PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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

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IX. *A further Minute Analysis by Electric Stimulation of the so-called Motor Region of the Cortex Cerebri in the Monkey* (Macacus sinicus).*

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[Plates 40–42.]

INTRODUCTION.

In a former paper published in the 'Philosophical Transactions,' B., vol. 178 (1887), pp. 153–167, a minute account was given by us of the effects produced by electrical stimulation of the so-called motor area in the cerebral cortex for the upper limb. In continuation of this work we have investigated in a similar manner the effects produced by stimulating the rest of the so-called motor region on the convexity of the cortex, with the exception of the lower parts of the ascending frontal and parietal convolutions. The parts examined in the present research comprise the posterior third of the frontal convolutions, the upper third of the ascending frontal convolution, the superior parietal lobule, and the posterior half of the ascending parietal convolution. The movements evoked by stimulating these areas were respectively those of the head and eyes to the opposite side, conjoined movement of both opposite limbs, movements of the lower limb, and movements of the upper limb. In order to avoid discrepancies in the arrangement of the cerebral sulci in different species, and so to obtain exact localisation of the effect produced, the same variety of Monkey was alone used, viz., *Macacus sinicus*. In all we have performed twenty-three experiments, the animal in each case having been narcotised with ether and killed before recovery from the anæsthetic.

PART I.—ANATOMY.

In the paper above referred to, a description was given of the position in the Monkey of the fissure of Rolando, the præcentral sulcus, and a small fissure above

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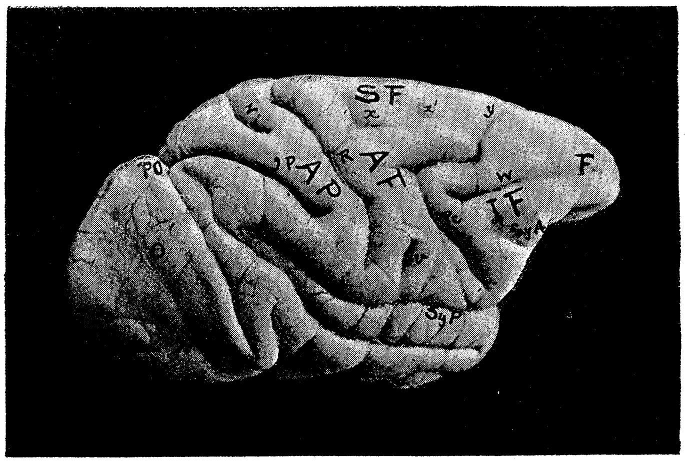
this, called by Professor SCHÄFER "*x*." The excitable region investigated in the present paper is limited below, where it lies in front of the præcentral sulcus, by the horizontal level* of the lower end of that sulcus, the superior and anterior part being bounded above by the middle line, and in front by a sulcus which Professors HORSLEY and SCHÄFER provisionally named "*y*" (see fig. 1). Below, it is partially bounded by a sulcus which we have temporarily called "*w*." This sulcus, "*w*," runs horizontally from near the tip of the frontal lobe backwards to within a very short distance of the vertical limb of the præcentral sulcus, thus lying below and approximately

Fig. 1.



Photograph of the external surface of the right half of the brain of a Monkey (*Macacus sinicus*).

Sulci SyA. Fissure of SYLVIUS, anterior limb.
SyP. Fissure of SYLVIUS, posterior limb.
R. Fissure of ROLANDO.
PO. Parieto-occipital fissure.
IP. Intra-parietal sulcus.
Pc. Præcentral sulcus.
v.
w.
x.
x'. Supplementary to *x*, occasionally found.
y.
z.
(*v.* – *z.*) Sulci, so named.

Convolutions or Gyri. F. Tip of frontal lobe. SF. Superior frontal.
IF. Inferior frontal. AF. Ascending frontal.
AP. Ascending parietal. O. Occipital lobe.

parallel to the upper limb of the præcentral sulcus. The homology between this sulcus and corresponding parts of the human brain has not as yet been made out. The middle part of the region investigated in the present research is bounded above

* *I.e.*, a line parallel to, and a short distance above, the Sylvian fissure.

by the longitudinal fissure and below by the sulcus "x." The remaining part of this region, situated behind the fissure of ROLANDO, is bounded above by the longitudinal fissure, behind by the intraparietal sulcus, and below by the horizontal level of the lower end of that sulcus. The upper part of the ascending parietal convolution, or as it is also called the superior parietal lobule, is divided by a small sulcus which is usually vertical, and which has been designated "z" by Professors HORSLEY and SCHÄFER (see fig. 1).

(As we showed in our previous paper, we consider that the sulcus "x" separates the superior from the middle frontal convolution, and is consequently homologous with the superior frontal sulcus of Man.)

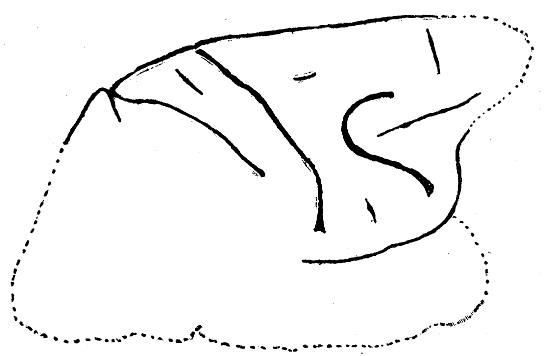
On looking at fig. 1 it will be seen that the portion of the cortex treated of in this paper partly surrounds the area in which the upper limb is chiefly represented—as described in our former paper—on two sides, viz., in front and above. These parts of the cortex in front and behind the area for the upper limb form the anterior and posterior limits respectively of the cortex which is excitable. The present research completes the investigation of the upper part of the excitable region of the outer convex surface of the hemisphere.

TOPOGRAPHICAL DETERMINATION OF THE SULCI.

The position of the sulci in different Monkeys of the same species and of about the same age varies considerably. These variations were noted in the following way:—the brain of each Monkey was exposed, and the part to be investigated was drawn the exact size, the distance of the sulci from each other and the size of the convolutions being measured by compasses; thus an accurate representation of each individual brain was recorded. As can be well seen by referring to figs. 1A and 1B, noteworthy variations in the outlines of the sulci were thus revealed.

Fig. 1A.

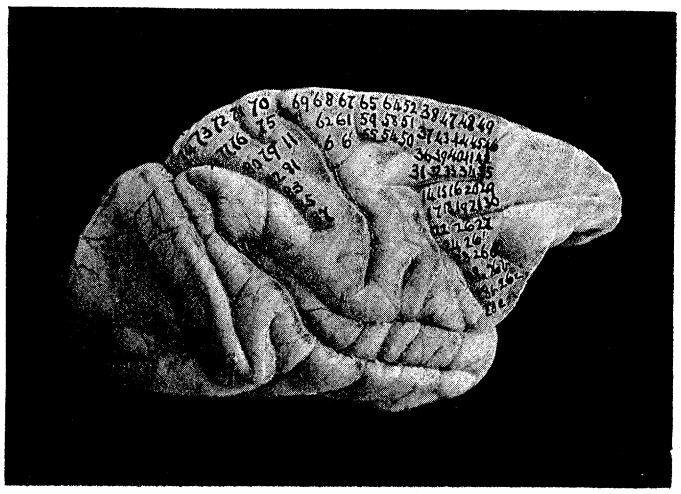
Fig. 1B.



PART II.—METHOD OF NOTATION OF THE VARIOUS POINTS STIMULATED.

Method of Experimentation.—We have, as before, divided up the area to be examined into centres* of 2 mm. square; but, although in our former research we investigated the contiguous borders as well as the middle point of these minute divisions, we thought it sufficient then to record only the latter half of these observations. In describing our present research we have thought it better to record the result obtained at every point stimulated. Consequently, in any given linear centimetre there will be five points of stimulation: that is to say, the electrodes being as before, 2 mm. apart, the middle of each centre will be 2 mm. distant from the middle point of an immediately contiguous one. The mere difference in size of the brain of some of the Monkeys investigated compelled us to slightly alter this arbitrary arrangement

Fig. 2.



This is a similar photograph to fig. 1, and shows the area of the cortex, which is the subject of this paper; the numbers denote the different individual points of stimulation, of which 74 are here given. Each number denotes a centre of the size of 2 sq. mm. Centres 35, 42, and 46 apparently pass anterior to the sulcus y (see fig. 1), but the deep shadow is caused by a large vein which happened to be present in this brain.

by suppressing a row of these centres where the approximation of the sulci reduced the surface area of the excitable cortex, so that there was only room for two in place of three rows of numbers. Moreover, occasionally we have been compelled to spread out the numbers, but the error of position so caused was never more than ·5 mm. As the method of notation of these small centres was quite arbitrary, and as numbers had to

* By the word centre, we mean each of the 2 mm. square divisions into which we have partitioned the region investigated. We reserve the term area to designate the total cortical surface in which movements of one part (*e.g.*, a limb) are wholly represented, *i.e.*, the upper limb area, the face area, etc.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

be occasionally omitted owing to the inequalities and irregularities of a convex surface such as that of the brain, it has been impossible to maintain a perfect continuity in sequence of the numbers employed. (Reference to figs. 1 and 2.)

Method of Stimulation.—We have used as before the faradic current, employing such an one as would only just evoke a movement, and for the detection of the primary movement (see 'Phil. Trans.,' *l.c.*, p. 163) the method of momentary application of the stimulus. The sole change made in the apparatus has been the substitution of one litre bichromate of potash cell for the single DANIELL cell.

The parts of the cortex relegated to the representation of the various parts of the body observed to move on excitation of the different centres must now be described, in order to make clear the details of the subsequent analysis.

PART III.—THE TOPOGRAPHY OF THE REPRESENTATION OF THOSE PARTS OF THE BODY, OF WHICH MOVEMENTS WERE OBSERVED IN THE PRESENT RESEARCH. (See fig. 3.)

(I.) *The Head and Eyes.*—The area of representation of the fundamentally important movement of turning the head and eyes to the opposite* side is a very extensive one, reaching from the longitudinal fissure above almost to the fissure of SYLVIUS below. It is limited in front and above by the small transverse or perpendicular sulcus *y* before referred to. The limitation anteriorly is continued downwards, in the same direction as *y*, to the horizontal sulcus which we have called *w*, along which the imaginary boundary runs backwards to the narrow gyrus surrounding the hinder end of this sulcus, and which bounds in front the vertical limb of the præcentral sulcus. Below *w* the border line of the area extends downwards parallel to the vertical limb of the præcentral sulcus, this portion of the line frequently corresponding with a small oblique sulcus which seems to us to be the anterior limb of the fissure of SYLVIUS. Posteriorly the area is limited by the vertical limb of the præcentral sulcus, and by a line continuing the direction of this same upwards to the middle line, passing a little in front of the anterior extremity of the sulcus *x*. The area of representation of this part has, therefore, roughly speaking, the outline of a flag, the staff of which forms the lower part (see fig. 3).

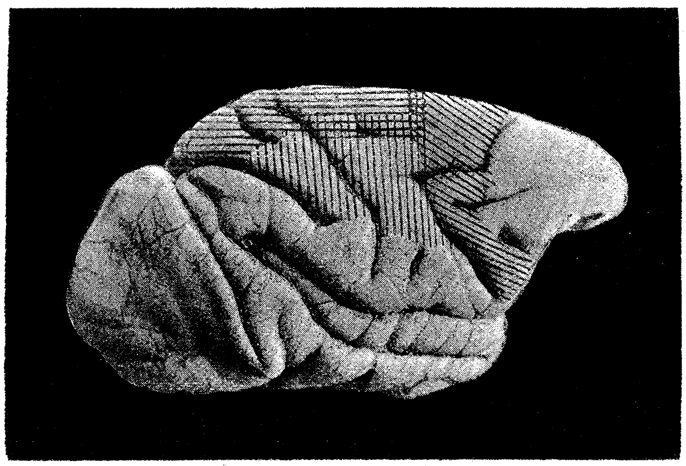
The synchronous conjugate deviation of the eyes to the opposite side is represented in the same region, but to a less extent than the movement of turning the head (*vide* page 212).

(II.) *The Lower Limb.*—The area of representation of the movements of the lower limb is limited in front by a line passing vertically through the anterior extremity of the sulcus *x*, and sometimes a little in front of this point; behind, it extends to the junction of the intra-parietal sulcus with the longitudinal fissure; upwards it extends to the

* By this is meant, of course, the turning away of the head so that the face looks away from the hemisphere stimulated.

median line, where it is continuous with the marginal convolution; below it is limited by the sulcus x, and by an imaginary line drawn backwards from this across the fissure of ROLANDO and through the middle of the sulcus z to the intraparietal sulcus. The shape of the area is in the form of a horizontal strip along the top of the hemisphere.

Fig. 3.



A similar photograph, shaded to show the parts of the cortex, excitation of which produces movements of the head and eyes to the opposite side, and movements of the upper and lower limbs; it comprises the areas which were investigated in our previous paper, as well as those which are the subject of the present one.

Oblique shading represents the area of the movements of the head and eyes.
Vertical shading " " " upper limb.
Horizontal shading " " " lower limb.

The places where the lines, having different directions, intersect, denote the overlapping of the contiguous areas; and at these points the functions of these different areas are represented together.

(III.) *The Upper Limb.*—The area of representation of this limb we have already described in part in our former paper, in which, however, we left for future observation the analysis of the margins of the upper limb region. This we have now done, and we find that the upper limb is represented over the whole of the ascending parietal convolution below the line given above in limitation of the representation of the lower limb. For the discussion of the limitation of the rest of the upper limb region see page 238, where the localities of the fusion of the different contiguous centres are treated of in detail.

We do not here treat of the area of representation of the face, jaws, &c., and the observations on these points will form the subject of a future paper.

PART IV.—REPRESENTATION OF THE MOVEMENTS OF THE HEAD ACCOMPANIED BY CONJUGATE DEVIATION OF THE EYES. (Plate 40, figs. 3, 4, 4A, 5.)

The movements of the head and eyes were observed by Professor FERRIER as being simultaneous. We find on further analysis that, though this synchronous action is by far of commonest occurrence, yet that considerable differentiation exists, and of this we shall now speak, reserving the discussion of the simultaneous movements to pp. 213 to 215, when we consider the march of movements in this region.

The different movements, therefore, which have to be considered in this part are—

I. *Movements of the Head.*—The head moves in one of the following modes or in combination of the same:

(*a*) Simple horizontal rotation to the opposite side.
(*b*) Rotation with elevation of the muzzle.
(*c*) Rotation with adduction of head to the (opposite) shoulder.

II. *Movements of the Eyes.*—

(*a*) Both eyes open.
(*b*) Both eyes turn horizontally to opposite side.
(*c*) Both eyes turn to opposite side and upwards.
(*d*) Both eyes turn to opposite side and downwards.
(*e*) Both eyes return to the middle line (from the side stimulated) or turn only through a few degrees.

III. *Movements of the Pupils.*—

(*a*) Contraction.
(*b*) Dilatation.

I. *Movements of the Head:*

(*a*) Simple horizontal rotation to the opposite side. This occurs as a primary movement most markedly in the part of the cortex above the horizontal fissure of the præcentral sulcus, *i.e.*, the middle frontal convolution, and especially in the centres 32, and to a slightly less degree in 33, 40, 44, and 45 (see fig. 2). This movement of turning the head to the opposite side is also represented* over the whole area included by the centres 14–52.† From this it follows that the principal focus of the representation of this act, as a primary movement, is most marked at centre 32, from which point the representation gradually diminishes (*vide* fig. 4).

(*b*) Rotation to opposite side with elevation of the muzzle. It is a matter of common observation that the movement of the head to either side is often accompanied by a tilting of the head backward so that the face looks upwards as well as outwards. We have never observed this elevation of the muzzle below the horizontal

* *I.e.*, absolute or total representation.

† Excepting, of course, centres 27, 30 (see pp. 242 and 244).

limb of the præcentral sulcus. Further, this combined action, we find, is most represented in the superior frontal convolution close to the margin of the hemisphere, and most especially in the centre 48; in addition it is present in the centres 38, 47, 44, 45, 40, 41, 42, 34, and 35.

(*c*) Rotation with adduction of head to the opposite shoulder. In a few instances we noted that the rotation of the head was scarcely so marked as a rolling over and adduction to the opposite shoulder. This action was observed at 46 and 48 only, thereby showing that it occurs very rarely as a primary movement. It will be seen later on that it was observed occasionally as a secondary movement along the lower border of the horizontal limb of the præcentral sulcus.

II. *Movements of the Eyes:*

(*a*) Both eyes open. Before entering into the detailed account of the representation of this movement, we must observe that no great stress can with justice be laid on the frequency of the observation of this action; for the reason that unless the animal be very profoundly narcotised the eyes remain open, while on the other hand, if it be so deeply narcotised, the cortex is no longer excitable to the currents we employ. With this reservation, we will now discuss the frequency and position of its occurrence. Since we have obtained this movement of opening the eyes at almost every point in which turning of the head is represented, we are inclined to believe that this movement constantly occurs in association with that of the head; but, owing to the error of observation above referred to, we do not wish to speak more positively on this point. From two special experiments made to answer this question, we find that the movement was most represented at centre 32; from this point it diminished upwards and downwards, and especially in the former direction. With one doubtful exceptional case, the movement of opening the eyes is not represented along the middle line of the hemisphere or along the vertical line of centres immediately behind the sulcus *y*.

We are fortified in our opinion stated above by the fact that Professor FERRIER, in his work 'On the Functions of the Brain,' 2nd edit., p. 242, states that he obtained by stimulating his centre 12, which mainly corresponds to the region now under discussion, the following associated movements:—"the eyes open widely, the pupils dilate, and head and eyes turn to the opposite side."

(*b*) Both eyes turn horizontally to the opposite side. The eyes rarely turn to the opposite side as a primary movement; this action is best represented in the convolutions situated in front of the præcentral sulcus, and to a less degree behind the sulcus *y*. Just as the movement of opening the eyes is associated with that for rotation of the head, so in like manner the turning of the eyes is found in connection with the same movement of the head.

The further consideration of this movement is continued under the heading of "March," *vide* p. 213.

(*c*) Both eyes turn to the opposite side and upwards. This movement was very rarely observed, and only in centres 15, 16, 17, 19, 20, and very slightly at 33 and 31.

(*d*) Both eyes turn to opposite side and downwards. This movement was noticed but twice, and only at centre 22.

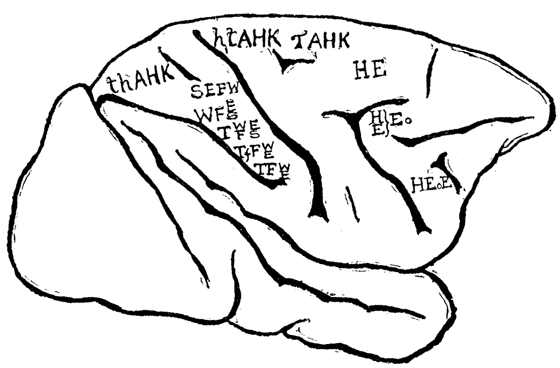
(*e*) Both eyes turn to the middle line, or only through a few degrees to the opposite side.

This action was observed to occur frequently in the centres 28, 28*a*, 26*a*, 26*b*. It consisted in a limited rotation of the eyes through a few degrees, such as would suffice to restore the direct position of the visual axes, if the eyes happened to be in position of slight conjugate deviation towards the hemisphere stimulated, and if any external strabismus happened to be present it was similarly instantly corrected.

In watching the rotation of the eyeballs we occasionally observed nystagmus of the eyes; this was only seen at the centres 15, 16, 29, and always consisted of rapid jerking movements towards the opposite side. This was probably merely a result of fatigue.

III. *Movements of the Pupils.*—In the vast majority of instances there was no movement of the pupils; when it occurred dilatation was always noted. This dilatation of the pupils exists simply in association with turning of the head and eyes to the opposite side. It appeared to be represented most round the horizontal limb of the præcentral sulcus, but we did not observe it many times.

Fig. 14.



This figure is illustrative of the march or sequence of muscular spasm at those points in the areas investigated which appeared to be most constantly the seat of origin of such sequence. The letters indicating the joints moved are placed in the order of the successive movements.

A = Ankle.	*f* = Index finger.	S = Shoulder.
E = Eyes turning to opposite side.	H = Head turning to opposite side.	T = Thumb.
E*o* = Eyes opening.	**H** = Hip.	τ = All toes.
E = Elbow.	*h* = Hallux.	*t* = Small toes.
F = All fingers.	K = Knee.	W = Wrist.

March or Sequence of Movement of the Head and Eyes. (See fig. 14.)

The relation of the movements of the turning of the head and eyes to the opposite side to that of opening the eyes varies as regards sequence of movement in the different parts of the cortex now under consideration. The sequence or order in which these movements occur forms the march for the part stimulated.

We shall take first the movements described above as an aid in dividing up the large area for the movements of the head and eyes, for the purpose of investigating the "March." It will be remembered that we postponed for later consideration the simultaneous movement of the head and eyes. The primary representation of this most important synergic action is given in Plate 40, fig. 5. It will be seen that its representation has a very wide distribution, which for the most part corresponds in mere extent with the representation of the movements of the head alone. As a primary movement, its importance entitles it to first consideration, for a review of the facts given in Table I.* will exhibit the very remarkable result that, of the 104 occasions on which this movement was observed to occur, in 100 instances it was primary. This is, no doubt, a demonstration of the necessity that this primitive movement should precede all others.

Taking first, then, the simultaneous movements of turning the head and eyes to the opposite side, the following march can be made out for a considerable number of centres. The order of this march is as follows:—

1. Simultaneous turning of the head and eyes to the opposite side.
2. Opening of the eyes wide.
3. Continuation of turning of the head.

And this occurs at centres 14 to 17 inclusive and 34.

The part next to be considered is the region below the sulcus *w*, which extends downwards in front of the vertical limb of the præcentral sulcus. The following movements here form the march:—

1. Turning of the head to the opposite side.
2. Opening of the eyes wide.
3. Turning of the eyes to the opposite side.

And are represented in the following centres, 19 to 28*b* inclusive. At the centres below *w* the opening of the eyes occurred earlier in the march than is just stated.

We would here direct special attention to the fact that occasionally the representation of the movements of the head and eyes is continued downwards, in front of the præcentral sulcus as far as its lower extremity, this area being limited in front by the subordinate sulcus (often very slightly marked) in the inferior frontal convolution, which probably represents the anterior limb of the Sylvian fissure.

We believe that it was owing to the very large proportion of negative results (*i.e.*, recorded nil) observed in stimulating this region, that Dr. FERRIER was led to consider it (*i.e.*, the part below the sulcus *w*) inexcitable.

We, however, find from a large number of observations that it is really excitable, although not invariably so. Of course, too, this excitability diminishes from above downwards. Not only is the representation in this region relatively less, but also the

* See p. 242, *et seq.*

amount of movement evoked is much inferior in force and extent to that obtained in the centres above w.

The relative amount of representation in the two parts is best shown by comparing the number of times in each in which no movement was obtained.

This will be made clearer by inspection of the following columns. In the left side are set forth, in position corresponding to their arrangement in the cortex, the centres above and below the sulcus w, viz., all those below the horizontal limb of the præcentral sulcus. On the opposite side of the central line are correspondingly arranged fractions, the numerators of which denote the number of negative results obtained, while the denominators give the number of observations on each particular centre.

	Centres.			Nils.		
	14	15	16	$\frac{0}{19}$	$\frac{1}{19}$	$\frac{1}{19}$
	17	18	19	$\frac{1}{16}$	$\frac{3}{16}$	$\frac{6}{17}$
Level of w	—	—	—	—	—	—
	22	26	27	$\frac{2}{18}$	$\frac{13}{18}$	$\frac{17}{18}$*
	24	26′		$\frac{3}{15}$	$\frac{6}{14}$	
	28	26a		$\frac{3}{18}$	$\frac{5}{16}$	
	28a	26b		$\frac{4}{16}$	$\frac{7}{16}$	
	28b	26c		$\frac{7}{13}$	$\frac{5}{11}$	
	28c	26d		$\frac{6}{9}$	$\frac{3}{5}$	

(The thick black line in each group of figures denotes the level of the sulcus w.)

To return to the existence of marked inferiority of functional activity of this region, we would repeat that this is the part of the head and eye area where excitation evokes rotation of the head and eyes through only a few degrees, such, for instance, as is requisite to direct the face to the middle line, if it be a little diverted towards the side stimulated.

In discussing the bearing of the less forcible character of the representation in this region as compared with that around the horizontal limb of the præcentral sulcus, it must be observed that the negative results occurred in Monkeys with small brains, in which case consequently this portion of the brain was only slightly developed.

PART V.—REPRESENTATION OF THE MOVEMENTS OF THE LOWER LIMB. (See figs. 3, 6, 6A, 7, 8, 9, 10, 11, 12, 13, Plates 40 and 41.)

Before classifying and discussing the representation of the movements of the lower limb, it will be advisable to consider a few generalisations. In the first place, as we showed in our former paper, certain segments of the limb are of more importance than

* The one positive observation noted here was obtained in a Monkey in which the sulcus w was extremely short, so that centre 27 was brought near to the focus of representation.

others ; thus we demonstrated in the upper limb that its extremities, *i.e.*, the shoulder and the hand, possessed the greatest primary representation, the intermediate joints being only of subsidiary importance.

It is interesting to find that the same phenomenon is present in the lower limb, the foot and the hip taking the lion's share of primary movement, while the knee, the intermediate joint, occupies quite a subordinate position. Indeed, in many cases it was obvious that the movement of the knee was only consequential to that of the hip, thus mechanically relieving the tension necessarily produced by flexion of the former joint.

The differentiation of the movements of the lower limb is not nearly so minute and distinct as in the upper limb. This is extremely well exemplified in the mode of sequence of the movements of the segments in the two limbs. For instance, in the upper limb excitation of the middle of the ascending frontal convolution* produces a comparatively slow and orderly successive flexion of digits, wrist, elbow, and shoulder ; whereas excitation of the same convolution above and behind the posterior extremity of x evokes rapid movement of all the toes, almost instantly followed by movement of the ankle and hip with, as before remarked, the subsequent and subordinate movement of the knee. Indeed the rapidity with which movement of one segment followed that of another was so great as to make it appear that each, with the exception of the knee, was represented equally in point of time. In this way it was frequently difficult to discover the exact march of the spasm produced even by minimal stimuli.

