of ROLANDO, was here in the Orang observed to be just in front of the latter fissure at a homologous level, *i.e.*, at squares 120, 121, 122, 123, 124, 125, 126. (See fig. 3, Plate 18.) The lids of both eyes closed, but those of the same side far less completely than those of the opposite side.

Movements of the Face.

We shall next consider the movements of the lower part of the face, including the lips, mouth, and tongue, but before doing so, we must call special attention to the great development and mobility of the lips in the Orang, especially in the young animal (see p. 136).

The movements of the mouth and lips are very varied, and we have arranged them according to the following list.

Movement	
Elevation of upper lip, opposite side	Unilateral.
Retraction of angle of mouth, opposite side	
Eversion of lip, opposite side	
Rolling in of both lips	Bilateral.
Pursing of lips	
Pouting of lips	
Closing of mouth	

(4) *Elevation of upper lip of opposite side.*—This movement was obtained at squares 95, 96, 97, 121, 127; it was most marked at square 97; thus at 96 the latent period was long,† and at 127 the movement was very slightly marked. The representation of this movement is thus found as a narrow band in the ascending parietal gyrus close behind the Fissure of ROLANDO, and above the horizontal level of the lower end of the intraparietal sulcus (see fig. 4, Plate 18).

(5) *Retraction* (*horizontal*) *of the opposite angle of the mouth.*—Retraction (*i.e.*, with no elevation) of the angle of the mouth was elicited at squares 100, 101, 102, 103, 7, 8, 98, 99, 9, 10, 11, 12, 13, 14, 96.

The position of representation of this movement thus covers the middle third of that portion of the ascending frontal gyrus, which extends between the Fissure of SYLVIUS and the well-marked genu which we have in previous communications shown

* Not yet published. † *Cf.* next article on "Retraction," square 96.

to exist in the Fissure of ROLANDO. The focus, or point of most intense representation, is situated in the line of squares 9, 10, 11, *i.e.*, just above the middle of the part now being considered. See fig. 5, Plate 18.

All the squares for this movement are, with the exception of No. 96, situated in front of the Fissure of ROLANDO. Excitation of No. 96 producing a very interesting result, viz., the mouth was first retracted and *subsequently* elevated. Thus this square 96 forms a "border" square between the movements of retraction and elevation respectively, but the former predominates.

(6) *Eversion of the opposite lower lip.*—We obtained the representation of this movement at only one spot, viz., square 104. See fig. 6, Plate 18.

(7) *Bilateral. Rolling in of both lips, especially of the lower and of the opposite side.*—This movement consists in an incurving or inversion of the red margin of the lips over the teeth, so that the mouth being shut the skin of both lips comes into contact. It involved the whole length of the oral fissure, but the opposite half more powerfully, and the movement of the lower lip was more extensive than that of the upper. It was elicited from squares 15, 16, 17, 20, 21, 22, 23, being most represented at Nos. 22 and 23. See fig. 7, Plate 18.

Before proceeding to describe the representation of pursing and pouting of the lips, it will be well that we should explain distinctly our means of recognising the difference between these two movements.

Mr. DARWIN* refers to the compression of the lips together in the performance of a delicate manual act by a young Orang; he says, *loc. cit.*, "at each attempt the lips were firmly compressed, and at the same time slightly protruded." We have expressed this combination of drawing together of the lips with some protrusion by the term pursing. According to Professor THANE† the facial portion of the orbicularis oris acting alone projects the lips, whilst the two parts of the muscle acting as a whole, draw the lips together, the result being an action similar to that we have described as pursing.

When, on the other hand, we have eversion of the lips combined with extreme protrusion in anthropoids and children, a movement is produced which Mr. DARWIN (*loc. cit.*, p. 140) describes and figures as pouting, and which he considered to be an expression of disgust and disappointment, although, as he also states, a similar expression is used to denote the antithesis. We may incidentally remark that we observed the same pouting when the administration of the ether in the present research was begun.

(8) *Pursing of both lips.*—This bilateral movement was obtained from two squares only, viz., 85 and 86, and was more marked at the former of these. See fig. 8, Plate 18.

(9) *Pouting of both lips.*—Pouting was represented much more extensively than pursing, and as we consider it to be a further development of the latter by the superposition of eversion of the lips by means of the levator menti (THANE, *loc. cit.*, p. 281),

* 'Expression of the Emotions,' 1872, p. 142.

† QUAIN'S 'Anatomy,' 9th Edition, vol. 1, 1882, p. 280.

it is most interesting to observe that its representation was nearer than that of pursing to the Fissure of ROLANDO, passing round its lower end to reach towards the square in which eversion is most represented. Pouting was observed at squares:—(*a*) In front of Fissure of ROLANDO, 87, 88, 89, 90. (*b*) Behind Fissure of ROLANDO, 91, 92, 93, 94.

The focus was situated at No. 90, and the representation decreased from this point to No. 87, and as far as to No. 94 behind the Fissure of ROLANDO. See fig. 9, Plate 18.

(10) *Twitching of the opposite half of the upper part of the Orbicularis Oris.*—This remarkably specialised movement was restricted to the small triangular area lying between the upper end of the secondary sulcus in the foot of the ascending parietal gyrus, and reaching nearly to the genu of the Fissure of ROLANDO, viz., at squares 128, 129, 130, 131, 132, 133, 134, 135, 136, 137, and was most marked at the vertical line passing through the middle of this region, viz., at squares 130, 134, 136. See Plate 19, fig. 10.

In passing to the next group of movements a prefatory explanation is needed of our use of the term, movements of the mouth. By such term we wish to imply the opening and closure of the oral cavity, *i.e.*, lowering and raising of the lower jaw. Although we shall show that the lower jaw may be occasionally depressed within the closed lips, but that, if combined with compression of the lips, the mouth may remain shut, it is nevertheless more convenient and in accordance with general usage that the mandibular movements and the opening or closing of the labial fissure should be considered together.

Contrary to that which we had observed in the Bonnet (*Macacus sinicus*), in the Orang we never obtained evidence that the movement of mastication was represented in the cortex. We, of course, only credit this fact with the value generally attached to negative evidence. The various combinations of movements associated with the opening of the mouth we will consider in the chapter on the "Marches" observed, see p. 146.

(11) *Opening of the Mouth.*—This fundamentally important movement we found to be represented, exactly as in the Bonnet Monkey, at the foot of the ascending frontal and parietal gyri, around the lower end of the Fissure of ROLANDO, viz., at squares (*a*) in front of Fissure of ROLANDO, 20, 21, 22, 84, (*b*) behind the Fissure of ROLANDO, 91, 92.

It is universally well marked in the squares in front of the Fissure of ROLANDO, but only moderately in those which lie behind it (at 91, 92). See Plate 19, fig. 11.

Movements of the Tongue.

We have found in the Bonnet Monkey (in some experiments shortly to be published) that the movements of the tongue are highly differentiated in cortical representation, constantly localised in the same position, and arranged in a definite order of grouping. The movements of the tongue that we have found to be distinctly evoked by stimulating the cortex in the Orang we shall arrange in the order in which the varieties of representation are successively grouped in the cortex from above down.

Div. 1. Protrusion of whole organ.	Tongue flattened posteriorly, tip directed to opposite side.
	Tongue heaped up on the same side, tip directed to opposite side.
Div. 2. Rolling over of whole organ to side.	Tongue rolled over to opposite side.
Div. 3. Retraction of whole organ.	Tongue heaped up posteriorly, rolled over to opposite cheek.
	Tongue flattened throughout, the tip of the opposite side being retracted horizontally.

On summing up this table it will be seen that the movements are consecutively arranged in the cortex, so as to pass gradually one into the other from protrusion to retraction.

(12) *Tongue protruded, flattened posteriorly, tip directed to opposite side.*—This occurred at squares 7, 8, 98, 99, 9, 10, 11, 11′. This movement, shown in fig. 12, is the one upon the loss of which most stress has hitherto been laid in cases of destruction of the internal capsule and cortex in Man, but in our opinion it is but one and not the most important of a series of movements differing one from another, as will subsequently be seen. See Plate 19, fig. 12.

(13) *Tongue protruded, heaped up on the same side, and tip directed to the opposite side.*—This movement is represented next below the one just described, No. 12, and was noted at squares 12, 13, 14. See fig. 13.

It was seen that by "heaping up" to one side (for instance, the left) the tongue was narrowed transversely, the left side being thickened in the vertical diameter, so that that side and border bulged upwards.

(14) *Tongue neither protruded nor retracted, but rolled over to opposite side.*—This we found to occur at the next level below, viz., at squares 15, 16, 17.

It is a very important movement which has not hitherto received attention. In its execution the same side of the tongue rose and then the whole organ was tilted up and rolled over on its longitudinal axis, so that the previously horizontal dorsum was inclined towards the opposite cheek. See fig. 14.

(15) *Tongue retracted, heaped up posteriorly and rolled over to the opposite cheek.*—It is clear that this movement is a further extension of the last one (No. 14) with the addition of retraction. It was observed at squares 20, 21, 22. See fig. 15.

We need only add that the raising of the posterior part of the tongue was bilateral and occurred before the rolling over began. See "Marches," p. 146.

(16) *Tongue retracted slightly, flattened throughout, and the tip of the opposite side retracted horizontally.*—This rather singular movement we have never seen before; it was found at the lowest point of the representation of the tongue at squares 23, 84, 85, 86, 87, 88, 89, 90.

In this movement the tongue appeared to be adjusted horizontally to the floor of the mouth, while the upper surface of the opposite half was slightly hollowed (see fig. 16) and its tip retracted from the teeth.

Movements of the Upper Limb.

Proceeding now to investigate the mode of representation of the limbs, we will commence with that of the upper limb, taking the segments in order from below upwards, beginning with the thumb. But we cannot forbear from pointing out that it will be seen, especially now, how extremely integrated is the representation in this animal, and in the case of the upper limb we actually found it quite exceptional, with a minimal stimulus, for more than one segment to be represented at any given point.

Further, owing to the exaggeration of the bend of the ascending gyri above the genu of the Fissure of ROLANDO, the foci of the segments of the upper limb are arranged along a curved line which is horizontal at its lowest point and becomes vertical where the limb areas are contiguous, whereas, in the Bonnet Monkey, as we have shown, the foci are arranged in a straight but oblique line, parallel to the Fissure of ROLANDO. The functional arrangement and sequence of the representation of the segments being the same in the two animals, we think it is clear that this difference in horizontal level is simply due to the extreme bending of the Fissure of ROLANDO in the Orang. In illustration of this we show, in fig. 4, p. 150, the curve of the Fissure of ROLANDO in the two animals, with words indicating the foci of the segmental representation.

(17) *Movements of the Thumb.*—We observed the thumb to execute the following simple movements at the points indicated.

Action.	Square.
Flexion	38
Adduction, flexion	35, 36, 36′
Adduction	39, 83
Extension.	37, 37′, 138

We now have to point out the arrangement of the respective order of representation of these movements, and we shall compare that order with the simpler order, as seen in the Bonnet Monkey.

Thus, to begin :—Extension of the thumb we see is represented at 37 and 37′, *i.e.*, in the foremost part of the area of representation. Now this is exactly the localisation we have demonstrated to occur in the Bonnet Monkey.

With a stronger current (8·5 cm.) we once obtained extension of the thumb at 138, which is, of course at the opposite pole of the thumb area.

The movement represented next to extension is that of adduction-flexion at squares 35, 36, 36′.

The above movements are represented in the ascending frontal gyrus: the next to be described are in the ascending parietal gyrus. See fig. 17, Plate 19.

Of these the first is flexion at square No. 38, the second, adduction at squares Nos. 39 and 83.

As before stated, these movements of the thumb were single and unaccompanied by movement of any other joint, although the electrodes were finally kept applied for 5 seconds, a time more than sufficient in the lower Apes to generate movements in all segments of that limb, and probably, these in addition, be followed by others in the limb of the same side. See conclusions, p. 149.

Finally, just as we have seen, extension is represented most anteriorly and superiorly, so now by reference to fig. 3, Plate 17, it appears that flexion and adduction are placed posteriorly and inferiorly.

The remarkable individual clearness of these and other movements is discussed on pp. 151, 152.

(18) *Movements of the Index Finger*.—The index finger is always represented in the Bonnet Monkey in the cortex next to the thumb area, and its focus in that animal is found to be in the ascending parietal gyrus (see fig. 18). It is therefore of great interest, and we may add importance to note that also in the Orang the principal (indeed, almost the only) representation of this segment is situated next behind and above the thumb area, and in the ascending parietal gyrus, viz., at centres 40, 41, 83.

The kind of movement produced at each square was the well-known purposive or voluntary movement of extension; the subordinate or associated movement of the index is alluded to in the next paragraph. The focus of movement appeared to be at 40, and the representation diminished towards 41 and 83. At 83 there was also observed adduction of the thumb, but there was no abduction of the index by the *abductor indicis* as might have perhaps been expected, the finger moved only in extension, *i.e.*, in its most highly integrated character.

(19) *Movements of the Fingers*.—The fingers (all moving in association) were represented in the ascending frontal gyrus at squares 28, 29, 30, *i.e.*, above and behind the thumb area. The movement evoked at each was invariably extension, and this of a remarkably deliberate character, so that the sequence of the segments in action was very clearly demonstrated. Thus the first digit to move was the little finger, which completely extended, next the ring finger, and finally, less marked extension of the remaining middle and index fingers. No flexion of the fingers was noted to occur. See fig. 19.

(20) *Movements of the Wrist*.—We have previously ('Phil. Trans.,' 1887, 1888) urged that the wrist and elbow should be regarded as joints subordinate in primary importance to those of the digits and shoulder. In harmony with this view, we found in the Orang that the former was represented only in association, *e.g.*, with extension of the fingers, and with the following movements :—

Pronation at square No. 29.
Ulnar adduction at square No. 30.

See also Table of "Marches," and fig. 20, Plate 19.

(21) *Movements of the Elbow.*—The elbow we only saw move at one spot, viz., on exciting square No. 31, *i.e.*, next above and behind the wrist and fingers. The movement was flexion, and of primary character, no other segment being affected or associated with it, and the representation, though limited in area, was thus of a very high order (see p. 152). See fig. 21, Plate 19.

(22) *Movements of the Shoulder.*—In accordance with what has just been said about the subordination of the elbow and wrist to the shoulder and digits, it is evident why the shoulder should be represented at so many squares as we found it to be, viz., at Nos. 32, 33, 42, 43, 34, 44, 45, 46, 47.

It was represented around and below the hinder end of the superior frontal sulcus, see fig. 22, Plate 20, as in the Bonnet Monkey, while, owing to the special configuration of the sulci in the Orang, the representation shaded off at squares Nos. 46 and 47, into the area for the lower limb. In character the movement was always adduction, and was never associated with that of any other segment.

Movements of the Lower Limb.—Probably, in all the higher animals the representation of the lower limb is less integrated than that of the upper limb, but it was especially necessary to see what was the condition in an anthropoid like the Orang, whose customary vertical posture places it in an intermediate position between the Macacques and Man.

In the Bonnet Monkey, the lower limb area extends over the hinder third of the superior frontal gyrus, into the paracentral lobule on the mesial surface and backward into the ascending frontal convolution and superior parietal lobule, *i.e.*, the upper end of the ascending parietal gyrus.

In the Orang we found that, except with currents of such intensity (7 cms.) that obvious escape resulted, no movement was obtained on exciting the upper third of the ascending parietal gyrus. It is, however, of noteworthy interest that what we regarded as the effect of escape consisted only in extension and flexion of the hallux, viz., at squares 139, 140, 141, and this occurred between the postcentral sulcus and the Fissure of ROLANDO. Consequently, the representation of the lower limb in this anthropoid was confined to the part in front of the Fissure of ROLANDO (extending also over the mesial margin into the paracentral lobule*); and we shall now consider this region in detail, under the headings of the segments of the limb.

(23) *Movements of the Hallux.*—Omitting the squares 139, 140, and 141 just referred to, we obtained movements of the hallux at squares 56, 63, 64, 69, 76, 77, 78. See fig. 23, Plate 20.

Of these, the hallux moved primarily at 56 (where it was associated with movement

* See "Marches" and Right Hemisphere, p. 143.

of the ankle only) and 77 (where it was associated with movement of the small toes as well as of the ankle).

Character of the Movement evoked.—Flexion was noted at 56, 77, 78, and extension at 63, 64, 69, 76; consequently, the representation of flexion is anterior to that of extension. It will be seen that the hallux is at the highest point (*i.e.*, nearest the middle line) of the area only associated with the ankle and other toes. (*Vide infra.*)

(24) *Movements of the Small Toes.*—The small toes were represented at 54, 63, 64, 69, 70, 71, 76, 77, 78, 109, 110.

At squares Nos. 109, 110, which were situated on the anterior frontier of the lower limb area, we obtained the unique movement of very slight extension of the second toe, which is homologous with the index finger.

The primary movement of the small toes occurred on exciting squares Nos. 70, 71, 54, 78, No. 70 being the point of intensest representation; in fact, at 70 and 71 the small toes were the only segments which moved at all. See fig. 24, Plate 20.

Character of Movement.—This was in all cases extension. See also "Marches," p. 143.