Hence the march and also, as will be subsequently shown in detail, the primary movement, both show the same character of the representation of the lower limb as is revealed in the performance of so-called volitional efforts. Whereas the upper limb performs movements of great complexity and speciality of purpose, those of the lower limb are engaged in actions of a lower grade which are far less individualised.

We now proceed to discuss the seat of primary movement in each segment of the lower limb, as we have observed such to occur, and in each instance also the character of the movements evoked at each point excited.

The segments of the lower limb may best be considered in the order from below upwards, inasmuch as the smallest segments possess the most extensive primary representation.

For accuracy and convenience it is necessary to refer to the movements of the toes, not only under the two headings of hallux and the rest of the toes respectively, which, for further convenience, we shall speak of as the small toes, but also to the movements of all the digits acting simultaneously as a whole, under the expression "all toes."

The movements of the segments will consequently be described in the following order :—

* Centre 3, *vide* former paper.

Hallux,
All toes,
Small toes,
Ankle,
Knee,
Hip.

In describing the movements of each of these segments we shall give (i.) the total or *absolute* representation in each instance, (ii.) the *primary* representation, (iii.) the character of the movements comprising (a) the total or absolute representation of the part, and (b) the primary representation.

By the expression *total or absolute representation* of any segment, we mean that we have extracted from our records every single movement of each given segment at every one of our centres where that segment happened to be represented. The summation of these facts gives correctly the actual total amount of representation of each joint at each centre, and consequently tells us to what extent, as determined by electrical stimulation, that joint or segment is represented in the cerebral cortex.

The second heading under which we have classified our observations, viz., that of *primary representation*, requires little explanation, since, unlike the first heading just described, it defines the region in which any particular joint begins the general movement of the limb, excluding, of course, secondary, tertiary, or even quaternary representations of the segment of the limb, all these being included under the first heading.

The determination of the representation of the primary movement is of the greatest importance, since upon this rests the exact localisation of the starting point of epileptiform convulsions.

Finally, by the *character of the movement* we mean whether it be one of flexion, extension, &c., and this is separately considered, according as the movement is referable to (a) absolute or (b) primary representation.

Representation of the Hallux (see Plate 40, figs. 6, 6a).

(i.) *Total or Absolute Representation.*—The movements of the hallux are represented * at the following centres in order of diminishing frequency :—

$$71,\ \left\{\begin{matrix}69\\68\end{matrix}\right\},\ \left\{\begin{matrix}70\\62\end{matrix}\right\},\ \left\{\begin{matrix}61\\65\end{matrix}\right\},\ \left\{\begin{matrix}67\\64\\72\end{matrix}\right\},\ 59,\ 55,\ \left\{\begin{matrix}54\\73\\75\\77\\6'\\6\end{matrix}\right\}\ 76,\ \left\{\begin{matrix}58\\52\end{matrix}\right\}.$$

* The centres enclosed vertically in brackets are those in which the degree of representation was equal.

On reference to Plate 40, figs. 3 and 6, it will be seen that this is tantamount to saying that the hallux is frequently represented all over the area for the movements of the lower limb, with the exception of its hindermost extremity, viz., centre 74. The maximum representation of the hallux is thus grouped round the upper end of the fissure of ROLANDO, and by reference to Table I., p. 250, &c., and fig. 6 it is evident that the representation of this segment decreases rapidly in intensity posteriorly, but more gradually anteriorly and inferiorly, reaching a minimum at each end of the lower limb area (*cf.* the region for absolute representation of "all toes"). The total number of times that the hallux was observed to move was 138.

(ii.) *Primary Representation* (see fig. 6A).—The hallux is primarily represented at

69, 68, 71, 62, 70, 61, 67, 65, 72, 75, 59, 58,

the centres being here arranged in order of decreasing intensity of representation.

It occurred to us that the order of these centres of primary representation ought to be decided by different considerations to those by which were determined the relative positions of the centres of *total* representation. Consequently we have gauged the intensity of the *primary* representation, not only by the greater proportionate* frequency with which it actually occurred, but also by its being accompanied or not by the occasional primary representation of other segments, *e.g.*, the small toes.

It will thus be seen that the hallux is represented in primary movement in a very large proportion of the centres which are relegated to the movements of the lower limb, in fact it occurs primarily in the proportion of over 50 per cent. While noting that the hallux is represented as a primary movement to such a degree, it is important to remember that its chief region of primary representation is close around the upper end of the fissure of ROLANDO. This latter generalisation not only assumes special importance in connection with the diagnosis of the seat of disturbance in an epileptiform convulsion beginning in the hallux, but also because it points to the fact, upon which stress will later be laid, that this part is the focal region of the representation of the lower limb. A total number of 82 primary movements of the hallux were observed.

III. *Character of Movement.*—(*a.*) *Absolute.* (*b.*) *Primary.*

We have found, somewhat unexpectedly, that there is no distinct localisation of any particular movement; extension and flexion† being apparently equally represented in any centre for movement of the hallux. It is true that there is a slight difference,

* By "proportionate" we mean the ratio of the primary movement of the hallux to all other primary movements occurring at the same segment (see p. 220, "Primary Representation of All Toes").

† In employing the term flexion of the hallux we have found it advisable to include therein not only direct flexion but also the more specialised movements of adduction and opposition. Although in this species of Monkey the hallux is employed as a thumb, nevertheless the special movements just mentioned were so frequently accompanied by the action of flexion, that the representation was most accurately described as that of flexion into the sole.

according as the movement is a primary movement or not; thus we find that out of 82 instances of primary movement of the hallux, 47 were flexion adduction and opposition, *i.e.*, mainly flexion, while only 35 were the converse, viz., extension abduction.

When, however, we come to enumerate the total or absolute number of instances in which the hallux moved, we find that this relationship is reversed, and that extension distinctly predominates. For instance, if we take the focus of representation of the hallux, viz., centres 69,71, and summate the absolute representation of movements, we find that "extension" occurs fifteen times, whereas "flexion" was observed only 6 times. Flexion is primarily represented at

$$70,\quad \left\{\begin{matrix}69\\71\end{matrix}\right\},\quad \left\{\begin{matrix}68\\67\end{matrix}\right\},\quad \left\{\begin{matrix}61\\62\\72\end{matrix}\right\},\quad \left\{\begin{matrix}65\\75\\59\end{matrix}\right\},\quad 58;$$

while on the other hand extension is represented at

$$\left\{\begin{matrix}69\\62\\71\end{matrix}\right\},\quad 61,\quad 65,\quad \left\{\begin{matrix}67\\72\\75\\77\end{matrix}\right\},\quad \left\{\begin{matrix}70\\58\end{matrix}\right\}.$$

Hence, although flexion is the more frequent *primary* movement of the hallux, extension is the more important from an *absolute* point of view.

In our previous paper we drew attention to the combination of these movements as affecting the fingers, but in the lower limb it is most interesting to note that we have only observed extension of the hallux followed by flexion in one instance, viz., in Monkey 38, centre 64, where slight extension of the hallux preceded flexion. In connection with this it is proper to state that in Monkey 40 we thrice observed, viz., at centres 59, 61, 62, that adduction of the hallux was preceded by a slight movement of extension. The converse combination of these two exists, which merits attention, viz., the antecedence of extension by flexion—the movement of flexion being slight, and being instantly followed by a more powerful and permanent extension. When it is taken into account that the exceptional instances of flexion being preceded by extension are the only ones of the kind out of 138 recorded movements of the hallux, it is clear that some very remarkable relation exists between these two fundamental movements of this segment, though hitherto we have failed to discover any reason why the one combination should exist to the exclusion of the other—*cf.* representation of movement of toes, p. 222.

Representation of Movements of All Toes, acting simultaneously.

(See Plate 40, fig. 7.)

(i.) *Total or Absolute Representation.*—The movement of all toes occurs at the following centres, in order of diminishing intensity,

$$71,\ 68,\ \left\{\begin{matrix}67\\58\end{matrix}\right\},\ \left\{\begin{matrix}69\\65\\61\end{matrix}\right\},\ \left\{\begin{matrix}73\\76\\77\\64\\54\end{matrix}\right\},\ \left\{\begin{matrix}62\\59\\52\end{matrix}\right\},\ \left\{\begin{matrix}72\\70\end{matrix}\right\},\ \left\{\begin{matrix}75\\6\end{matrix}\right\},\ 74,\ 6',\ 55.$$

Although we here give a list of the localities at which we have observed combined simultaneous movement of all the toes, we wish most particularly to remark that, on *a priori* grounds, it is not to be expected that such simultaneous movements should be as constantly localised as those of a highly specialised segment, like the hallux; further, we wish to draw attention to the fact that it may well happen that occasionally in those localities where the movement of the toes succeeds that of the hallux the time-interval may be so short that the movements are practically synchronous. For example, we have several times obtained, first, synchronous movements of all the digits; and, later, by carefully repeated minimal stimulation, discovered that occasionally there was a distinct interval between the movement of the hallux and the rest of the digits. It might have seemed justifiable to ignore those instances where the time-interval was exceedingly short, but we have thought it more accurate to record all the movements exactly as they occurred.

(ii.) *Primary Representation* of "all toes" occurs in diminishing intensity at centres,

$$77,\ 74,\ \left\{\begin{matrix}58\\52\end{matrix}\right\},\ 73,\ 54,\ 64,\ \left\{\begin{matrix}61\\67\end{matrix}\right\},\ 59,\ \left\{\begin{matrix}65\\72\\71\\76\end{matrix}\right\},\ 68,\ 70,\ 69.$$

We have drawn up the above list, as in the case of the hallux, according to the degree of intensity of the primary representation of "all toes" at any given centre.

This intensity has been estimated by taking the proportion of the primary representation of "all toes" as compared with frequency of occurrence of movement of other segments of the lower limb; these proportionate numbers have furnished the indices for each centre.

This order reveals a very definite symmetrical arrangement, not only constant as regards the position of the representation of all toes, but also with reference to the primary representation of the hallux. This latter, it will be remembered (see page 218), was grouped in greatest intensity round the upper end of the fissure of ROLANDO, this being the middle third of the lower limb area. In striking contrast to this (*cf.* figs. 6 and 7), we find that the representation of "all toes" is grouped at each extremity of the lower limb area, from which points it gradually diminishes in intensity towards the focus of representation for the hallux. Now, the hindermost centres of the lower limb area being 77 and 74, whereas 52 and 58 are the most anterior; these four centres are seen to head the above list of the primary representation of "all toes," showing that in the combination of the hallux and small toes

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

forming the group of all toes, it is the smaller digits which take the larger share of the primary representation. Primary movement of "all toes" was observed 78 times.

(iii.) *Character of Movements.*

(*a.*) *Absolute.*—The first point of interest to be noted in the character of movements of "all toes" is that to which we drew attention, in discussing those of the hallux (p. 219), viz., that extension is the more frequent movement. Thus, out of 138 simultaneous movements of "all toes," only 21 were flexion, all the rest being extension. But a still more remarkable fact is brought out in considering the localities where these two opposite movements are represented; we have just seen that the simultaneous movement of "all toes" is most represented in positions exactly complementary to that of the hallux, it is now interesting to observe that the most important movement of the digits, *i.e.*, extension, is characteristic of the chief foci of representation of "all toes," while the far rarer movement of flexion is only to be found in those centres where the primary representation of "all toes" is overshadowed by that of the hallux.

The centres where flexion was most observed (arranged in successive order of decreasing importance) were :—

$$\left\{\begin{matrix}69\\68\\64\end{matrix}\right\}, \quad \left\{\begin{matrix}6\\76\\58\\67\end{matrix}\right\}, \quad \left\{\begin{matrix}70\\71\\65\\61\end{matrix}\right\}.$$

Comparison of figs. 6A and 8 with fig. 10 will show still more clearly than this list the relative position of the proportionate frequency of flexion.

(*b.*) *Primary.*—The character of the primary movement of "all toes" corresponds so closely with that of the absolute movement that it need not be separately considered.

Representation of Movements of Small Toes. (See fig. 10.)

(i.) *Total or Absolute Representation.*—Movements of the small toes we have observed to occur on excitation of the following centres, in order of decreasing intensity :—

$$62, \quad 65, \quad \left\{\begin{matrix}69\\67\end{matrix}\right\}, \quad 64, \quad \left\{\begin{matrix}55\\59\\68\\70\\72\\73\end{matrix}\right\}, \quad \left\{\begin{matrix}78\\6'\end{matrix}\right\}, \quad 61, \quad \left\{\begin{matrix}54\\74\\75\\76\\77\\6\end{matrix}\right\}.$$

On referring to Table I. for further details of this list, it is apparent how much less frequently the movement of small toes is represented than that of "all toes" or hallux, the figures being respectively 92, 138, and 138.

(ii.) *Primary Representation.*—The intensity of primary representation is given in the following order :—

$$78,\ 55,\ 64,\ \left\{\begin{matrix}62\\72\end{matrix}\right\},\ 67,\ 65,\ 73,\ 74,\ 6',\ 77,\ 6,\ 70,\ 76,\ 69.$$

Owing to the comparative rarity with which primary movement of "small toes" occurs, it is necessary to be cautious in forming generalisations from this list; but it is abundantly clear that the fundamentally important generalisation which was so obviously true for the movements of all toes, also applies in the case of the small toes, viz., that the representation of the small toes is complementary to that of the hallux. For not only does movement of the small toes occur primarily but once at centre 69, and but twice at 70, where other primary movements occur to the number of 14 and 16 respectively, but also the "small toes," as such, are not so represented at 68 and 71. Primary movement of the small toes was noted 44 times.

At the same time it is evident, from the general rarity of primary movement of the small toes, that it is of very inferior importance among the movements of the lower limb. This conclusion is completely confirmed by observation of the so-called voluntary movements of the toes; primary simultaneous action of the small toes being extremely rare, and, perhaps, scarcely ever performed by Man, or by this species of Monkey.

(iii.) *Character of Movement.*

(*a.*) *Absolute.*—Again we find that, as in the case of "all toes," the movement of extension is much more largely represented than that of flexion. Thus, out of a total of 92 movements, 78 were extension and 14 flexion.

A further point of material interest in connection with this remarkable preponderance of the movement of extension is to be seen in the fact that the movement of flexion, when it happened, was observed only at centres

$$67,\ \left\{\begin{matrix}68\\62\end{matrix}\right\},\ 69,\ 64,\ 54,\ 6';$$

these, with one exception, form a group immediately in front of the fissure of ROLANDO, and in the same region which we have already seen in the case of "all toes" to be connected especially with the flexion movements of those digits as well as the general representation of the hallux.

As we shall now leave the consideration of the movements of the toes for that of the movements of the ankle, it seems to us very desirable to make further reference to the fact just mentioned, viz., the peculiar localisation of the rare movement of flexion of the small toes in what we may call the hallux region of the lower limb area.

To put the matter in a simpler light than is offered by the bare record of observations, let us state again that the whole region of representation of the lower limb is a narrow strip running along and forming the upper fifth of the convex outer surface of the excitable region in the hemisphere; further, that the middle of this strip, or more strictly speaking, the junction of its middle and posterior thirds, is essentially the seat of representation of the hallux, while each extremity is essentially the seat of representation of the small toes.

To continue: the commonest primary movement of the hallux differs from that of the small toes in being flexion for the former and extension for the latter. Consequently we may say that, other things being equal, the movement of flexion will be characteristic of the more central portion of the lower limb area, while extension will be more marked at each extremity of this part. Under these circumstances it seems to us justifiable to entertain the belief that possibly a movement which is characteristic of any given segment in its focus of representation may be overshadowed by a different movement, if the representation of that segment is carried (diminishing in intensity, of course) into the focal region of some other segment whose characteristic movement is of an opposite nature. To be more particular, we would suggest then that this is the reason why flexion of the small toes is observed more frequently as the representation of those digits (whose characteristic primary movement is extension) invades, as it were, the region of the hallux (whose characteristic primary movement is flexion). We do not wish to press this point unduly, for the reason that the actual number of times that flexion of the small toes occurred is not large; but, as will be seen on reference to figs. 6, 8, and 9, the existence of this remarkable relation between the representation of flexion and extension in the toes is undeniable.

Representation of the Movements of the Ankle (Plate 41, fig. 11).

(i.) *Total or Absolute Representation.*—Movement of the ankle occurs in order of decreasing frequency at the centres—

$$68, 61, \begin{Bmatrix} 65 \\ 72 \end{Bmatrix}, \begin{Bmatrix} 62 \\ 67 \\ 70 \\ 71 \end{Bmatrix}, \begin{Bmatrix} 59 \\ 76 \end{Bmatrix}, \begin{Bmatrix} 69 \\ 73 \end{Bmatrix}, \begin{Bmatrix} 58 \\ 64 \\ 6' \end{Bmatrix}, \begin{Bmatrix} 55 \\ 77 \end{Bmatrix}, 54, 75, \begin{Bmatrix} 52 \\ 78 \\ 6 \end{Bmatrix}, \begin{Bmatrix} 51 \\ 74 \end{Bmatrix}, 80.$$

On comparing these numbers with fig. 1, it is clear that the ankle is not specially represented in any one portion of the lower limb area, its focus only being situated in the centre of the area, and its intensity decreasing towards the borders with that of the limb generally.

The total number of times that we observed movement of the ankle was 198, a number which, as might have been expected, owing to the relative position of the joint in the limb, is far in excess of that of any other part.

(ii.) *Primary Representation.*—In marked contrast to the segments already described, primary representation of the ankle is of rare occurence, being observed only 36 times out of 198 actual movements. Although occurring so rarely, it is nevertheless important to remark that it was observed at no less than two-thirds (16 out of 23) of the centres in the lower limb area, thus again showing the general and subordinate character of the representation of this joint as compared with the focal character of that of others.

The infrequency of occurrence of primary movement of this joint diminishes, of course, the value of any arrangement in order of intensity of the same, and therefore we shall do no more now than state the arrangement we have found—

$$62,\ 59,\ 68,\ 74,\ \begin{Bmatrix}58\\61\end{Bmatrix},\ \begin{Bmatrix}70\\72\end{Bmatrix},\ \begin{Bmatrix}64\\69\\73\end{Bmatrix},\ 77,\ \begin{Bmatrix}71\\76\end{Bmatrix},\ 75,\ 6.$$

(iii.) *Character of Movement.*—(*a.*) *Absolute.*—The movements of the ankle are :—

(a.) *Dorsal flexion.* (By this we mean what is frequently called *flexion* of the joint, *i.e.*, when the toes are brought upwards, so as to approach to the front of the leg.)

(b.) *Plantar extension.* (By this we mean the opposite to dorsal flexion, *i.e.*, when the toes are pointed downwards, the heel being drawn upwards. This movement is frequently called *extension* of the ankle.)

NOTE.—We have preferred to employ these arbitrary terms as conveying a distinct notion of the direction in which the foot moves, thus, at the same time avoiding the homologically false use of the simple terms flexion and extension.

(c.) *Eversion.*

(d.) *Inversion.*

These movements (of an absolute total of 198) occurred in the following order of frequency :—

Dorsal flexion	116 times
Eversion	31 ,,
Plantar extension	26 ,,
Inversion	21 ,,

Confusion between dorsal flexion and plantar extension was noted in four instances.

The analysis of the localisation of the movements of dorsal flexion and plantar extension respectively gives no further information than that dorsal flexion is represented in proportion to the amount of general representation of the limb as a whole. Further that, apparently for the same reason, plantar extension was only observed in the middle of the lower limb area, especially since that part, as we have just shown, is essentially the region of representation of true, *i.e.*, homologous, flexion rather than of extension.

The movements of eversion and inversion deserve a passing notice. Their distribution in the lower limb area appears to be guided only by the relative degree of representation of the limb in the various parts of its cortical area.

In examining the question as to whether there exists any correlation between dorsal flexion and plantar extension, on the one hand, and eversion and inversion, on the other, we have found that the synergic relation between these movements was no more than the simple relation of probable frequency in proportion to the amount of actual representation of each. Hence it is impossible to make any generalisations on this point.

(*b.*) *Primary Movement.*—The number of times that primary movement was observed was 36. Of this number,

Dorsal flexion occurred	. .	14 times
Eversion ,,	. .	12 ,,
Plantar extension ,,	. .	8 ,,
Inversion ,,	. .	2 ,,

Beyond the obviously altered relation in the degree of representation which these movements bear to one another when primarily represented and when arranged in the order of the number of total representation, *i.e.*, all movements observed, there is nothing further to be remarked upon this point, save to mention that this small degree of primary representation is found, as might be expected, just in the middle of the lower limb area, *i.e.*, around and especially in front of the upper part of the fissure of Rolando.

Representation of the Movements of the Knee (Plate 41, fig. 12).

(i.) *Total or Absolute Representation.*—Movement of the knee occurs in order of decreasing frequency at the centres :—

$$\begin{Bmatrix}65\\68\end{Bmatrix}, \begin{Bmatrix}67\\71\end{Bmatrix}, 70, \begin{Bmatrix}54\\69\\73\\6'\end{Bmatrix}, \begin{Bmatrix}55\\64\end{Bmatrix}, \begin{Bmatrix}61\\62\end{Bmatrix}, \begin{Bmatrix}72\\77\end{Bmatrix}, \begin{Bmatrix}75\\76\\59\\6\end{Bmatrix}, 58, \begin{Bmatrix}52\\74\\98\end{Bmatrix}.$$

The knee is thus represented all over the entire lower limb area, the total number of movements observed being 141 (*cf.* Ankle).

Further on we shall draw attention to the fact that the movements of the knee are essentially dependent upon those of the hip.

(ii.) *Primary Representation.*—The knee we have observed to move primarily only ten times, *i.e.* $\frac{1}{27}$th of the total primary movements of all the segments of the lower limb. And, moreover, of these ten times, in four it was associated with other synergic primary movements, *i.e.*, of hip and other joints. Consequently its *rôle* as a joint of primary movement is most insignificant, and we shall return to this question in discussing the representation of "purposive" actions of the limb.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the total number of movements observed,

Flexion occurred	. . . .	118 times
Extension ,,	. . . .	12 ,,
Rotation in ,,	. . . .	7 ,,

and confusion was noted in four instances.

The movement of extension, it is important to observe, occurred at the following centres in order of frequency :—

$$6,\ \left\{\begin{array}{c}55\\61\end{array}\right\},\ \left\{\begin{array}{c}54\\68\\69\\75\end{array}\right\},$$

and hence, though rare, it is represented about the same region as is the equally rare movement of flexion of the small toes, *i.e.*, close to the fissure of ROLANDO. This, as we have pointed out before, is the focus of representation of the limb, and perhaps the rare movements of extension and rotation in, which occur at the centres :—

$$68,\ \left\{\begin{array}{c}6'\\6\\69\\70\\73\end{array}\right\},$$

owe their representation to the fact that, this being the middle of the lower limb area, the cortex here is most highly organised, and thus possesses centres for every movement of all the joints.

(b.) *Primary.*—The 10 primary movements of the knee were all flexion, with one exception, viz., rotation in.

REPRESENTATION OF THE MOVEMENTS OF THE HIP (see Plate 41, fig. 13).

(i.) *Total or Absolute Representation.*—Movement of the hip occurs in order of decreasing frequency at the centres :—

$$67,\ \left\{\begin{array}{c}65\\6\end{array}\right\},\ \left\{\begin{array}{c}61\\68\\71\end{array}\right\},\ \left\{\begin{array}{c}55\\70\end{array}\right\},\ \left\{\begin{array}{c}54\\62\\64\\73\\6'\end{array}\right\},\ \left\{\begin{array}{c}59\\69\\72\\75\\76\end{array}\right\},\ 77,\ 58,\ 52,\ \left\{\begin{array}{c}74\\78\end{array}\right\}.$$

The hip is thus represented most in the middle or focus of the lower limb area, moving altogether 177 times.

(ii.) *Primary Representation.*—The hip is primarily represented in the following centres in order of diminishing intensity :—

$$54,\ 76,\ 75,\ \left\{\begin{matrix} 6' \\ 6 \end{matrix}\right\},\ 55,\ \left\{\begin{matrix} 64 \\ 65 \end{matrix}\right\},\ 52,\ 59,\ 61.$$

We must first call attention to the important deduction which these figures reveal, namely, that the hip is *primarily* represented in but 11 out of the 23 centres of its total or absolute representation ; further that the centres, where it was observed to move primarily, are exactly the counterpart of those where the hallux is especially primarily represented. In accordance with the same fact, it is to be noted that behind the fissure of ROLANDO the hip is only represented in two centres, viz., 76 and 75, and that these centres are situated at the lower border of the area of representation of the limb. This localisation of the hip to the lower border of the area is equally strongly marked in front of the fissure of ROLANDO, and culminates in the fact that the centre in which most primary representation of the hip was found to occur is the lowest and most anterior of the whole lower limb group, viz., centre 54.* Primary movement of the hip was observed only 27 times.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of 177 movements,

Flexion occurred	. . . . .	118 times
Rotation out	,, ...	35 ,,
Extension	,, ...	23 ,,
Confusion	,, ...	4 ,,
Abduction	,, ...	2 ,,
Rotation in	,, ...	1 ,,

Extension, remarkably rare in occurrence, was observed at the following centres in order of decreasing frequency—

$$6,\ 6',\ \left\{\begin{matrix} 55 \\ 61 \\ 75 \end{matrix}\right\},\ \left\{\begin{matrix} 52 \\ 64 \\ 62 \\ 69 \\ 72 \end{matrix}\right\}.$$

It is evident from these figures that this infrequent movement is most represented in the neighbourhood of centre 6, both behind and in front of the fissure of ROLANDO.

Rotation out occurs at centres :—

* Here we should remark that centre 51, although a border centre, where various parts of the body are represented (see p. 238), is also a centre where the hip is notably represented in primary movement (see also Table I.).

$$68,\ 59,\ \left\{\begin{matrix}65\\67\end{matrix}\right\},\ \left\{\begin{matrix}55\\61\end{matrix}\right\},\ 70,\ \left\{\begin{matrix}52\\58\\64\\72\\76\\6'\end{matrix}\right\}.$$

But there does not seem to be any definite localisation of the movements.

(b.) *Primary.*—Of the 27 primary movements :—

12 were flexion,
10 ,, extension,
5 ,, rotation out.