(25) *Movements of all Toes.*—All the toes moved in synchronous association at squares 63, 64, 69, 76, the movement being invariably extension with separation of the digits. See also "Marches," p. 143.

(26) *Movements of the Ankle.*—The total of absolute representation of movements of the ankle is situated at squares 54, 55, 56, 60, 61, 62, 63, 64, 76, 77.

The primary movement was obtained at squares Nos. 55, 60. At 60 it was the only movement, consequently this affords another instance of the unique character of the localisation in the Orang. See p. 152, and fig. 25, Plate 20.

Character of Movement.—The nature of the movements observed was as follows:—

Eversion obtained at squares			No. 54.
Dorsal flexion	,,	,,	Nos. 55, 56, 76, 77.
Plantar extension	,,	,,	,, 60, 61, 62, 63, 64.
Inversion	,,	,,	No. 77 (observed only once on a repeated trial).

(27) *Movements of the Knee.*—The representation of the knee was found at squares 54, 55, 61, 62, 63, 64, 68. See fig. 26.

No primary movement was obtained, as was evidently probable from the condition of representation in the Macacque of such a subordinate joint.

Character of the Movement.—The movement was extension, except at square No. 68, where it was flexion.

(28) *Movements of the Hip.*—The total or absolute representation of the hip was found at the squares 48, 49, 50, 51, 52, 53, 61, 62, 63, 64, 65, 66, 68.

Primary Movement.—Just as with the shoulder, so the cortical representation of the hip in the Orang is not only very extensive, see fig. 27, but also singularly integrated; thus movement of the hip (only) occurred at no less than eight squares, viz., Nos. 48, 49, 50, 51, 52, 53, 65, and 66.

The very large majority of these will be found to be aggregated on the upper border of the upper limb region, close to where the shoulder is most represented. See "Marches," p. 144, and conclusions, p. 151.

Character of the Movements.—In contradistinction to what we found in the Bonnet Monkey (*loc. cit.*) the character of the movement was extension of the hip (and knee), indeed with but three exceptions of which only one was a pure flexion. The explanation of this we offer on p. 151. The movements observed may be thus arranged:—

Extension observed at squares Nos.	48, 49, 50, 51, 52, 53, 61, 62, 63, 64.
Adduction	52, 53.
Flexion	68.
Rotation	65, 66.

See also next chapter, "Marches."

(A.) *Cortex.—Right Hemisphere.*

After the excitation of the left hemisphere had been completed as far as possible (*i.e.*, until the fall in blood pressure began to affect the excitability) we proceeded to rapidly expose the right hemisphere and to explore it with the same stimulus.

We found that the so-called motor points were symmetrically situated in the two hemispheres, and in consequence that the inexcitable regions (*vide infra*) which we were careful to explore first, as soon as the brain was exposed, were also similarly situated on the two sides. The only trifling difference we noted was that at squares 121, 125 on the right side we obtained marked closure (blinking) of the opposite eyelids. This means, of course, simply that on this side the representation of this movement was rather more highly differentiated.

We made an observation on the paracentral lobule in vertical line with square 78, *i.e.*, 7–8 mm. in front of the upper end of the Fissure of Rolando of this hemisphere, and found that the lower limb was alone represented there, *i.e.*, without the abdomen. See "Marches."

Marches.

Since, as a rule, the effect obtained by exciting the cortex of the Orang was a single primary movement, a march of the spasm from one group of muscles to another was exceptional. We, therefore, have deemed it best to collect together under one heading all such "Marches" as follows:—

Area.	Square.	Primary movement.	Secondary movement.	Tertiary movement.	Quaternary movement.
Lower face	20, 21, 22	Mouth open	Tongue retracted, heaped behind, rolled to right		
	91, 92	Lowering of lower jaw	Lips pouted		
Upper face	96	Retraction of angle of mouth	Elevation of upper lip		
	121	Closure of both eyelids, especially of opposite side	Elevation of upper lip, marked		
	24, 25, 26, 27, 111, 112, 113, 114, 115, 116, 117, 118, 119	Eyelids open	Both eyes turn to opposite side	Head turns to opposite side	
Upper limb	83	Adduct thumb . . .	Slight extend index		
	28	Extend little finger . .	Extend ring finger . .	Extend other fingers	
	29	,, ,, . .	,, ,, . .	,, ,, .	Pronate wrist
	30	,, ,, . .	,, ,, . .	,, ,, .	Ulnar adduction of wrist
Lower limb— Hip	61, 62	Extend hip and knee .	Plantar-extend ankle		
	63, 64	,, ,, .	,, ,, . .	Extend digits	
	68	Flex hip and knee			
Ankle	55	Dorsoflex ankle . . .	Extend knee		
Small toes	54	Extend small toes . .	Evert ankle	Extend knee	
	78	,, ,, . .	Flex hallux		
All toes	76	Extend all toes . . .	Dorsoflex ankle		
Hallux	56	Flex hallux	Dorsoflex ankle		
	77	,, ...	Extend small toes . .	Dorsoflex ankle	

From an inspection of the foregoing table which, with the exception of the combination of facial and oro-lingual movements to be mentioned later, is an absolute record of all the "marches" noted to have occurred, the extreme paucity of such combinations shows more clearly than words to what a remarkable extent the representation of each individual segment is integrated in the cortex of the Orang. Too much stress cannot be laid upon this point since it demonstrates incontestably the great advance in evolution of function of the Orang's cortex above that of the Macacque, for, in the latter animal, single primary* movements were only rarely obtained, and even then by only momentary application of the electrodes.

In complete harmony with this view we also see that at only two groups of squares was there a combination of segmental movements in the upper limb (viz., 83, and 28, 29, 30), and these only involved the digits and wrist, whereas in the lower limb no less than nine such combinations were observed, and those (owing to duplication) at eleven squares.

The limited extent of such combinations is also manifested by the fact that all the segments of the lower limb were thrown into action at only two squares (63 and 64), and at a large number of the remainder only two segments were involved.

We have now to consider four points in this connection, these are :—

(1.) Combination of facial and oro-lingual movements.
(2.) Juxtaposition of synergic segments.
(3.) Character of movements in each march.
(4.) Relative position of squares from which marches were obtained.

* *I.e.*, a single movement not followed by any other movements, which latter we have termed secondary, tertiary, &c., in the successive order of their appearance ('Phil. Trans.,' B, 1887, 1888).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(1) *Combination of Facial and Oro-lingual Movements.*

Square. (List of squares in which face or tongue were represented.)	Tongue.	Face.
7, 8, 98, 99, 9, 10, 11, 11′	Flattened, protruded to opposite side .	Opposite angle of mouth retracted
12, 13, 14	Tip to opposite side, heaped on same side	" " "
15, 16, 17	Rolled over to opposite side	Rolling in of both lips, especially of lower (bilateral)
20, 21, 22	Retracted, heaped posteriorly and rolled to opposite side	Rolling in of both lips followed by mouth opening
23	Retracted slightly, flattened throughout, tip of opposite side retracted horizontally	" " "
24		Opening of mouth
85		Pursing of lips
86		" "
87		Pouting of lip
88		" "
89		" "
90		" "

The foregoing list shows which facial and oral movements are related with each other in synchronous action, and we do not see that it can be profitably amplified by further discussion.

(2) *Juxtaposition of Synergic Segments.*—Without a single exception the march involved segments in series according to their successive anatomical juxtaposition. The most striking instance of this phenomenon, and shown more minutely than anything noted by us in the Bonnet, is seen at square 29, where the successive order of segments involved was little finger, ring finger, second and index, wrist.

(3) *Character of Movements in each March.*—We find that the character of the movement in the stages of the march is simply a repetition of the character of the primary movement of the segment involved.

(4) *Relative Position of Squares from which Marches were Obtained.*—We have thought it important to note the regions where combinations of movements more frequently occurred, to see whether there was any definite relation among the squares one with another which would reveal any explanation of the phenomena in question.

Face Region.—Combination appeared to be universally distributed over the region for the face.

Upper Limb.—Combination was only found in the squares for representation of the small muscles (at squares 83, 28, 29, 30), *i.e.*, at the highest part of the hand region.

Lower Limb.—Combination occurred most at the squares situated in the vertical line drawn towards the middle of the lower limb region.

These facts are simply examples of the principle which we have previously enunciated, viz., that the representation of function is most intense on the summits of the gyri, and shades off to the sulci, where the excitability becomes nil.

(B) *Internal Capsule.*

We next proceed to raise the upper half of the right hemisphere (after ligature of the middle cerebral artery deeply in the Sylvian fissure just in front of the anterior limb of that fissure) by a horizontal section carried through the brain, as shown by the dotted line in fig. 1, Plate 16, so as to expose the internal capsule. See fig. 5, Plate 17.

Description.—The section exposing the internal capsule of the right hemisphere was a horizontal cut passing through (from before backwards) the third frontal gyrus, the foot of the ascending frontal and parietal gyri respectively, and crossing the posterior limb of the Sylvian fissure just where it turns upwards, viz., at about the junction of the middle and posterior thirds. The cut surface, viewed from above, exhibited, as is shown in the accompanying photograph, fig. 5, taken in the fresh state after the excitation, the following points. In front is seen the upper part of the anterior commissure, only the middle portion of which appears, as it is soon lost between the outer and middle zones of the lenticular nucleus. Posteriorly, in the middle line, the splenium of the corpus callosum limits the field of white fibres. Only the two outermost zones of the lenticular nucleus are visible, and the caudate nucleus is only represented by a small portion of its head separated by a few white fibres from the putamen or outer zone of the lenticular nucleus. Of the anterior limb of the capsule, besides these fibres, there remains only a bundle of fibres about 4 mm. long, running directly backwards from the posterior surface of the anterior commissure. The hinder limb of the capsule extends from the inner border of the second or middle zone of the lenticular nucleus, and on section it is seen that the bundles of transversely cut fibres terminate posteriorly opposite the lamina medullaris situated between the zones.

We mapped out by compasses the cut surfaces of the basal ganglia and capsule, upon paper ruled with squares of 1 mm. side, taking care that the posterior limb was drawn parallel to the vertical lines of the squares.

Arbitrary numbers were then applied to each square from which result was obtained on excitation, and we now furnish the records of stimulation.

No. of square.	Distance of secondary coil.	Result.
	cm.	
1	10	Both eyes turn to opposite side
2	10	Both eyes turn to opposite side (more markedly than at No. 1) and open at the end of excitation
3	10	Both pairs of eyelids blink, then both eyes turn to the opposite side
4	10	Both pairs of eyelids blink, the mouth is strongly retracted to opposite side, tongue flattened, protruded, tip turning to the opposite side. Next opposite wrist flexed, doubtful movement of fingers
5	10	Both eyelids blink, both eyes turn to opposite side Mouth strongly retracted to opposite side, tongue protruded, tip to opposite side, opposite fingers and thumb flexed
5′	10	Nil
6	10	Mouth strongly retracted to opposite side. Tongue flattened, protruded to opposite side. Flexion of fingers (strong), flexion of fingers (slight). Flexion of wrist, doubtful flexion of elbow
6′	10	Doubtful flexion of fingers
7	10	Flexion of fingers, of thumb, of wrist, later mouth retracted to opposite side
7′	10	Flexion of finger and thumb, later flexion of wrist.
8	10	Flexion of fingers and thumb (very strongly), flexion of wrist, abduction of shoulder
8′	10	Flexion of fingers (less than 8)
9	10	Flexion of fingers
9′	10	Flexion of fingers and wrist, later eversion of ankle
10	9	Flexion of all toes, plantar extension of ankle, later pronation of wrist
10′	9	Very slight adduction of shoulder. Slight flexion of toes

As will be seen on fig. 5, Plate 17, the length of the posterior limb of the internal capsule is 18 mm. It will now be convenient to show more plainly the extent of distribution of the fibres for each particular movement.

Movement.	Extends	
	From—	To—
	m.	m.
Eyes turn to opposite side	1 max. 2	5
Eyelids closing (blinking)	3	5
Retraction of angle of mouth to opposite side	4	7
Tongue flattened and tip directed to opposite side	4	6
Flexion of thumb	5	8
Flexion of fingers	5	9′
Flexion of wrist	4	10
Flexion of elbow	6	..
Abduction of shoulder	8	..
Adduction of shoulder	..	10′
Flexion of toes	10	10′
Eversion of ankle	9′	..
Plantar extension of ankle	10	..

That this order of arrangement of the fibres in the capsule is mainly correct we have no doubt, in the light of our experiments on the capsule of the Bonnet Monkey

(Paper read to the Royal Society, December 12, 1889), but whether we obtained complete results is questionable, since after we had observed the above-mentioned facts, and were proceeding to amplify and control them, the animal died suddenly, evidently from syncope.

SUMMARY AND REVIEW.

We are now in a position to review the facts detailed above, and to examine into their real value.

I. *Condition of the Animal.*

(*a*) *Health.*—It had been in England about two months, and appeared to be in perfect health, and although the day before the experiment its appetite had begun to fail a little, to all appearances it was vigorous and healthy. It moved about in the vertical posture, and all its acts were per ormed completely, and with the deliberation special to the Orang.

(*b*) *Age.*—The animal was estimated to be about 2½ years old. Since the animal was a young one, we wish it to be understood clearly that the facts which we put forward concerning the limitation of representation are not necessarily typical, as it is possible that this may be more extensive in an older animal. Bearing on this point we may mention that we have found that, given the same species of Macacque Monkey, a more extensive representation occurs with a larger, *i.e.*, an older, brain, and the converse also holds, but that the chief details and general plan are the same under the two circumstances.

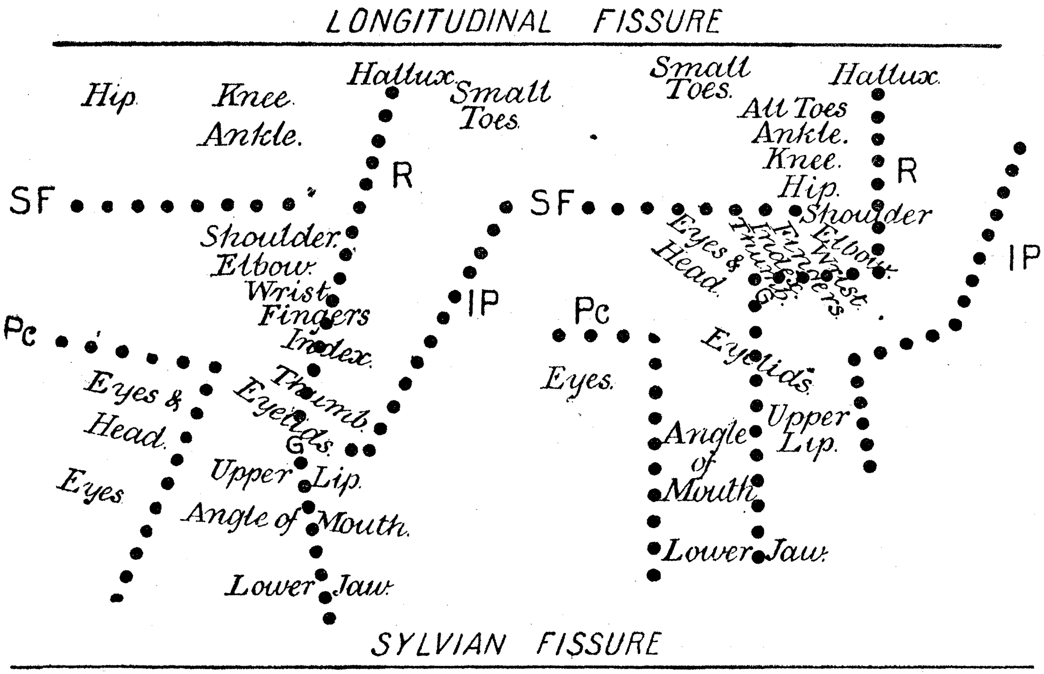
Future investigation can alone decide this point.

II. *Vertical arrangement of the Representation of each Segment in levels transverse to the Fissure of* ROLANDO.

In the Bonnet Monkey (*Macacus sinicus*) we have shown that the representation of the segments of the various parts of the body is arranged along the Fissure of ROLANDO in horizontal levels, and that the boundary lines of these pass across the fissure. In the Orang the same arrangement holds as is well seen in the photograph on Plate 21. This photograph is constructed by writing on an enlarged copy of fig. 1, Plate 18, the various foci of representation. If we place the segments in successive order as we see them in the Bonnet and the Orang, the relations are as follows :—

Fig. 4.

BONNET. ORANG.



SF = Superior frontal sulcus.
R = Fissure of Rolando.
G = Genu of ditto.
Pc = Præcentral sulcus.
IP = Intraparietal sulcus.

We cannot but feel that the foregoing fig. 4 clearly shows that the general plan of the arrangement of the representation of the segments in the two animals corresponds closely, and that the variations are rather due to the exaggeration of the sinuosities in the gyri of the Orang than to any special characters in that animal. Indeed, if the Fissure of ROLANDO in the Orang could be drawn out straight, the arrangement would be practically identical.

It is extremely interesting to see that the plan of the segments of the lower limb is truly horizontal in the Orang, *i.e.*, transverse to the Fissure of ROLANDO, but antero-posteriorly placed in the Bonnet. We believe that this depends upon the following considerations, which we venture to suggest are not merely fanciful, and which we connect with the great representation in the Orang of extension of the hip as contrasted with the usual flexion of that joint in the Bonnet.