Flexion as a primary movement was most marked at 54 (6 times), then at 76 (twice), 59, 64, 6′, 75.

Extension was most marked at 6, then 75, 52, 61, 64, 61′.

Although so seldom moving primarily, it is interesting to note that when this did occur, the hip was nearly as often extended as flexed; while on the other hand, as noted above, in the movements of the joint of secondary, tertiary, and quaternary sequence, extension was extremely rare as compared to flexion.

March or Sequence of Movements in the Segments of the Lower Limb.
(See fig. 31; p. 213.)

The sequence of movements successively invading the various segments of the limb, when any given point in the cortex is excited, varies in mode according to the segment in which the movement commences. For this reason the facts are best grouped together according to the seat of the primary movement. Thus we have different types named after the various segments of the limb. We commence with the most frequent.

Class I.—*Hallux Type*, observed at centres 61, 62, 65, 67, 68, 69, 70, 71, 72.

The march of the muscular spasm when commencing with movement of the hallux is very constant, the order of joints affected being almost invariably :—

Hallux, Small Toes, Ankle, Hip, and *Knee*.

In a relatively considerable number of instances the hip and knee moved simultaneously, and in one the movement of the knee preceded that of the hip.

The character of movement in the march was as follows :—

Hallux $\left\{\begin{matrix}\text{flexed*}\\ \text{or}\\ \text{extended}\end{matrix}\right\}$; *Small Toes* extended; *Ankle* dorsally flexed; *Hip* flexed; *Knee* flexed.

* Flexion more frequently than extension (see p. 219).

The general effect produced was thus, of course, a drawing up of the limb with extension of the digits. The movement of flexion of the knee might thereby gain a fictitious importance, if we did not at this moment explain that it was very frequently simply secondary to, and necessitated by, the flexion of the hip. It has already been pointed out what a very subordinate position the knee occupies among the joints of the limb, and especially that it is practically never primarily represented.

Class II.—"*All Toes*" *Type*, observed at centres 64, 58, 59, 72, 52, 54, 73, 77.

The character of the movement and the order was :—

All Toes extend ; *Ankle* dorsally flexed ; *Hip* flexed ; *Knee* flexed.

At each of the three last centres mentioned above there was once presented a slight variation in the order of the march ; but, being so infrequent, these variations were not deemed sufficiently important to merit separate description.

Class III.—"*Small Toes*" *Type*, observed at 55, 64, 78.

This type, only occurring three times, presents considerable confusion of arrangement, which deprives it of much importance. The localisation of the commencement of the march was fairly constant, viz., movement of the small toes, followed by that of the hallux. Consequent on the movement of the hallux we should naturally have expected movement of the ankle, and then of the hip and knee. At centres 64 and 78 this was indeed the case, but at centre 55 movement of the ankle terminated the march.

It will be remembered that in a few, comparatively rare, instances the ankle, knee, and hip commenced movement in the limb. It appeared to us likely that some interesting facts might be obtained by analysing these exceptional cases. This we did, and the results are best arrived at in the following order :—

(*a*.) *Ankle Type*.—The study of the march, when the movement is begun by the ankle, gave the following order, which was fairly constant, viz. :—

Ankle, Toes, Hip, Knee.

(*b*.) *Knee Type*.—Similarly, summation of the instances when the primary movement began in the knee was productive of the following result, as the most usual order of the march, viz. :—

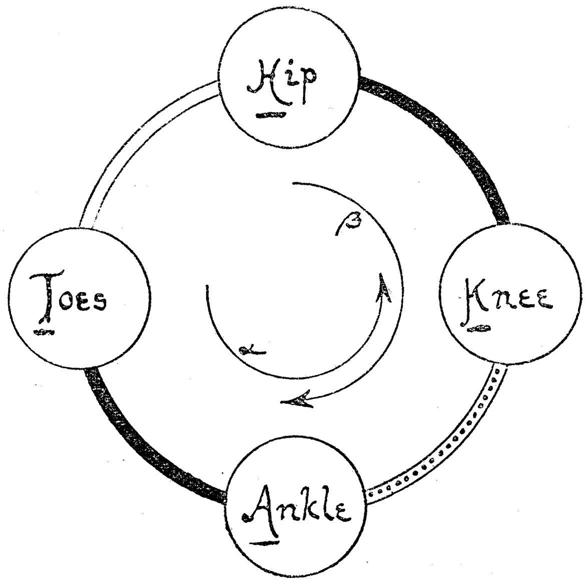
Knee, Hip, Ankle, Toes.

(*c*.) *The Hip Type*.—The commonest order of movement in this type was found to be :—

Hip, Knee, Ankle, Toes.

Comparison of arrangement in each of these more unusual marches with that of the common types described on pp. 228, 229 seems to us to suggest that the mechanism of a cortical motor centre is almost constant in arrangement, and that for the lower limb it may schematically be represented thus (fig. 15).

Fig. 15.



In this schematic figure the lines connecting the limb segments are made dark, dotted, or white to show the difference in amount or degree of association existing between the representation of the knee and hips, and between that of the ankle and toes respectively. (It must not be forgotten that this association is not only psychical in origin, but is also conditioned by the anatomical configuration of the muscles moving the various segments, whereby it happens, for example, that the hip cannot be notably flexed without similar movement of the knee, and again, that the powerful flexion of the toes causes plantar extension of the foot.)

Now the flow of energy which most frequently follows excitation is from T along the direction of the arrow α to H, but occasionally it is in the reverse direction, from H along the direction of the arrow β to T. This simple reversion of the current Dr. HUGHLINGS JACKSON fully described many years ago, as occurring in disease of the cortex in Man, and therefore we need not further consider it here. But, as we have just stated, in certain exceptional cases the flow of energy may start from A or from K. Of these two A is by far the more important, the movements of the knee being so very largely conditioned by those of the hip. Now, when the initial spasm affects the ankle, it is clear from the order in the ankle type of march that the energy flows in the more unusual direction of the arrow β, and so really simply continues the hip type of march. This mode of regarding the ankle type of march is of value as enabling us without exaggeration to harmonise what might otherwise appear to be conflicting observations.

Moreover, the *Knee Type* also probably conforms to the same system, although the order, viz., K, H, A, T seems at first sight to be wholly exceptional. The explanation of this may possibly be that the movements of the knee are so dependent on those of the hips as to bring their seats of representation in far closer connection than the union of the knee division of the area with its other neighbour (anatomically and schematically speaking) the ankle division. Hence, given the movement commencing in K, the course it will theoretically, and actually as observed by experiment, take is K, H, A, T, and not K, A, T, H.

PART VI.—REPRESENTATION OF THE MOVEMENTS OF THE UPPER LIMB.

In our former Paper in the 'Philosophical Transactions,' *loc. cit.*, we considered the representation of the upper limb as it occurred in the anterior half of the ascending parietal convolution. In the present paper we supplement our former account by a description of the movements obtained when the posterior half of that convolution is stimulated.

It will be useful if we now give in their positions the figures indicating the centres into which we divided the anterior half of the middle two-fourths of the ascending parietal convolution in our previous paper, and those of the posterior half adopted in the present research—

80	79	11
82	81	9
	83	8′
	85	8
	87	7′
		7

Above 80, 79, 11 is the parietal lobule. (See also fig. 2.)

In our former paper we contented ourselves with describing in one table the primary movement, the march, and the character of all the movements obtained. In the present instance, however, we shall follow the more minute arrangement adopted in the foregoing pages.

We shall now describe the movements of the various segments in the order of thumb, fingers, wrist, elbow, shoulder.

Representation of the Movements of the Thumb.

(See fig. 16, which with figs. 17, 18, 19, and 20 are extensions of the diagrams of the representation of the upper limb segments given in our former paper).

(i.) *Total or Absolute Representation.*—The thumb is represented along the posterior part of the ascending parietal convolution in the lowest four centres only, as follows, commencing with the most important, 87, 85, 83, 81.

The total number of times movement was observed was 40 (39 at centres 87, 85, 83).

(ii.) *Primary Movement.*—The thumb moved primarily at centres 87, 85, 83. It is most essential that we should here point out that at centre 87 not only did every movement of the thumb occur as a primary movement, but also that no other segment of the limb participated in such primary movement. It is further to be remarked that at centres 85 and 83 the primary movements almost equalled in number the absolute representation. (See Table I., p. 252.)

(iii.) *Character of the Movements.*—(a.) *Absolute.*—Of the 40 movements of the thumb,

26 were flexion and
14 ,, opposition.

Consequently the *general* movement of flexion of the digit into the palm was the only movement obtained.

(b.) *Primary.*—Of 37 movements,

25 were flexion and
12 ,, opposition.

These facts, coupled with those we noted in our previous paper, leave it beyond doubt that this region, viz., the middle third of the ascending parietal convolution, is the focus of representation of the movements of the thumb.

Representation of the Movements of the Fingers (See Plate 42, fig. 17).

(i.) *Total or Absolute Representation.*—The fingers are represented, in order of diminishing intensity, at the centres :—

$$85,\ 83,\ 87,\ 82,\ 11,\ \left\{\begin{matrix}79\\80\\81\\6\end{matrix}\right\},\ 6'.$$

It is worthy of remark that at 85 the representation of the fingers was found to be present 15 times, in contrast to 8 times at 87 and 7 times at 83.

The total number of movements observed was 54.

(ii.) *Primary Representation.*—Primary movement of the fingers was observed at the following centres, in order as before :—

82, 85, 83, 81.*

On close scrutiny we found that at centre 85 the index finger was primarily

* Note complete absence of primary representation of the fingers at centre 87.

represented no less than 4 times in association with the thumb. The chiefest representation of the fingers all moving together is centralised at 82. Thus there exists, as might have been surmised, a gradation from above down of primary representation of all fingers, index, and thumb at the centres 82, 85, and 87 respectively.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the total number of 54 movements,

35 were flexion,
15 ,, extension,
4 ,, "interosseal position."

At centre 85, where the greatest number of movements occurred, of 15 observations flexion occurred 14 times. And at 87 also flexion was alone obtained.

In striking contrast to this representation of flexion at the lowest part of this region, we find the movement of extension is alone represented at the highest part of the region, viz., at centres 11 and 79. In front of the fissure of ROLANDO, a somewhat different arrangement prevails at the upper part of the upper limb area. Here, as we showed in our previous paper, movement of the fingers occurred very slightly in degree and very late in time, and the character of this late and feeble movement was flexion. This fact we have now confirmed in our re-examination of the border centres 6 and 6′ (situated between the upper and lower limb centres).

(b.) *Primary.*—Of 11 movements,

4 were flexion,
3 ,, extension,
4 ,, abduction of the index.

The rarity of primary movement of the fingers here indicated is explicable by the fact that in the ascending parietal gyrus the movements of the fingers are almost universally secondary to those of the thumb. Thus of fifteen absolute movements of the "all fingers" (*i.e.*, excluding primary movements of the index), only 1 was a primary movement, and that was associated with the thumb. Reference also to the plate in our former paper and to fig. 14 shows this important preponderating influence of the thumb.

REPRESENTATION OF THE MOVEMENTS OF THE WRIST. (See fig. 18.)

(i.) *Total or Absolute Representation.*—The movements of the wrist are represented in the following centres, arranged in order as before:—

$$83,\ 85,\ \left\{\begin{matrix}87\\82\end{matrix}\right\},\ \left\{\begin{matrix}81\\80\\11\\6\end{matrix}\right\},\ \left\{\begin{matrix}79\\6'\end{matrix}\right\}.$$

The total number of movements observed was 40.

(ii.) *Primary Representation.*—The wrist initiated movement of the limb at the following centres :—

$$\left\{\begin{matrix}80\\81\\82\end{matrix}\right\},\ 83,\ 6',\ 85,\ \left\{\begin{matrix}11\\79\end{matrix}\right\},\ 6.$$

Altogether 16 movements were observed. The universality of representation of this joint in nearly all* the centres for the upper limb now under consideration, again demonstrates the condition described in our former paper, viz., that this joint is subordinate to the movements of the other segments of the limb, and notably to those of the digits.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the 40 movements observed, no less than

21 were pronation,
14 ,, extension,
4 ,, supination,
1 was ulnar adduction.

Thus, while in no case was flexion observed, it is most noteworthy that pronation was the commonest movement. We would like again to quote the opinion expressed in our former paper as to the important part played by the movement of extension of the wrist in fixing the hand as a prefatory procedure in delicate movements of the digits, but we would insist that, even more than extension, pronation is absolutely essential to the correct performance of accurate and minute movements of the thumb and forefinger, the most highly specialised of the fingers. We therefore find the wrist represented immediately above (*i.e.*, preceding functionally) the areas for the latter segments. The movement of supination was noted at centres 87 and 85, but nowhere else, and occurred at the end of the act (*vide* March, *infra*).

(b.) *Primary.*—Of a total of 16 primary movements every one was pronation (*vide* March).

The intensity or degree of representation of this movement corresponds to the order given in (ii.) that of the primary representation of the joint.

Representation of the Movements of the Elbow. (See Plate 42, fig. 19.)

(i.) *Total or Absolute Representation.*—The movements of the elbow are represented at the following centres, arranged in order of decreasing intensity :—

$$6,\ 11,\ 79,\ 6',\ 83,\ \left\{\begin{matrix}81\\82\\85\end{matrix}\right\},\ \left\{\begin{matrix}80\\87\end{matrix}\right\}.$$

The total number of movements observed was 50.

* Nine out of ten.

(ii.) *Primary Representation.*—The elbow initiated the movements of the limb in 9 instances at 7 centres :—

$$80, \left\{\begin{matrix}81\\82\end{matrix}\right\}, 6, 6', 11, 83.$$

Proportionately we thus see that the elbow is very generally though feebly primarily represented (*cf.* the Wrist).

(iii.) *Character of Movement.* (a.) *Absolute.*—Of the 50 movements,

26 were extension,
23 ,, flexion,
1 was confusion.

These opposed movements were grouped thus: extension alone was obtained at 6 (12 times), 6′ (5 times), and 81; whereas flexion alone was obtained at

$$83, \left\{\begin{matrix}82\\85\end{matrix}\right\}, 87.$$

At centres 11, 79, and 80, viz., the neutral ground between the two extremes just detailed, both flexion and extension were nearly equally represented, with, however slight predominance of the former.

(b.) *Primary.*—Of the 50 total or absolute movements of the elbow, only 9 were primary, this notably illustrating its subordinate importance. Of these, 6 were extension and 3 were flexion. The distribution of these primary movements was the same as that of the absolute movements.

Representation of the Movements of the Shoulder. (See Plate 42, fig. 20.)

(i.) *Total or Absolute Representation.*—Altogether 62 movements of the joint were observed, occurring at the following centres, in order of diminishing frequency :—

$$11, 79, 6', 81, 82, \left\{\begin{matrix}80\\83\end{matrix}\right\}.$$

The important fact here exhibited, namely, that the shoulder is not represented at centres 85 and 87, will not escape notice (*vide* March, *infra*). On the other hand, of 14 total primary movements at centre 79, the shoulder claims no less than 13; and for centre 11, out of a total of 14, it claims 12. Thus, the localisation of the shoulder, like that of the thumb, is very perfectly defined.

(ii.) *Primary Representation*—The shoulder, like the thumb, being an important joint in the initiation of movements, moved primarily 34 times at the following centres, in the order of diminishing intensity :—

$$79, 11, 81, 6, \left\{\begin{matrix}80\\82\end{matrix}\right\}.$$

(iii.) *Character of Movement.* (a.) *Absolute.*—Of the total of 62 movements,

28 were adduction,
15 ,, advancing,
11 ,, retraction,
4 ,, elevation,
3 ,, rotation in,
1 was rotation out.

Adduction.—Occurred at :—

$$11, \quad 79, \quad \begin{Bmatrix} 6 \\ 81 \end{Bmatrix}, \quad \begin{Bmatrix} 80 \\ 82 \\ 83 \end{Bmatrix}, \quad 6'.$$

More than half (15) of the instances were observed at 11 and 79. The same thing was observed for the movement of retraction, the explanation probably being that these movements are associated, as we have shown in addition that this is the region of greatest representation of the joint.

Advancing.—This movement—one of great importance and interest—with the exception of being once observed at centre 82, was represented solely in front of the fissure of ROLANDO, namely, at 6 and 6′ (8 times and 6 times respectively).

Elevation was noted 3 times at 79 and once at 11 out of the total of the 4 occasions on which it was observed, thus being closely localised.

(b.) *Primary.*—Of the 36 primary movements of the shoulder (*i.e.*, including combinations),

22 were adduction,
9 ,, retraction,
4 ,, elevation,
2 ,, advancing.

Primary movement of adduction was observed at :—

$$\begin{Bmatrix} 11 \\ 79 \end{Bmatrix}, \quad 6, \quad 81, \quad \begin{Bmatrix} 6' \\ 80 \\ 82 \end{Bmatrix};$$

11 and 79 equally gave 7 instances of this movement, so that it was represented 14 times out of 22. Retraction occurs almost entirely at 11 and 79.

It will now be fitting to discuss the order of combination of the movements of the various segments.

March or Sequence of Movements in the Segments of the Upper Limb (see Table II. and fig. 14).

As the centres in which the upper limb is represented are so few in number in the present research, we have deemed it best to give the march of the movements in full at each spot, in a tabular form.

Table II.

Centre.	Primary.	Secondary.	Tertiary.
11	Shoulder add., retract.	Elbow flex.	Fingers extend. Wrist ext.
79	Shoulder, add., retract., elevate.	Elbow flex.	Fingers ext.
80	Border centre	See p. 238.	
81	Border centre	See p. 238.	
82	Wrist pronated	Fingers interosseal flex.	Elbow flex. Shoulder adduct.
83	Thumb flexed, opposed	Wrist pronated. Fingers flexed.	Elbow flexed. Shoulder add. (2)
85	Thumb flexed, opposed. Index opposed	Fingers flexed	Wrist extend. Elbow flex.
87	Thumb flexed, opposed	Fingers flexed	Wrist extend, supinate. Elbow flex.

The march in this, the posterior half of the ascending parietal convolution, is more differentiated than that of the anterior half and, *a fortiori*, than that of the ascending frontal convolution.

In the upper part of the region it passes steadily down the limb, and in the lower part as steadily up the limb.

In this connection it is very important to observe the real position and value of the index finger. Thus, at centre 85 the march is very distinctly in the order of: thumb, index finger, the other fingers, wrist, and elbow. So at this part, where, as we have already seen, the index possesses some primary representation, it forms a distinct item in the march. Further, it is most noteworthy that the wrist is invariably pronated in the upper part of the region now under consideration. The importance of this fact has already been alluded to in considering the necessary succession of movements in the performance of the highly evolved actions of the thumb and index finger.

At the same time, it is of great interest, in connection with the development of psychical energy, to see that the representation of the shoulder does not proceed lower than centre 83, while at the same time also the representation of the thumb extends upwards to, but not beyond, the same centre.

Character of Movement in the March.

There are several differences in the character of the successive movements represented in the ascending parietal convolution and those in the ascending frontal convolution. Thus, the shoulder in the parietal gyrus, instead of exhibiting the representation of "advancing," as in the frontal gyrus, is almost invariably adducted and retracted (rarely elevated) at the centres 11 and 79.

PART VII.—MISCELLANEOUS FACTS.

There are several facts of general interest which have come to light in the course of our experiments.

(1) *The Border Centres* (see fig. 3).

We have employed this term to denote those centres which are situated along the lines separating continuous areas of representation.

The centres which come into this category are :—

31, 36, 37, 38, 39, 50, 51, 6, 6′, 80.

The representation of function at each of these centres is best seen by summing the absolute representation at each point, and the results of this method we shall now state.

Thus, for example, at centre 31—

Head turned to the opposite side	7	times
Head and eyes turned	3	,,
Eyes opened	5	,,
Eyes turned to opposite side	3	,,
Shoulder advanced	7	,,
Shoulder rotated	3	,,
Elbow extended	5	,,
Elbow flexed	2	,,
Wrist extended	4	,,

Thus centre 31 is clearly the seat of a simple fusion of the movements of the upper limb and those of the head and eyes. Centre 31 thus serving as an example, it will be similarly found on referring to Table I. that at—

Centre 36	We have fusion of the movements of the	Head and eyes and Upper limb.
,, 37 ,, 38 ,, 39	,, ,, ,, ,,	Head and eyes, Upper limb, Lower limb.
,, 50	,, ,, ,, ,,	Head and eyes, Upper limb, Lower limb.
,, 51	,, ,, ,, ,,	Head and eyes, Upper limb, Lower limb.
,, 6 ,, 6′ ,, 80	,, ,, ,, ,,	Upper limb, Lower limb.

From the extreme limitation of the effects of excitation in the thumb region, it is clear that the fusion of representation observed at the above described border centres cannot be due to spread of the current, but is to be interpreted as evidence of the gradual character of the evolution of representation of movements in the cortex. Such evolution would suggest the overlapping of the function of one region by that of another, and the more so in proportion as the parts are commonly moved in association.

(2) *Epilepsy.*

This we observed to follow the weak excitation, we always employed, at centres—

33, 40, 50, 51[(2)], 54[(2)], 58, 62, 65[(2)], 67, 68, 69, 6′, 72, 75.

[(2)] Noted twice.

It will thus be seen that the focus of the area of representation of the lower limb is the commonest seat of epileptiform disturbance. This may be due to the fact that the different regions of the lower limb area do not equally respond to the same stimulus, so that the same current just sufficient to evoke movement from one centre may cause overaction of another. Though it is undoubtedly a fact that some centres are more easily excited than others, still we do not put this prominently forward in any other sense than as a suggestion towards the interpretation of the above-described localisation of the tendency to the development of epileptiform convulsions.

(3) *Movements of Second and Third Toes.*

In Monkey 40, centre 65, and in Monkey 38, centre 68, the second and third toes began the movement of the limb, independently of the other toes. The movement in the first case was that of extension of the second and third toes, in the other it was that of opposition. Of course, in the Monkey, the second toe is the homologue of the index finger, and consequently is occasionally associated in movement with the hallux, as a primary movement; thus, at centres 65 and 68 in Monkeys 25 and 40 respectively, separation of these two digits was observed in the former, followed by extension of all the toes, while in the latter opposition took place. The march of the movements at these centres makes it quite clear that in these instances the second and third toes occupy undoubtedly a truly primary position, since movement of these is followed by that of all the other toes.

(4) *Purposive Movements.*

(a.) *Head and Eyes.*—It is well worth while to shortly review the so-called voluntary or purposive movements in the light of the facts detailed in the foregoing pages. In the first place, rotation of the head and eyes to one side is a necessary accompaniment of all the highest movements. This will probably explain the fact that this rotation of the head and eyes is represented over the whole breadth of the hemisphere reaching from near to the fissure of SYLVIUS below to the middle line above. It is thus in close apposition, from below upwards, to the areas for the face, the upper, and the lower limbs, respectively. It is, moreover, the area which intervenes between the presumably higher psychical centres of the præfrontal region and the lower areas for the face and limbs; hence, it seems probable that impulses proceeding from these higher centres will traverse the area for the head and eyes on their way to the areas for the limbs.

(b.) *Upper Limb.*—We can, with advantage, add to what we said about the movements of the upper limb in our former paper. Some of these movements we have already discussed in considering the mode of the march (p. 237), but to these considerations we would like to add one or two more of a wider nature. It is time to consider whether we cannot elucidate the fundamental principles which underlie the development of the mechanism for the performance of so-called voluntary actions. In the first place, we cannot pass by the obvious fact upon which we think we are now entitled to speak with some degree of certainty, viz., the suggestive difference between the functional activity of the ascending frontal and ascending parietal portions of the upper limb area.

While at the upper part (especially anteriorly) of the ascending frontal portion we find represented, as an initial movement, advancing of the whole limb with extension of all the joints, behind the fissure of ROLANDO the converse exists, and accordingly we find there the function of adduction and retraction of the shoulder with flexion of the elbow.

Summing all these facts together, we would advance the suggestion that an exact parallelism exists between the topographical relations just described and the sequence of movements in such a very frequent purposive action as that of, first, directing the gaze upon an object; next, reaching forward of the upper limb with extension of the joints to seize it; and, thirdly, the withdrawing of the arm with adduction of the shoulder, and carrying of the hand to the mouth by flexion of the elbow.

We are loath to lay too much stress on these deductions, as they are necessarily speculative, and also because we feel that a great deal has yet to be done in explanation of the fact that there are several movements relatively frequently performed by the head and eyes or the limbs, and yet which we have not been able to elicit by electrical stimulation from the regions in which they are presumably represented.

For instance, we have never observed the movement of direct upward rotation of the eyeballs, nor even circumduction of the shoulder, nor, to any marked degree, extension of the hip.

It seems to us probable that the absence of these special movements is owing to the method of analysis. The excitation of the so-called motor cortex by a faradic current is most obviously a very different effect-producing agency to the normal passage of a nerve impulse from the sensory perceptive areas, as occurs in the early stages of an effort of volition. What we mean, in short, is, that we cannot, with the present means at our disposal, apply a minutely localised excitation to one small group of corpuscles, and so cause them to discharge, without at the same time arousing into equal, or perhaps under certain circumstances even greater, activity other contiguous and possibly allied combinations of movements.

(5) *Opening of the Eyes.*

In one Monkey (No. 25) we observed in stimulating centres 32 and 33, that the two eyes did not open synchronously, but that the eyelids of the eye on the opposite side to that of the cortex stimulated opened before the eyelids of the same side. The time between the two movements was very slight, but still it shows that, although this movement is usually strictly bilateral, yet in exceptional instances the eyelids of the opposite side tend to act before those of the same side.

Abbreviations.

Hd. = Head.
Hd. E. } = Simultaneous deviation of Head and Eyes.
L. = Left, *i.e.*, opposite side to that stimulated.
E. = Eyes.
Sh. = Shoulder.