The habits of the two animals appear to afford an explanation of the difference of the mode of representation in their brains.

The Bonnet Monkey saves itself in flight by climbing, for which the first purposive movement of the lower limb is of necessity flexion of the hip. This, therefore, we find represented most anteriorly in the lower limb region, and therefore localised exactly in the psychical order of events, *i.e.* (1), direction of the head towards the danger; (2) initial movement of flight.

In the Orang the case is otherwise. The vertical posture requires much purposive action. An Orang placed under the same circumstances as the Bonnet rises on to its hind limbs by extension of the hip; we, therefore, find that this movement is represented in this animal to great excess compared to that of flexion.

Further, in accordance with the now well recognised fact that as the foci of function are more spread over the convex surface of the hemisphere from the longitudinal towards the Sylvian fissure, so they are more highly, *i.e.*, purposively evolved, it is clear that in the Orang the hip possesses a far higher character of representation than it has in the Bonnet, and we believe that this subserves the vertical posture. In addition, just as in the Bonnet the anatomical juxtaposition of the foci corresponds with the psychical order of events, in the Orang it is seen also that the focus of direction of the head towards the source of danger is situated *below* the focus for the hip—below because, as will be seen, what in the upper part of the hemisphere is horizontally directed in the Bonnet Monkey becomes vertically arranged in the Orang.

III. *Integration of Foci.*

The extraordinarily integrated character of representation of individual movements in the several foci thus observed is of such extreme importance in elucidating the mode of localisation of function in the brains of the highest animals, the main object of the present research, that we shall now examine their arrangement in successive detail from this standpoint.

The most important facts to notice in the comparison of the representation of the Anthropoids and Man with that in the Macacque and similar Monkeys, the highest animals on which experiments on the brain have hitherto been conducted, are that—

1. Instead of the excitable area of the cortex being continuous, it is (in the Orang) much interrupted by spaces from which no effect could be obtained even by the application of strong stimuli.

The inexcitable areas are indicated on fig. 3, and it will be noticed that they separate the areas of representations of the larger divisions of the body, and do not separate those for the segments of such divisions.

2. Reference to the figures shows also that a large part of the cortex generally considered to be excitable was not so in the Orang. This is especially the case in the frontal lobe, the whole of which in front of the ascending frontal gyrus was inexcitable, with the exception of the area for the representation of turning the eyes to the opposite side, which is just in front of the præcentral sulcus. See figs. 1 and 3.

Similarly, the ascending parietal gyrus gave relatively much fewer results than the same gyrus in the Bonnet Monkey, being practically wholly inexcitable in its upper third (the superior parietal lobule).

3. The chief fact in this connection, and indeed possibly the most important new point observed in this investigation, is the frequent limitation of movement to one segment when a point is excited, instead of, as in the Bonnet, a sequence of movements being thus produced. As an extreme instance of this singularity of function we may mention square 31, where flexion of the elbow and nothing else was obtained. The elbow in the Macacque, it will be remembered, was never unaccompanied by movements of other segments and rarely initiated a "March," whereas in the Orang we found it represented absolutely alone. (See "Marches," p. 144.)

It is well known that in the lower orders of animals the integration of representation becomes less perfect as we descend in the scale*—that, in fact, it is increasingly difficult to differentiate the areas for the limbs; while, on the contrary, in ascending the scale, we have shown in our previous communications that it is easy to differentiate between the areas of representation of even the segments of the limbs; and finally, when we now arrive at the Orang, the segments are not only differentiated in representation, but the nature of that representation is that of single movements.

There is now, from direct observation, reason to believe that in Man a similarly interrupted mode of representation exists.

The excitability to faradic stimulation of the human brain was established by the observations of BARTHOLOW† and SCIAMANNA.‡

The detailed results, however, are not sufficiently accurate to throw light upon the present question. Four observations, however, have been made under more favourable circumstances, although they cannot be fully accepted as deciding this question.

I. In October, 1886,§ one of us (V. H.) explored (under anæsthesia, with morphia $\frac{1}{10}$ gr. and chloroform), for purposes of exact localisation, the right facial area in a boy, the subject of epileptic attacks, and found that excitation with an interrupted induced current of a strength just felt by the tongue only produced movements in the opposite (left) side of the face at points distant from each other, and not at intermediate points. In this case, however, the surface of the brain had been freely irrigated with 5 per cent. carbolic acid solution in water. The application of this lotion Professors SCHÄFER and HORSLEY had already found to soon depress the excitability of the cortex. This observation, therefore cannot stand alone.

II. In May, 1888, Dr. KEEN of Philadelphia‖ excited (under anæsthesia with morphia $\frac{1}{8}$ gr. and ether) with a faradic current of sufficient strength to cause contraction of the muscles of his own hand, the cortex in a man also the subject of epilepsy, and obtained movements as follows—"The wrist (as observed by MORRIS J. LEWIS) moving in extension in the mid line and to the ulnar side at different

* FERRIER, 'Functions of the Brain.'

† BARTHOLOW, 'Amer. Journ. Med. Sciences,' April, 1874.

‡ 'Arch. di Psichiatria e Scienza Penale,' 1882.

§ 'Brit. Med. Journ.,' April 23, 1883.

‖ 'International Journal of Medical Science,' 1888.

touches, and the fingers being extended and separated. Above this centre were the shoulder and elbow centres and below, the face centre."

After Dr. KEEN had excised the focal representation of the wrist thus ascertained, he again excited the cortical surface above and below the point of removal and observed movement as follows:—"At the remaining part of the convolution at the upper margin of the excised portion, movements of the left elbow (flexion and extension) and shoulder, especially of the latter, which was raised and abducted, were noticed. Touching the part of this convolution remaining at the lower border of the excised portion produced an upward movement of the whole left face, no one muscle being noticeable in isolated contraction. The platysma was not contracted nor was the angle of the mouth drawn downwards. Touching the white matter at the bottom of the excision, produced again movements of the hand. . . ."

Immediately after the operation, the left hand was found to be paralysed as to all movements both of fingers and wrist. The elbow was paretic, the shoulder and face perfectly unaffected.

Dr. KEEN's careful observation seems to us to bear out what we have said above as to the nature of localisation in the highest animals, including Man, and the more so since, although the current employed was evidently so very strong, it only produced movement of one or, at the most, two segments at each spot.

III. In June, 1888, Dr. LLOYD and Dr. DEAVER similarly explored* (under anæsthesia with ether preceded by chloroform and morphia $\frac{1}{4}$ gr.), the region of the middle of the Fissure of ROLANDO with a faradic current (strength not given). Dr. LLOYD observed numerous and complex movements of the opposite upper limb and face. As he says (*loc. cit.*) "the exact muscular movements which occur in the fit." Reference to his description makes it probable that he elicited epileptiform spasms. Of immediate interest to us is his summary of the effects observed, as follows:—"I observed, especially in making these applications of faradism to the cortex, that considerable areas of it did not appear excitable at all to the strength of current employed, at least did not give muscular response anywhere, while the two comparatively narrow points above-mentioned reproduced almost exactly the muscular contractions of the epileptic seizures, and seemed to stand for more 'centres' than the diagrams of those who have experimented would allow to any such narrow areas."

IV. In a fourth case† published by Dr. NANCREDE, who operated for the relief of focal epilepsy, both the high integration of representation and, at the same time, the remarkable strength of current required to evoke the same were strikingly demonstrated. Dr. NANCREDE found that excitation of "a spot in the ascending parietal convolution," corresponding to the point indicated by ourselves, "*i.e.*, in the second fourth from below upwards, the thumb suddenly flexed," and an epileptic fit followed. And further, he found that "the shoulder, elbow, forearm, and facial centres were

* 'International Journal of Medical Science,' November, 1888, p. 480.

† 'Medical News,' Philadelphia, 1888, p. 586.

readily picked out," and were situated as indicated by our previous observations. In the discussion that followed the reading of Dr. NANCREDE's paper, Dr. MORRIS J. LEWIS, to whom had been intrusted the provision of the excitation, and, in part, observation of the effect, made the following important remarks. He said, "No effect was produced by the application to the cortex until the current was so strong as to produce powerful and painful tetany of his first dorsal interosseous muscle," the skin being wet and metallic electrodes employed. The battery was "one of FLEMMING's largest faradic batteries in perfect order, one half of the secondary coil being used with the graduating tube half withdrawn."

Finally, displacement of the electrodes laterally of the $\frac{1}{16}$th of an inch "caused the movement to cease," showing how extremely focal the effect produced was.

The objection to observation 1 does not apply in the same degree to observations 2, 3, and 4, since in 2 and 3 a weak solution of perchloride of mercury, and in 4 sterilised water was employed in irrigation of the surface of the brain. On collating the observations, moreover, they all point in the same direction, viz., that the representation of movement in Man is very integrated, *i.e.*, in isolated areas, and requires powerful excitation for its demonstration.

Another example has recently occurred to one of us (V. H.) :—

V. R.L. ♂, age 39, operated upon for focal epilepsy at the request of Sir JAMES CRICHTON BROWNE, F.R.S.

The attacks began with a confused aura in the left hand and upper limb, which was then raised at the shoulder in extension, the motor spasm spreading rapidly to the lower limb and face of the left side, and subsequently to the right side, but the left was far more affected. It was concluded that a previous diffused injury to the head had caused lesion of the right so-called motor area, and that the focus for the movements of the shoulder was the starting point of the attack.

The cortical area for the upper limb was therefore exposed. The dura mater having been raised carefully, the cortex was excited with platinum electrodes, 2 mm. apart, a secondary current being obtained from a KRONECKER coil, furnished with a HELMHOLTZ side wire, and supplied by a weak GRENET (bichromate) cell.

The first excitation with the coil at 7000 gave no result, etherisation was then diminished, but as no result followed application of the electrodes to the point marked 1 in the table on p. 155, the strength of the coil was raised to 8000, and subsequently to 9000; this last, together with diminished etherisation, produced a single movement of the thumb, consequently this strength of current was retained. Tested after the excitation was completed, this stimulus was found to be distinctly painful to the tongue and was, therefore, far in excess of that which would have sufficed to produce general epileptic convulsions in the Bonnet Monkey. At the same time, it is interesting to note that the strength of current required to produce a movement from the cortex of the Orang was intermediate between these two extremes.

The cortical surface exposed included the two central quarters of the Fissure of

ROLANDO, the posterior extremity of the superior frontal sulcus (superior præcentral sulcus of JENSEN), and consequently a small piece of the ascending parietal, and a considerable part of the ascending frontal convolution, with very small portions of the superior and middle frontal convolutions. All these were explored with the current mentioned above, but only the ascending frontal gave any result.

No final conclusions can be ascribed to this fact, owing to reasons which have been already stated, although care was taken to irrigate with the mercurial lotion instead of carbolic. In the ascending frontal, the points indicated below by the numbers 1, 2, 3, 4, 5 from above downwards, were found to be excitable and produced movement as follows :—

The movements were observed by Sir JAMES CRICHTON BROWNE, Drs. BUXTON, WALTON, and RUSSELL.

ASCENDING Frontal Convolution.

Number.*	Character of movement.
1	Shoulder abducted, whole upper limb extended with pronation of wrist
2	Wrist, pronation; elbow movement (? character)
3	Fingers all flexed. Wrist extended with (?) pronation
4	Index finger flexed
5	Thumb, slight abduction followed by flexion towards palm

We wish to point out that the order of representation in the above table is precisely the same as that observed in the Orang and also in the Bonnet Monkey. The movements were, for the most part, single, *i.e.*, affecting only one segment of the limb, and were evidently primary in character (*vide* 'Phil. Trans.,' 1887). It was, of course, impossible to investigate these points more minutely as the object of the exploration had been attained, but it seemed as if the portions of cortex intervening between the above foci were either altogether inexcitable or much less excitable than the foci themselves.

We think that it will be now admitted that we are in a position to assert that the character of the motor function of the cortex, whether topographical or physiological, is the same in the higher animals, proceeding from the lower Apes through the Anthropoids to Man.

4. In complete accord with this we find that in the Orang no border centres of amalgamated function of contiguous areas of representation exist, such as, for instance, that in the Bonnet Monkey between the areas for the limbs and face.

5. We never observed epilepsy to follow excitation of any part, although, as has been already described (p. 140) the electrodes were occasionally kept in contact

* No. 1 was situated just below the level of the superior frontal sulcus, and No. 5 just above the middle of the genu, which was well marked.

for 5 seconds. In view of the increasing readiness with which epilepsy follows cortical excitation as we pass from Apes to the Carnivora this observation is not without meaning.

Conclusion.

In conclusion we feel obliged to advert once more to the fact that the foregoing account is founded upon but one experiment. In view of the difficulty and expense of obtaining material we have, however, thought it best to publish the results at once.

Description of Plates.

Plates 16, 17 (Figs. 1–5).

PLATE 16.

Fig. 1. View of left hemisphere (external surface) which was analysed by excitation, and photographed directly after the experiment, with the meninges intact. Natural size. The photograph has been unavoidably reversed in printing.

- *Sy.* Fissure of Sylvius.
- *G.* Fissure of Rolando, placed just behind its genu.
- *Pr.c.* Præcentral sulcus.
- *S.F.S.* Superior frontal sulcus.
- *I.F.S.* Inferior frontal sulcus.
- *P.c.* Postcentral sulcus.
- *I.P.* Intra-parietal sulcus.

Fig. 2. View of the same hemisphere after hardening in bichromate of ammonia and alcohol, and subsequently removing the meninges. Natural size (shrunk in hardening).

The letters are the same as in fig. 1.

PLATE 17.

Fig. 3. Photograph of the original drawing of the portion of the cortex examined, made at the time of the experiment. The exact size, on paper ruled with 2 mm. squares, as described on p. 133.

The letters are the same as in fig. 1, except that the Fissure of Rolando is called *R.*

The numbers are referred to in the text.

Fig. 5. Horizontal section of the right hemisphere, showing the level where the internal capsule was excited (*vide* p. 147).

- *i.c.* Internal capsule.
- *pu.* Putamen, or outermost zone of lenticular nucleus.
- *m.z.* Middle zone of lenticular nucleus.
- *o.th.* Optic thalamus.
- *s.l.* Septum lucidum.

PLATES 18–20 (Figs. 1–27).

PLATE 18.

Fig. 1. Photograph of the external surface of the left hemisphere, which is tilted laterally, so that the genu of the Fissure of ROLANDO is opposite the centre of the lens. Natural size.

The letters refer to the same parts as in fig. 1, Plate 16.

In figs. 1 to 27, the shading shows the area of representation of the various movements, the depth of shading showing the degree of representation. The numbering of these figures corresponds to the description in the text (pp. 134–147).

Figs. 2–27 are photographs of the central convolutions corresponding to fig. 1.

Fig. 1. Both eyes move conjugately to the opposite side.

Fig. 2. Combined movement of eyelids opening briskly, eyeballs turning to the opposite side, and head turning to the opposite side.

Fig. 3. Bilateral closure of the eyelids, but those of the opposite side more strongly than those of the same side.

Fig. 4. Elevation of upper lip of opposite side.

Fig. 5. Retraction (horizontal) of the opposite angle of the mouth.

Fig. 6. Eversion of the opposite lower lip.

Fig. 7. Rolling in of both lips, especially of the lower and of the opposite side.

Fig. 8. Pursing of both lips.

Fig. 9. Pouting of both lips.

PLATE 19.

Fig. 10. Twitching of the opposite half of the upper part of the orbicularis oris.

Fig. 11. Opening of the mouth.

Fig. 12. Tongue protruded, flattened posteriorly, tip directed to opposite side.

Fig. 13. Tongue protruded, heaped up on the same side, and tip directed to the opposite side.

Fig. 14. Tongue neither protruded nor retracted, but rolled over to opposite side.

Fig. 15. Tongue retracted, heaped up posteriorly, and rolled over to opposite cheek.

Fig. 16. Tongue retracted slightly, flattened throughout, and the tip of the opposite side retracted horizontally.

Fig. 17. Movements of the thumb.

Fig. 18. Movements of the index finger.

Fig. 19. Extension of the fingers.

Fig. 20. Movements of the wrist.

Fig. 21. Flexion of the elbow.

PLATE 20.

Fig. 22. Adduction of the shoulder.
Fig. 23. Movements of the hallux.
Fig. 24. Extension of the small toes.
Fig. 25. Movements of the ankle.
Fig. 26. Movements of the knee.
Fig. 27. Movements of the hip.

PLATE 21.

This is a photograph (enlarged twice the size) of fig. 1, Plate 18, upon which are written the names of the foci of representation in their proper relative positions.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

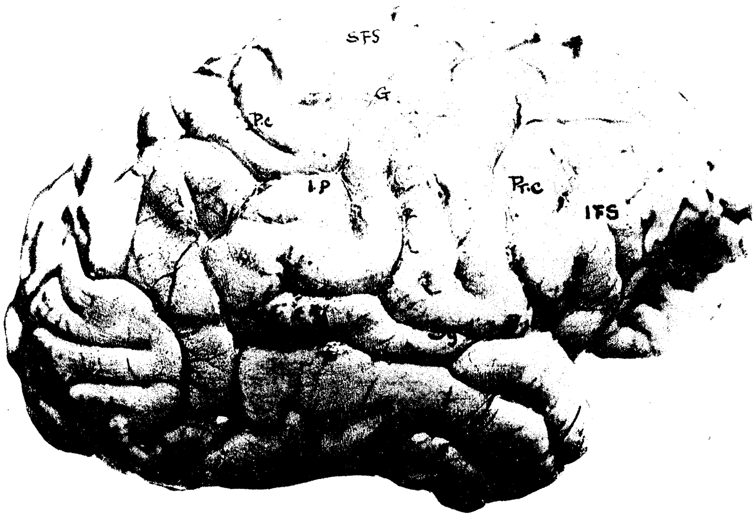


Fig. 1

Fig. 2

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

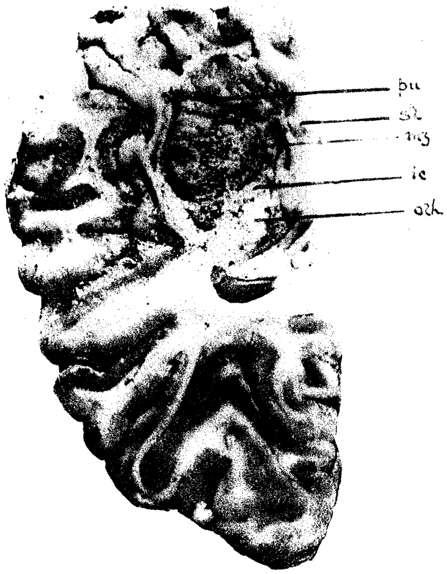


Fig. 5

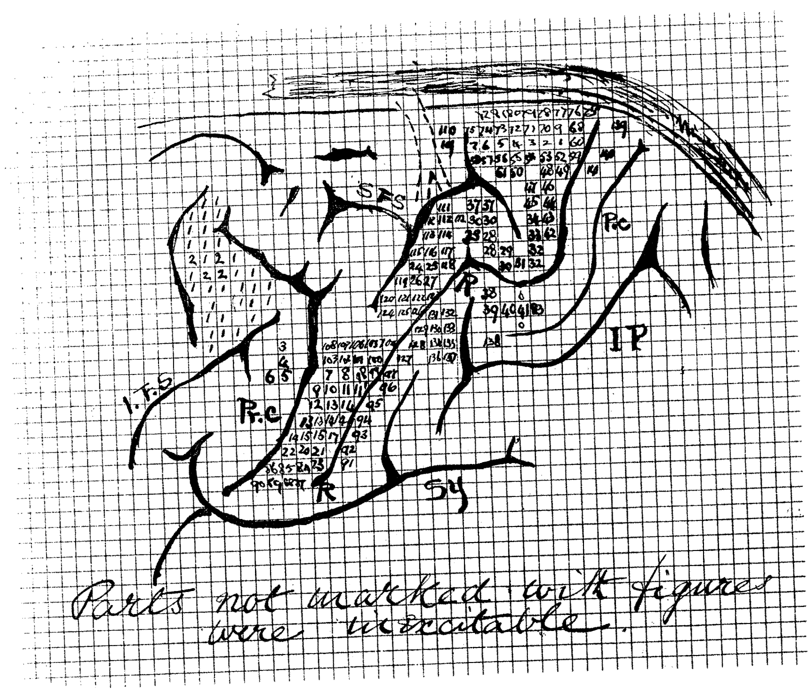


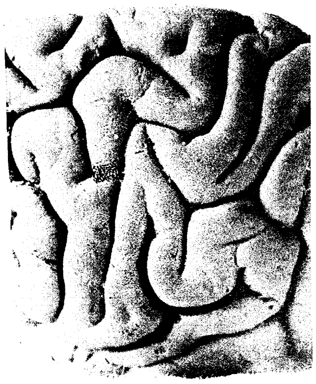
Fig. 3

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

1

2.

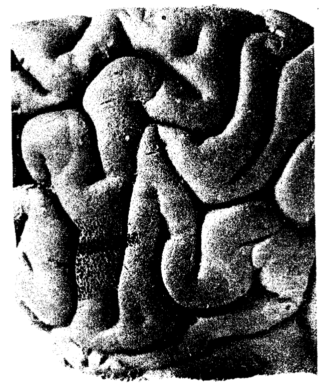
3.



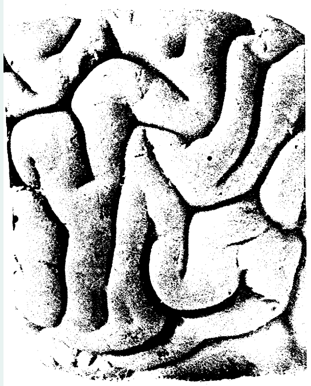
B

4.

5.



6.



7.

8.

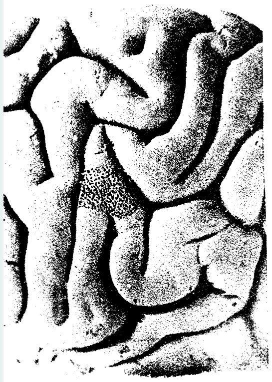
9.

…t.

L.B. Fleming Hanwell.

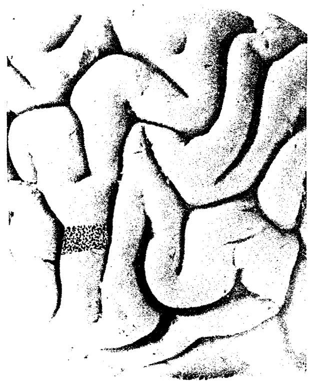
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

10.

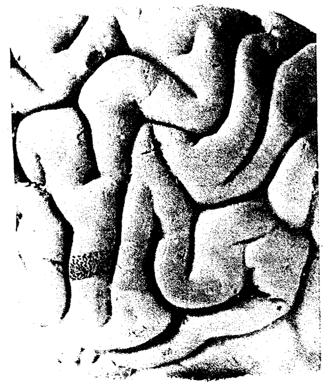


11.

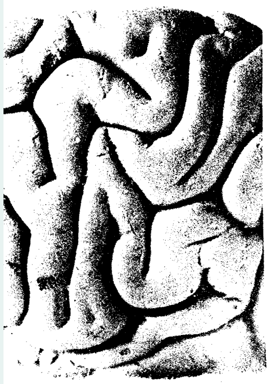
12.



13.

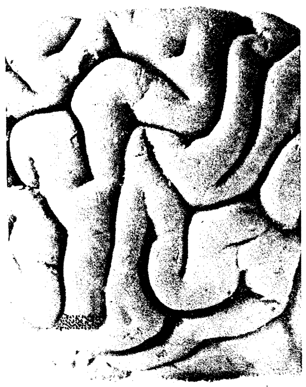


14.

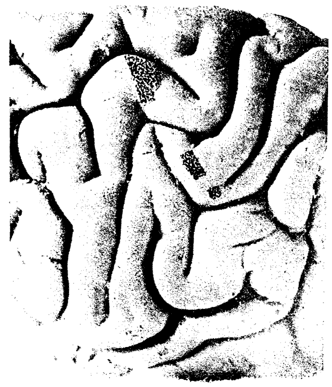


15.

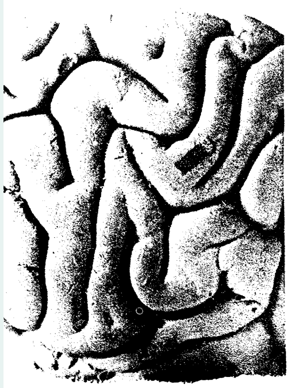
16.



17.

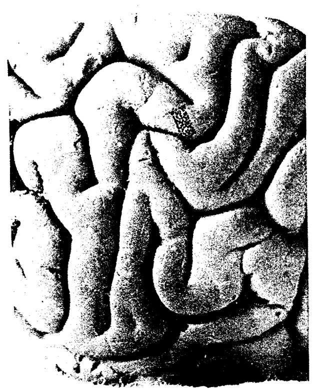


18.

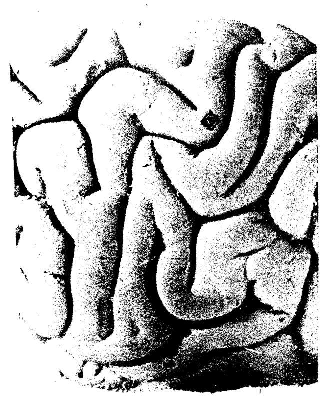


19.

20.

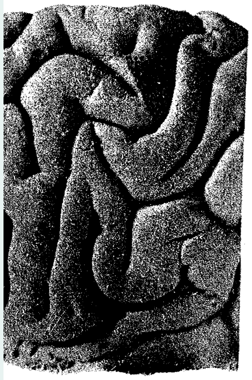


21.



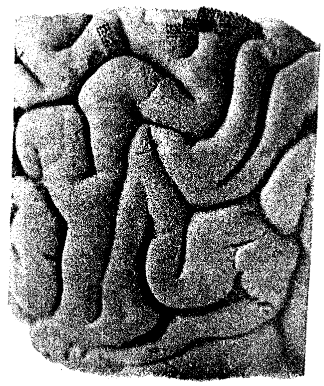
oto-Print. L.B. Fleming Hanwell.

22.

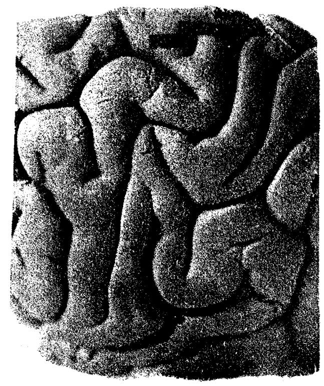


23.

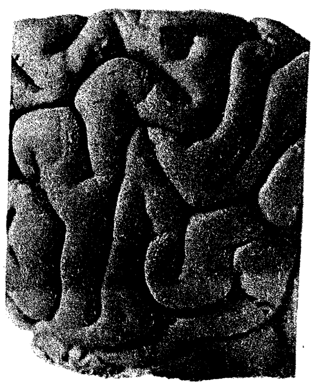
24.



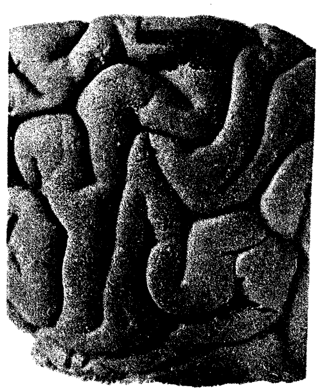
25.



26.



27.



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

ote-Print. L.B. Fleming Hanwell.

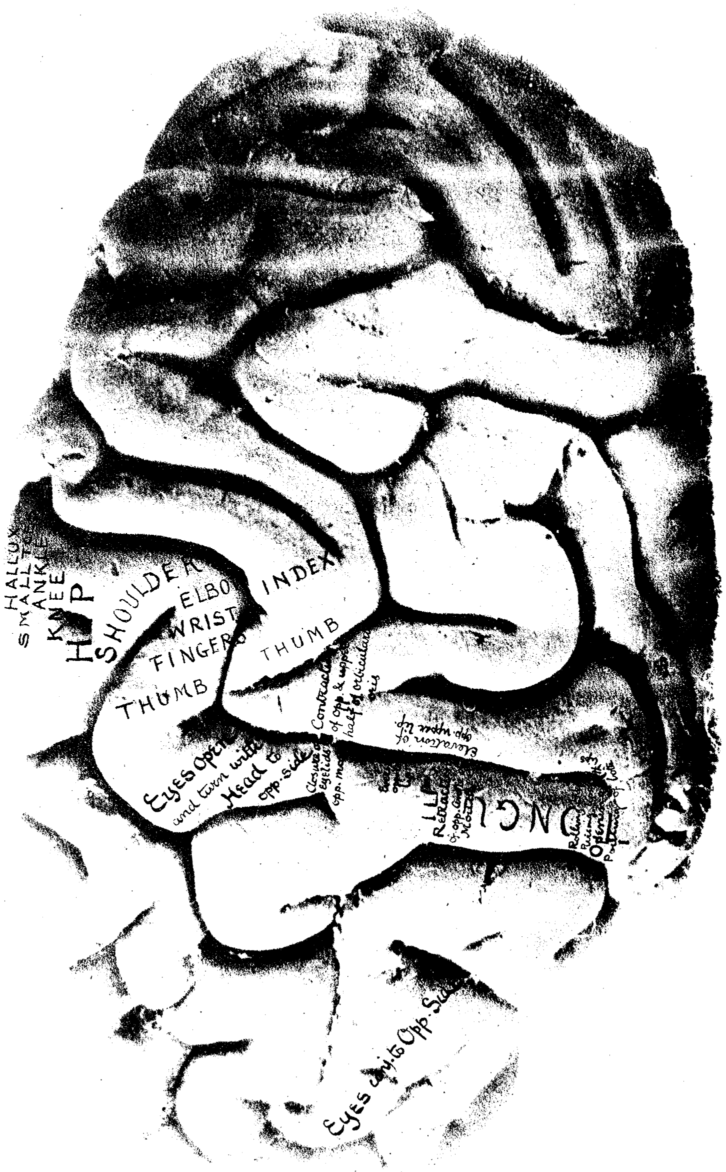


Photo-Print L.B. Fleming Hanwell.