TABLE

Centre.	Primary movement.			Secondary.		Tertiary.
14	Hd. E. } 13	Hd. to L., 3 E. to L., 3–5		Eyes open, 4 Hd. to Sh., 1		
15	Hd. E. } 9	Hd. to L., 5 E. to L., 3		Eyes open, 2 Hd. to Sh., 3		
16	Hd. E. } 7	Hd. to L., 6 Eyes to L., 2 Eyes open, 3		Hd. to L., 3 Eyes to L., 4 Eyes open, 1 Hd. to Sh., 2		
17	Hd. E. } to L., 11	Hd. to L., 3 Eyes to L., 3 Eyes open, 1		Hd. to L., 3 Eyes to L., 2 Eyes open, 2 Hd. to Sh., 1		Hd. to Sh., 3
18	Hd. E. } to L., 7	Eyes to L., 2 Eyes open, 2 Hd. to L., 1 Hd. to Sh., 1		Hd. to L, 2 E. to L., 2 Eyes open, 1 Hd. to Sh., 2		
19	Hd. to L., 5	Hd. E. } to L., 3 Eyes open, 2 Eyes up, 1		Eyes to L., 4 Hd. to L., 2 Eyes open, 1		Eyes to L., 2
20	Hd. to L., 7	Hd. E. } to L., 3 Eyes open, 3	Eyes to L., 1	Eyes to L., 5 Hd. to L., 2 Hd. E. } to L., 2		Hd. to Sh., 1
21	Hd. to L., 5	Eyes open, 1 Eyes to L., 1		Eyes to L., 2 Hd. to L., 1 Eyes open, 1		Eyes to L., 2
22	Hd. to L., 8	Hd. E. } to L., 5	Eyes to L., 2 Eyes open, 1	Eyes to L., 6 Eyes open, 2		Hd. to L., 1 Eyes open, 1
24	Hd. to L., 5	Eyes open, 3	Hd. E. } to L., 2 Eyes to L., 2	Hd. to L., 2 Eyes to L., 2 Eyes open, 1		Eyes fixed, 1
26	Hd. to L., 2 Eyes open, 2	Eyes to L., 1		Eyes open, 2		
27	Eyes open and turn, 1 (Very slight and slow)					
26′	Hd. to L., 5	Eyes open, 3		Eyes to L., 3		
26*a*	Hd. to L., 6	Eyes open, 4	Hd. E. } to L., 1	Eyes open, 3 Eyes to L., 2 Hd. to L., 1		Hd. to L. (25°), 1 Eyes open, 1 Eyes straighten, 1
26*b*	Hd. to L., 5	Eyes open, 4		Eyes to L., 2 Eyes open, 2 Hd. turns, 2		Hd. to L., 1
26*c*	Hd. to L., 2 Eyes to L., 2	Eyes open, 2				
26*d*	Hd. to L., 1 Eyes to L., 1					
28	Hd. to L., 7	Eyes open, 5	Hd. E. } to L., 2 Eyes to L., 1	Hd. to L., 2	Eyes to L., 1 Eyes open, 1	

1.

Quaternary.	Nil.	Total.	Remarks.	Centre.
	0	19		14
	1	19	Weaker than 14 in 7 out of 18; nystagmus to L., 1	15
	1	19	Nystagmus, 1; eyes up and out (secondary), 1; horizontal (secondary), 1	16
Eyes up and out, 1	1	18	Less than 14, three times	17
	3	18		18
	6	17	Two cases more than 18	19
	4	18	Less than 14, 15, or 16, once; less than 14, once; greater than 16, once; eyes fixed, not turn, twice	20
	10	17	In one case included in the "nil" column the left ear retracted	21
	2	18	Eyes down, twice; eyes and head moved to opposite side in jerks	22
	3	15	All movements were slow and slight, and one noticed in jerks	24
	13	18		26
	17	18	The one positive result was probably due to "*w*" extending less posteriorly than usual	27
	6	14		26′
	5	16		26*a*
	7	16		26*b*
	5	11		26*c*
	3	5		26*d*
	3	18		28

TABLE

Centre.	Primary movement.			Secondary.		Tertiary.	
28*a*	Hd. to L., 6	Eyes open, 4	Hd., E. } to L., 1 Eyes to L., 1	Hd. to L., 3	Eyes to L., 2 Eyes open, 1		
28*b*	Hd. to L., 2 E. to L., 2 E. open, 2			Hd. to L., 1			
28*c*	Hd. to L., 1 E. open, 1 E. to L., 1			Hd. to L, 1			
29	Hd. to L., 4	Hd., E. } to L., 3	E. open, 1 E. to L., 1	E. to L., 2	Hd., E. } to L., 1 E. open, 1		
30	Hd. to Sh., 1 (?) E. open, 1 (?) E. to L. 1 (?)						
31	Hd. to L., 7	Hd., E. } to L., 3 E. open, 3	E. to L., 1 Wrist ext., 2 Sh. adv., 1	Hd. to L., 3 Elbow ext., 3	E. open, 2 E. to L., 2 Sh. adv., 2 Elbow flex., 2	Sh. adv., 4	
32	Hd. to L., 12	E. open, 1 Hd. to L., E. open } 1	Hd. to L., E. to L. } 1	E. to L., 5 E. open, 6		E. to L., 3 E. up, 2 Finger ext., Wrist ext. } 1	
33	Hd. to L., 10	E. open, 2 Hd., E. } to L., 2	Hd. to L., E. open } 1	E. to L., 7	E. open, 6	E. to L., 2	
34	Hd., E. } to L., 6	E. to L., 3 Hd. to L., 4	Hd. to L., E. open } 2	E. open, 4 E. to L., 4	Hd. to L., 1	Hd. to L., 2 E. to L., 1	
35	Hd. to L., 4	Hd. to L., E. to L. } 2 E. to L., 2	Hd. to L., E. open } 1 E. open, 1	E. to L., 2	Hd., E. } to L., 1 Hd. to L., 1		
36	Hd. to L., 6	Sh. adv., 4 Hd., E. } to L., 3	Wrist ext., 1 Toes ext., 1 E. open, 1	Elbow ext., 3	Sh. adv., 2	Elbow ext., 3	Wrist ext., 2
37	Hd. to L., 5	Hd., E. } to L., 2 Hip, 2 Ankle, 2	Sh. adv., 1 E. open, 1	See "Remarks"			
38	Hd. to L., 6	Hip rot. out, 1 Hip flex., 1 Ankle evert., plant. ext., 1					
39	Hd. to L., 7	Hd. to L., Eyes open } 3	Hd., E. } to L., 2 E. open, 1 Ankle evert., 1	E. to L., 4	Hd to L., 1 E. open, 1		
40	Hd. to L., 7	Hd. to L., E. open } 4	Hd., E. } to L., 3 E. to L., 1	E. to L., 4	E. open, 2		
41	Hd. to L., 7	E. to L, 3	Hd., E. } to L., 2 Hd. to L., E. open } 2 E. open, 1	Hd. to L., 3 E. to L., 3	E. open, 1 Hd. to L., E. open } 1		

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre.
	4	16		28*a*
	7	13		28*b*
	6	9		28*c*
	6	15	Slight nystagmus at break of current	29
	11	14	Motor representation here probably very imperfect	30
Sh. rot. out, 3 Wrist ext., 2 Elbow ext., 2	1	18	As a tertiary movement, there occurred once each:—Hd. to L.; wrist extended; wrist pronated; flexion of fingers. As a quaternary movement, there occurred once each:—Hd. to L.; elbow flexed	31
	1	16	In Monkey 25, L. eye opened before R. at each of these centres. In 33 epilepsy noticed. Pupil dilated once	32
	2	17		33
	1	16	Muzzle up twice	34
	4	14	Muzzle up once. In two cases 35 < 34	35
	1	17	Fusion of movements of head and eyes with extension movements of upper limb occurred ten times. Movements of leg occurred twice	36
	3	16	There was fusion of head and eye movements with those of limbs, thus—with those of arm, 4; with leg, 3; with arm and leg together, 5	37
	5	14	No definite secondary movement, but there occurred twice:—extension of all toes, knee, and hip; and once each:—eyes open; eyes to L.; shoulder flexed; elbow extended; toes extended. As tertiary movement, once:—shoulder advanced, elbow extended; knee extended, confused. Muzzle raised up, 1	38
	0	14	As secondary movement there occurred once each:—shoulder advanced; elbow extended; hip and knee flexed; ankle inverted; toes extended. In one case there was observed after the secondary movement:—extended hallux; flexed hip and knee; arm advanced; head and eyes to L. In the primary movement of the eyes opening, occurring once, the L. eye opened before the R	39
	2	17	Muzzle raised up in two cases; pupils dilated in two cases; arm advanced late and slight in one case; leg once very late; L. eye open before R., once; epilepsy, once	40
	1	16	Pupil dilated, 1; muzzle raised up, 1; arm and leg affected together, but late, 1	41

TABLE

Centre.	Primary movement.			Secondary.		Tertiary.	
42	Hd. to L., 3 Hd. } E. } to L., 3 E. to L., 3			E. to L., 3	Hd. to L., 1		
43	Hd. to L., 6	Hd. } E. } to L., 1. Hd. to L. } E. open } 1		E. to L., 3			
44	Hd. to L., 7	Hd. to L. } E. open } 4	Hd. } E. } to L., 1	E. to L., 7			
45	Hd. to L., 5	Hd. to L. } E. open } 4	Hd. } E. } to L., 3	E. to L., 5	E. open, 1	E. to L., 1	
46	Hd. to L., 4	Hd. } E. } to L., 1	Hd. to L. } E. open } 1 E. to L., 1	E. to L., 4	Hd. to L., 1 E. open, 1	E. to L., 2	
47	Hd. to L., 8	Hd. } E. } to L., 1	Hd. to L. } E. open } 1	E. to L., 4	E. open, 1 Sh. add., 1	E. to L., 1	
48	Hd. to L., 8	E. to L., 1 Hd. } E. } to L., 1	Hd. to L. } E. open } 1 E. open, 1	E. to L., 5	Hd. to L., 2 E. open, 1	E. to L., 1	
49	Hd. to L., 5	E. to L., 1	Hd. to L } E. open } 1	E. to L., 2	Hd. to L., 1		
50	Hd. to L., 3 Upper limb, 5 Lower limb, 3	Hd. to L. } Sh. adv. } 1			See "Remarks."		
51	Hip, 3 Hallux } Toes } 3	Hd. to L., 2	Ankle dorso-flex., 1	Shoulder advanced, 3	E. to L. Hip flex., 1	Leg flexed, 1 Knee confused, 1 Ankle dorso-flex., 1	
52	All toes ext., 6	Knee flex., 1 Hd. to L., 1 Hip extend., 1	Sh. adv., 1 Hd. to L. } E. open } 1	Ankle dorso-flex., 3	Sh. adv., 2 Hallux extend., 2 Hip rot. out, 1 E. open, 1	Hip flexed, 3	Hd. to L., 1 E. to L , 1
54	All toes extend., 7	Hip flex., 5	Knee flex., 3	Ankle dorso-flex. } ,, invert. } 4	Hip flex., 2 Knee flex., 1 Hallux ext., 3 Hallux flex., 1 Small toes flex., 1 L. abdomen, 1 Arm, 1	Arm advanced, 8 Knee flex., 3 ,, ext., 1 Ankle dorso-flex., 1	
55	Small toes extend., 6	Hallux extend., 2 Hallux opposed, 2	Hip rot. out, 2 Hip flex., 1	Knee flex., 4	Ankle dorso-flex., 2 ,, ext. invert., 1 Hip flex., 1 Hip rot. out, 1	Ankle dorso-flex., 2 ,, invert., 1 Knee ext., 2 ,, flex., 1 Hip flex., 1 ,, ext., 1	Hip flex., 1 ,, ext., 1 Toes ext., 1 Hallux flex., 1

I (continued).

Quaternary	Nil.	Total.	Remarks.	Centre.
	6	15	Muzzle raised up, 2; Hd. to shoulder, 1; pupils dilated, 1	42
	6	14	Movements of head were associated with those of the arm and leg together, three times; with the arm only in two cases	43
	4	16	Muzzle raised up, 2. In one case there was:—ext. hallux, eversion ankle, flex. hip and knee. In another, L. hip was flexed and adducted	44
	4	16	Muzzle raised up twice	45
	5	12	Muzzle turned down at end of movement of turning head, 1. Hd. drawn to shoulder, once	46
	2	12	The upper limb was affected twice, and the lower limb, once. Muzzle raised up, 1	47
	3	15	Muzzle raised up, 3; arm and leg combined were affected, 1; Hd. drawn down to shoulder, 1	48
	5	12		49
	2	14	Epilepsy occurred once. This number being the border-land of the centres for movements of the head, the upper and lower limbs, it was impossible to find any definite march of movements, owing to the different results obtained	50
	1	10	Epilepsy occurred twice. The primary movements of the hip were extension, flexion, and abduction	51
	2	13		52
	1	14	Epilepsy twice in lower limb, not in the upper	54
Arm. adv., 5	3	14		55

TABLE

Centre.	Primary movement.	Secondary.	Tertiary.
58	All toes ext., 6 Hallux flex., 1 „ ext., 1 Ankle invert. Ankle dorso-flex. } 2 Sh. adv. slight., 1	Ankle dorso-flex., 2 Ankle ext., 1 All toes flex., 2 Hip Knee } flex., 2 Hip abd., 1	Hip, 3 Knee, 2 Ankle, 2 Toes, 1
59	All toes ext., 4 Hallux flex., 1 „ ext., 2 „ add., 1 } 4 Ankle evert., 1 Ankle dorso-flex., 1 Ankle invert., 1 } 3 Hip and knee flex., 1	Ankle, 6 Small toes, 4 Hallux add., 2	Toes (small), 2 Hip flex., rot. out, 6 Knee, 3 Sh., 1
61	Hallux ext., 4 Hallux add. and opp., 3 } 7 All toes ext., 5 „ „ flex., 1 } 6 Ankle evert., 2 Ankle dorso-flex., 1 } 3 Hip ext., 1	Ankle invert., 7 Ankle dorso-flex., 2 Ankle plant. flex., 2 Small toes ext., 2 All toes ext., 1 Hallux add., 1 Hip rot. out. flex., 1	Knee flex., 3 „ ext., 2 Hip flex., 3 „ rot. out, 2 „ ext., 1 Sh. adv., 2 Toes ext., 1
6	Hip extend., 4 Sh. add., 3 „ retract., 1 „ adv., 1 } 5 Ankle evert., 1 Hallux ext., 2 Small toes ext., 1 Elbow ext., 2 Wrist pron., 1	Elb. ext., 5 Sh. flex., 1 Knee ext., 2 All toes flex., 2 „ „ ext., 2 } Hallux ext., 2	Ankle plant. ext., 4 Ankle dorso-flex., 2 } 6 Hip ext., 3 „ rot. out, 1 } 4 Knee ext., 1 Sh. rot. in, 1 „ adv., 2 } 3 Wrist ext., 1
6′	Small toes ext., 2 Hallux ext., 1 abd., 1 opp., 1 } 3 Elbow ext., 1 Wrist pronat., 1 Hip rot. out flex. } 1 Hip ext., 1 Sh. add., 1 „ adv., 1 } 2	Hallux ext., 1 All toes ext., 2 Ankle dorso-flex., 1 Knee flex., 1 „ conf., 1 } 2 Hip rot. in, 1 Sh. adv., 1 „ rot. in, 1 „ add., 1 } 3 Elb. ext., 2 „ conf., 1 } 3 Fingers flex., 1	Small toes flex., 1 Ankle dorso-flex., 2 Knee ext., 1 Hip ext., 2 Sh. adv., 2 Wrist pron., 1
62	Hallux ext., 5 „ flex., 3 } 8 Small toes ext., 3 Small toes flex., 2 } 5 Ankle evert., 3 Ankle plant. ext., 1 Ankle dorso-flex., 1 } 5	Small toes ext., 4 „ „ flex., 1 „ „ conf., 1 Ankle invert., 2 Ankle dorso-flex., 1 } Hip flex., 2 „ ext., 1 } Hallux ext., 1 „ add., 1 }	Hip, 3 Ankle, 3 Toes, 4 Knee, 3
64	Small toes ext., 5 All toes ext. and sep., 4 All toes flex., 1 } Hip ext., 1 „ flex., 1 } Ankle evert., 2 Arm adv., 1	Hallux ext., 3 „ conf., 1 „ flex., 2 } 6 Ankle dorso-flex., 2 Ankle evert, 1 } 3 Small toes ext., 1 „ „ flex., 1 } 2 Arm adv., 1 „ add., 1 } 2	Knee flex., 4 Hip flex., 2 „ rot. out, 1 } 3 Ankle invert., 1 „ evert., 1 } 2 Hallux ext., 1
65	All toes ext., 3 „ „ flex., 1 } 4 Small toes ext., 4 Hallux ext., 3 „ flex., 2 } 5 Hip rot. out, 2	Ankle dorso-flex., 3 Ankle plant. ext., 1 Ankle evert., 1 „ invert., 1 } 6 Small toes ext., 4 Small toes flex., 2 } 6 All toes ext., 2 Hallux ext., 2 „ flex., 1 } 3 Knee flex., 2	Ankle invert., 4 Ankle dorso-flex., 1 } 5 Hip flex., 2 „ rot. out., 2 } 4 All toes ext., 2 Sh. 2
67	All toes ext., 4 „ „ flex., 2 } 6 Hallux flex., 2 „ ext., 2 „ opp., 3 } 7 Small toes ext., 2 Small toes flex., 2 } 4	Ankle dorso-flex., 4 Ankle plant. ext., 1 Ankle evert., 2 „ invert., 1 } 8 All toes ext., 3 Small toes ext., 1 Small toes flex., 1 } 2 Hip conf., 1 „ rot. out, 1 } 2	Hip flex., 2 „ rot. out., 3 } 5 Knee flex., 3 Small toes flex., 1 Small toes ext., 1 } 2 Ankle dorso-flex., 2 Ankle plant. flex., 1 Ankle invert., 1 } 4

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre.
Hip rot. out, 1 Knee flex., 1 Arm, 1	1	12	Epilepsy once	58
Sh. adv., 3 All toes ext., 2 Ankle invert., 2	1	12		59
Sh. adv., 3 Hip flex., 2 Hip abd., 1 Elbow ext. and conf., 2 Knee, 1	0	16		61
Elbow ext., 5 Sh. adv., 4 Wrist ext., 1 Fingers flex., 3 Toes ext., 3 Knee and hip flex., 3 Hip ext., 2 Pelvis rot. to L, 2 Knee conf., 1 " ext., 1	1	18		6
Small toes ext., 1 Knee and hip flex., 2 Pelvis rot., 1 Sh. adv., 2 Elbow ext., 2 Fingers flex., 1	1	12	Epilepsy occurs once	6′
Toes, 2 Knee, 3 Ankle, 1 Hip, 2 Arm, 4	0	13	Epilepsy occurred once. It is to be noted that, among the small toes, those which were most represented were the 2nd and 3rd, and the 2nd more than the 3rd. In two cases the hallux and 5th toe were associated as a primary movement, but the 4th toe never	62
Arm adv., 3 Hip and knee flex., 3 Toes flex., 2	1	14		64
Hip and knee flex., 6 Knee flex., 3 Ankle, 2 Arm, 2	0	16	Epilepsy occurred twice. Note 2nd and 3rd toes	65
Knee, 7 } conf. and flex. Hip, 6 } Sh., 4	1	17	Epilepsy once	67

TABLE

Centre.	Primary movement.	Secondary.	Tertiary.
68	Hallux flex., 5 ,, ext., 5 } 10 All toes ext., 3 ,, ,, flex., 1 } 4 Ankle plant. ext., 3 Ankle dorso-flex., 1 } 4	All toes ext., 4 ,, ,, flex., 1 ,, ,, conf., 1 } 6 Small toes ext., 3 Small toes conf., 1 Small toes flex., 1 } 5 Ankle dorso-flex., 2 Ankle evert., 1 Ankle plant. ext., 1 } 4 Hip rot. out, 2 Hallux flex., 1 ,, ext., 1 } 2 2nd toe opp., 1	Ankle dorso-flex., 3 Ankle plant. ext., 1 Ankle conf., 1 ,, invert., 2 ,, evert., 1 } 8 Small toes flex., 2 Knee ext., 1 ,, flex., 1 } All toes flex., 1 ,, ,, ext., 1 }
69	Hallux flex., 6 ,, ext., 3 Hallux and 2nd toe ext., 2 } 11 All toes ext., 1 Small toes ext., 1 Ankle evert., 1 Ankle plant. ext., 1 } 2	All toes ext., 2 ,, ,, flex., 2 } 4 Small toes ext., 3 Small toes flex., 1 } 4 Ankle dorso-flex., 2 Ankle plant. ext., 1 } 3 Hallux ext., 1	Small toes ext., 2 Small toes conf., 1 } 3 All toes ext., 1 ,, ,, flex., 1 } 2 Hip and knee ext., 1 Hip and knee flex., 1 } 2 Ankle plant. ext., 1 Ankle dorso-flex., 1 } 2
70	Hallux flex., 7 ,, abd., 1 } 8 Small toes ext., 2 Knee flex., 2 ,, rot. in, 1 } 3 Ankle evert., 1 Ankle dorso-flex., 1 Ankle plant. ext., 1 } 3 All toes ext., 1 ,, ,, flex., 1 } 2	Small toes ext., 4 All toes ext., 2 Hallux ext., 2 Ankle dorso-flex., 1 Ankle plant. ext., 1 Ankle evert., 1 } 3 Hip flex., 1	Ankle dorso-flex., 5 ,, confusion, 1 } 6 All toes ext., 1 Sh. rot. out, 1
71	Hallux flex., 6 ,, ext., 5 } 11 All toes ext., 4 ,, ,, flex., 1 } 5 Ankle dorso-flex., 1 Ankle plant. flex., 1 } 2	All toes ext., 9 Hallux ext., 4 Ankle dorso-flex, 3 Ankle evert., 1 ,, invert., 1 } 5 Hip flex., 3 Knee flex., 2	Hip and knee flex., 5 Ankle dorso-flex., 4 ,, conf., 1 } 5
72	All toes ext., 5 Small toes ext., 5 Hallux flex., 3 ,, ext., 2 } 5 Ankle plant. ext., 1 Ankle dorso-flex., 2 } 3	Ankle dorso-flex., 3 Ankle plant. ext., 1 } 4 Hallux ext., 2 Knee and hip flex., 1	Ankle dorso-flex., 5 ,, invert., 1 } 6 Knee and hip flexed, 4
73	All toes ext., 7 Small toes ext., 3 Ankle dorso-flex., 2 Hallux ext., 1 ,, flex., 1 } 2	Ankle dorso-flex., 6 Hallux ext., 2 Small toes ext., 2 Hip and knee flexed, 3	Knee and hip flexed, 3 Ankle evert., 1 ,, dorso-flex., 1
74	All toes ext., 3 Small toes ext., 1 Ankle dorso-flex., 1	Ankle Knee Hip } flex., 1	
75	Hallux flex., 2 ,, ext., 2 } 4 Hip ext., 2 Sh. add., 2 Knee and hip flex., 1 Ankle evert., 1	All toes ext., 3 ,, ,, flex., 1 } 4 Small toes ext., 1 Knee ext., 1 Ankle evert., 1 Ankle dorso-flex., 2 } 3 Knee and hip flex., 1	Knee and hip flex., 1 Arm add. adv., 1
76	All toes ext., 2 Hallux ext., 1 ,, flex., 1 } 2 Hip flex., 2 Small toes ext., 1 Knee flex., 1 Ankle dorso-flex., 1	Ankle dorso-flex., 3 Ankle invert., 1 } 4 All toes ext., 1 ,, ,, flex., 1 } 2 Hallux ext., 1 Hip flex., 1	Ankle evert., 2 ,, conf., 1 Ankle plant. ext., 1 Ankle dorso-flex., 1 } 5 Hip rot. out, 1
77	All toes ext., 5 Small toes ext., 1 Hallux ext., 1 Ankle dorso-flex., 1	Hallux ext., 3 All toes ext., 2 Ankle dorso-flex., 2 Hip flex., 1	Ankle dorso-flex., 2 ,, evert., 1 } 3 Knee and hip flex., 1

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre
Hip rot. out, 5 Hip and knee flex., 4 Ankle, 3 Knee flex., 3 } 5 „ conf., 2 }	0	16	Epilepsy occurred twice. The 2nd and 3rd toes, in Monkey 38, opposed towards hallux as a primary movement	68
Hip and knee flex., 5 Ankle dorso-flex., 3 Knee at 90°, 1 Toes confused, 1	0	15	Epilepsy once	69
Hip and knee flex., 5 Knee confused, 1 Hip abd., 1 } 3 „ rot. out, 2 } Arm adv., 2	0	18		70
Knee and hip flex., 3 Arm abd., 2	1	18		71
Hip flex., 1 } 2 „ ext., 1 } Toes sep., 1	1	18	Epilepsy once	72
Hip rot. out, 1 } 2 „ flex., 1 } Knee flex., 1 } 2 „ rot. in, 1 }	4	18		73
	8	14		74
	5	17	Epilepsy once	75
Hip and knee flex., 3 Toes sep., 2 All toes flex., 1 Ankle evert., 1	9	17		76
Hip and knee flex., 3 Knee flex., 1 Sh. adv., 1	9	17		77

TABLE

Centre.	Primary movement.	Secondary.	Tertiary.
78	Small toes ext., 4	Ankle dorso-flex., 2 Hallux ext., 1	Ankle dorso-flex., 1
11	Sh. add., 7 „ retract., 4 „ elevated, 1 } 12 Wrist pronated, 1 Elbow ext., 1	Elbow flex., 5 Sh. add., 1 „ retract., 1 „ rot. in, 1 } 3 Elbow ext., 1	Fingers ext., 4 Wrist ext., 2 Sh. rot. out, 1 Hip ext., 1
79	Sh. add., 7 „ retract., 3 „ elevation, 3 } 13 Wrist pronated, 1	Elbow flex., 5 Fingers ext., 3 Elbow ext., 2	Wrist ext., 1 Hip ext. rot. in, 1
80	Wrist pronated, 2 Elbow ext., 1 „ flex., 1 Sh. add., 1 Small toes ext., 1	Fingers inteross. ext., 2 Ankle dorso-flex., 1 Sh. add., 1	Wrist ext., 1 Fingers ext., 1
81	Wrist pronated, 2 Sh. add., 2 Elbow ext., 1 Fingers ext., 1	Sh. retract., 1 Elbow ext., 1 Thumb and fingers flex., 1	Sh. add., 1 Elb. ext. conf., 1 Wrist ext., 1 Fingers flex., 1
82	Wrist pronated, 2 Sh. add. retract., 1 Elbow flex., 1 Fingers flex., 1 „ ext., 1 } 2	Wrist pronated, 2 Fingers inteross. ext., 2	Wrist ext., 1 Elbow flex., 1 Fingers ext., 1
83	Thumb flex., 5 „ opp., 2 } 7 Wrist pronated, 4 Fingers flex., 2 „ ext., 1 } Elbow flex., 1	Fingers flex., 3 „ ext., 1 Index opp., 1 } 5 Wrist ext., 2 Wrist ulnar add., 1 } 3 Sh. add., 1	Elbow flex., 3 Wrist ext., 1 Fingers ext., 1 Sh. add., 1
85	Thumb flex., 10 „ opp., 4 } 14 Index opp., 4 Wrist pronated, 2 Fingers flex., 1	Fingers flex., 8 Index flex., 2 Thumb opposed, 2 Index opposed, 2 Fingers and thumb, 1 Wrist supin., 1	Fingers flex., 2 „ ext., 1 } 3 Wrist ext., 1 „ pron., 1 „ supin., 1 } 3
87	Thumb flex., 10 „ opp., 6 } 16	Fingers flex., 8 Wrist supin., 1	Wrist ext., 2 „ pronat., 1 Elbow flex., 1

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre.
Knee and hip flex., 1	7	11		78
Elbow ext., 1	1	12		11
	4	14		79
	12	16		80
	6	11		81
Sh. adv., 1 } 2 ,, add., 1 } Elbow flex., 1 All fingers ext., 1	8	15		82
Elbow flex., 1	3	17	Index finger opposed towards thumb, once as a secondary movement	83
Elbow flex., 3 Fingers flex., 1 Wrist ext., 1	3	19	Index finger opposed four times as a primary movement. Index finger flexed twice and opposed twice as a secondary movement	85
Wrist supin., 1 Elbow flex., 1	2	16		87

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Description of Plates 40–42.

PLATE 40.

The figs. 4 to 13 and 16 to 20 are stippled to show the representation of the absolute movements and the primary movements of the different joints. In all of these the intensity of the stippling denotes the degree of representation of the movements of the joint.

Fig. 4 shows the area of absolute representation of turning the head to the opposite side. The points of greatest intensity are seen to be just above the horizontal limb of the præcentral sulcus, and the part next to the longitudinal fissure. The area is seen to be very extensive.

Fig. 4A gives the representation of the primary movement of rotation of the head to the opposite side. When compared with fig. 4 it is seen that the point of greatest intensity here is also just above the horizontal limb of the præcentral sulcus, and also next to the longitudinal fissure. In the corner formed by the two limbs of the præcentral sulcus the representation is faint, as this is the place where the simultaneous movement of the head and eyes is most marked.

Fig. 5 shows the representation of the primary movement of the simultaneous action of turning the head and eyes to the opposite side. The point of greatest intensity is in the angle formed by the two limbs of the præcentral sulcus, and is in counter-distinction to fig. 4*a*, where this part has only a feeble representation of the primary movements for rotation of the head.

Fig. 6. Here the absolute representation of the movements of the hallux are given. The greatest intensity is seen to be in front of the upper end of the fissure of Rolando, and to a less degree behind this end of the fissure; from these points the representation extends over the whole of the lower limb area, but in a very feeble degree.

Fig. 6A. The representation of the primary movement of the hallux is here seen to be localised almost entirely to each side of the upper end of the Rolandic fissure, and to have its seat of greatest intensity immediately in front of the fissure. The localisation is very sharply defined, and is more exact than any other joint of the lower limb. (*Cf.* figs. 7, 8, 9, and 10.)

Fig. 7 gives the absolute representation of all the toes acting together; the representation extends over the whole area for the lower limb, and has its greatest intensity just in front of and behind the most intense representation of the hallux.

PLATE 41.

Fig. 8. The representation of the movement of flexion of all the toes is here given, and it is seen to be almost entirely in front of the fissure of ROLANDO.

Fig. 9 gives the absolute representation of the movements of the small toes; the greatest intensity is seen to be in front of the fissure of ROLANDO, but in front of and below the part occupied by the hallux.

Fig. 10 shows the primary representation of the movements of the small toes, and, when compared with fig. 6A, it is seen to occupy that part of the area of the lower limb, which is not occupied by the representation of the primary movement of the hallux, *i.e.*, immediately in front of and behind the upper end of the fissure of ROLANDO.

Fig. 11 shows the absolute representation of the movements of the ankle. It is well marked over the whole of the lower limb area, and is better represented than the next joint, the knee (*cf.* fig. 12). Its greatest intensity is above the hinder end of the sulcus x, and in front of the area for the hallux.

Fig. 12 is the absolute representation of the movements of the knee; it has no special characters, but is fairly evenly distributed over the whole of the lower limb area, in conformity with the secondary character of the movements of this joint.

Fig. 13. The absolute representation of the movements of the hip is here given. While it extends over the whole lower limb area, it is most marked in front of the fissure of ROLANDO, and especially in the more anterior part; its greatest intensity here is further forward than the representation of the ankle (*cf.* fig. 11), and it is only slightly represented just in front of the fissure of ROLANDO, the area for the hallux.

PLATE 42.

Fig. 16 gives the absolute representation of the movements of the thumb as observed in the present research. It is seen in a very striking manner to be limited to the lower end of the intra-parietal sulcus and over a small area; its lower edge is sharply defined and its upper border exhibits only a very slight amount of shading off into the contiguous centres. It is the most highly defined of all the segments of the limb.

Fig. 17 shows the absolute representation of the movements of the fingers; it extends more or less over the whole upper limb area (examined in this present paper), and it is more extensive than the representation of the movements of the thumb (*cf.* fig. 16). But while it is only slightly represented in the upper part of the upper limb area, it is very marked at its lower part, and it will be noted that its point of greatest intensity is just above that of the representation of the thumb.

Fig. 18. The absolute representation of the movements of the wrist is here seen to extend over the whole upper limb area (here examined), and to be feebly represented at the upper part of this area, but to have its greatest intensity about the middle and just above the point of greatest representation of the fingers (*cf.* fig. 17).

Fig. 19 gives the absolute representation of the movements of the elbow. Though it is represented over the whole upper limb area (examined in this paper), it is very slightly marked in the part opposite the lower end of the intra-parietal sulcus; its chief seat being at the upper end of the upper limb area, on a level with the sulcus *x*, and its point of greatest intensity is at this level, immediately in front of the fissure of ROLANDO, and, to a less degree, in the contiguous part behind this fissure.

Fig. 20. Here the absolute representation of the movements of the shoulder is seen to be localised almost entirely to the upper limit of the upper limb area. It is most important to observe that the shoulder, alone of all the joints of the upper limb, is not represented at all in the lower part of this area, opposite the lower end of the intra-parietal sulcus—the seat of representation of the movements of the thumb and the fingers (*cf.* figs. 16, 17). The point of greatest intensity is seen to be in front of and behind the fissure of ROLANDO at the horizontal level of the sulcus *x*, the upper limit of the upper limb area.

On comparing figs. 16–20, it will be seen that the most intense representation of the movements of the segments of the upper limbs is arranged in a most perfect gradation from below upwards. The representation of the thumb occupies the lowest part of the upper limb area, *i.e.*, opposite the lowest point of the intra-parietal sulcus; the fingers have their seat of greatest intensity immediately above that of the thumb; the representation of the wrist is situated just above that for the fingers; while the elbow is represented higher up than the wrist, near the upper limit of the area. The representation of the shoulder forms the upper limit of the upper limb area, being localised rather higher up than that for the elbow.

It will also be noted as most important that, whereas the representation of the thumb is confined entirely to the lowest part of the upper limb area, the shoulder is represented almost entirely at the uppermost limit of this area, *i.e.*, the two extreme segments of the upper limb are limited in their representations to the extreme ends of the area.

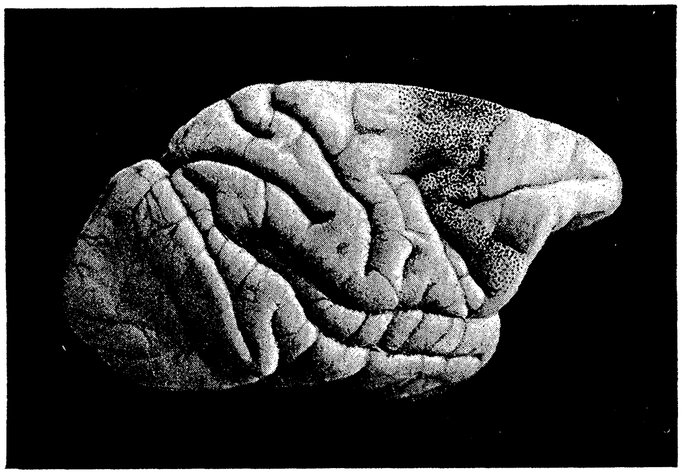


Fig. 4.—Absolute representation of turning of the Head towards the opposite side.

Fig. 4*a*.—Primary representation of turning of the Head towards the opposite side.

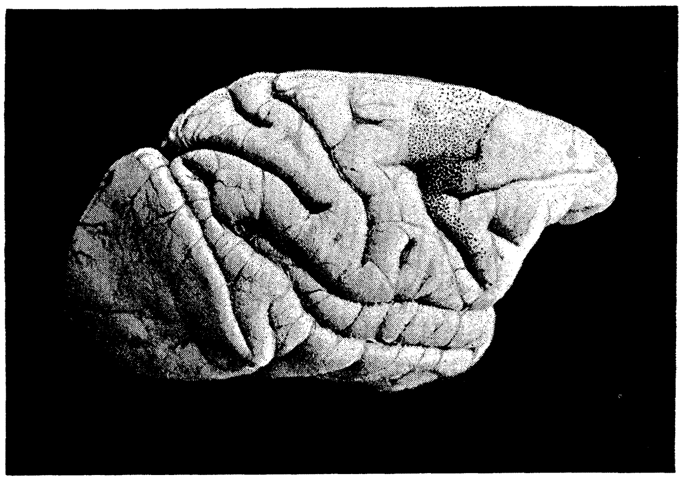


Fig. 5.—Primary representation of the simultaneous rotation of the Head and Eyes.

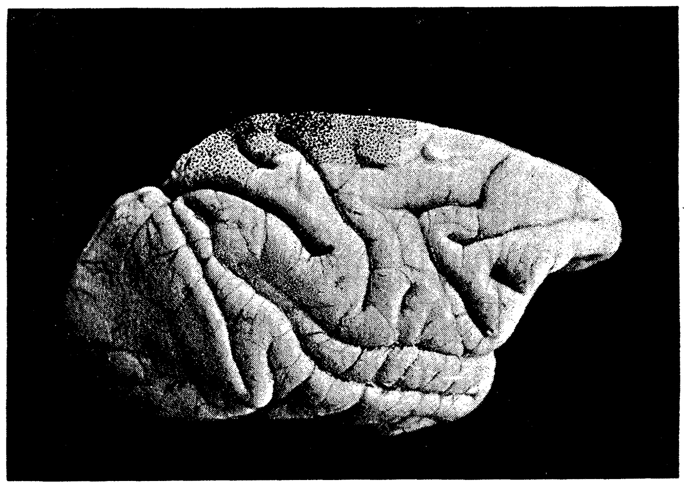


Fig. 6.—Absolute representation of the Hallux.

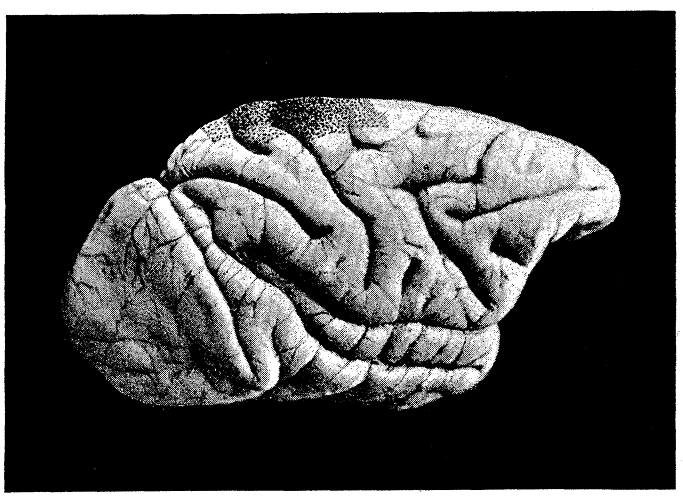


Fig. 6*a*.—Primary representation of the Hallux.

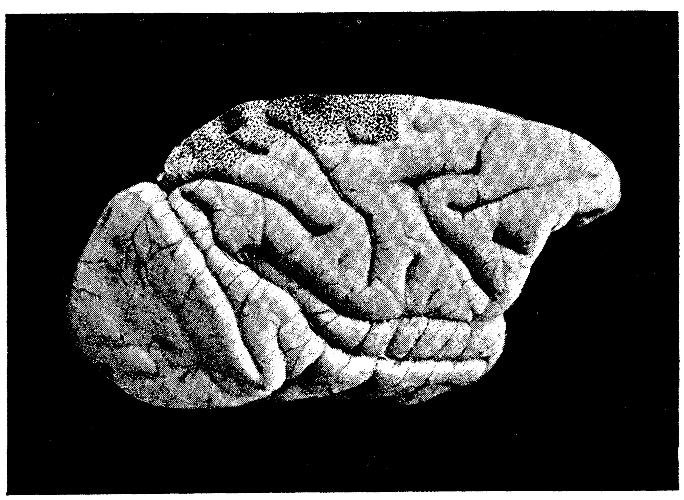


Fig. 7.—Absolute representation of All Toes.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

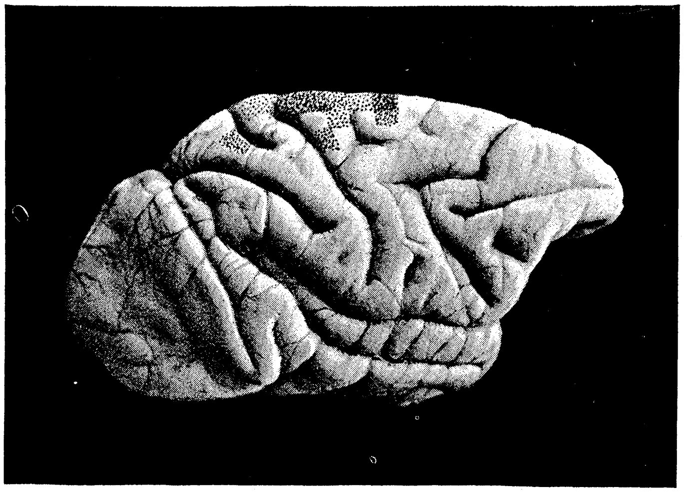


Fig. 8.—Representation of the movement of Flexion of All Toes.

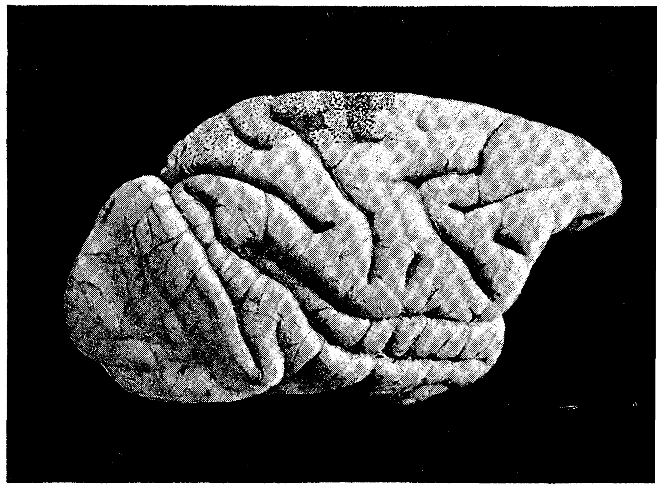


Fig. 9.—Absolute representation of the Small Toes.

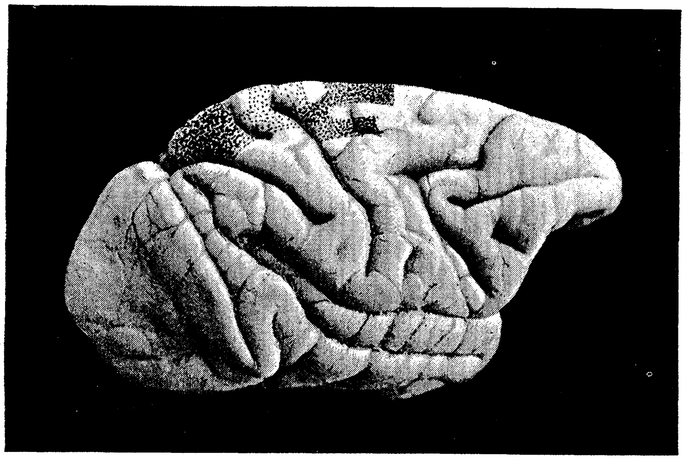


Fig. 10.—Primary representation of the Small Toes.

Fig. 11.—Absolute representation of the Ankle.

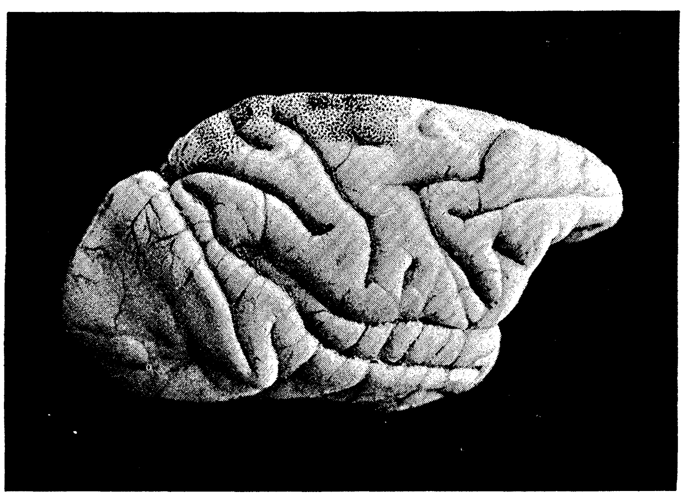


Fig. 12.—Absolute representation of the Knee.

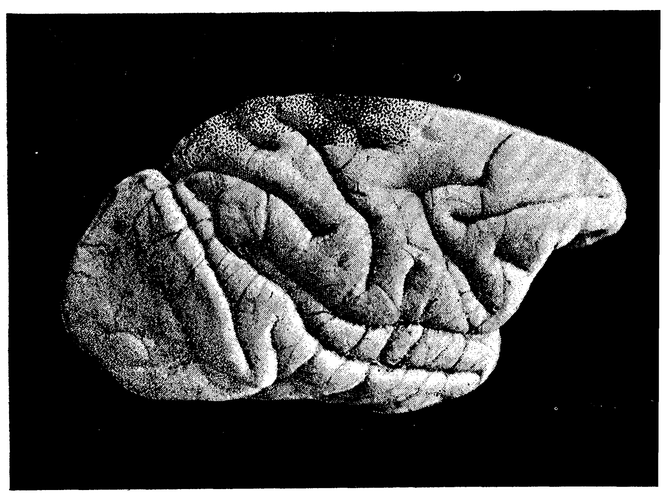


Fig. 13.—Absolute representation of the Hip.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

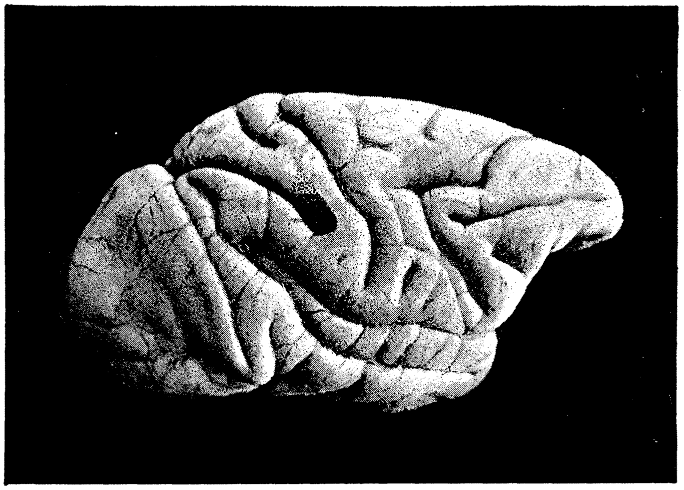


Fig. 16.—Absolute representation of the Thumb.

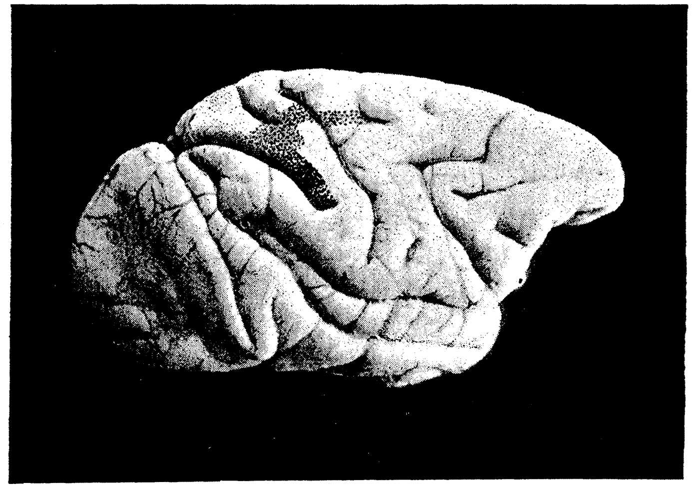


Fig. 17.—Absolute representation of the Fingers.

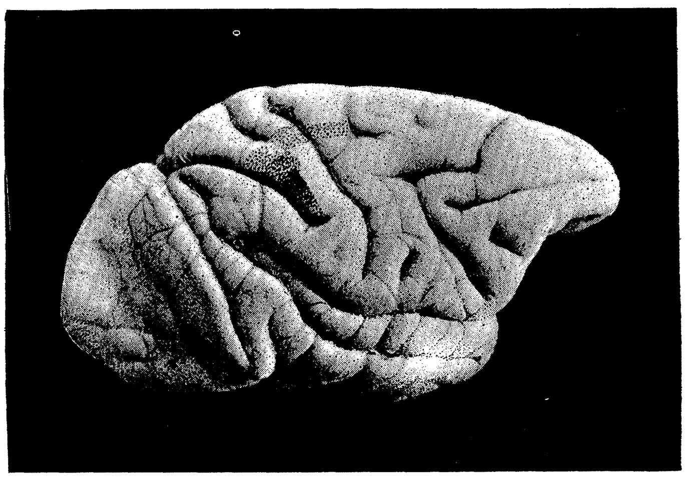


Fig. 18.—Absolute representation of the Wrist.

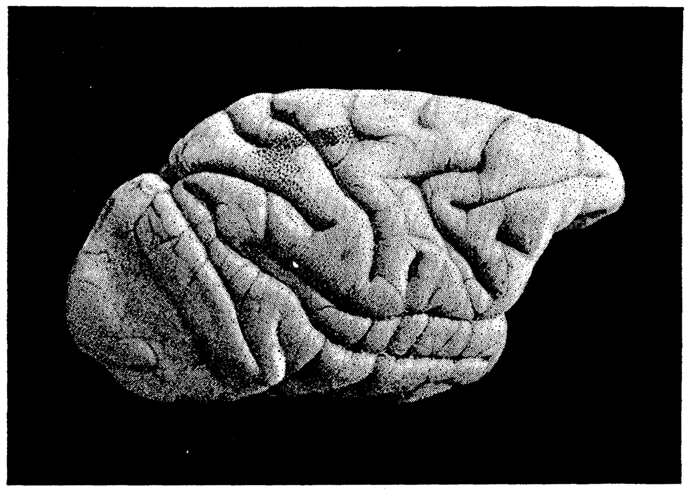


Fig. 19.—Absolute representation of the Elbow.

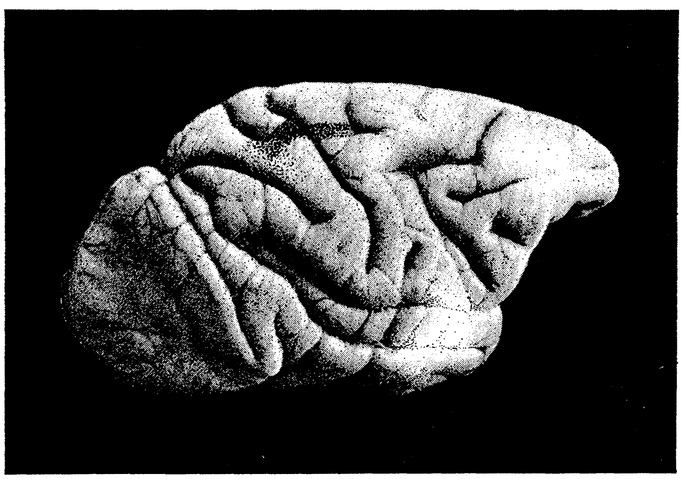
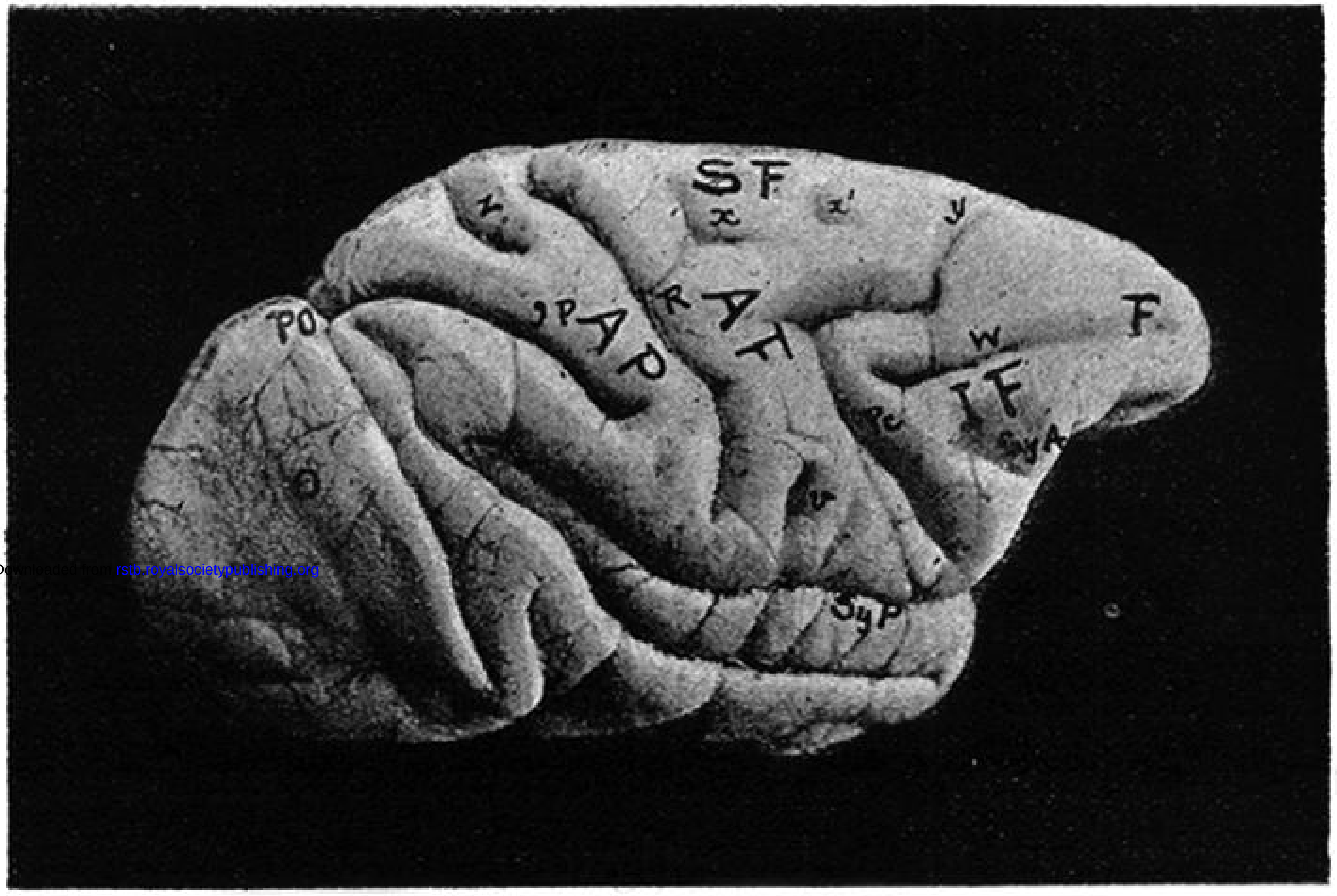


Fig. 20.—Absolute representation of the Shoulder.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Fig. 1.



hotograph of the external surface of the right half of the brain of a Monkey (*Macacus sinicus*).