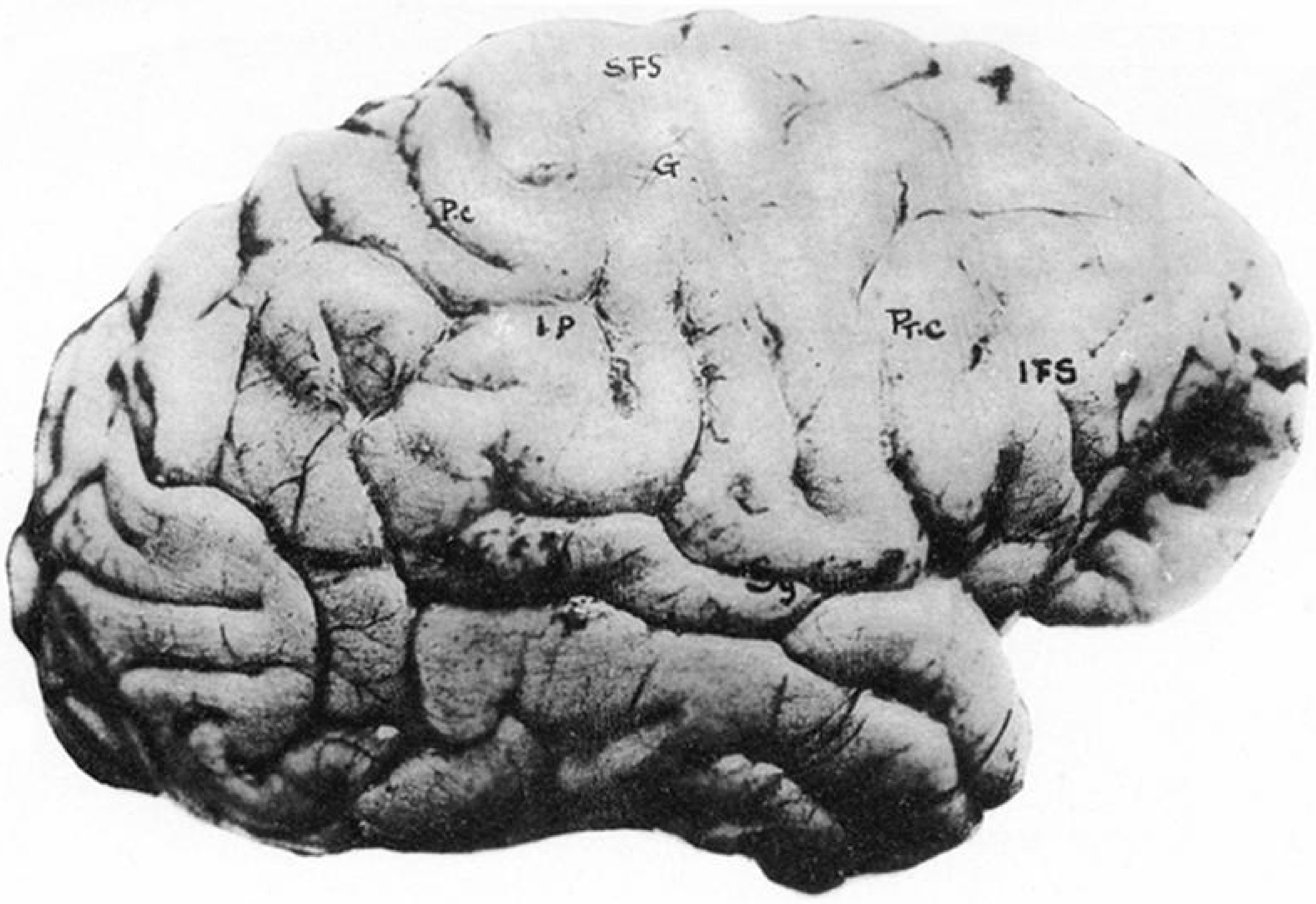


Fig. 1

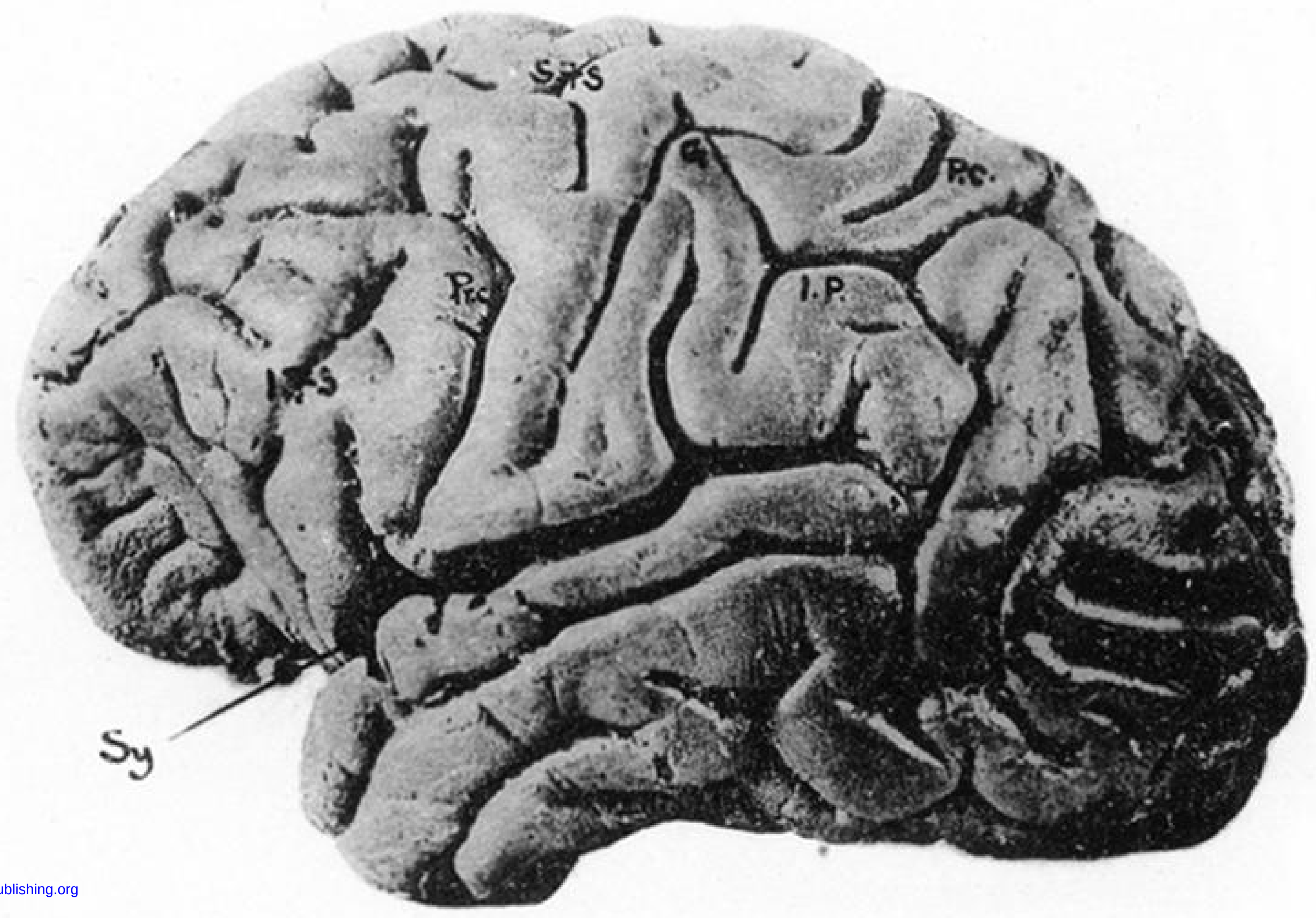


Fig. 2

PLATE 16.

Fig. 1. View of left hemisphere (external surface) which was analysed by excitation, and photographed directly after the experiment, with the meninges intact. Natural size. The photograph has been unavoidably reversed in printing.

Sy. Fissure of SYLVIUS.
G. Fissure of ROLANDO, placed just behind its genu.
Pr.c. Præcentral sulcus.
S.F.S. Superior frontal sulcus.
I.F.S. Inferior frontal sulcus.
P.c. Postcentral sulcus.
I.P. Intra-parietal sulcus.

Fig. 2. View of the same hemisphere after hardening in bichromate of ammonia and alcohol, and subsequently removing the meninges. Natural size (shrunk in hardening).

The letters are the same as in fig. 1.

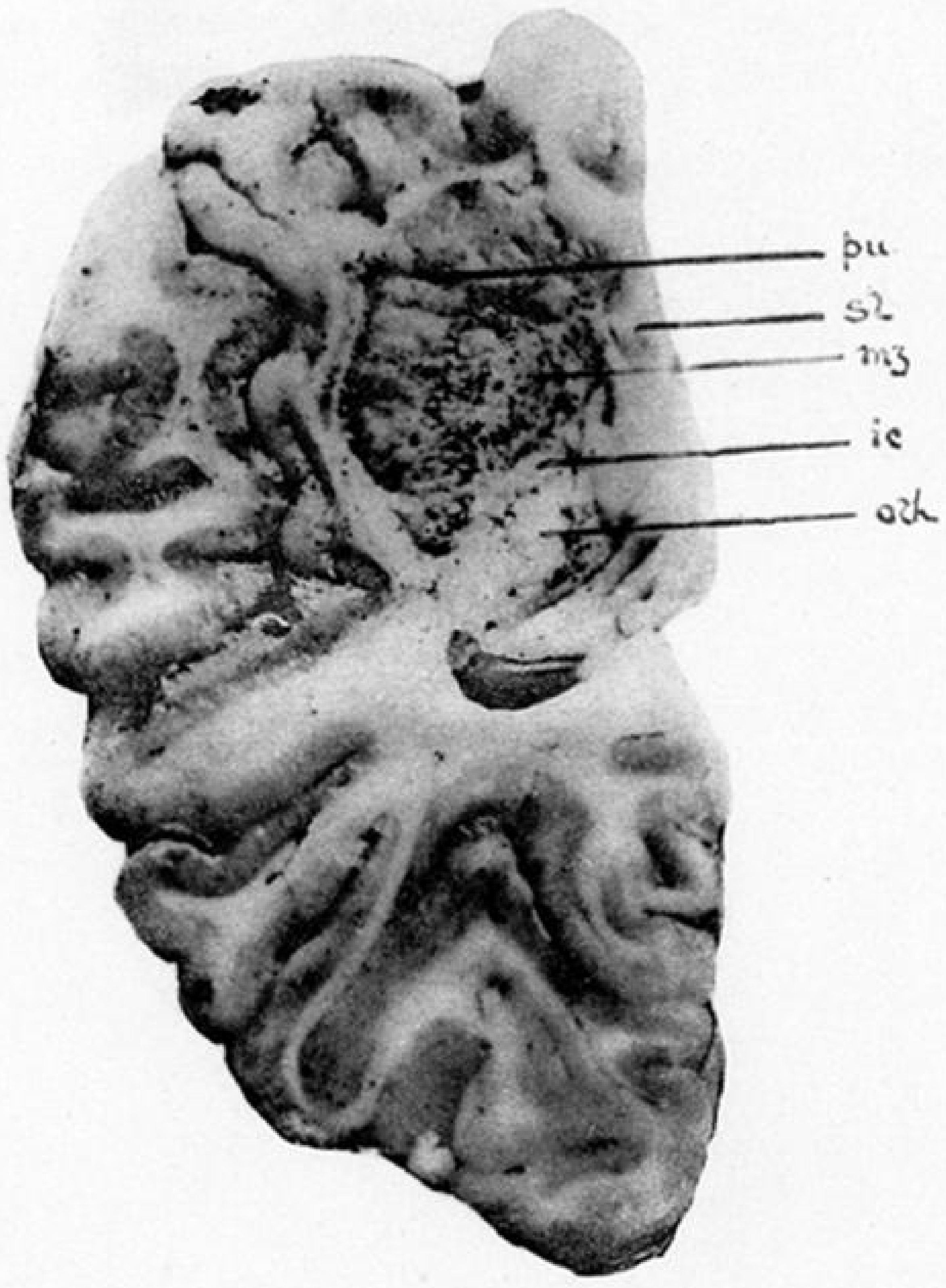


Fig. 5

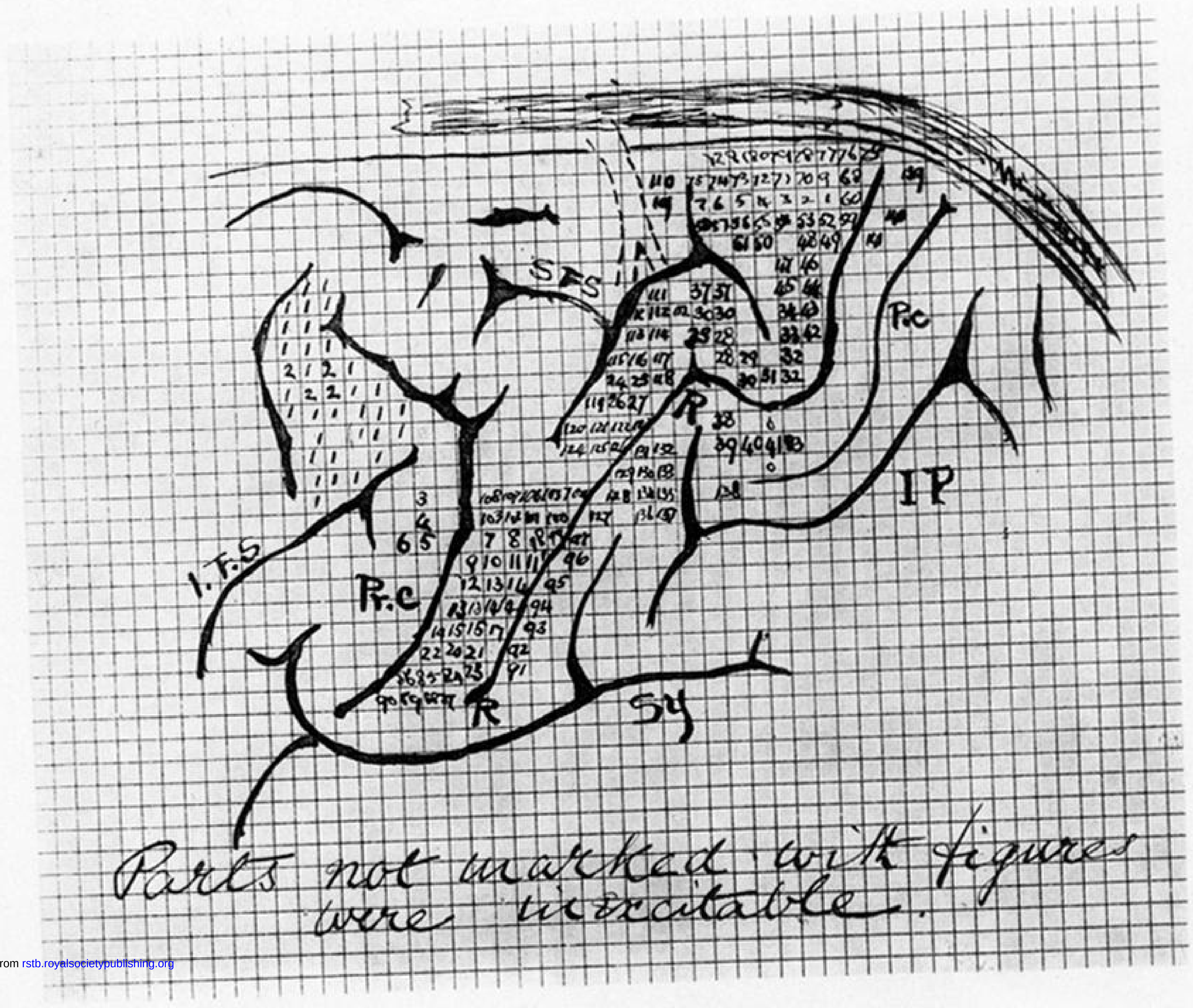


Fig. 3

PLATE 17.

Fig. 3. Photograph of the original drawing of the portion of the cortex examined, made at the time of the experiment. The exact size, on paper ruled with 2 mm. squares, as described on p. 133.

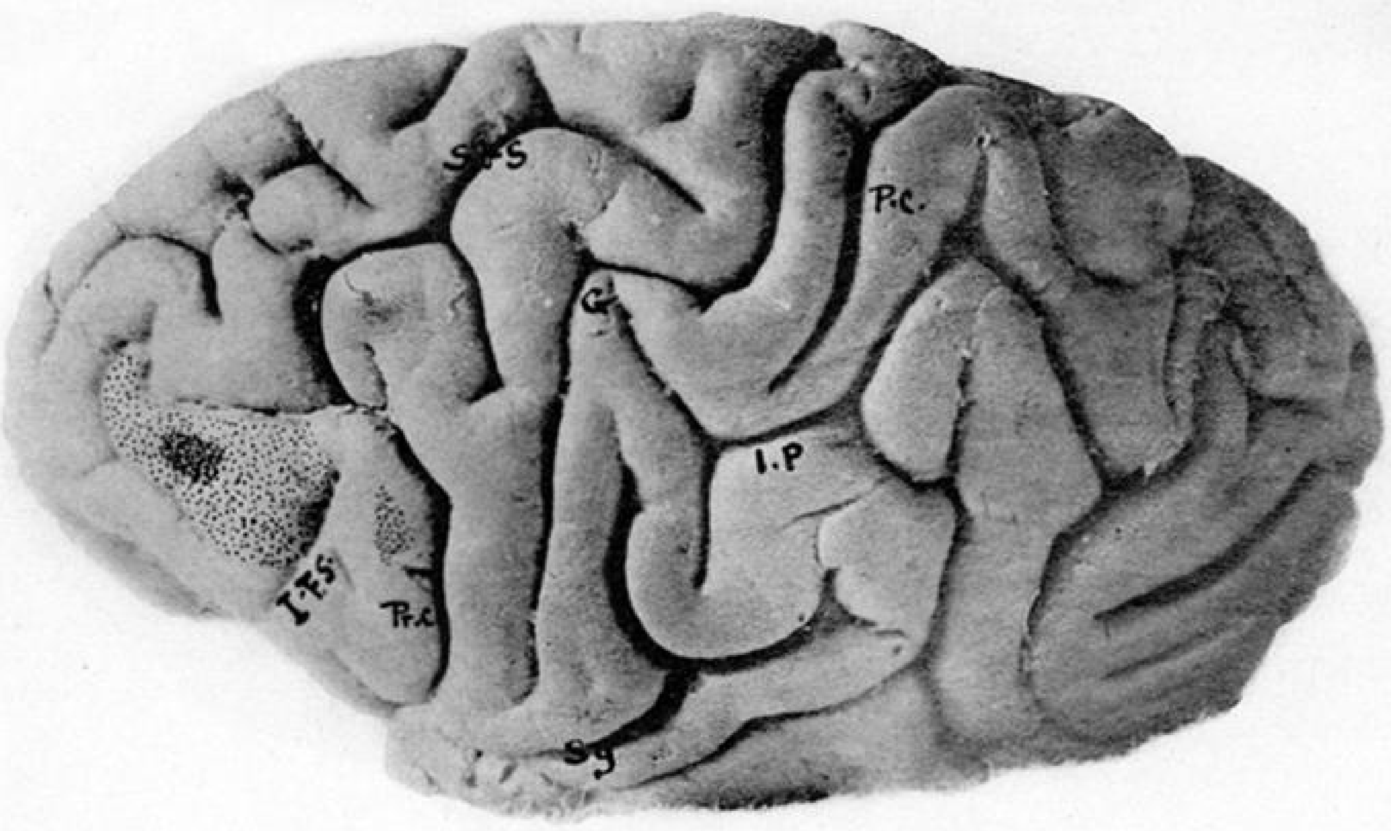
The letters are the same as in fig. 1, except that the Fissure of ROLANDO is called *R*.

The numbers are referred to in the text.

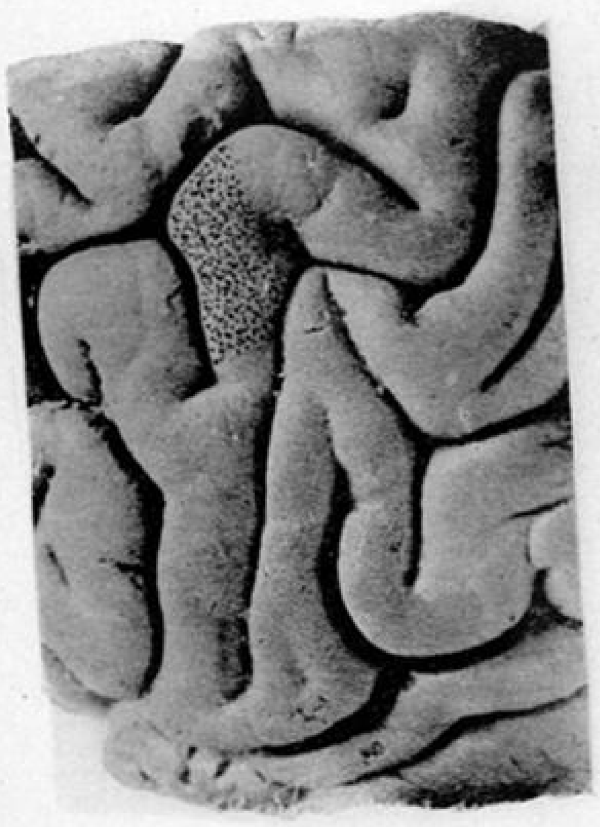
Fig. 5. Horizontal section of the right hemisphere, showing the level where the internal capsule was excited (*vide* p. 147).

i.c. Internal capsule.
pu. Putamen, or outermost zone of lenticular nucleus.
m.z. Middle zone of lenticular nucleus.
o.th. Optic thalamus.
s.l. Septum lucidum.

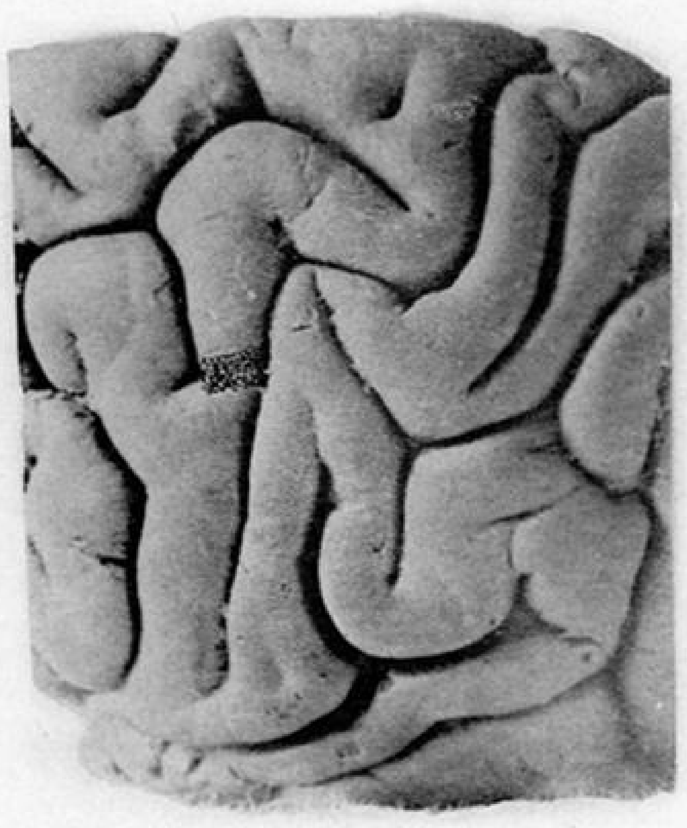
1



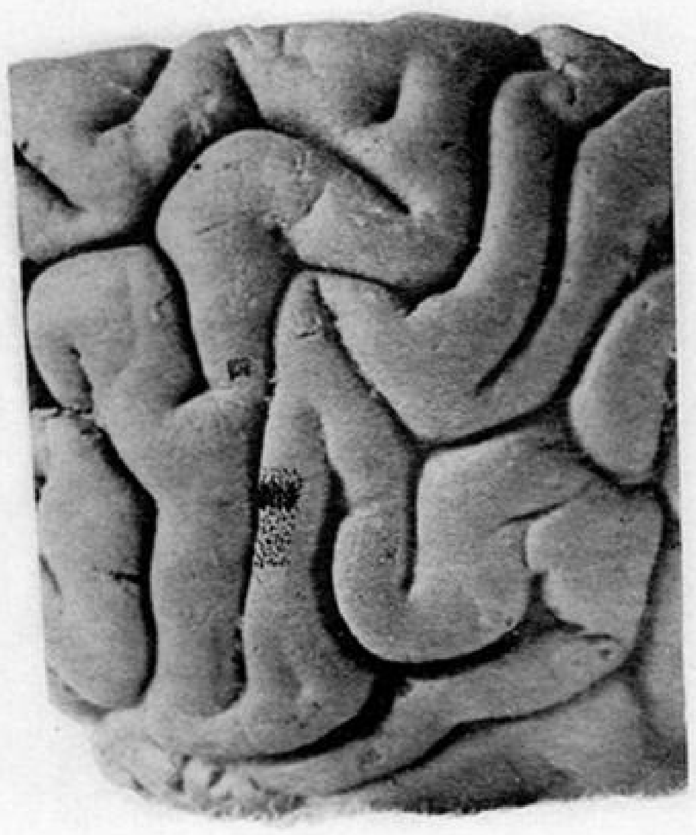
2.



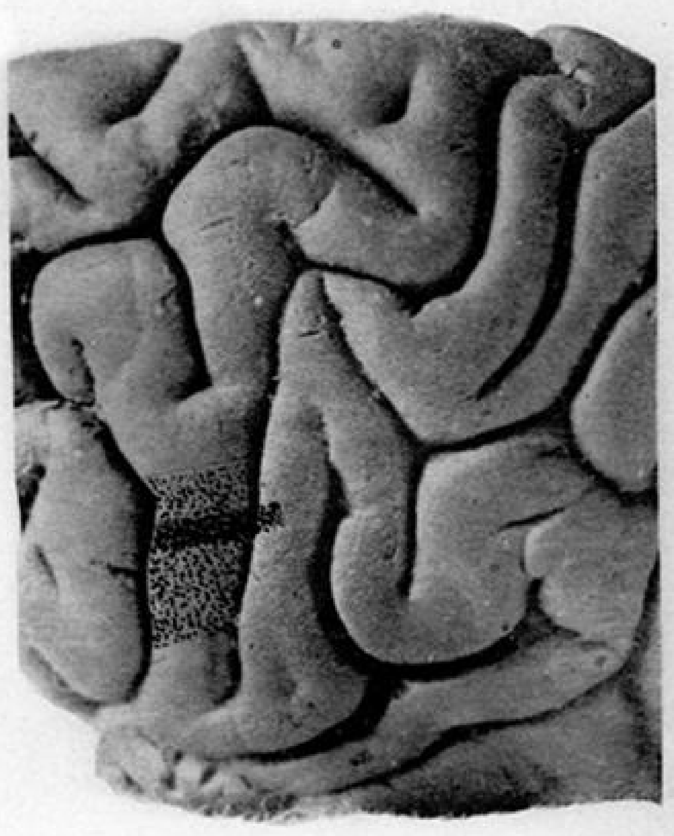
3.



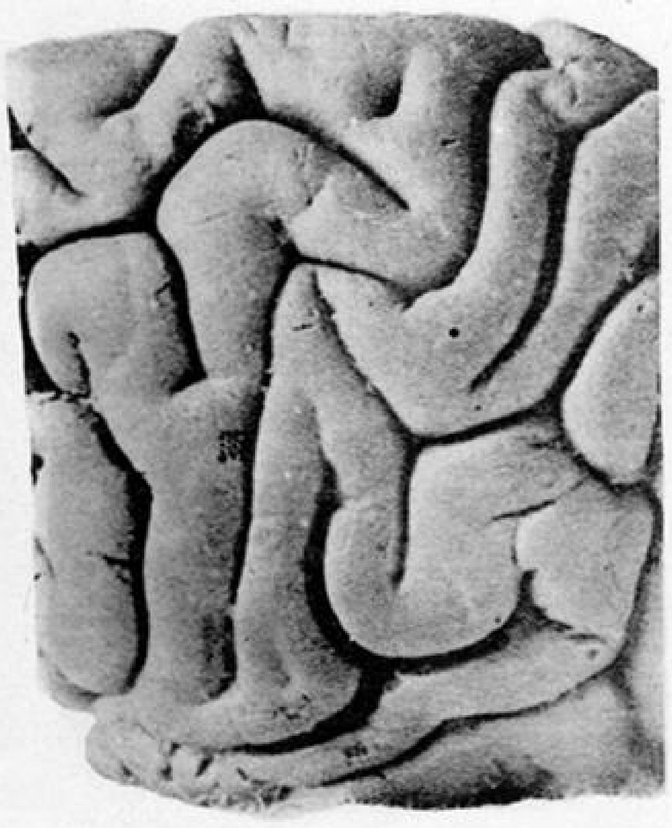
4.



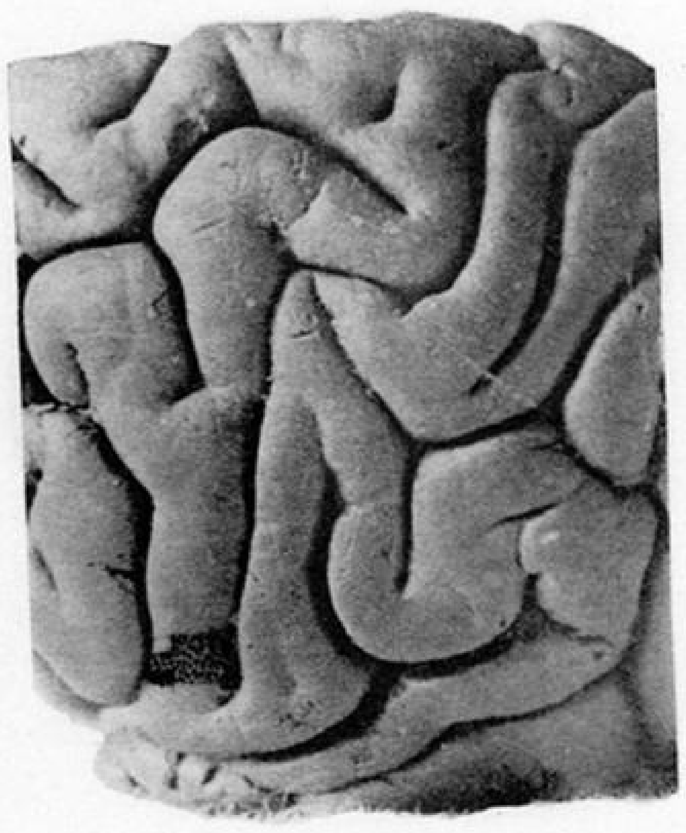
5.



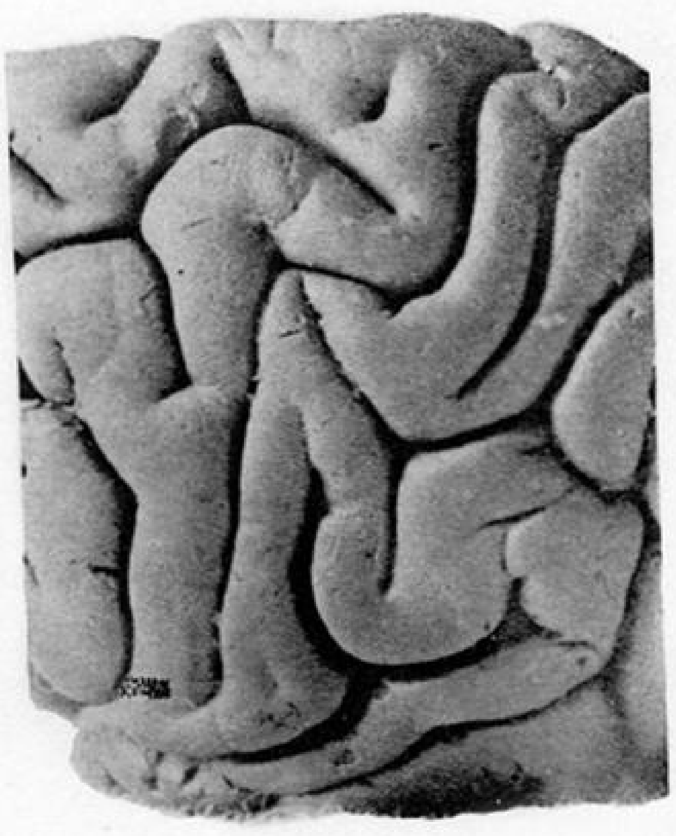
6.



7.



8.



9.

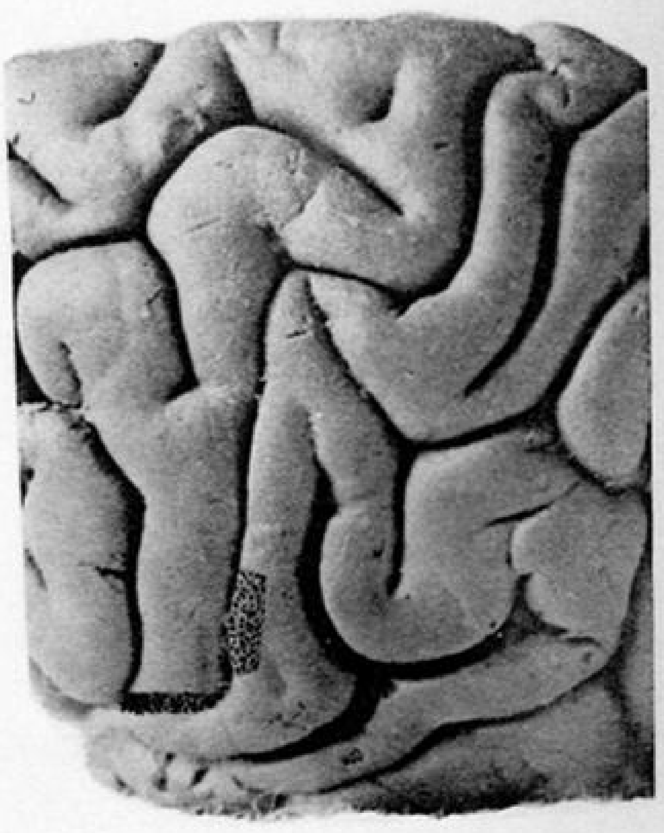


PLATE 18.

Fig. 1. Photograph of the external surface of the left hemisphere, which is tilted laterally, so that the genu of the Fissure of ROLANDO is opposite the centre of the lens. Natural size.

The letters refer to the same parts as in fig. 1, Plate 16.

In figs. 1 to 27, the shading shows the area of representation of the various movements, the depth of shading showing the degree of representation. The numbering of these figures corresponds to the description in the text (pp. 134–147).

Figs. 2–27 are photographs of the central convolutions corresponding to fig. 1.

Fig. 1. Both eyes move conjugately to the opposite side.

Fig. 2. Combined movement of eyelids opening briskly, eyeballs turning to the opposite side, and head turning to the opposite side.

Fig. 3. Bilateral closure of the eyelids, but those of the opposite side more strongly than those of the same side.

Fig. 4. Elevation of upper lip of opposite side.

Fig. 5. Retraction (horizontal) of the opposite angle of the mouth.

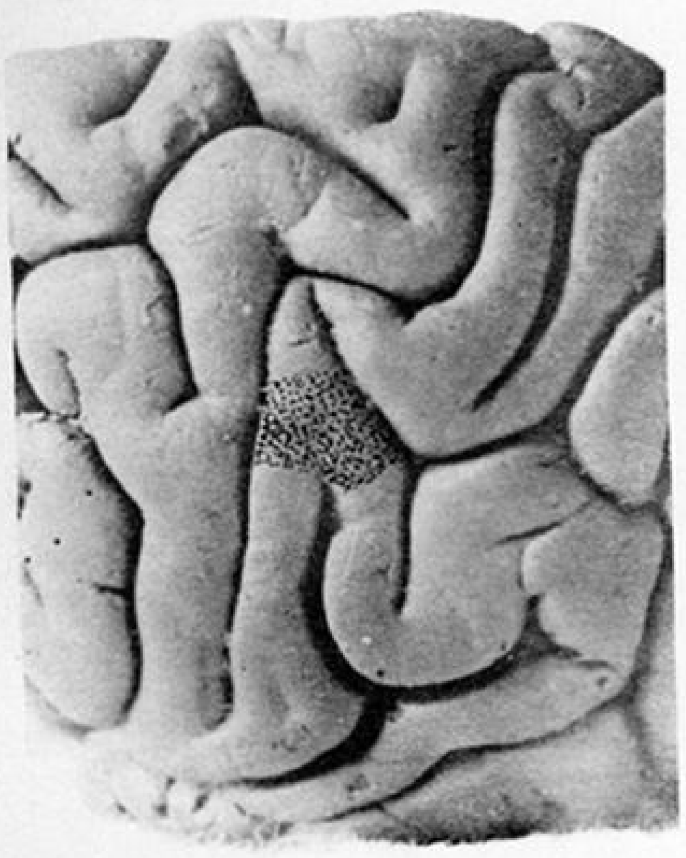
Fig. 6. Eversion of the opposite lower lip.

Fig. 7. Rolling in of both lips, especially of the lower and of the opposite side.