Sulci SyA. Fissure of SYLVIUS, anterior limb.

SyP. Fissure of SYLVIUS, posterior limb.

R. Fissure of ROLANDO.

PO. Parieto-occipital fissure.

IP. Intra-parietal sulcus.

P*c*. Præcentral sulcus.

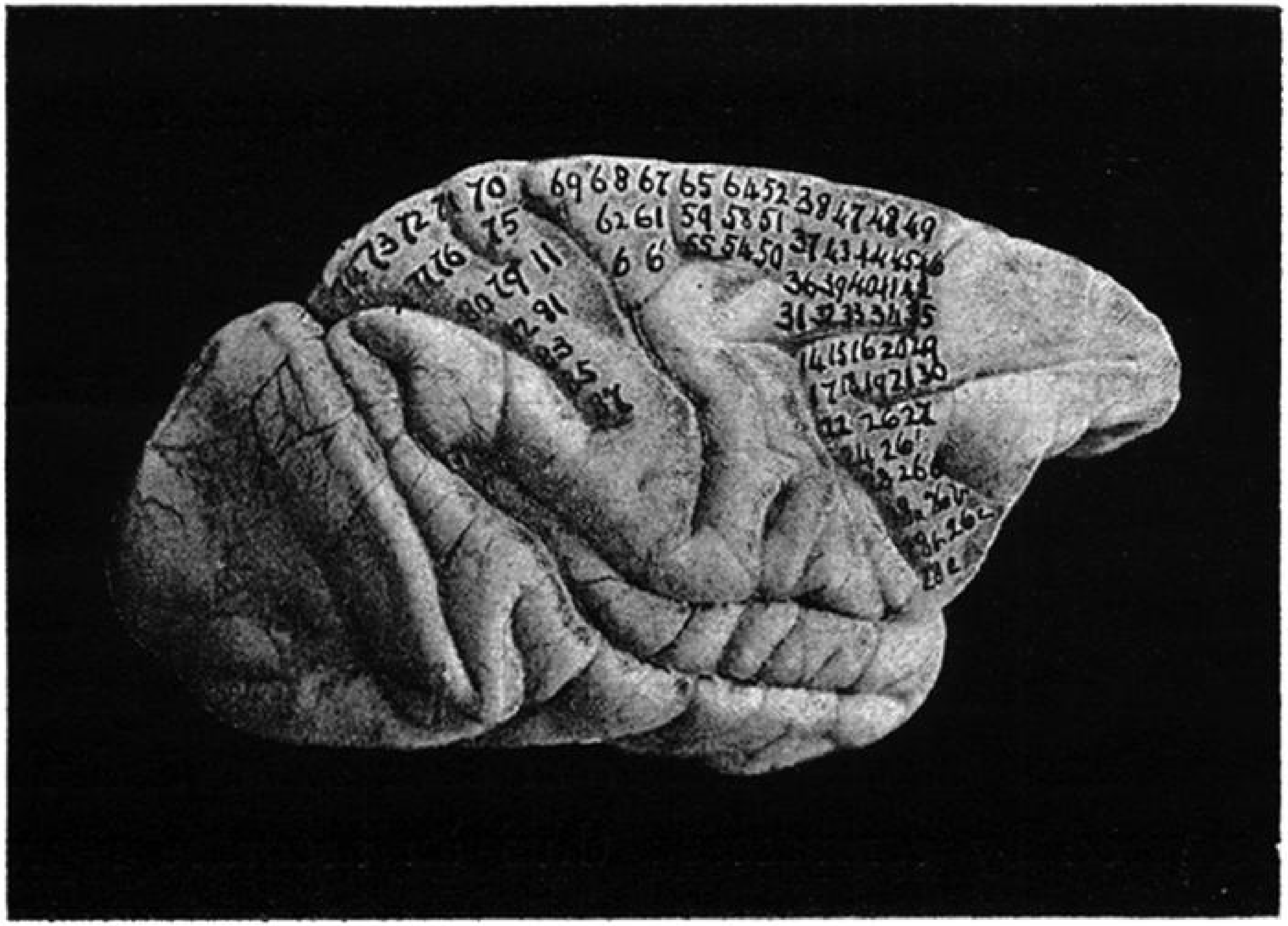
v.
w.
x.
x′. Supplementary to *x*, occasionally found.
y.
z.

} Sulci, so named.

Convolutions or Gyri.

F.	Tip of frontal lobe.	SF.	Superior frontal.
IF.	Inferior frontal.	AF.	Ascending frontal.
AP.	Ascending parietal.	O.	Occipital lobe.

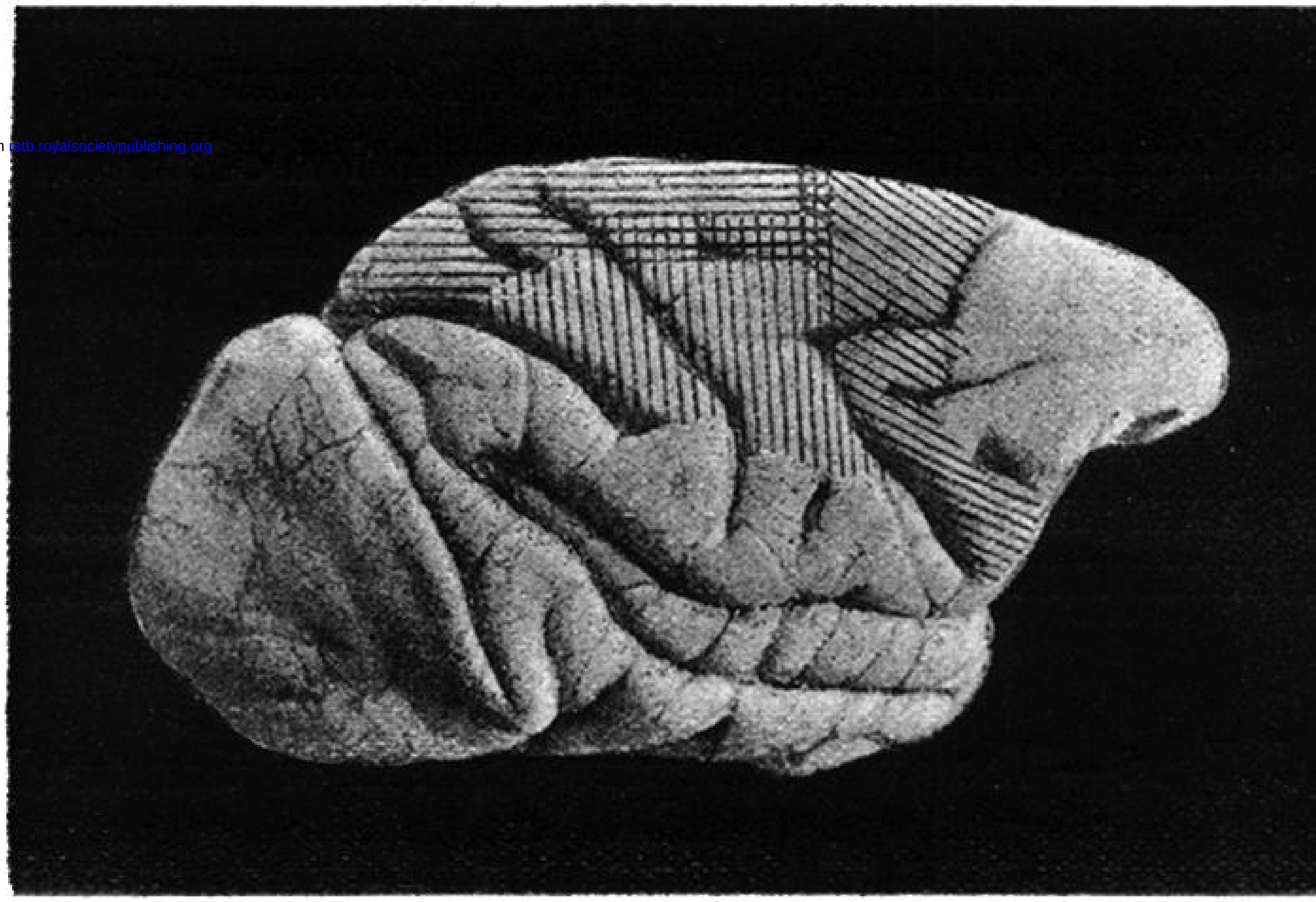
Fig. 2.



This is a similar photograph to fig. 1, and shows the area of the cortex, which is the subject of this paper; the numbers denote the different individual points of stimulation, of which 74 are here given. Each number denotes a centre of the size of 2 sq. mm. Centres 35, 42, and 46 apparently pass anterior to the sulcus *y* (see fig. 1), but the deep shadow is caused by a large vein which happened to be present in this brain.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Fig. 3.



similar photograph, shaded to show the parts of the cortex, excitation of which produces movements of the head and eyes to the opposite side, and movements of the upper and lower limbs; it comprises the areas which were investigated in our previous paper, as well as those which are the subject of the present one.

Oblique shading represents the area of the movements of the head and eyes.

Vertical shading ,, ,, ,, upper limb.

Horizontal shading ,, ,, ,, lower limb.

The places where the lines, having different directions, intersect, denote the overlapping of the contiguous areas; and at these points the functions of these different areas are represented together.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

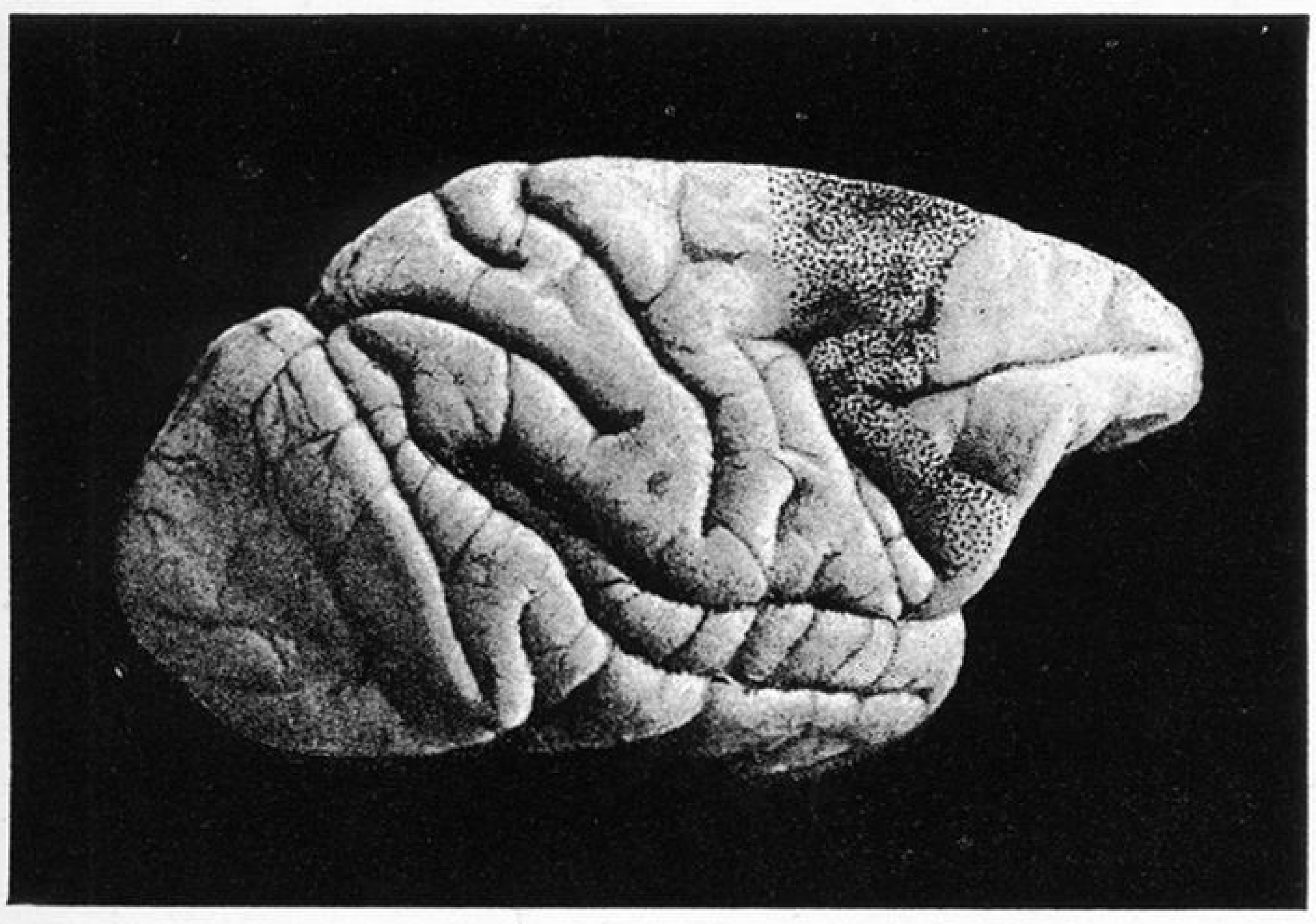


Fig. 4.—Absolute representation of turning of the Head towards the opposite side.

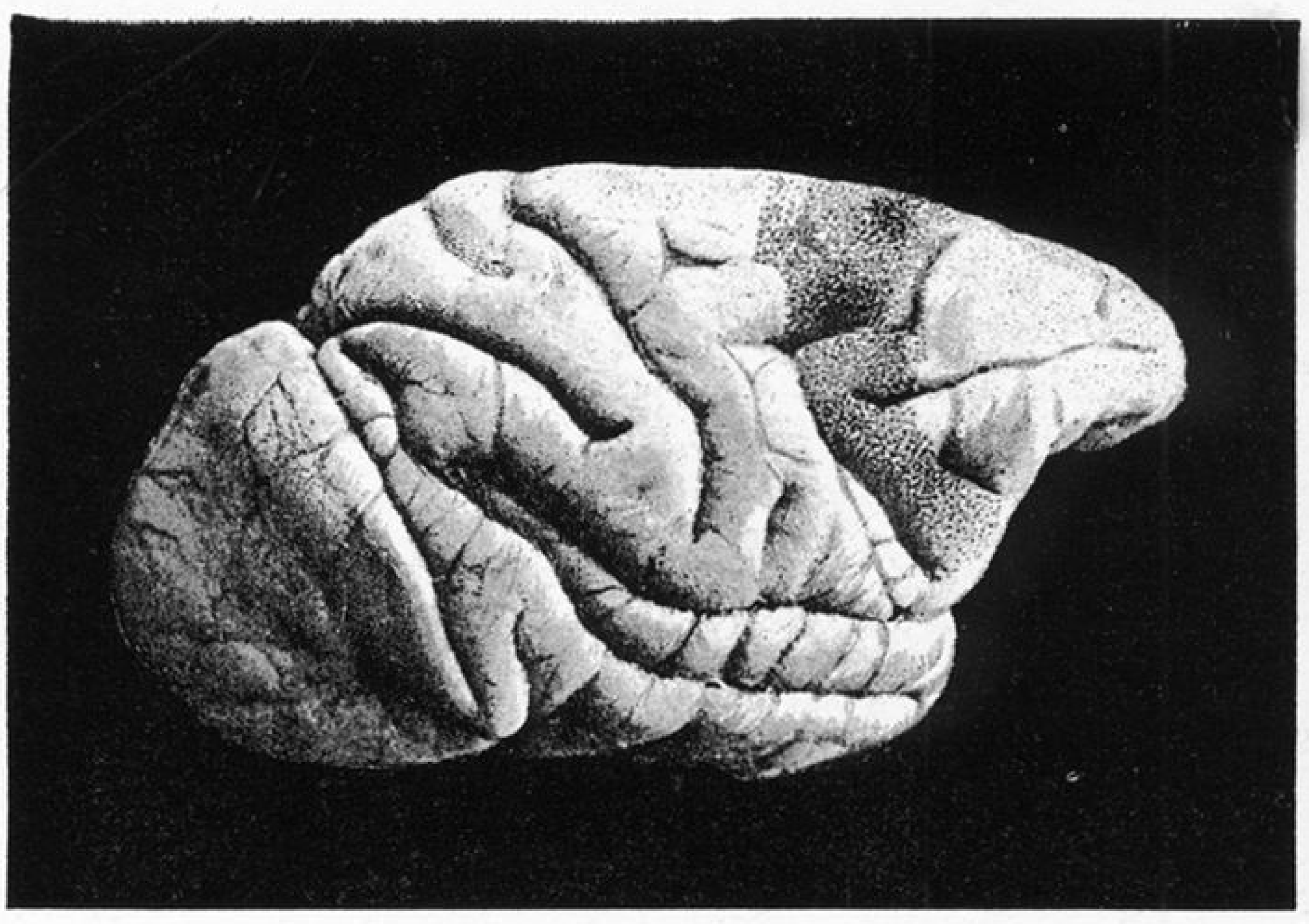


Fig. 4*a*.—Primary representation of turning of the Head towards the opposite side.

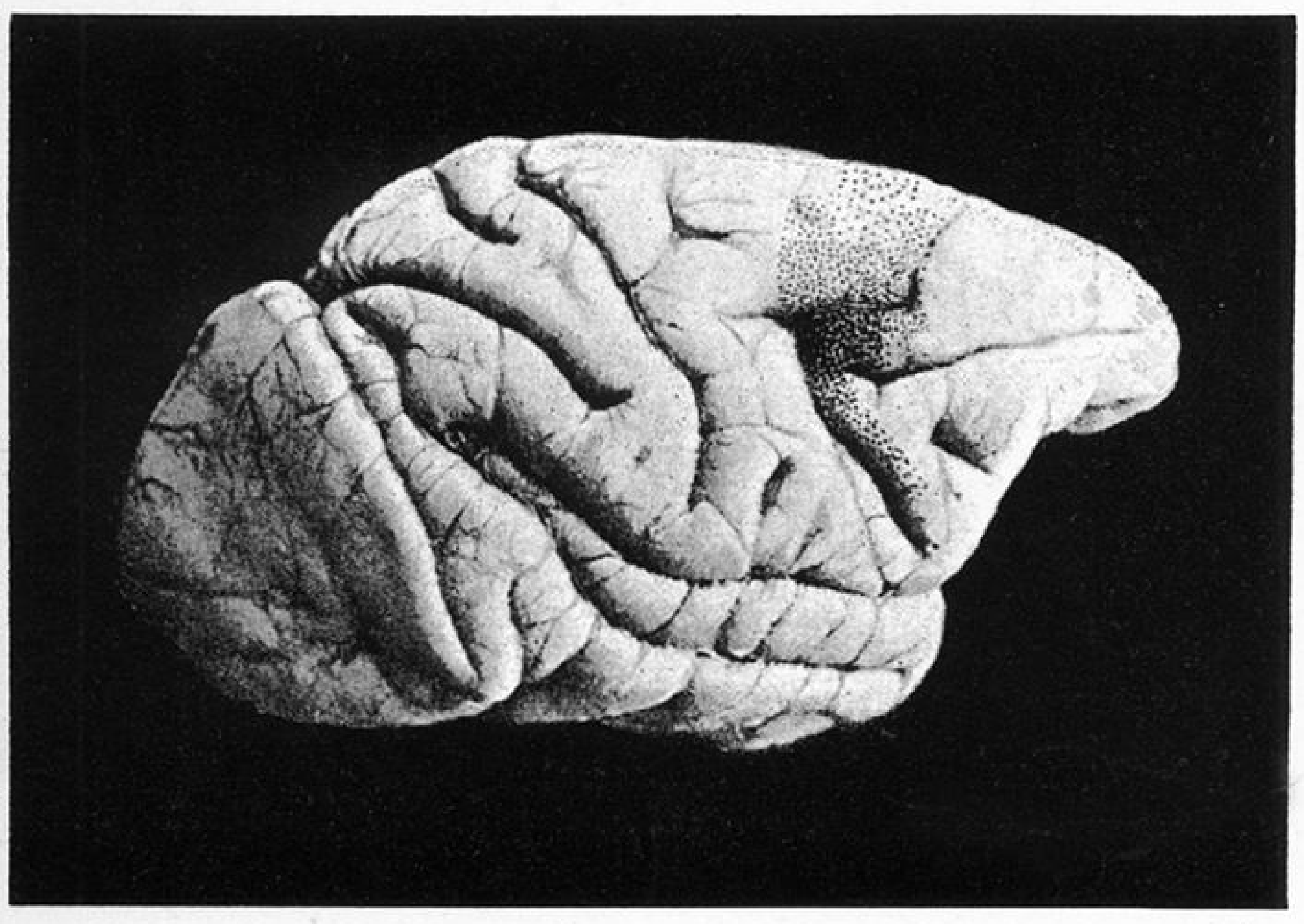


Fig. 5.—Primary representation of the simultaneous rotation of the Head and Eyes.

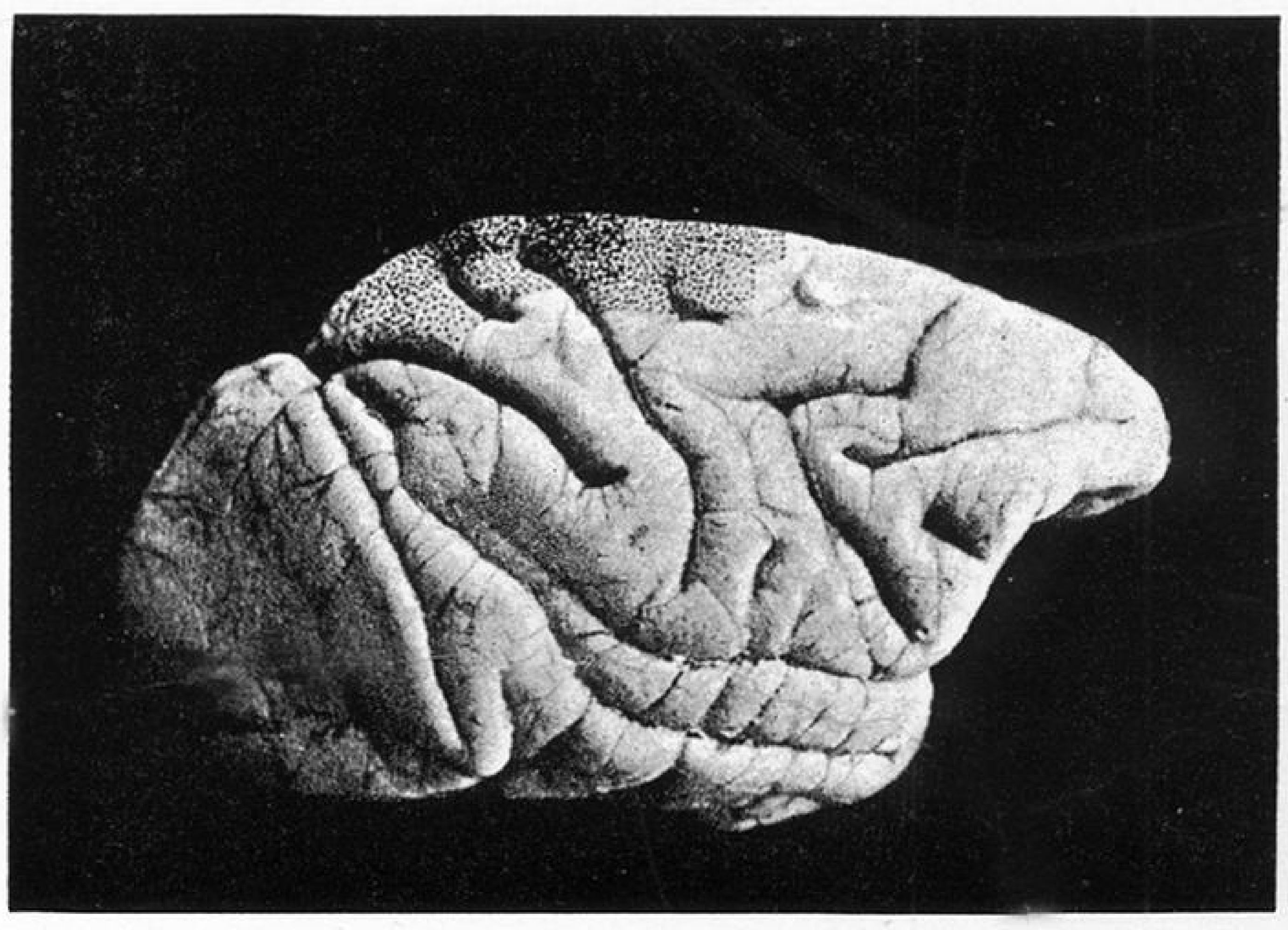


Fig. 6.—Absolute representation of the Hallux.

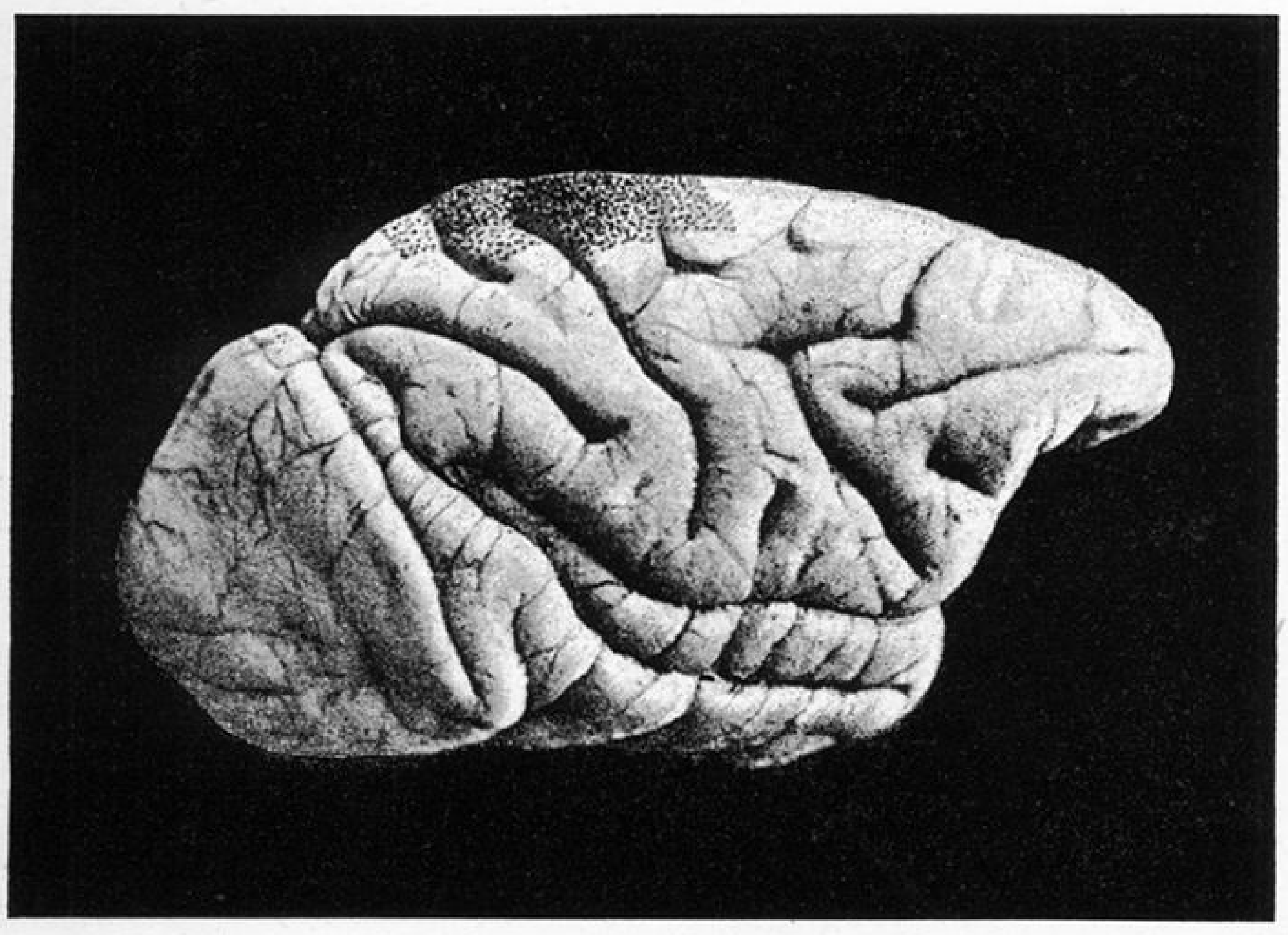


Fig. 6*a*.—Primary representation of the Hallux.

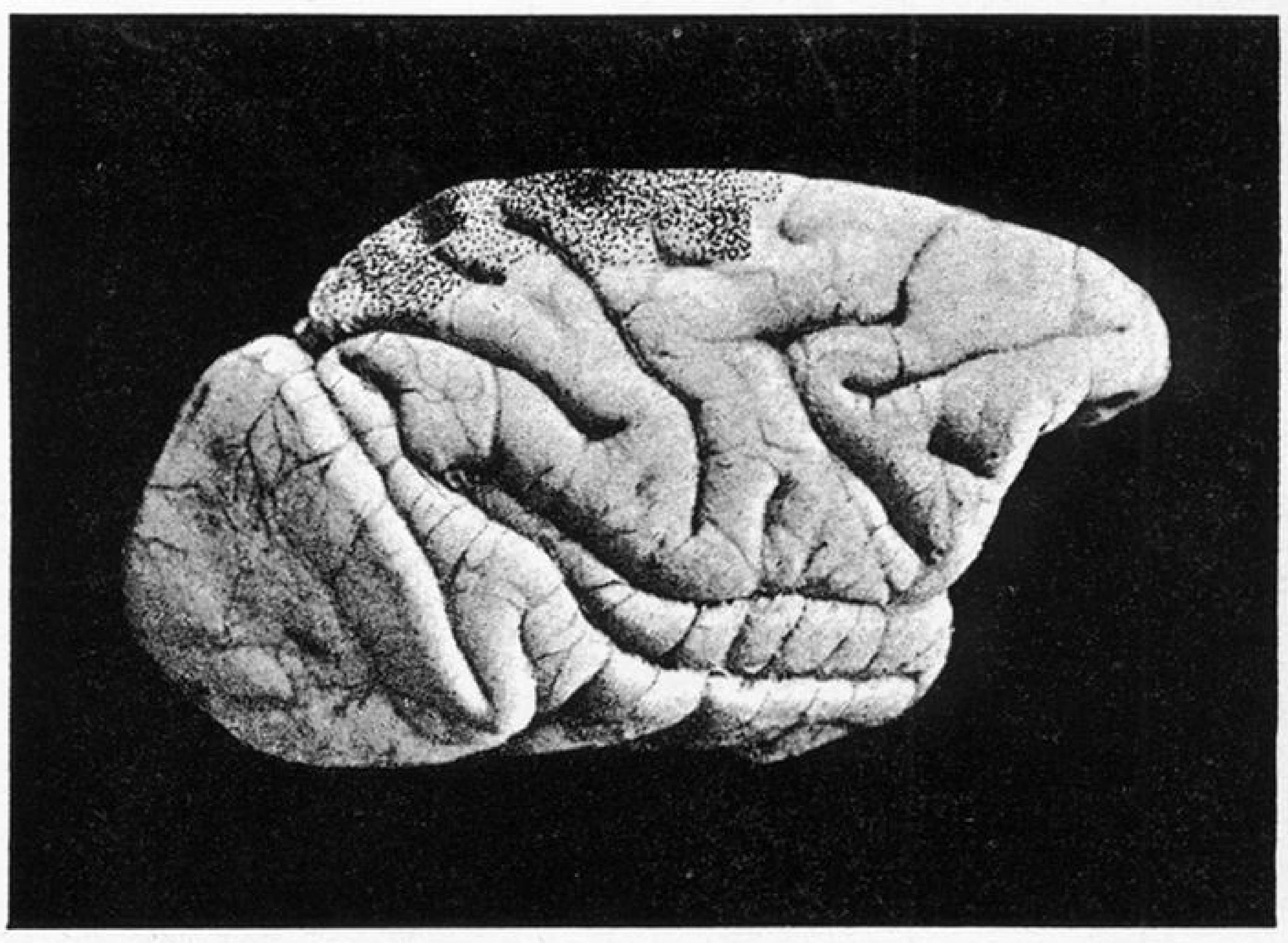


Fig. 7.—Absolute representation of All Toes.

PLATE 40.

The figs. 4 to 13 and 16 to 20 are stippled to show the representation of the absolute movements and the primary movements of the different joints. In all of these the intensity of the stippling denotes the degree of representation of the movements of the joint.

Fig. 4 shows the area of absolute representation of turning the head to the opposite side. The points of greatest intensity are seen to be just above the horizontal limb of the præcentral sulcus, and the part next to the longitudinal fissure. The area is seen to be very extensive.

Fig. 4A gives the representation of the primary movement of rotation of the head to the opposite side. When compared with fig. 4 it is seen that the point of greatest intensity here is also just above the horizontal limb of the præcentral sulcus, and also next to the longitudinal fissure. In the corner formed by the two limbs of the præcentral sulcus the representation is faint, as this is the place where the simultaneous movement of the head and eyes is most marked.

Fig. 5 shows the representation of the primary movement of the simultaneous action of turning the head and eyes to the opposite side. The point of greatest intensity is in the angle formed by the two limbs of the præcentral sulcus, and is in counter-distinction to fig. 4*a*, where this part has only a feeble representation of the primary movements for rotation of the head.

Fig. 6. Here the absolute representation of the movements of the hallux are given. The greatest intensity is seen to be in front of the upper end of the fissure of Rolando, and to a less degree behind this end of the fissure; from these points the representation extends over the whole of the lower limb area, but in a very feeble degree.

Fig. 6A. The representation of the primary movement of the hallux is here seen to be localised almost entirely to each side of the upper end of the Rolandic fissure, and to have its seat of greatest intensity immediately in front of the fissure. The localisation is very sharply defined, and is more exact than any other joint of the lower limb. (*Cf.* figs. 7, 8, 9, and 10.)

Fig. 7 gives the absolute representation of all the toes acting together; the representation extends over the whole area for the lower limb, and has its greatest intensity just in front of and behind the most intense representation of the hallux.

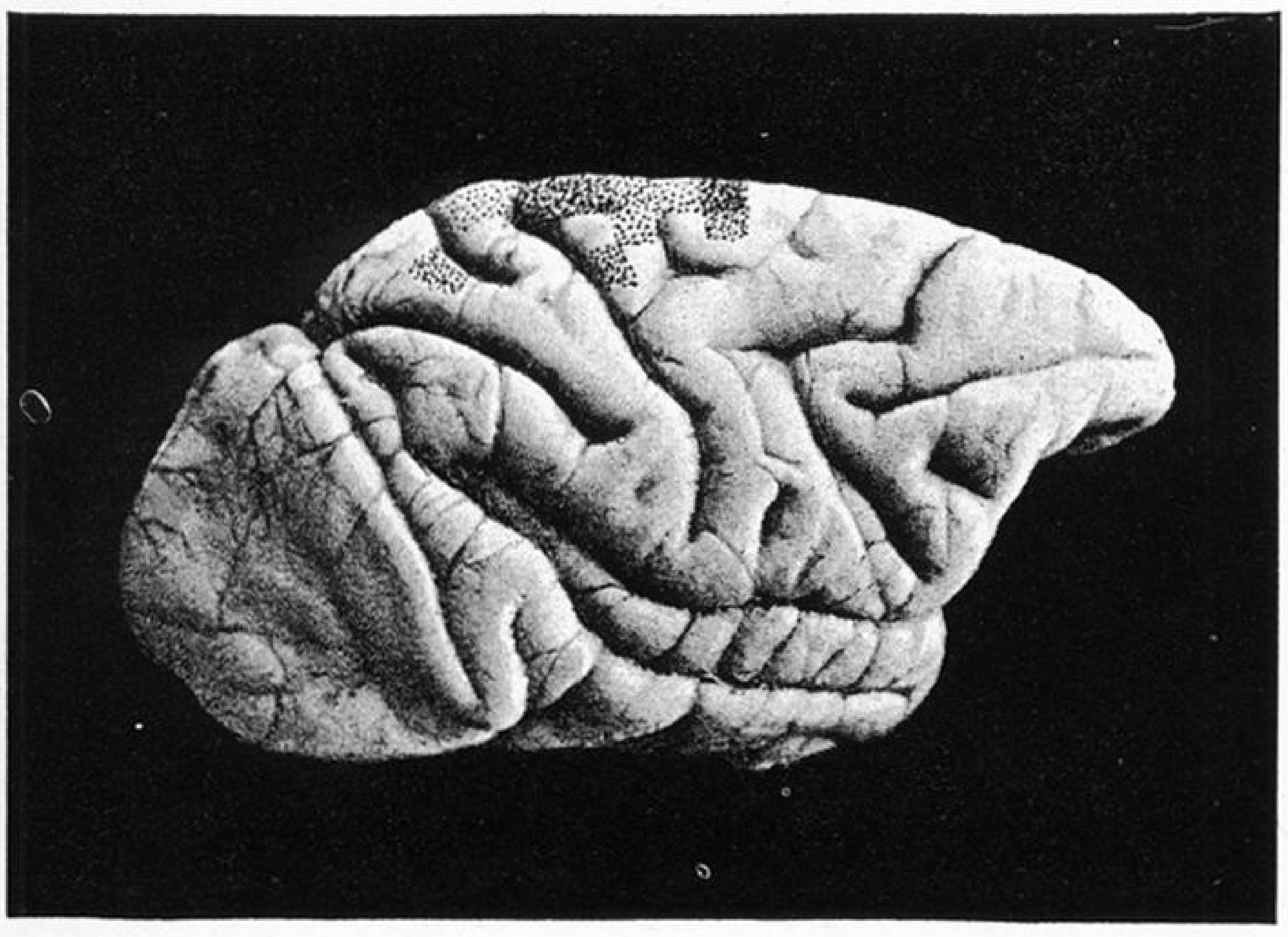


Fig. 8.—Representation of the movement of Flexion of All Toes.

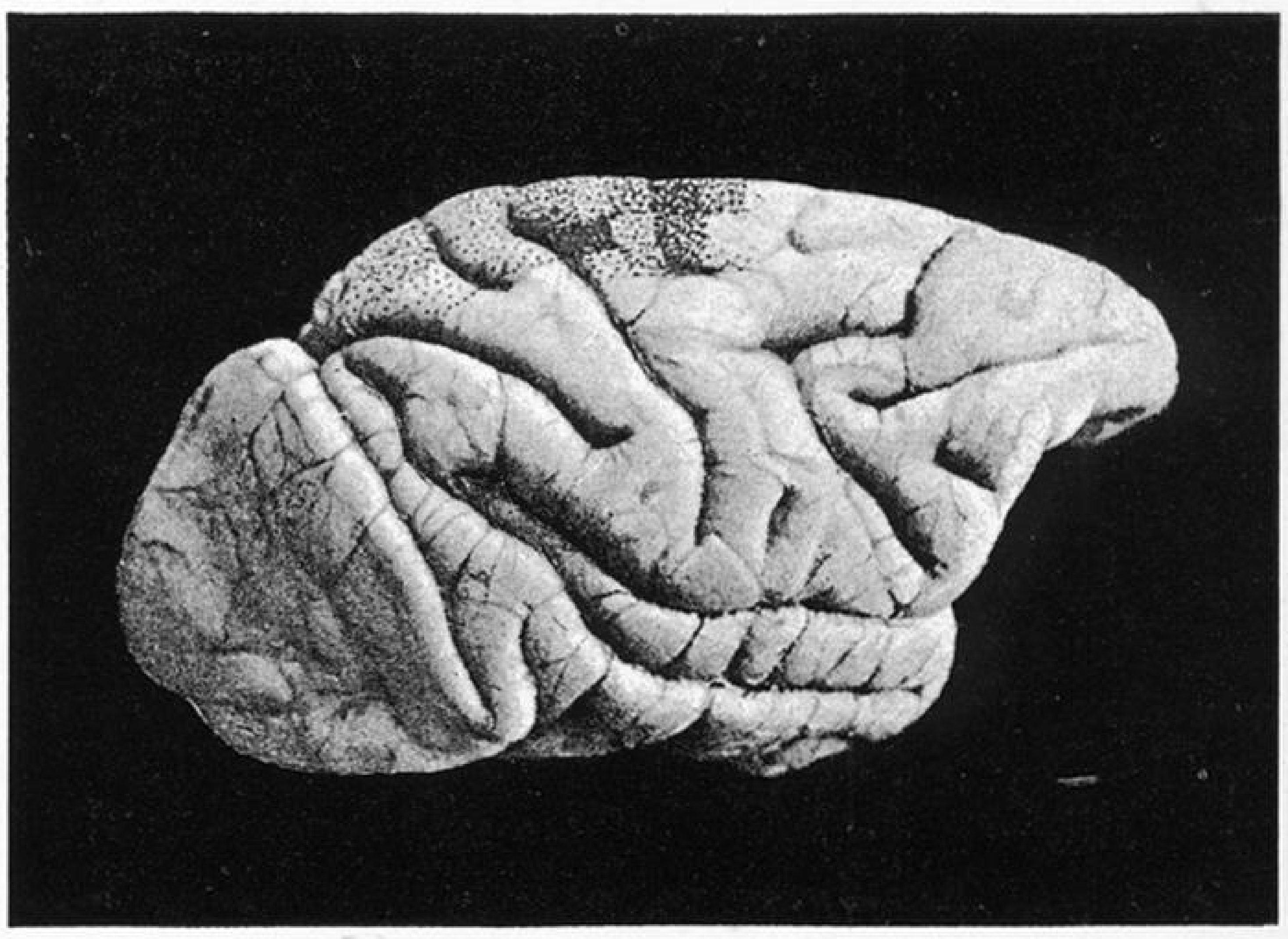


Fig. 9.—Absolute representation of the Small Toes.

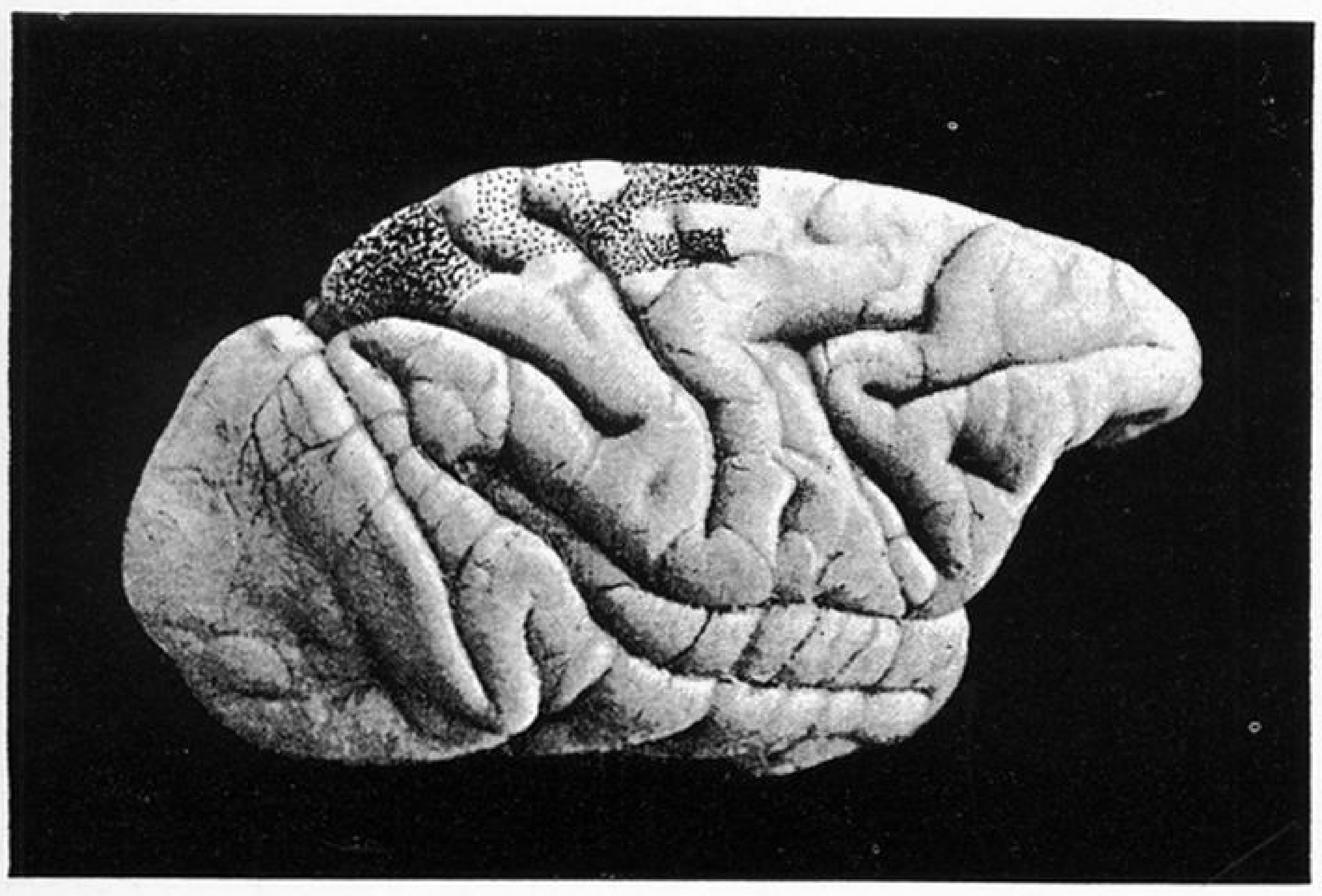


Fig. 10.—Primary representation of the Small Toes.

Fig. 11.—Absolute representation of the Ankle.

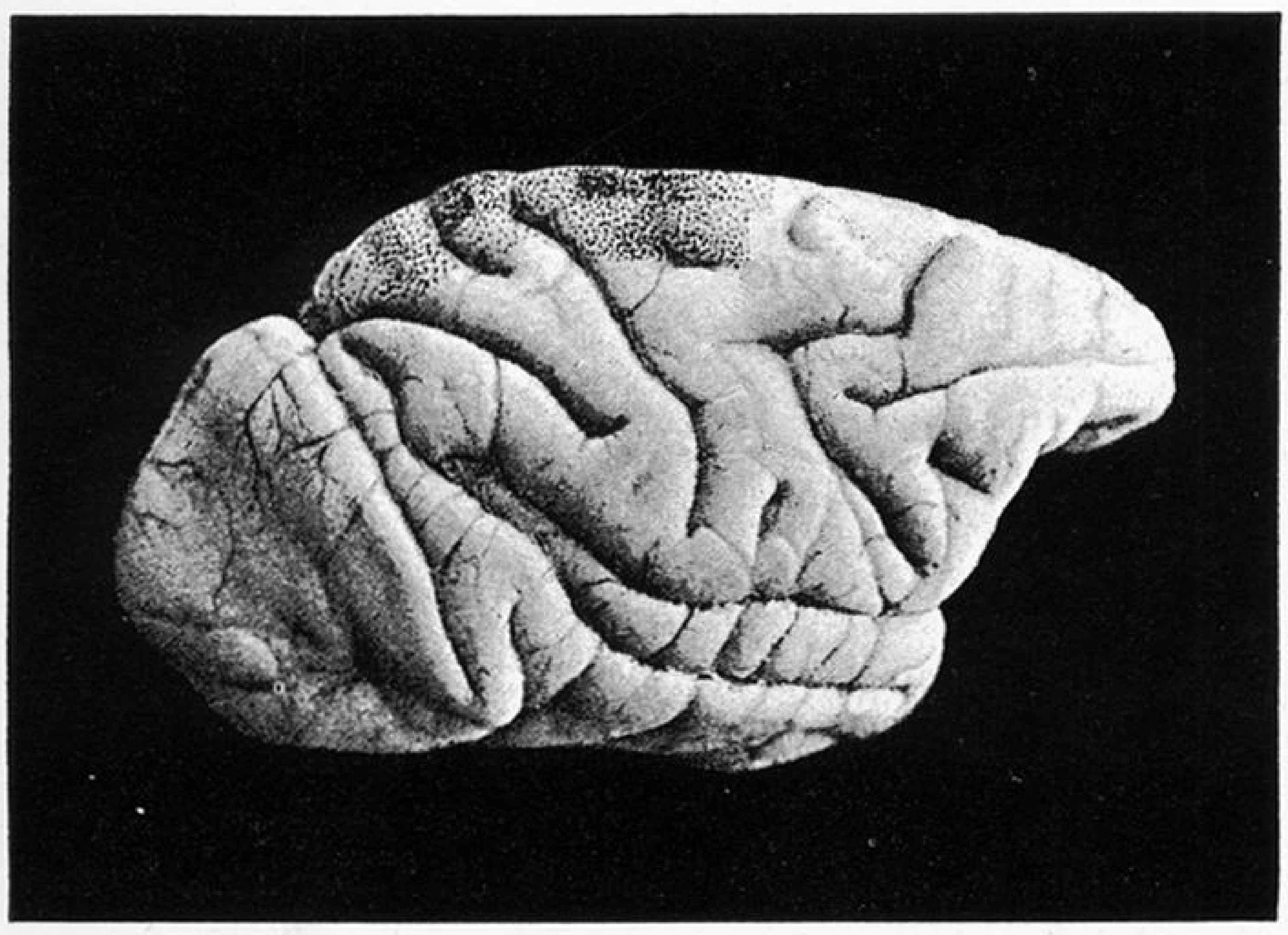


Fig. 12.—Absolute representation of the Knee.

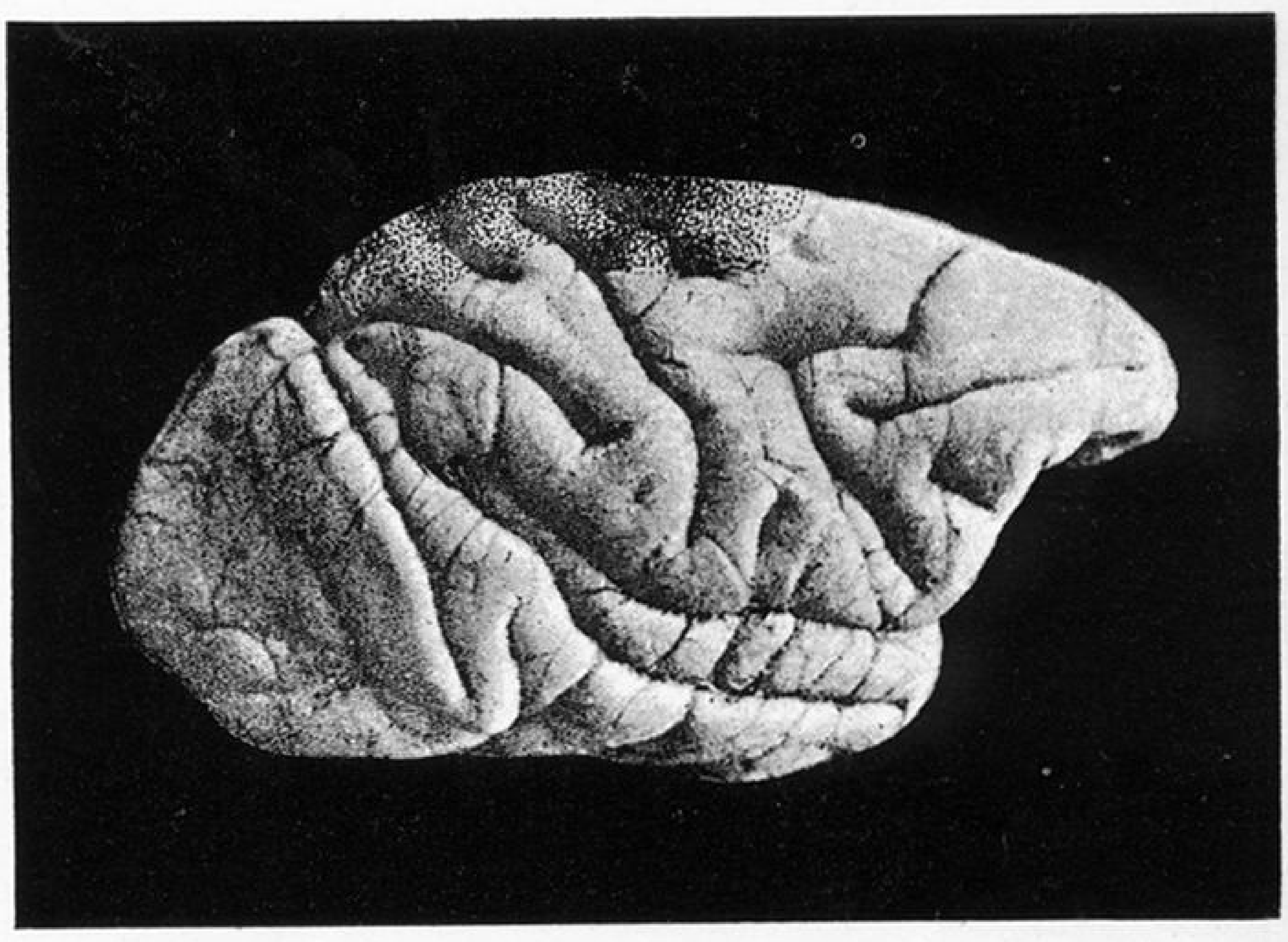


Fig. 13.—Absolute representation of the Hip.

PLATE 41.

Fig. 8. The representation of the movement of flexion of all the toes is here given, and it is seen to be almost entirely in front of the fissure of Rolando.

Fig. 9 gives the absolute representation of the movements of the small toes; the greatest intensity is seen to be in front of the fissure of Rolando, but in front of and below the part occupied by the hallux.

Fig. 10 shows the primary representation of the movements of the small toes, and, when compared with fig. 6A, it is seen to occupy that part of the area of the lower limb, which is not occupied by the representation of the primary movement of the hallux, *i.e.*, immediately in front of and behind the upper end of the fissure of Rolando.

Fig. 11 shows the absolute representation of the movements of the ankle. It is well marked over the whole of the lower limb area, and is better represented than the next joint, the knee (*cf.* fig. 12). Its greatest intensity is above the hinder end of the sulcus *x*, and in front of the area for the hallux.

Fig. 12 is the absolute representation of the movements of the knee; it has no special characters, but is fairly evenly distributed over the whole of the lower limb area, in conformity with the secondary character of the movements of this joint.

Fig. 13. The absolute representation of the movements of the hip is here given. While it extends over the whole lower limb area, it is most marked in front of the fissure of Rolando, and especially in the more anterior part; its greatest intensity here is further forward than the representation of the ankle (*cf.* fig. 11), and it is only slightly represented just in front of the fissure of Rolando, the area for the hallux.

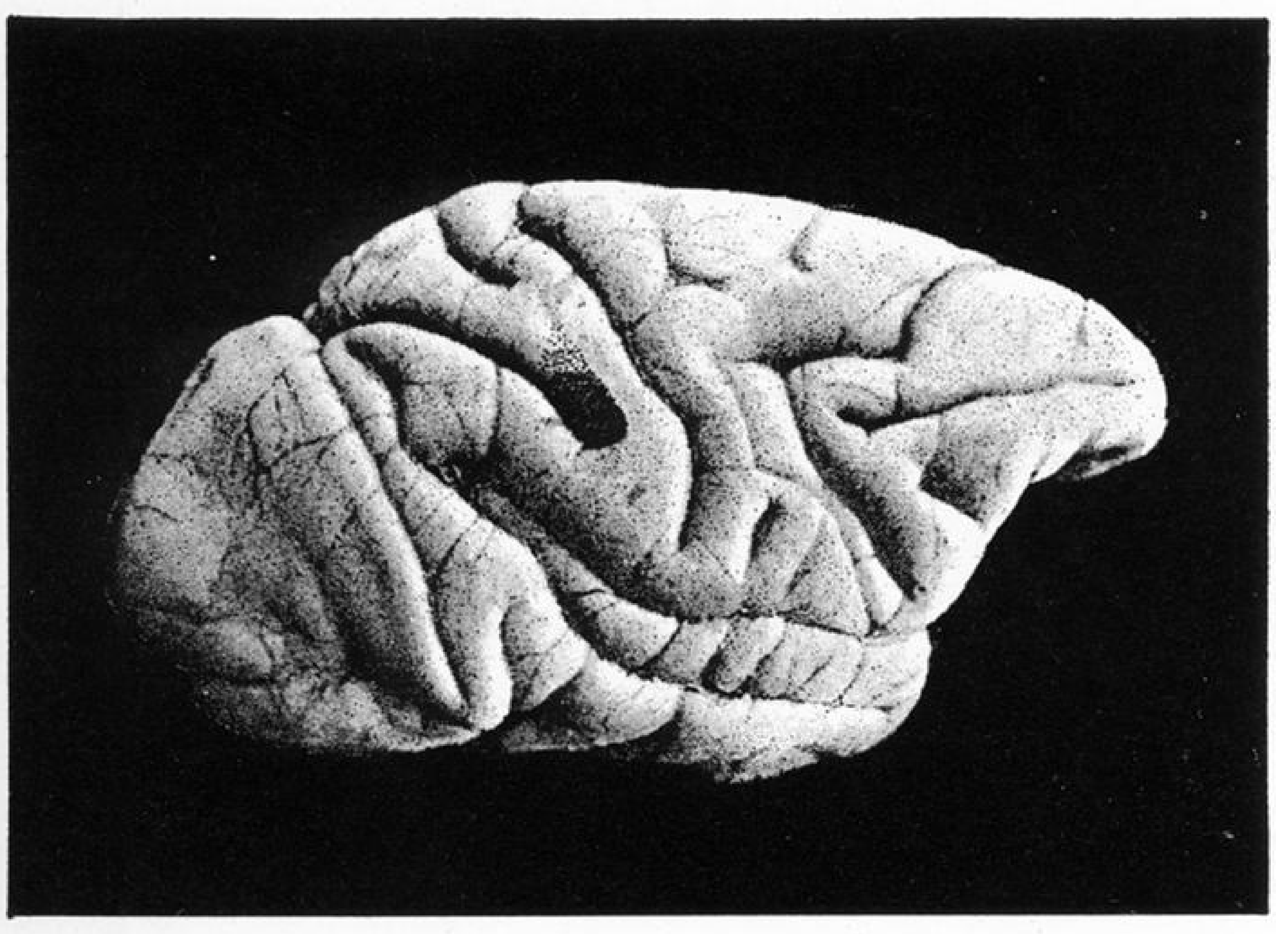


Fig. 16.—Absolute representation of the Thumb.

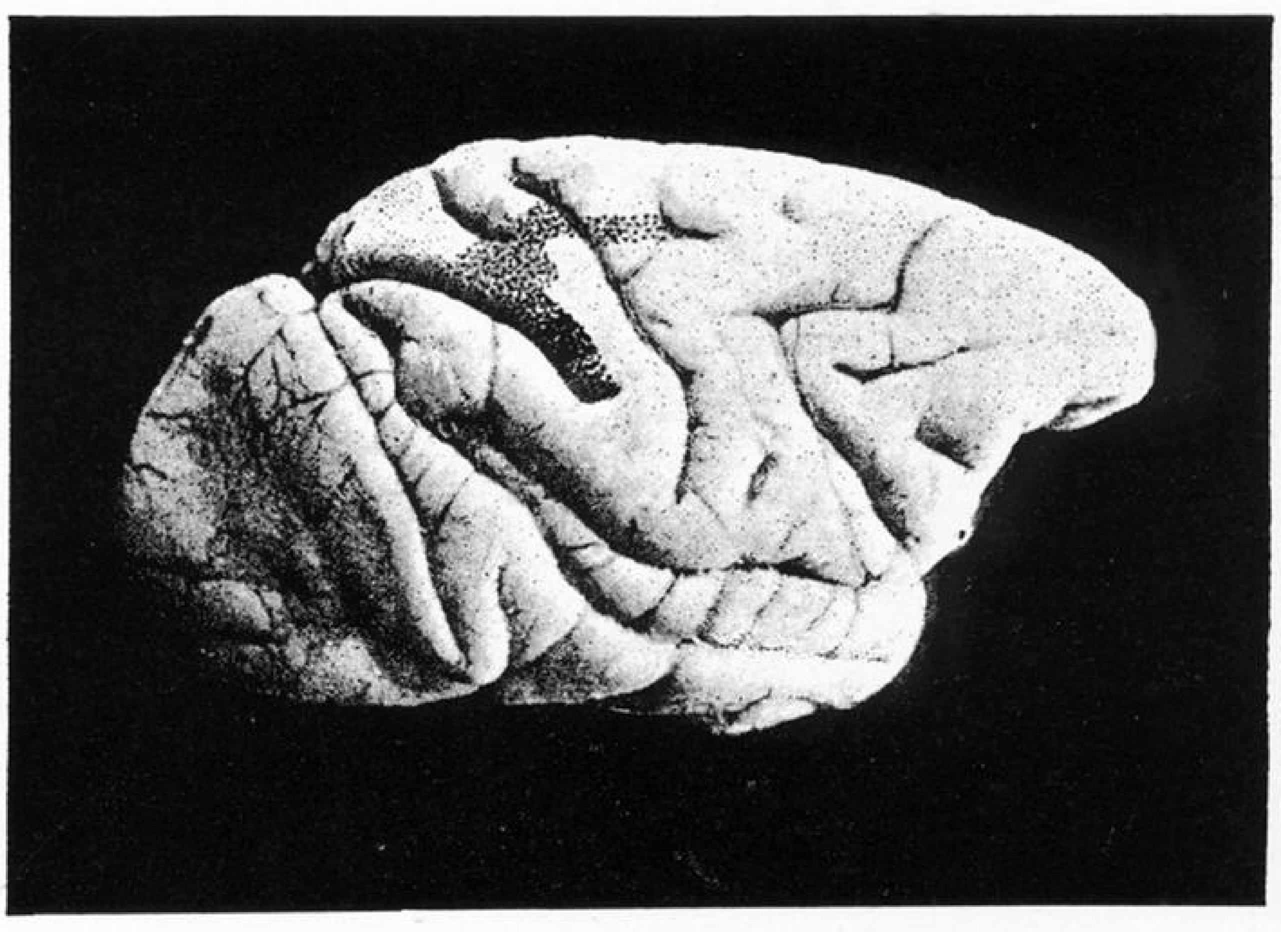


Fig. 17.—Absolute representation of the Fingers.

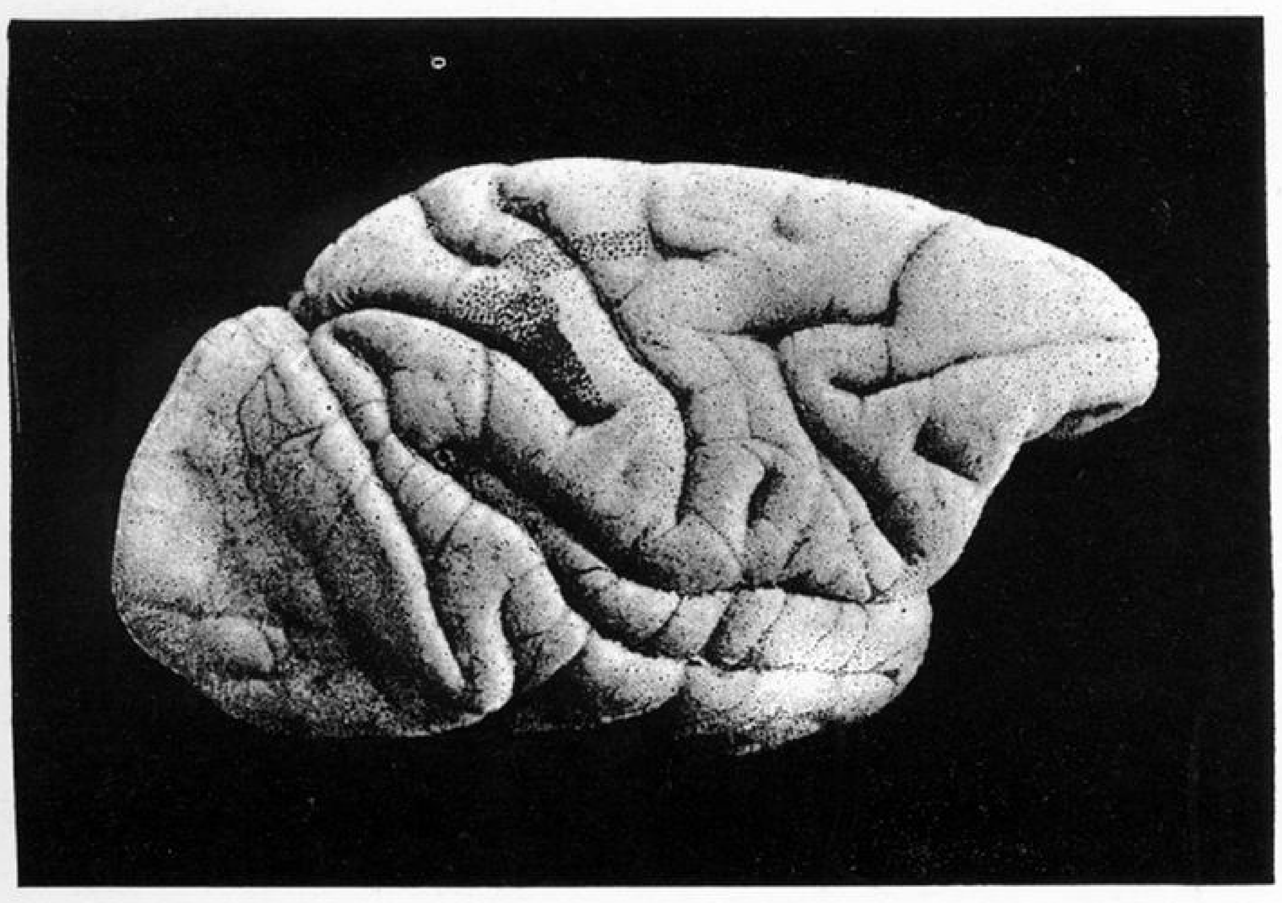


Fig. 18.—Absolute representation of the Wrist.

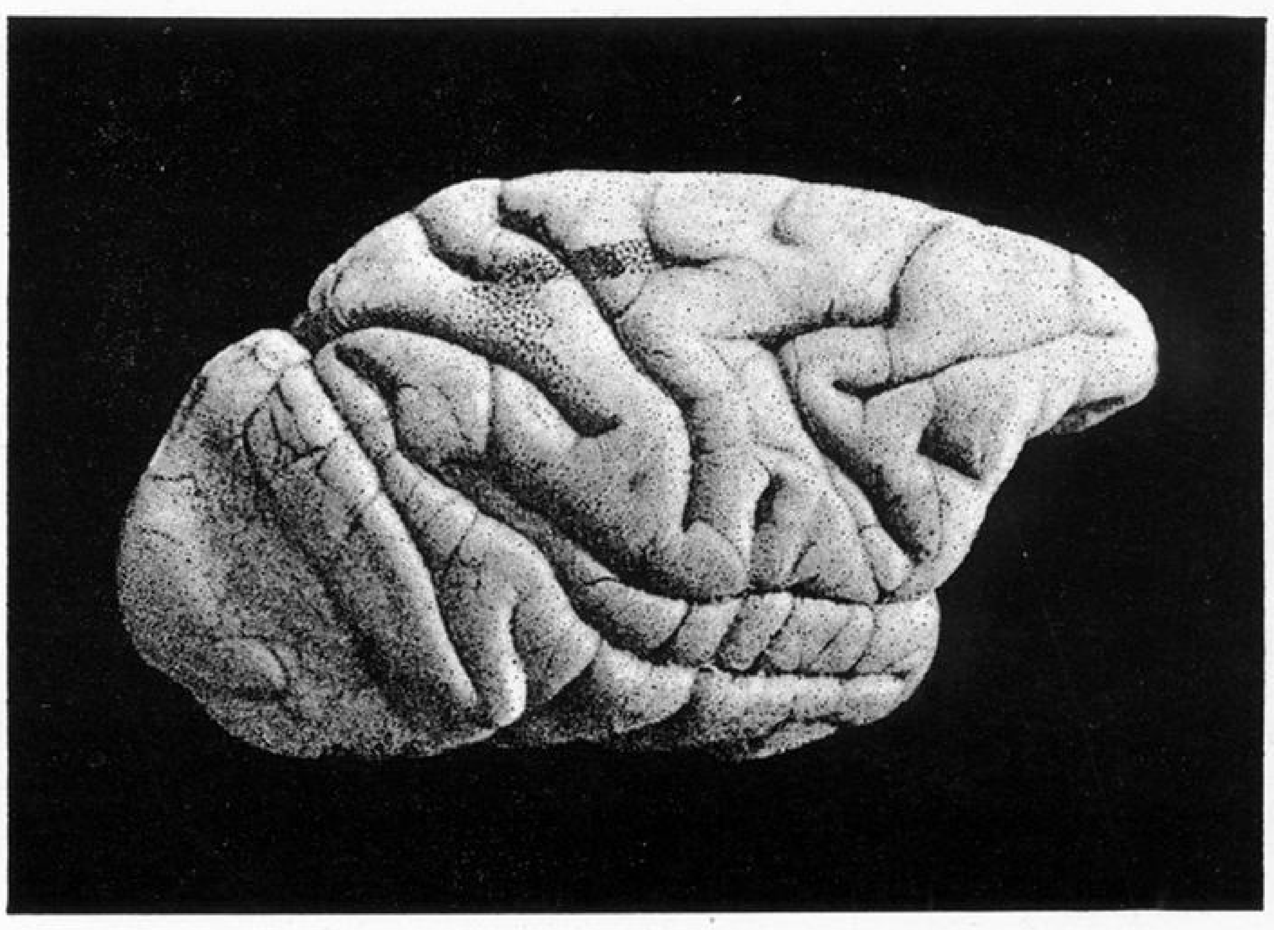


Fig. 19.—Absolute representation of the Elbow.

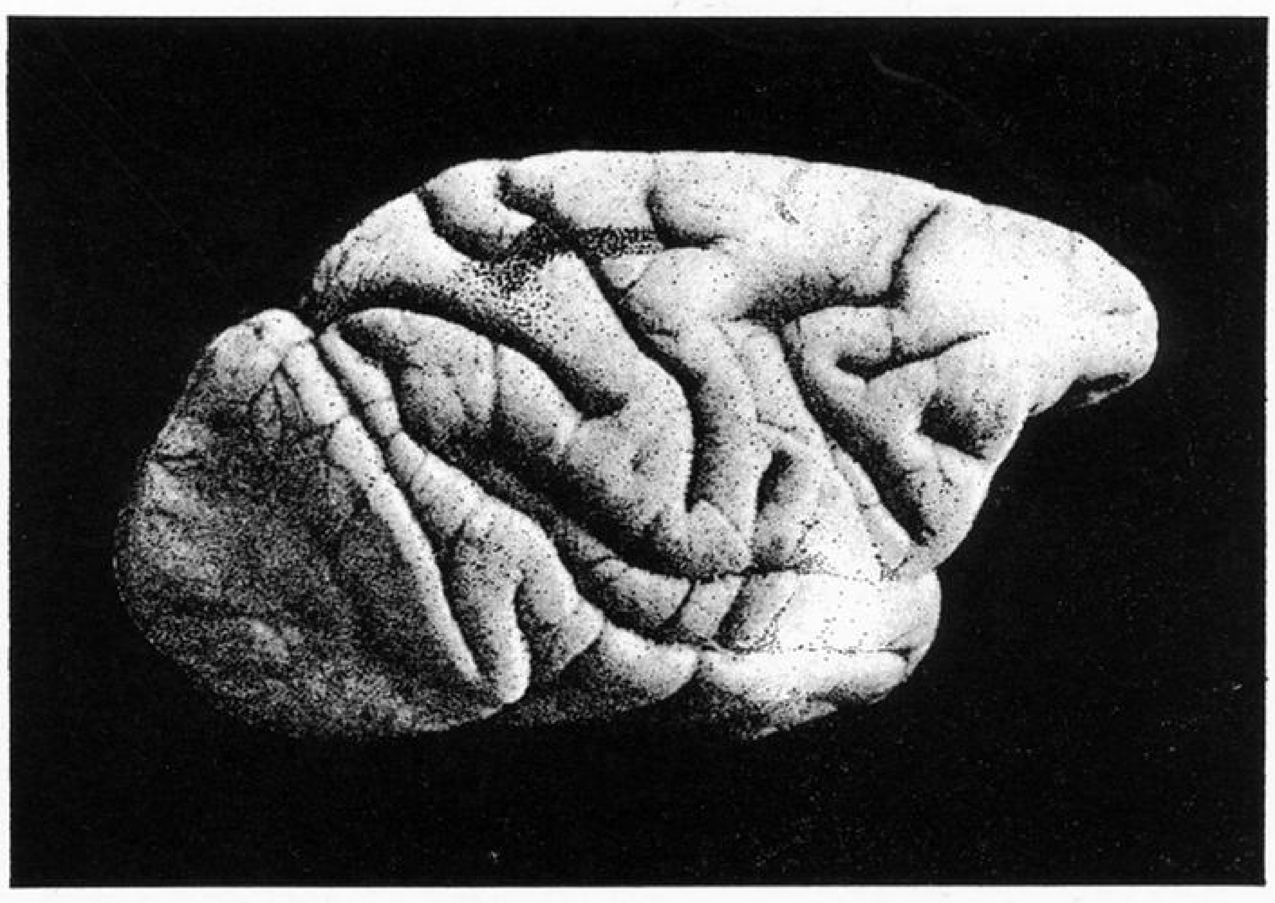


Fig. 20.—Absolute representation of the Shoulder.

PLATE 42.

Fig. 16 gives the absolute representation of the movements of the thumb as observed in the present research. It is seen in a very striking manner to be limited to the lower end of the intra-parietal sulcus and over a small area; its lower edge is sharply defined and its upper border exhibits only a very slight amount of shading off into the contiguous centres. It is the most highly defined of all the segments of the limb.

Fig. 17 shows the absolute representation of the movements of the fingers; it extends more or less over the whole upper limb area (examined in this present paper), and it is more extensive than the representation of the movements of the thumb (*cf.* fig. 16). But while it is only slightly represented in the upper part of the upper limb area, it is very marked at its lower part, and it will be noted that its point of greatest intensity is just above that of the representation of the thumb.

Fig. 18. The absolute representation of the movements of the wrist is here seen to extend over the whole upper limb area (here examined), and to be feebly represented at the upper part of this area, but to have its greatest intensity about the middle and just above the point of greatest representation of the fingers (*cf.* fig. 17).

Fig. 19 gives the absolute representation of the movements of the elbow. Though it is represented over the whole upper limb area (examined in this paper), it is very slightly marked in the part opposite the lower end of the intra-parietal sulcus; its chief seat being at the upper end of the upper limb area, on a level with the sulcus x, and its point of greatest intensity is at this level, immediately in front of the fissure of Rolando, and, to a less degree, in the contiguous part behind this fissure.

Fig. 20. Here the absolute representation of the movements of the shoulder is seen to be localised almost entirely to the upper limit of the upper limb area. It is most important to observe that the shoulder, alone of all the joints of the upper limb, is not represented at all in the lower part of this area, opposite the lower end of the intra-parietal sulcus—the seat of representation of the movements of the thumb and the fingers (*cf.* figs. 16, 17). The point of greatest intensity is seen to be in front of and behind the fissure of Rolando at the horizontal level of the sulcus x, the upper limit of the upper limb area.

On comparing figs. 16–20, it will be seen that the most intense representation of the movements of the segments of the upper limbs is arranged in a most perfect gradation from below upwards. The representation of the thumb occupies the lowest part of the upper limb area, *i.e.*, opposite the lowest point of the intra-parietal sulcus; the fingers have their seat of greatest intensity immediately above that of the thumb; the representation of the wrist is situated just above that for the fingers; while the elbow is represented higher up than the wrist, near the upper limit of the area. The representation of the shoulder forms the upper limit of the upper limb area, being localised rather higher up than that for the elbow.

It will also be noted as most important that, whereas the representation of the thumb is confined entirely to the lowest part of the upper limb area, the shoulder is represented almost entirely at the uppermost limit of this area, *i.e.*, the two extreme segments of the upper limb are limited in their representations to the extreme ends of the area.