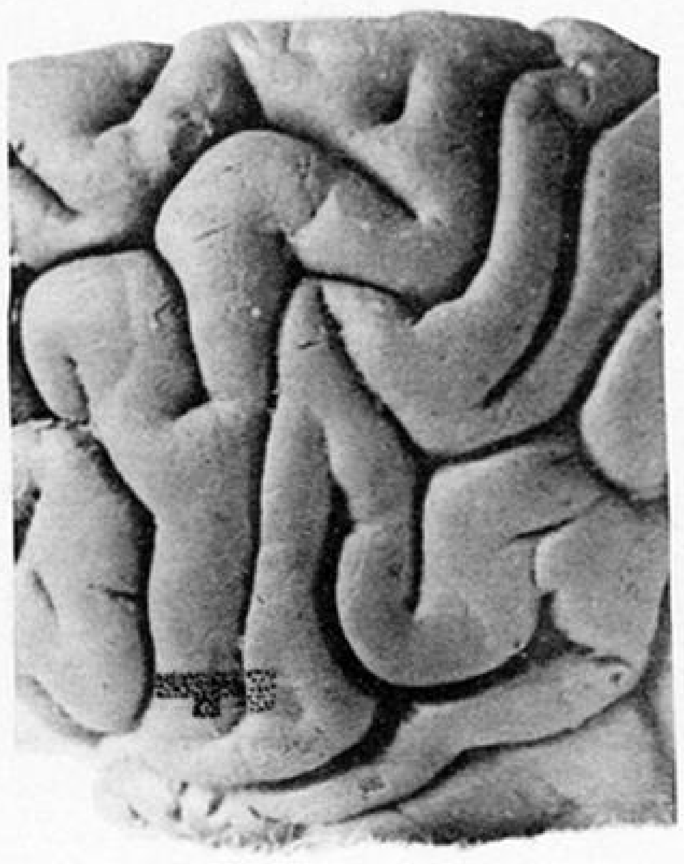
Fig. 8. Pursing of both lips.

Fig. 9. Pouting of both lips.

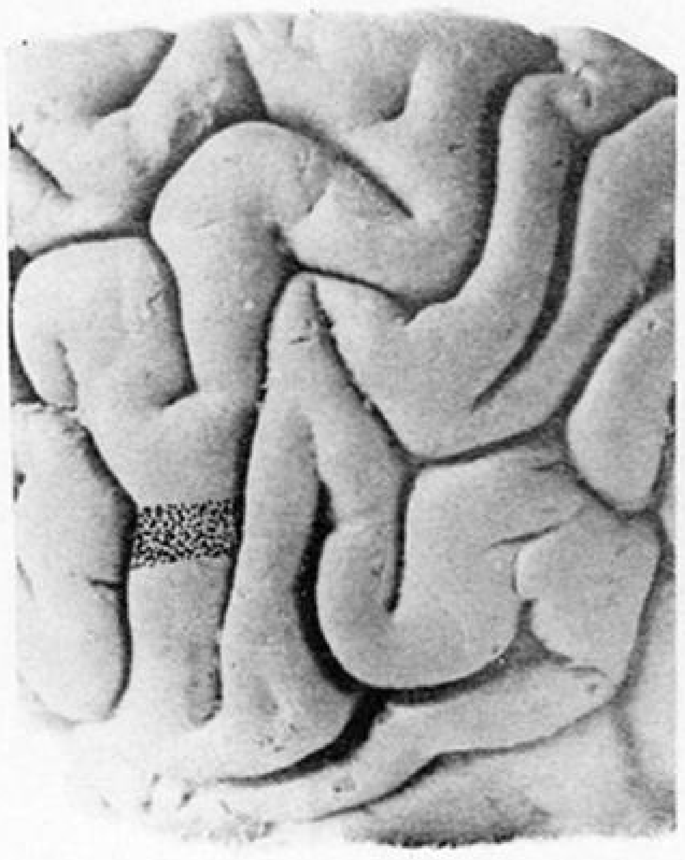
10.



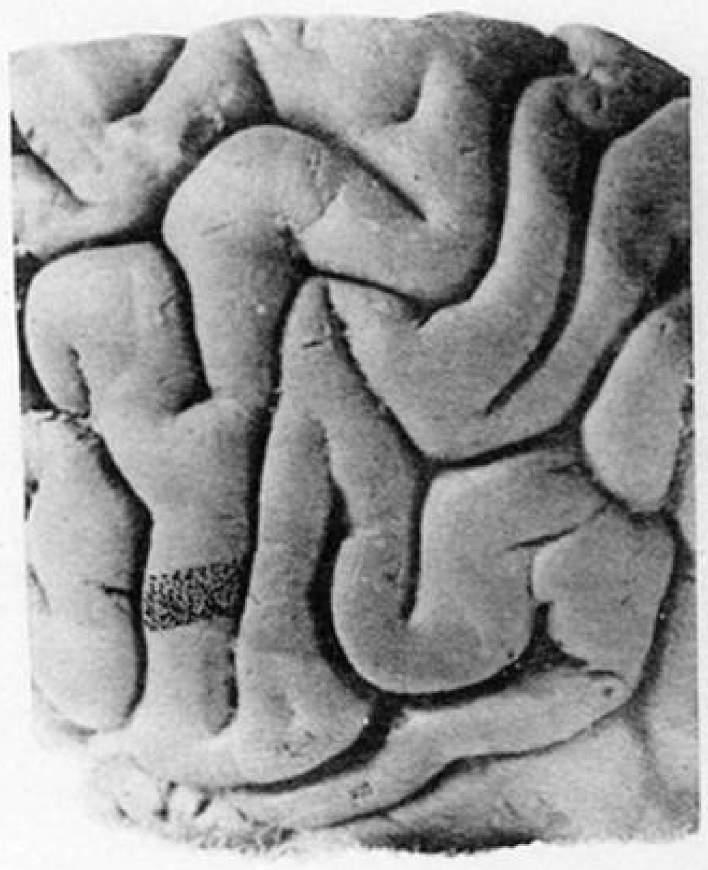
11.



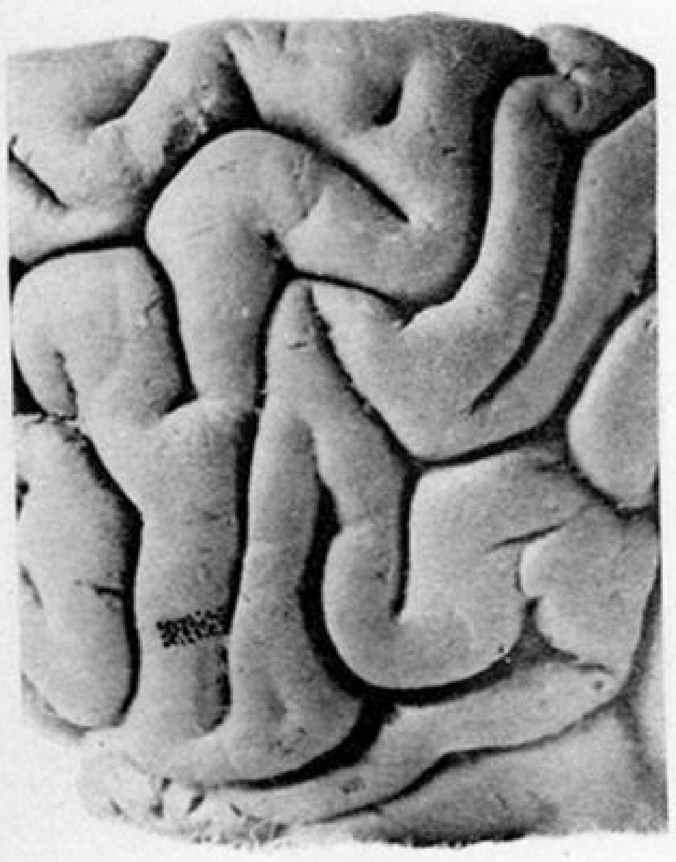
12.



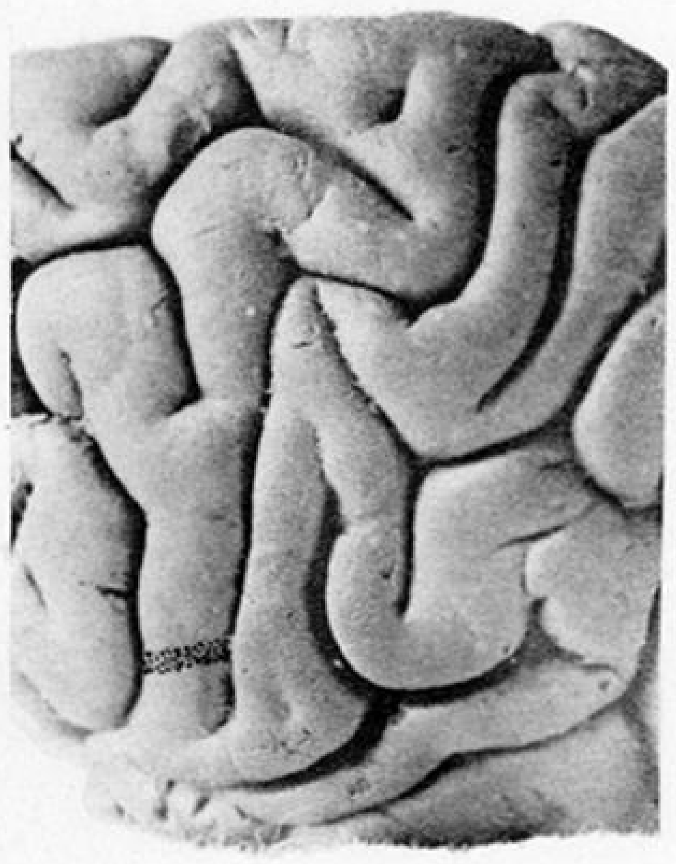
13.



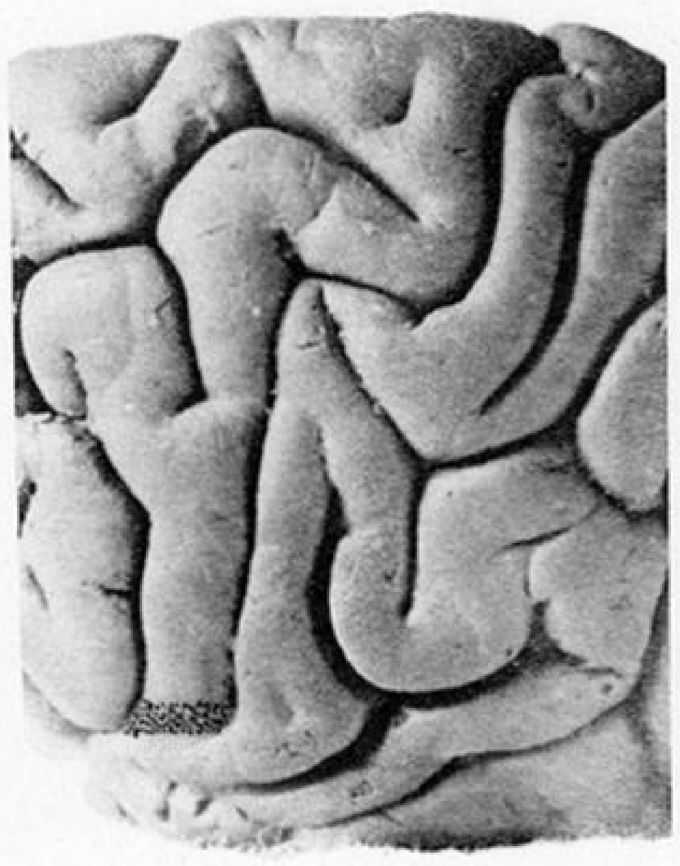
14.



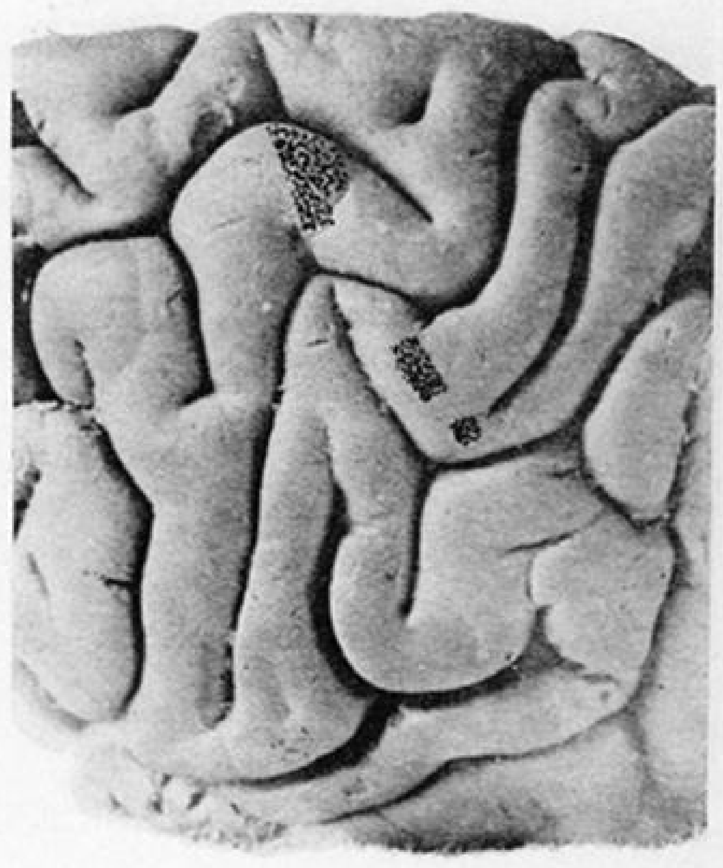
15.



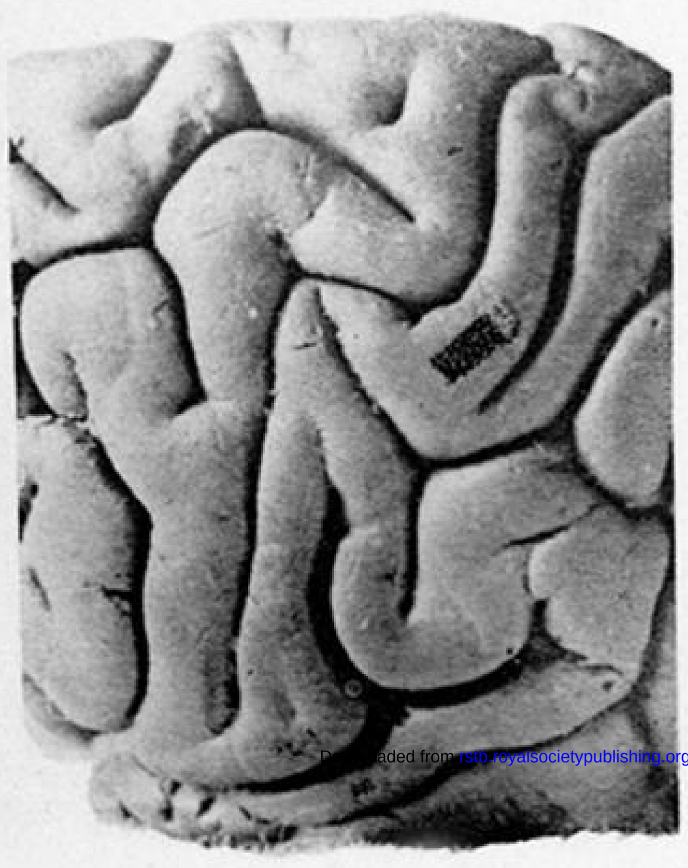
16.



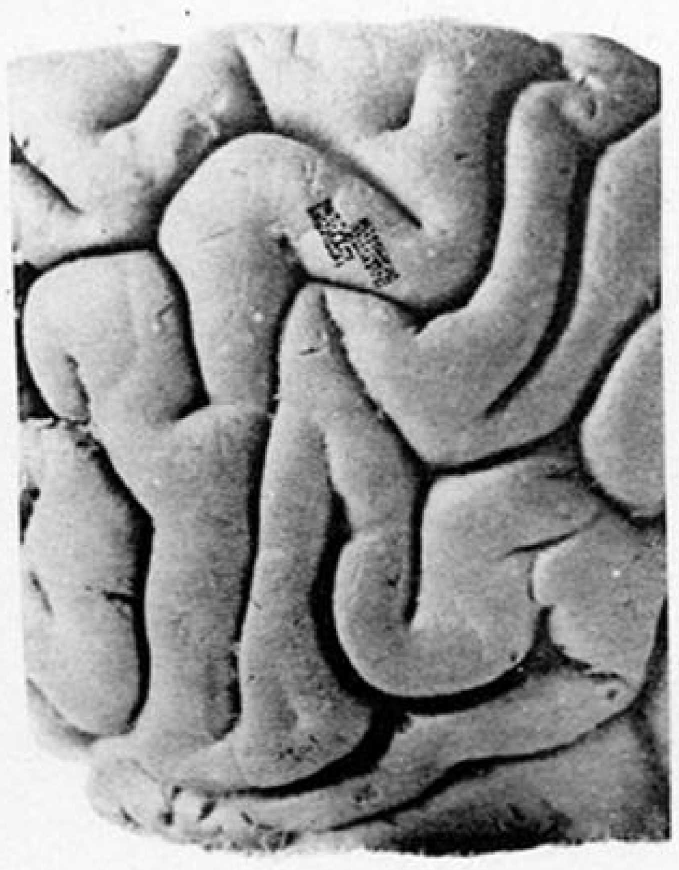
17.



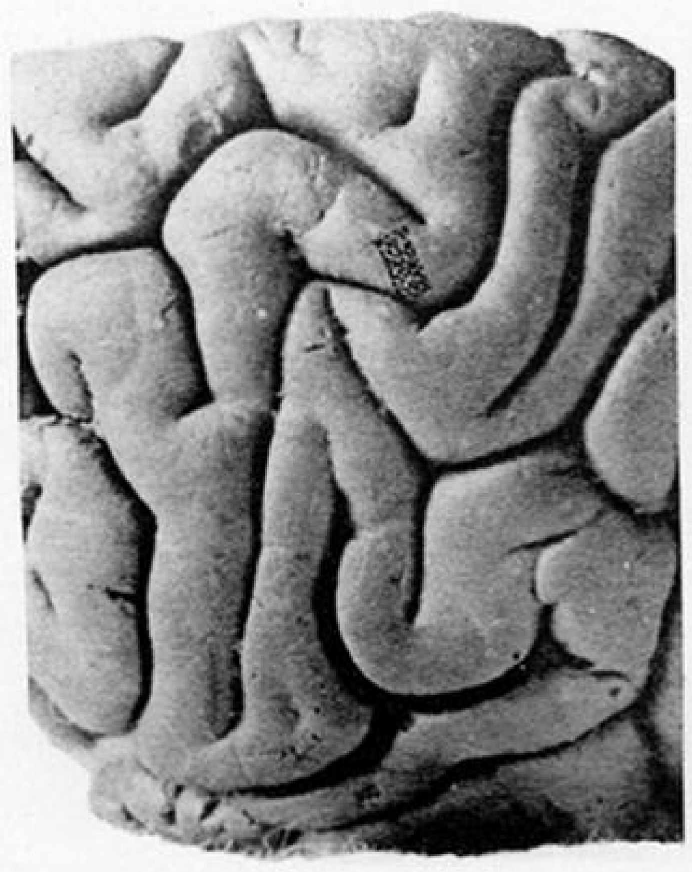
18.



19.



20.



21.

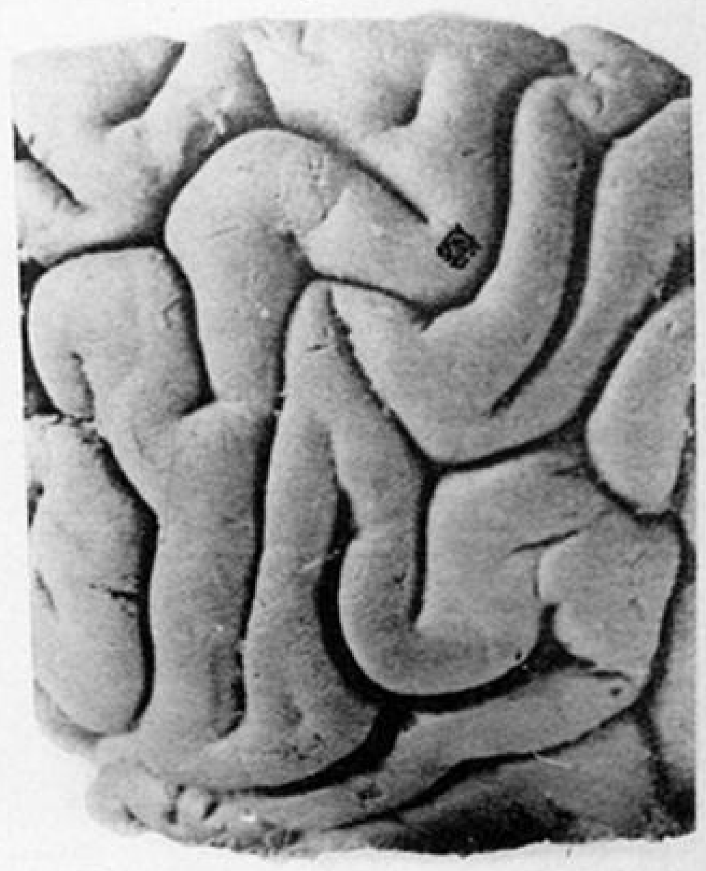


PLATE 19.

Fig. 10. Twitching of the opposite half of the upper part of the orbicularis oris.

Fig. 11. Opening of the mouth.

Fig. 12. Tongue protruded, flattened posteriorly, tip directed to opposite side.

Fig. 13. Tongue protruded, heaped up on the same side, and tip directed to the opposite side.

Fig. 14. Tongue neither protruded nor retracted, but rolled over to opposite side.

Fig. 15. Tongue retracted, heaped up posteriorly, and rolled over to opposite cheek.

Fig. 16. Tongue retracted slightly, flattened throughout, and the tip of the opposite side retracted horizontally.

Fig. 17. Movements of the thumb.

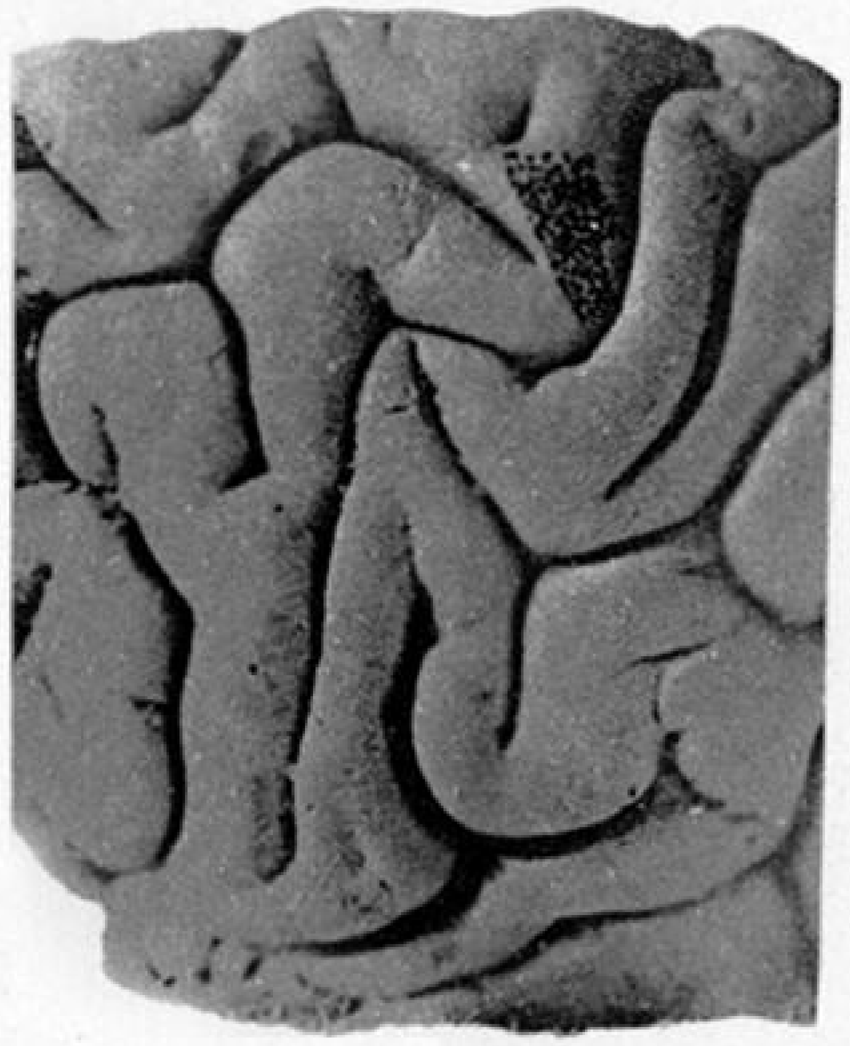
Fig. 18. Movements of the index finger.

Fig. 19. Extension of the fingers.

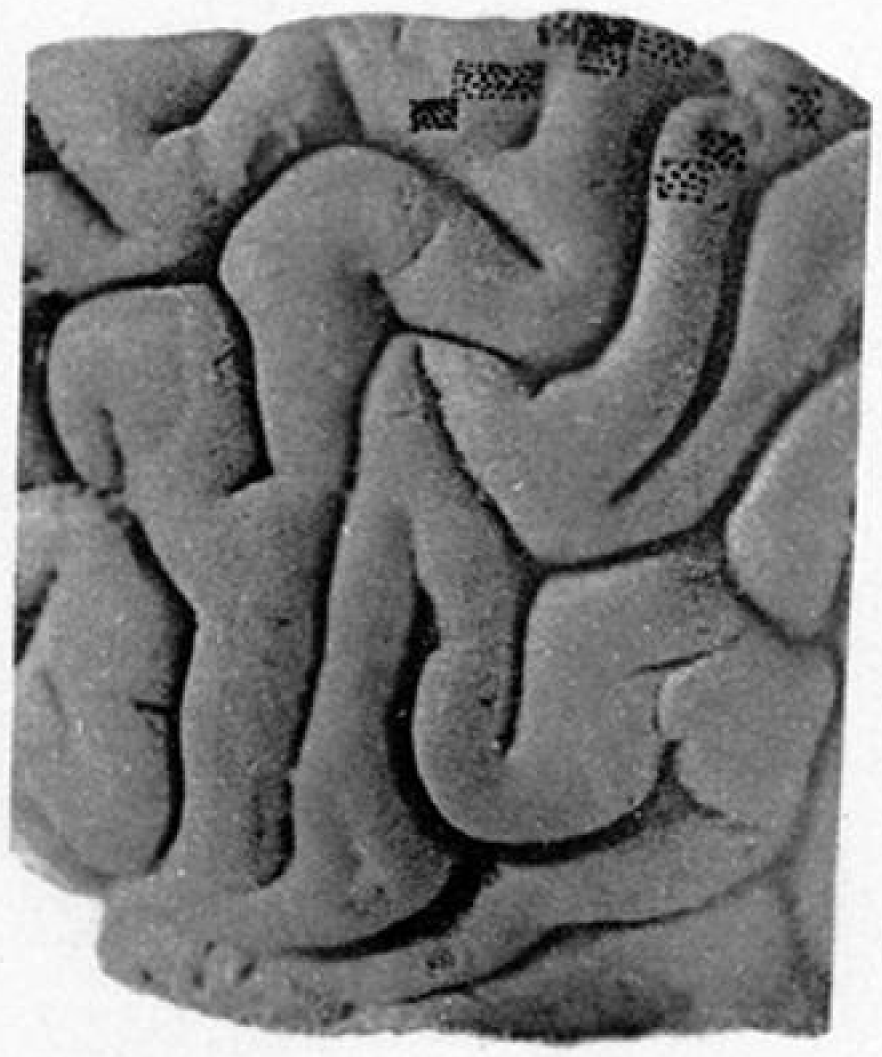
Fig. 20. Movements of the wrist.

Fig. 21. Flexion of the elbow.

22.

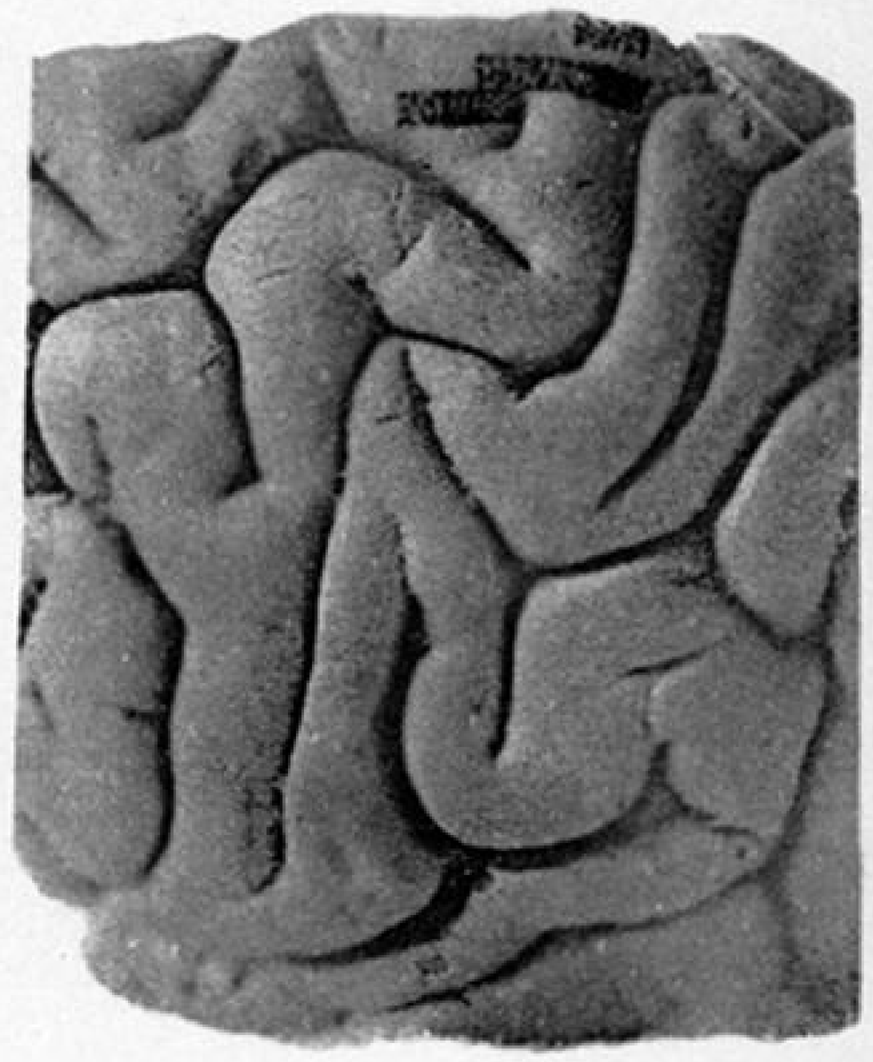


23.



24.

25.



26.

27.

PLATE 20.

Fig. 22. Adduction of the shoulder.
Fig. 23. Movements of the hallux.
Fig. 24. Extension of the small toes.
Fig. 25. Movements of the ankle.
Fig. 26. Movements of the knee.
Fig. 27. Movements of the hip.

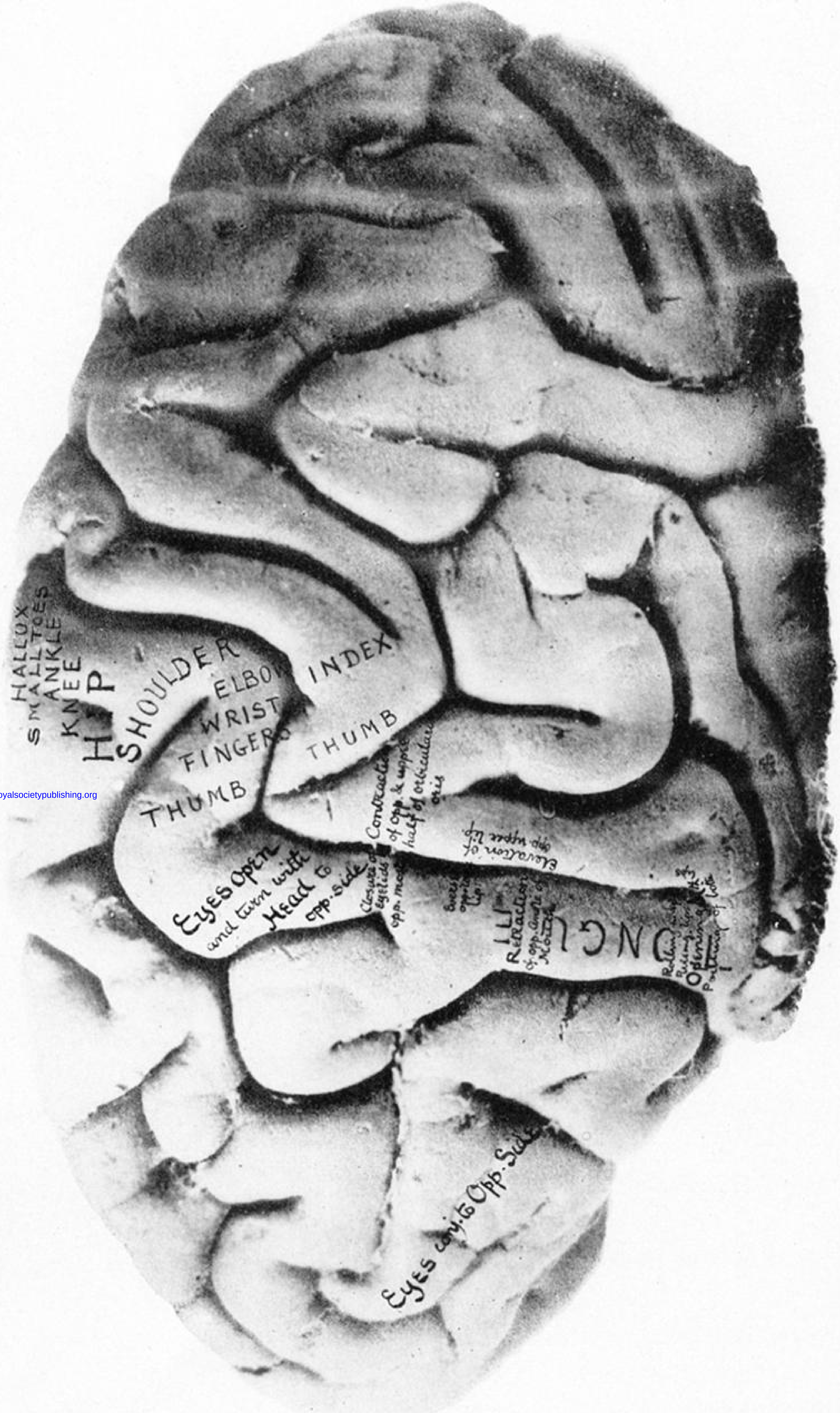


PLATE 21.

This is a photograph (enlarged twice the size) of fig. 1, Plate 18, upon which are written the names of the foci of representation in their proper relative positions.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES