VI. *A Minute Analysis (Experimental) of the Various Movements produced by stimulating in the Monkey different Regions of the Cortical Centre for the Upper Limb, as defined by Professor* FERRIER.

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[PLATE 7.]

THE following research was undertaken as a necessary preface to an investigation, which we are at present engaged upon, into the localisation of motor function in the cervical enlargement of the spinal cord.

Briefly speaking, the experiments from which the following conclusions have been drawn consisted in an elaborate examination of the movements elicited by stimulating with the interrupted induced current every part of the motor cortex in the Monkey, in which the upper limb is primarily represented, as first described by Professor FERRIER.

Before entering, however, on a detailed description of the present research, it will be necessary to discuss shortly the anatomical features of the parts of the cortex concerned.

Anatomy.—A glance at the accompanying diagram of the external or convex surface of the left cerebral hemisphere of the Macacque Monkey shows that FERRIER'S motor region is bounded inferiorly by the fissure of SYLVIUS, posteriorly by the intra-parietal sulcus, superiorly by the margin of the hemisphere, and anteriorly by a narrow strip of grey matter* in front of the vertical limb of the præcentral sulcus, and also by that sulcus itself. The central point of this area is the middle third of the ascending frontal convolution, and in this portion of the cortex and around it we have the cortical "centre" for the movements of the opposite upper limb.

Before enumerating the functions of this portion of the cortex it is incumbent upon us to draw attention to certain minute characteristics of the various sulci of this region, these being of great constancy, and therefore of primary importance in aiding exact localisation of function.

* By this is meant portions of the bases of the frontal convolutions, the extent of which can be mapped out by electrical excitation.

Proceeding from the best known of these to those which hitherto have escaped especial notice, we will commence with the fissure of ROLANDO.

The *fissure of* ROLANDO, in all the species of Monkey on which we have experimented, runs outwards, forwards, and downwards, forming an angle of 50° to 55° with the mesial margin of the hemisphere. In its course it presents the following changes of shape, which in our experience are perfectly constant. Thus, for the uppermost quarter of its extent it presents a distinct, though slight, curve with the convexity forwards; in the next, *i.e.* the second quarter, it is slightly curved, with the convexity in the opposite direction, viz., posteriorly; and this curvature, concave anteriorly, runs down into the third quarter, in which part of its course the fissure presents a well-marked bend forwards. To this bend we would now direct especial attention, for it can be demonstrated to exist perfectly distinctly in Man and most Monkeys. Further, in the *Monkeys* we have examined, this bend is situated, as we have already said, in the third quarter of the fissure; its apex or central point is rounded, and is just above the horizontal level of the lower end of the intra-parietal sulcus, while, at the same time, it is well below the level of the highest point of the præcentral sulcus. From the apex of this bend the fissure of ROLANDO in its lowest fourth slopes almost vertically downwards (vertically signifying at right angles to the longitudinal fissure) towards the Sylvian fissure.

The *præcentral sulcus* is directed upwards and distinctly backwards from the base of the ascending frontal convolution, which it limits anteriorly. Just before it reaches the level of the central point of the fissure of ROLANDO, it bifurcates into two horizontal limbs; the anterior and longer runs forwards, being slightly curved with the concavity downwards; the posterior, on the other hand, is directed upwards as well as backwards, and is extremely short, very rarely exceeding 2 mm. in length. The main stem of the sulcus presents a double curve, the upper half having a slight convexity backwards, while the lower half is markedly curved forwards. In this way the ascending frontal convolution is most narrow opposite the posterior superior limb of this sulcus, while below it widens broadly.

Superior Frontal Sulcus.—In December, 1883, Professor SCHÄFER published in the 'Journal of Physiology' an account of the brain of a Macacque Monkey, which was shown by Professor FERRIER at the International Medical Congress in London, in which account he drew attention to the existence of a small, but definitely marked, sulcus on the upper portion of the frontal lobe, having an antero-posterior direction, and dividing into two parts the surface of the brain between the upper end of the præcentral sulcus and the mesial margin of the hemisphere. This small sulcus lies just behind the line of direction upwards of the vertical stem of the præcentral sulcus. Professor SCHÄFER provisionally named this sulcus *x*.

We venture to think that this small sulcus is nothing less than the representative of the posterior extremity of the superior frontal sulcus of Man, and that, therefore, the portion of brain above it must be looked upon as the first or superior frontal con-

volution, and that that part which lies between it and the top of the præcentral sulcus is certainly the second or middle frontal convolution. Finally, all that portion of the cortex which lies below the anterior horizontal limb of the præcentral sulcus must at present be regarded as of uncertain denomination, since, for several reasons which need not be detailed here, the upper third of it would appear to belong to the middle frontal convolution, while there can be little doubt that the lower two-thirds are homologous with the third or inferior frontal convolution of Man. We will now return to the consideration of the evidence on which we ground the opinion that x is really the representative of the posterior extremity of the superior frontal sulcus in Man. This evidence we will consider under the following headings:—

1. Morphological significance as an important sulcus.
2. Functional significance as an important sulcus.
3. Anatomical form and direction.
4. Value as a determinant of localisation of function.

1. *Morphological Significance.*—We have already stated that Professor Schäfer had previously observed the constancy of this small sulcus, which opinion is fully confirmed by our experience. He has further shown on a transverse section that it was marked by a distinct folding in of grey matter—the sure indication of an important sulcus.

2. *Functional Significance.*—We have found that if electrodes are applied to the sulcus itself no movement follows, whereas, if they be just shifted to either border, the characteristic effects about to be described are obtained. Here we have a functional proof that this sulcus, although small, definitely divides two portions of the motor cortex. These portions, we shall see directly, have a different function.

3. *Anatomical Form and Direction.*—With one exception, we have found that the most constant direction of this sulcus is antero-posterior, though frequently it is slightly oblique. The exception referred to was found in a pig-tailed Monkey (*Macacus nemestrinus*), in which specimen the sulcus was almost vertical, and consequently parallel, to the fissure of Rolando. Now we would submit that we have here faithful imitations of the varieties of form presented by the superior frontal sulcus in Man. For, as is well known, that sulcus is most frequently a more or less straight antero-posteriorly directed line, while sometimes, though more rarely, it resembles a miniature præcentral sulcus in possessing a vertical stem parallel to the fissure of Rolando, from the middle of which there runs forwards an antero-posterior limb. If, therefore, we regard this sulcus, x, as the posterior extremity of the superior frontal sulcus, its variations in form will be most easily understood. Finally, we would observe that the superior frontal sulcus in Man commences posteriorly, well behind the line of the præcentral sulcus, directed vertically upwards; in fact, it begins posteriorly in the middle of the ascending frontal convolution. It is just this first part of the superior frontal sulcus which, lying over the anterior half of the breadth of the ascending frontal convolution, forms the sulcus, x, of the Monkey's brain.

4. *Value as a Determinant of Localisation of Function.*—We do not intend here to dwell on this point, because its full importance will be seen in the subsequent description of our experimental results obtained by stimulation, but we will anticipate so far as to say that this sulcus enjoys the distinction of separating the seat of the primary representation of the upper limb from that of the lower, a distinction which, it need hardly be added, is of the first importance.

Thus we have been led to designate this sulcus, x, by the more definite term of superior frontal sulcus, and we trust that the above evidence will be accepted as tending to establish this position.

The Intra-parietal Sulcus.—There is one variation in the form of this sulcus which we will notice, not merely because, so far as we know, it has not been described before, but also because it alters slightly the localisation of certain movements of the digits. This variation simply consists in a bending horizontally forwards of the lower end of the sulcus towards the fissure of ROLANDO, from which, in extreme cases, it is sometimes separated by only 3 mm. of surface of grey matter. This is particularly marked in the pig-tailed Monkey (*Macacus nemestrinus*). We shall refer to this point further.

Ascending Parietal Convolution.—We would draw attention to the fact that the upper end of this convolution—in other words, that part which represents in Man the parietal lobule—is invariably subdivided vertically by a subordinate sulcus, which is situated at the junction of the anterior and middle thirds of the convolution and runs down parallel to the fissure of ROLANDO. The lower end of this subordinate sulcus extends most frequently to the level of x, the upper end always being separated from the margin of the hemisphere by a few millimetres of cortex.

With the foregoing observations we conclude the anatomical description of the part under consideration.

PREVIOUS RESEARCHES IN THE SAME DIRECTION.

We will now describe the results obtained by Professor FERRIER on stimulating the same region, quoting verbatim from his 'Functions of the Brain,' 1st edition, 1876.

From the account there given we have drawn up the following Table, showing the relation between his nomenclature of centres stimulated and ours, and in the third column the results he obtained.

We find, however, that the area of cortex in which the upper limb is represented extends a little further towards the fissure of SYLVIUS than he has indicated; it is difficult also to make out the exact position of our centres 2 and 2′ in relation to his, but perhaps we may include them in his centre 6.

With these trifling differences, it will be seen that the broad facts in our account are practically identical with his, all minuteness of detail contained in the following pages being of course superadded by us.

TABLE 1.

FERRIER'S Centre.	Authors' Centre.	FERRIER'S Result.
3	12, 1′	Movements of the tail, generally associated with complex movements of thigh, leg, and foot, with adapted movements of the trunk by which the foot is drawn to the middle line of the body, as when the animal grasps with its foot or scratches its chest and abdomen.
4	1 9 (?) 11	Retraction, with adduction of opposite arm, palm of hand being directed backwards. This action . . . is such as may be ascribed to the latissimus dorsi.
6	3 3′ 4 4′	Supination, flexion of forearm by which the hand is raised to the face.
a *b* *c* *d*	7 7′ 8 behind 8′	Individual and combined movements of the fingers and wrist, ending in clenching the fist. Centres for the extensors and flexors of individual digits could not be differentiated, but the prehensile movements of the opposite hand are evidently centralised here.

We will now proceed to describe our method of experimentation, the results in full detail, and the generalisations which can be deduced therefrom.

Method of Experimentation.—The animal being thoroughly anæsthetised with ether, the left cortex was exposed *lege artis*, and the dura mater raised. A careful drawing was then made of the arrangement of the sulci, upon which was represented the position of the various points stimulated. The cortex, after being carefully dried to prevent diffusion of the current, was excited as follows. The apparatus employed was one DANIELL cell and an ordinary DU BOIS-REYMOND coil, but no attempt was made to equalise the make-and-break shock by means of a HELMHOLTZ wire. The electrodes were the ordinary platinum pattern, and were 2 mm. apart. The coil consisted of a primary bobbin wound round an iron core, with secondary bobbin sliding on a sledge over it, the distance between them being registered in centimetres, so that the strongest current would be at zero when the secondary coil completely covered the primary one. The primary current was interrupted by means of an ordinary NEEF'S hammer, and the secondary currents with this arrangement were of a strength sufficient to produce the sensation of slight pricking on the human tongue when the secondary coil was at 8, *i.e.*, 8 cm. from the primary. This very weak secondary current* was always employed so as to obviate the fallacy of diffusion. That this object was attained was obvious, for, if a certain movement was always obtained at one place, shifting the position of the electrodes for even one millimetre was sufficient to produce a totally different result.

* This was the weakest current which would produce a contraction in the muscles.

. Since in all the brains we have experimented upon the positions of the principal sulci were perfectly constant, we regarded them as definite landmarks by which we could accurately ascertain in different brains the position of each centre.

Thus, commencing above in the ascending frontal convolution, we took as our first landmark the sulcus x, and in the horizontal line behind it we placed our two first centres, 1 and 1′ (these to be explained directly, see fig. 1), and then placed opposite the level of the upper end of the præcentral sulcus the centres 3, 3′. Dividing the interval between these points (which in the average brain of the animals we employed, *i.e.*, nine out of the ten experiments, was 1 cm. in length) into two equal parts, we designated the point of division by the ciphers 2 and 2′. Below 3 and 3′ we placed 4, 4′ and 5, 5′ at distances equal to that between 2, 2′ and 3, 3′.

(The distance between the electrodes was 2 millimetres, and they were applied parallel to the longitudinal fissure at the points designated by the figures described above. These points or centres were about 4 mm. apart. Thus a considerable interval was left between the centres, which we explored in the same way, but we have not deemed it necessary to give the results of exciting the cortex at these intervals, since in every case they simply corroborated the effects obtained by stimulating the parts bounding them.)

We further found that the ascending frontal and middle-frontal gyri were so broad as to necessitate a vertical subdivision. To meet this contingency, we employ the plain figures for the centres of the posterior half, and figures dashed thus, 1′, for the anterior half; both, of course, being on the same horizontal level.

On reference to Table 3 it will be seen that, with the exception of the fingers and thumb, the absolute number of times that any movement is produced is much less in the ascending parietal than the ascending frontal convolutions, and further that the representation of even the thumb and index decreases as the gyrus is explored from below upwards.

From our experiments it appears to us that the ascending parietal convolution has less claim than the ascending frontal to be considered as an area of extensive representation of movement. We have been so impressed with the importance of deciding this fact that we have usually explored the former gyrus with the current directly after the skull has been removed, and subsequently repeated our examination of it at various intervals during the experiment, so as to eliminate any error in the direction of loss of excitability of the cortex of this gyrus.

We would call attention to the extraordinary degree of symmetry which exists in all the Monkeys on which we have experimented, and also that this is not merely morphological, but also physiological. Although this is a matter of great interest, we cannot enter into it in further detail.

Before giving the detailed results of our work, we would lay down the following axioms founded on our experiments.

Axiom 1.—Viewing as a whole the "motor area" of the cerebral cortex for the

upper limb, as defined by Professor FERRIER, we find that the regions for the action of the larger joints are situated at the upper part of that area, close to the middle line, while those for the smaller and more differentiated movements lie peripherally at the lower part of the area.

Axiom 2.—As a general rule, *extension* of all the joints, particularly of the wrist and elbow, is the most characteristic movement of the upper part of FERRIER'S arm centre; while *flexion* is equally characteristic of the movements obtained by stimulating the lower part. Finally, between these two regions there is a small portion where alternate flexion and extension predominate, a condition to which we have given the name of *confusion.**

We shall now proceed to give by means of tables the details of the experiments upon which the foregoing axioms are based.

In the following Table 2 we give general conclusions respecting the different movements of each joint obtained by stimulating the upper and lower half of the above-mentioned area.

TABLE 2.

Upper part of Area.	Lower part of Area.
Shoulder.—**Advancing.**	**Adduction** (nil in lower $\frac{1}{3}$).
Elbow.—**Extension** (uppermost $\frac{1}{5}$). Confusion (second $\frac{1}{5}$).	**Flexion** (remaining $\frac{3}{5}$).
Wrist.—(1) **Pronation** (upper $\frac{1}{3}$).	**Supination** (lower $\frac{2}{3}$).
,, (2) **Extension.**	**Extension** (flexion at end of action).
Posterior part of Area.	*Anterior part of Area.*
Digits.—**Flexion.**	**Extension.**
Thumb.—**Flexion** (nil in upper $\frac{1}{5}$).	**Flexion-Extension.**

Expansion of the foregoing Table (compare Table 2).

Shoulder.—In the above Table it will be noticed that rotation of the shoulder does not appear; this movement, though frequently observed, is but one of association. Rotation out occurs as the result of stimulating the lower three-fourths of the area, at least of that part which lies in front of the fissure of ROLANDO. In almost every case this rotation outwards was accompanied by flexion of the shoulder, so that the elbow was brought forward as well as rotated outwards.

Pure abduction was practically never seen by us, but it entered into the composition of the advancing movement, which we have shown to be characteristic of the upper fourth of the area. It will thus be seen that the movement of the shoulder, which we have called advancing of the arm, is neither pure flexion nor pure abduction, but a combination of these two.

Adduction is strongly characteristic of the movement of the shoulder in the lower

* Here both flexors and extensors are contracting at the same time, and consequently the joint is usually fixed in a median position, each group of muscles alternately dragging it in opposite directions.

half of the area. Indeed, a glance at Table 3 will show that it is almost the only movement in the lower third of the area, in which portion of the cortex, too, the joint is very feebly represented, movement of it only being met with once in ten times on stimulating the centre 5′. (See fig. 2 and Table 3.)

Adduction is the characteristic movement of the shoulder "centres" in the ascending parietal gyrus. Retraction (*i.e.*, extension with rotation out and some adduction) is especially represented in the anterior half of the upper third of the ascending parietal gyrus in the centres marked 9 and 11. (See Table 3.)

Circumduction was never seen.

Elbow.—We need only draw especial attention to the remarkably exact manner in which representation of extension of the elbow is limited to the upper fifth of the area experimented on, while flexion is equally the function of the lower three-fifths ; and to the existence of a very important zone of cortex, where the phenomenon of confusion is represented, this forming a border-land between the regions of extension and flexion. The explanation of this zone of confusion is easy, since the representation of the elbow—the movements of which occur in only one plane—admits necessarily of closely limited localisation. (See Table 3 and fig. 3.)

Wrist.—In tabulating the movements of this joint, it was obviously necessary to separate its two distinct functions, viz., pronation and supination, on the one hand, and flexion and extension on the other. We will first discuss the latter function, as by far the more important. On Table 3 it is seen how extremely constant is the movement of extension, and a moment's consideration will show that it is of fundamental importance, for it is clear that the delicate movements of the fingers could not possibly be performed with any degree of accuracy and force unless the wrist be previously fixed in moderate extension, and consideration of this fact also explains why the wrist is especially provided with powerful extensor muscles which act with considerable independence. (See fig. 4.)

In returning to the first-mentioned movements of the wrist, viz., pronation and supination, we have only to add that, as might be expected, supination is most marked in the lower two-thirds of the area, since it is here that we have also flexion of the elbow, *i.e.*, bicipital action. The converse equally holds, viz., that pronation is associated with extension of the elbow. This association is clearly the outcome of the two great classes of action in animal life, viz., that of defence and that of feeding. The former of these is a coarse violent movement, and is naturally associated in the upper part of the region with the centres for the large trunk and leg muscles, while the latter, more delicate, is represented near to the centres for the face and mouth.* (See Table 2.)

Digits.—The representation of the fingers must be considered apart from that of the thumb, the movements of which are the most highly specialized in the limb.

* Similar ideas have been previously suggested by Dr. LAUDER BRUNTON, F.R.S. See 'Brain,' vol. 4, p. 431.

We would first draw attention (see fig. 5) to the fact that the movement of simple extension is alone represented in the posterior extremity of the middle frontal convolution (according to our view), viz., at centres 12, 13, 12′, and 13′ (see Table 3 and fig. 5). It will be observed on Table 3 that in three instances we noted interosseal flexion in this region. Discussion of the relation between interosseal flexion and extension of the digits we shall enter into further on.

As regards the movement of flexion, we find that it is represented over the whole of the area which has been the subject of our investigations, with the exception of the centres above mentioned, viz., 12, 13, 12′, and 13′. We have now to draw attention to some extremely important considerations concerning the relative representation of the movements of flexion and extension. We have just seen that pure extension was limited to certain centres; we have now to add that we have only seen pure flexion at centres 1, 1′, 4, and 4′. We are not inclined to lay much stress on this limitation of the representation of the movements of pure flexion and extension, but we note the foregoing facts for the purpose of recording them.

We will now consider what appears to us the much more important co-operation of these two movements of flexion and extension of the digits. On this point we have obtained the exceedingly definite result that both movements are represented in the middle $\frac{1}{3}$ of the ascending frontal and parietal convolutions, and that, while in the ascending frontal convolution extension precedes flexion, in the ascending parietal convolution this order is reversed, and so extension follows flexion. In view of the fact that pure extension is only represented in 12, 12′, 13, and 13′, *i.e.*, in those centres which are immediately in front of the middle $\frac{1}{3}$ of the ascending frontal convolution, we readily understand how it comes about that in the ascending frontal extension *precedes* flexion, whereas behind the fissure of Rolando it *follows* flexion. We have observed interosseal flexion to precede long flexion in three cases, and only in the centres 8′, 2, 2′, 12, and 3. It is obviously possible that this interosseal flexion of the digits, consisting of flexion of the metacarpo-phalangeal joints and extension of the phalangeal joints, should co-exist in perfect harmony with long extension of the digits. It must not be understood that in all the remaining cases interosseal extension of the phalanges leads the way for the action of the long extensors; indeed, in many instances it appeared to us that preliminary extension of the digits was so sharp and complete as to be explained only by rapid and perfect action of the long muscles. We must add, however, that, although this preliminary extension of the fingers was extremely well marked, it was of very brief duration, whereas the subsequent flexion was very powerful, and was maintained as long as the electrodes were applied to the cortex.

Although we have thus written at some length on the relation between flexion and extension of the digits, we do not consider that the results were sufficiently absolute to permit of our speaking dogmatically, and we hope that further research will ultimately solve this problem.

Thumb.—The limitation of the representation of the thumb in the cortex (see fig. 6) is a matter of great interest, considering that it is the most highly differentiated member of the body. The representation is limited to the ascending frontal and parietal convolutions. No movement could be elicited by stimulating the centres 1, 1′, 5, and 11 ; to these we must add 2 and 2′, as being centres in which the thumb was only exceptionally represented, *i.e.*, in one-third of the total number of cases for 2, and one-fifth for 2′. It is interesting to observe that the thumb obeys the same general rules respecting the relations of the movements of flexion and extension as do the digits ; thus extension *precedes* flexion in the ascending frontal and *follows* flexion in the ascending parietal. The movement of opposition, which is, of course, the most highly differentiated one, was only obtained on stimulating the lowest part of the thumb area, viz., the centres 7 and 5′ ; this is in perfect harmony with the general plan of representation, as we have found it to exist in the outer convex surface of the cortex. (See Axioms 1 and 2.)

We may here refer to the fact that in 5′, in the ascending frontal gyrus, we obtained in two cases abduction of the thumb, whereas adduction was present in two cases in centre 7 in the ascending parietal ; this is a further illustration of the fact that extension is represented in the ascending frontal, and flexion in the ascending parietal convolutions.

Before leaving the consideration of the representation of the thumb, we would briefly draw attention to the fact that the representation of the thumb extends lower down anteriorly, *i.e.*, just behind the præcentral sulcus, than that of any other part of the upper limb. Thus it is represented at centre 5′, but not in centre 5, &c. (See Table 3.)

We employ throughout our paper this expression—Primary Movement—in a very definite sense, namely, to express that movement which is represented above all others at one particular spot in the cortex. This use of the expression is in harmony with Dr. HUGHLINGS JACKSON's view, viz., that cerebral localisation is in the main a matter of degree of representation of several movements, and not the close limitation of any one. We were brought to the necessity of closely examining this point, not from the considerations of theories, but by observing with what remarkable constancy the various joints of the limb took up movement in series according to the part of the cortex stimulated, and how invariably one joint would commence the action when we adopted a method of excitation which we may call instantaneous or minimal stimulation.

PRIORITY IN THE ORDER OF MOVEMENTS. (See fig. 7.)

We may now return with advantage to a detailed consideration of Axiom 1, viz., that the larger muscles are represented in the upper part of the motor area for the upper limb, while the smaller ones have their centres in the lower part of that area.

It seemed to us highly important, as bearing on this point, to note the order of movement of the different segments of the limb,—in fact, the "march," as it has been termed by Dr. HUGHLINGS JACKSON, of the nerve discharge,—since we consider that a complete series of observations of this kind would enable us to construct a definite scheme which would show at a glance where certain primary movements are really centralised.

By this we mean that we applied the electrodes to the cortex just long enough to evoke movement in one joint only, and then noted which moved first, and in what direction. This first movement we considered to be the primary or fundamental movement in the given portion of cortex stimulated. (The current employed in every case was only just adequate to produce such movement, and the secondary coil was usually 10 cm. distant from the primary coil.)

On fig. 8 is exhibited that joint in which primary movement occurs in each portion of the area.

In taking each joint separately, it is found that the shoulder presents priority of movement in the centres 1, 1′, 11; while the wrist is the first to move when we stimulate the centres 2, 2′, 12, 13, 3′. It is important to notice that the elbow does not present any absolute priority of movement over the other joints, for its only approach to priority is seen at centres 8, 8′, and 9, where it is associated with, and shares this action synchronously with, other joints, viz., the thumb and wrist. With regard to the fingers alone, the same thing is to be observed, viz., that they are not represented in primary movement in the cortex, and indeed are only associated once with a true primary movement, viz., in centre 12. Starting now with the series of joints moved as represented schematically in fig. 8, we will take up the order in which the other joints of the limb are secondarily moved.

Tabulating these joints in the order of centres stimulated, we have the following list:—

Centre.	Order of Joints moved.
Ascend. Frontal Convolution.	
1.	**Shoulder** { elbow, wrist, fingers.
1′.	**Shoulder**, elbow { wrist, fingers.
2.	**Wrist,** fingers, elbow, shoulder.
2′.	**Wrist** { fingers elbow } shoulder.
3.	**Thumb,** fingers, wrist, elbow, shoulder.
3′.	**Wrist** { thumb fingers } elbow, shoulder.
4.	**Thumb,** wrist, fingers, elbow, shoulder (4).
4.′	**Thumb** { fingers wrist } elbow, shoulder (2).
5.′	**Thumb,** fingers, elbow { wrist (1), shoulder (1).
Ascend. Parietal Convolution.	
11.	**Shoulder** { wrist elbow } fingers.
9.	**Thumb** **Elbow** } fingers, wrist, shoulder.
8′.	{ **thumb** **wrist** **elbow** } { shoulder fingers }
8.	{ **thumb** **elbow** } fingers, wrist.
7′.	**Thumb,** elbow, shoulder (1).
7.	**Thumb,** fingers, wrist, elbow (1).
Middle Frontal Convolution.	
12.	{ **Wrist** **Fingers** } { elbow shoulder }
13.	**Wrist**, fingers, elbow, shoulder.

The figures in parentheses show the greatest number of times out of a total of 10 in which a movement in the joint was produced.

As is shown in this Table, the sequence in the movement of the joints is fundamentally similar to that which had been arrived at from clinical observation by Dr. Hughlings Jackson in cases of epilepsy, in which he had recorded the "march" of the movements of the joints.

As all the facts which we have accumulated on the subject of the primary representation of movement of joints and the representation of secondary, &c., movements are collated in a very demonstrative manner in the accompanying figs. 7 and 8, a detailed description is hardly called for, but we cannot leave this pathologically very important subject without dwelling for a moment on some of the more salient features of our results.

We have already pointed out on page 163 why the shoulder, wrist, and thumb are the joints, *par excellence,* in which primary movement takes place.

We will now, therefore, discuss the march, *i.e.*, the order in which the movements of the various joints follow each other after the primary movement. The first and most fundamental fact concerning the successive invasion of the various joints has already been determined by Dr. Hughlings Jackson, viz., that when a movement emanating from the cortex, *e.g.*, of the upper limb, begins in the shoulder it proceeds downwards, involving successively the elbow, wrist, and fingers; and inversely, when it begins in the thumb and fingers, the "march" proceeds up the limb. We are here referring to movements presenting the characters of deliberate purpose, "voluntary" efforts, which also can be evoked by electric stimulation of the cortex, besides being exhibited in convulsive and epileptiform seizures. The observation of these movements as produced in our experiments has enabled us to form certain definite generalisations concerning the order of their march. Among these generalisations, the following appear to us to be the most important.

1. Movement of the upper limb, commencing with the shoulder, is not completed by a movement of the thumb; and, while this result is obtained at the extreme upper limit of the area, on the other hand, we have the exact converse at the lowest limit, viz., movement of the limb, commencing in the thumb, and ultimately involving the elbow, which is not completed by movement of the shoulder. In fig. 8 is shown diagrammatically the order of the march of movements occurring at each point in the area for the upper limb.

2. We wish next to point out the very remarkable constancy in the order of march in the centres 2, 2′, 13 (fig. 8). Here we are dealing with the very nucleus of the upper limb area, *i.e.*, that part of it in which the most frequent and most ordinary movement of the limb is represented, viz., preliminary fixation of wrist in extension, intended, as we think, for the purpose of permitting accurate movement of the digits; following this, flexion of the digits; next flexion of the elbow and subsequent adduction and rotation out of the shoulder, producing the complex movement which has been popularly styled the hand-to-mouth action, and which is unquestionably one of the most

important of the limb. The remarkable way in which this movement is represented in a nearly horizontal line on the cortex must not be overlooked.

Finally, fig. 8 illustrates most clearly how the mode of march is in harmony with the representation of primary movements in the various points in the area. Thus the movements consequential to the first movement obey the law we have already dwelt upon, viz., that the joints are represented from above down in the area, in the order of shoulder, elbow, wrist, digits, and thumb. The truth of this statement is rendered very evident when fig. 7 is compared with fig. 8.

To summarise briefly the facts contained in the foregoing pages, we consider :—

1. That sulcus x (SCHÄFER) corresponds to the superior frontal sulcus of Man.

2. That the muscles of the upper limb are progressively represented from above downwards, in the outer or convex surface of the hemisphere, in the order of their size and the movements of the joints: in the order of shoulder, elbow, wrist, finger, thumb.

3. That the joints are moved in the order of shoulder, elbow, wrist, and hand when the highest part of the area is stimulated, and in the converse order—thumb, fingers, wrist, elbow, shoulder—when the lowest part is excited, whilst between these extreme points the sequence of movement is commenced by a middle joint, *i.e.*, the elbow (incompletely), in the ascending parietal convolution, and the wrist to a very large extent in the ascending frontal.

4. That with regard to the quality of movements of the different joints represented in the cortex, the *shoulder* presents the following sequence from above down: advancing, abduction, rotation out, adduction; the *elbow:* extension, confusion, flexion; the *wrist:* extension, flexion, and pronation, confusion, supination. In the fingers and thumb the sequence is altered, and we have, broadly, extension anteriorly and flexion posteriorly. (For details refer to diagrams.)

5. That there is no *absolute* line of demarcation between the area of localisation in the cortex of one movement and that of another; each movement having a centre of maximum representation, this gradually shading off into the surrounding cortex.

TABLE 3.—*Résumé.* (Ten Experiments ; one incomplete.)

Gyrus	Centre	*Thumb.*	*Fingers.*	*Wrist.*		*Elbow.*	*Shoulder.*
Ascending Frontal Gyrus.	1.	Nil.	Flexion, 5.	Extension, 3.	Pronation, 4.	Extension-flex., 90°, 9.	Advancing abd., 10.
	1′.	Nil.	Flexion, 7.	Extension, 3.	Pronation, 5.	Extension, 10.	Advancing abd., 9.
	2.	? Flexion-extension, 4.	Ext.-flexion, 10.	Extension, 3.	Pronation-Sup., 4 to 4.	Flexion-confusion, 5 to 5.	Rot. out. add. abd., 7.
	2′.	Slight extension-flexion, 3.	Ext.-flexion, 9.	Extension, 7.	? Sup. 3.	Flexion-confusion, 5 to 5.	Rot. out. add. abd., 8.
	3.	Slight ext.-flex., 5 to 2.*	Ext.-flexion, 1 to 8.	Extension, 4.	Supination, 5.	Flexion, 10.	Rot. out. add. abd., 8.
	3′.	Ext.-flex., 2 to 1.	Ext.-flexion, 4 to 2.	Extension, 5.	Supination, 4.	Flexion, 5.	Rot. out. add. abd., 6.
	4.	Ext.-flex., 2 to 4.	Flexion, 5.	Ext.-flex., 3.	Sup.-pron., 5.	Flexion, 9	Add. rot. out., 5.
	4′.	Ext.-flex., 3 to 5.	Flexion-ext., 8.	Extension, 2.	Sup.-pron., 5.	Flexion, 9.	Add. 4.
	5.	Probably *nil.*	1 exception, same as 4′.				
	5′.	Ext.-opp.-abd., 8.	Ext.-flexion, 4.	Extension, 1.	.. ..	Flexion, 2.	Add., 1.
Ascending Parietal Gyrus.	7.	Flexion-add.-opp., 6.	Flexion-ext., 4.	Slight flexion, 1.	Slight sup., 1.	Flexion, 2.	Nil.
	7′.	Slight flex.-ext., 2.	Inteross. flexion, 1.	.. ..	.. ..	Flexion, 1.	Rot. out., 1.
	8.	Flexion-ext., 3 to 1.	Flexion-ext., 7.	.. ..	Sup.-pron., 2.	Flexion, 4.	Rot. out., 1.
	8′.	Flexion-ext., 3.	Flexion-ext., 6.	Extension, 2.	Supination, 1.	Flexion, 3.	Abd. confusion, 1; add. retr., 1.
	9.	Extension, 1.	Ext.-flexion, 3.	Extension, 2.	.. ..	Flex.-conf., 2.	Add., 2.
	11.	Nil.	Flexion-ext., 2.	Extension-flex., 2.	Pronation, 1.	Conf.-flexion, 3.	Adduction with retraction (Lat. dors.), 4.
Middle Frontal Gyrus.	12.	Nil.	Extension, 6; inteross. flex., 1.	Extension, 6.	Pronation, 1.	Confusion, 7.	Rot. out. abd., 5.
	12′.	Nil.	Extension, 1; interosseal flex., 2.	.. ..	.. ..	Confusion, 2.	Rot. out., 1.
	13.	Nil.	Extension, 2.	Extension, 3.	Supination, 1.	Flexion, 4; 90°, 2.	Rot. out. add., 2.
	13′.	Nil.	Extension, 1.	.. ..	Supination, 1.	Flexion, 1; 90°, 2.	Rot. out. add., 2.

N.B.—The sequence of movement is indicated by the amount of underlining, thus:—The primary movement is denoted by one line, the secondary by two lines, and the third and fourth by three and four lines respectively.

Note.—The numbers *following* the record of each movement indicate the number of times that any action was obtained by stimulating the given centre. As before mentioned, we do not here give the results of stimulating the centres indicated by fractions, *i.e.*, the areas of cortex intervening between the above enumerated centres, because they simply corroborated the observation that the representation in one centre gradually merged into that of the next.

* Adduction in one case.

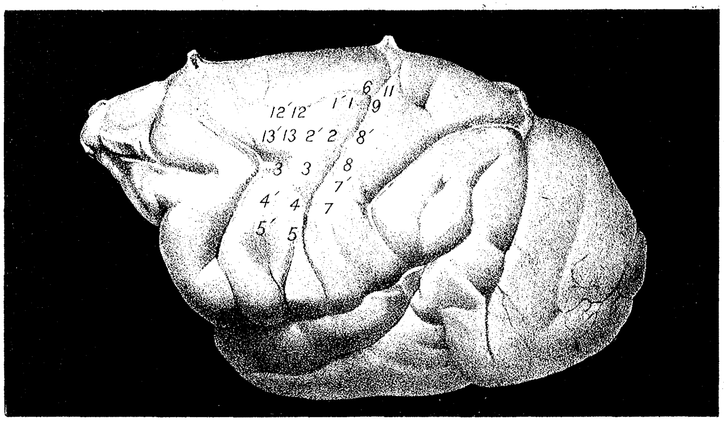

Fig. 1

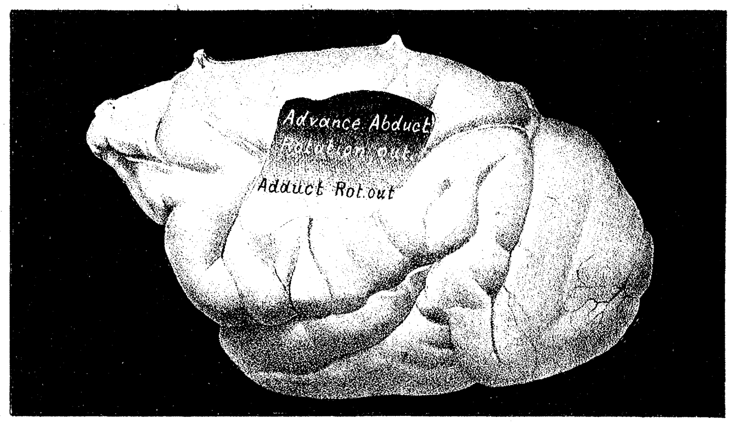

Fig. 2

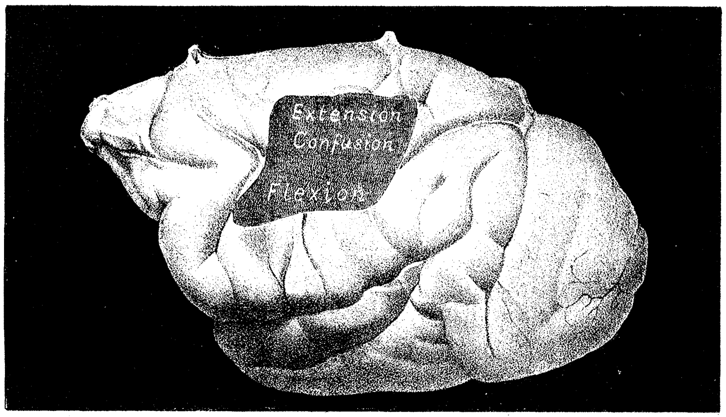

Fig. 3

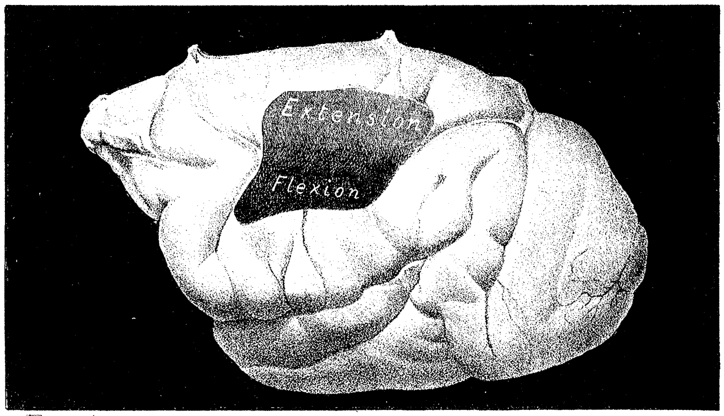

Fig. 4

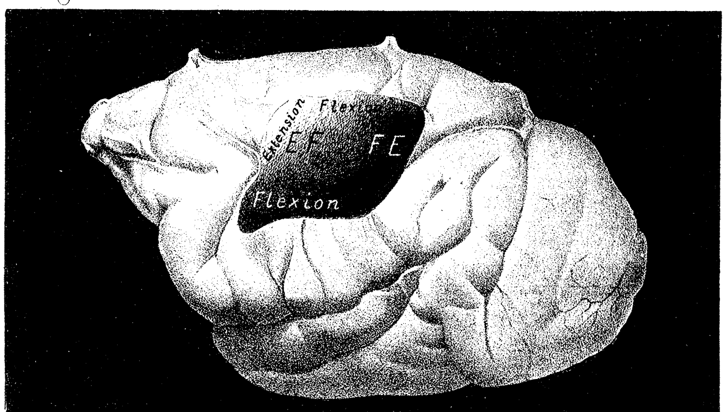

Fig. 5

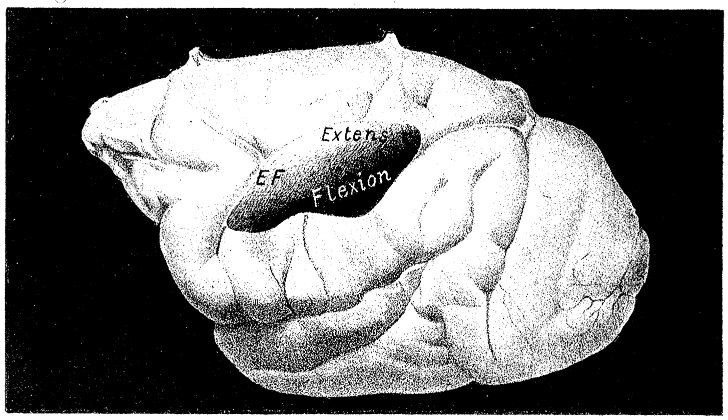

Fig. 6

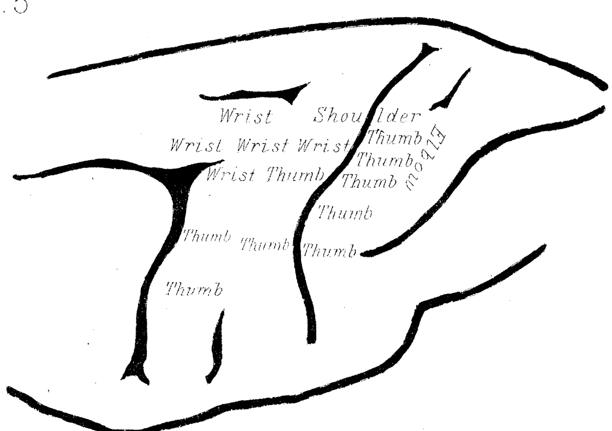

Fig. 7

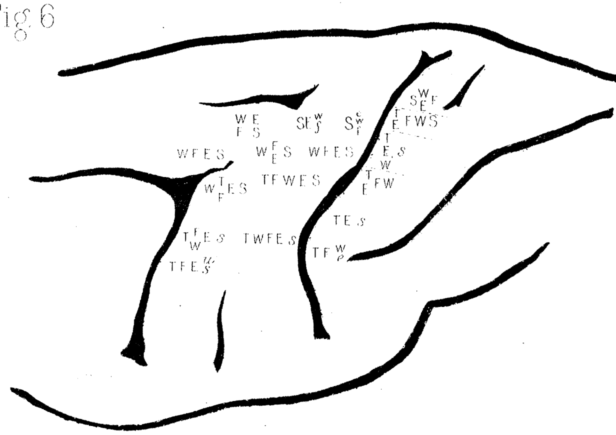

Fig. 8

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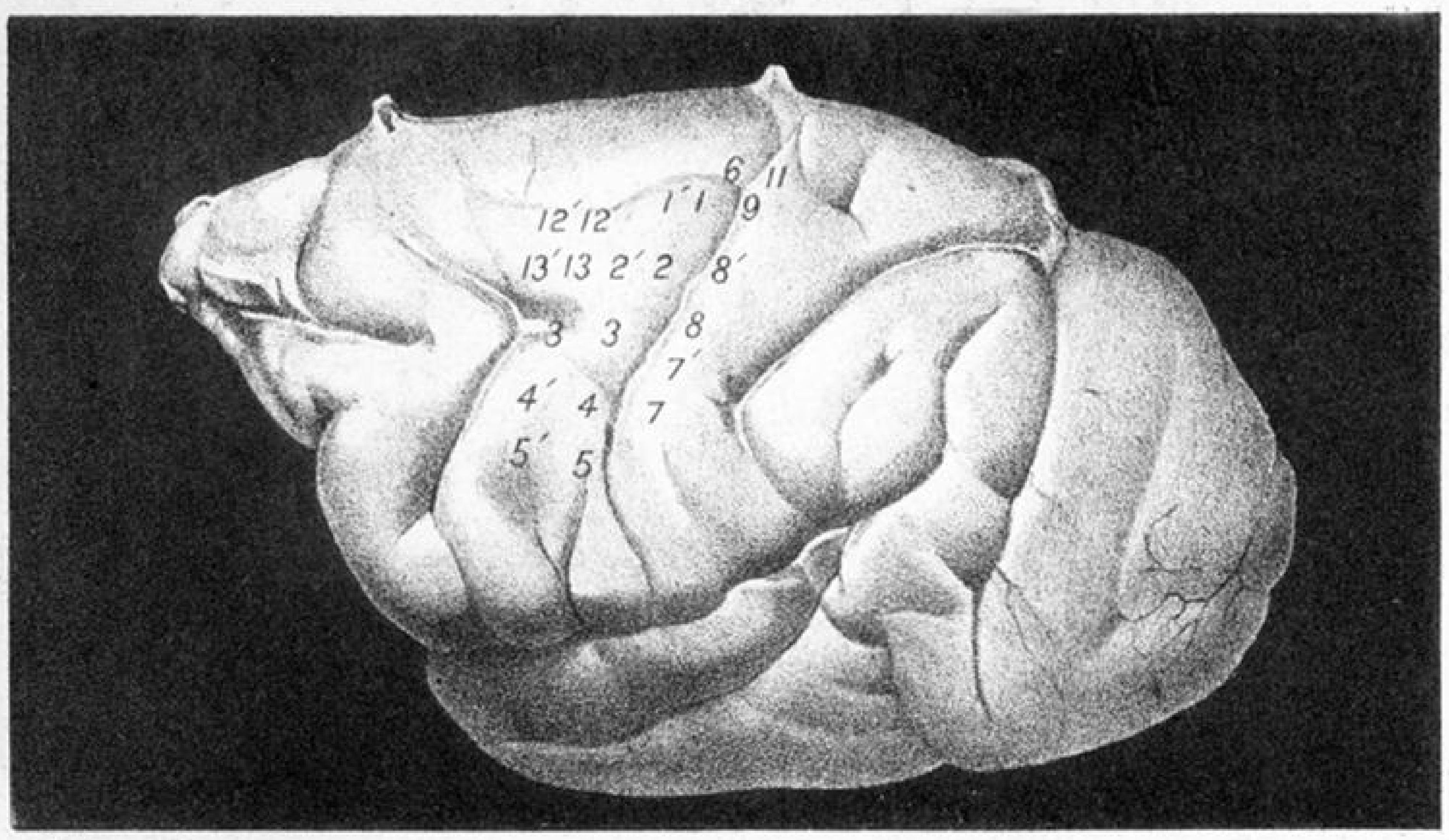

Fig. 1

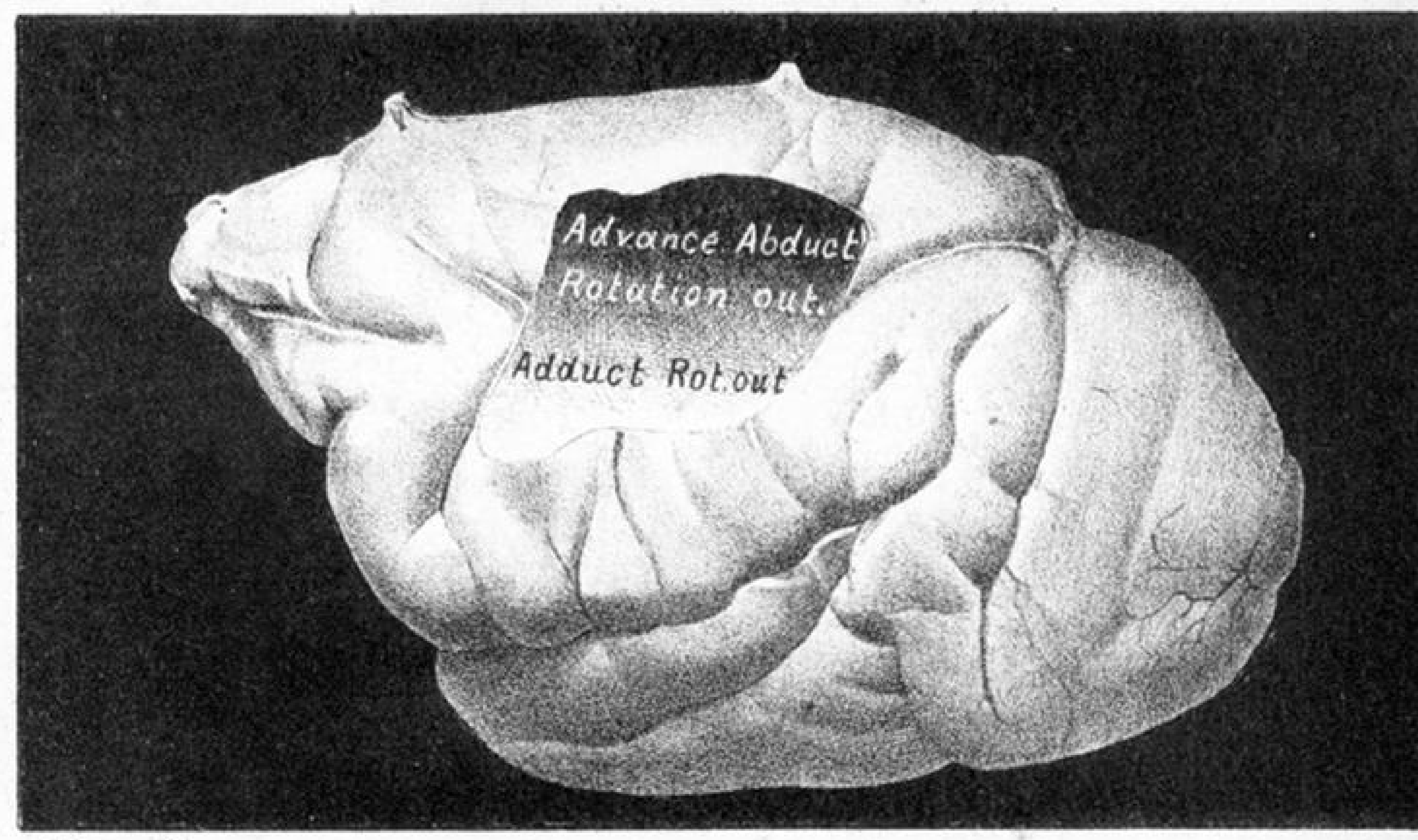

Fig. 2

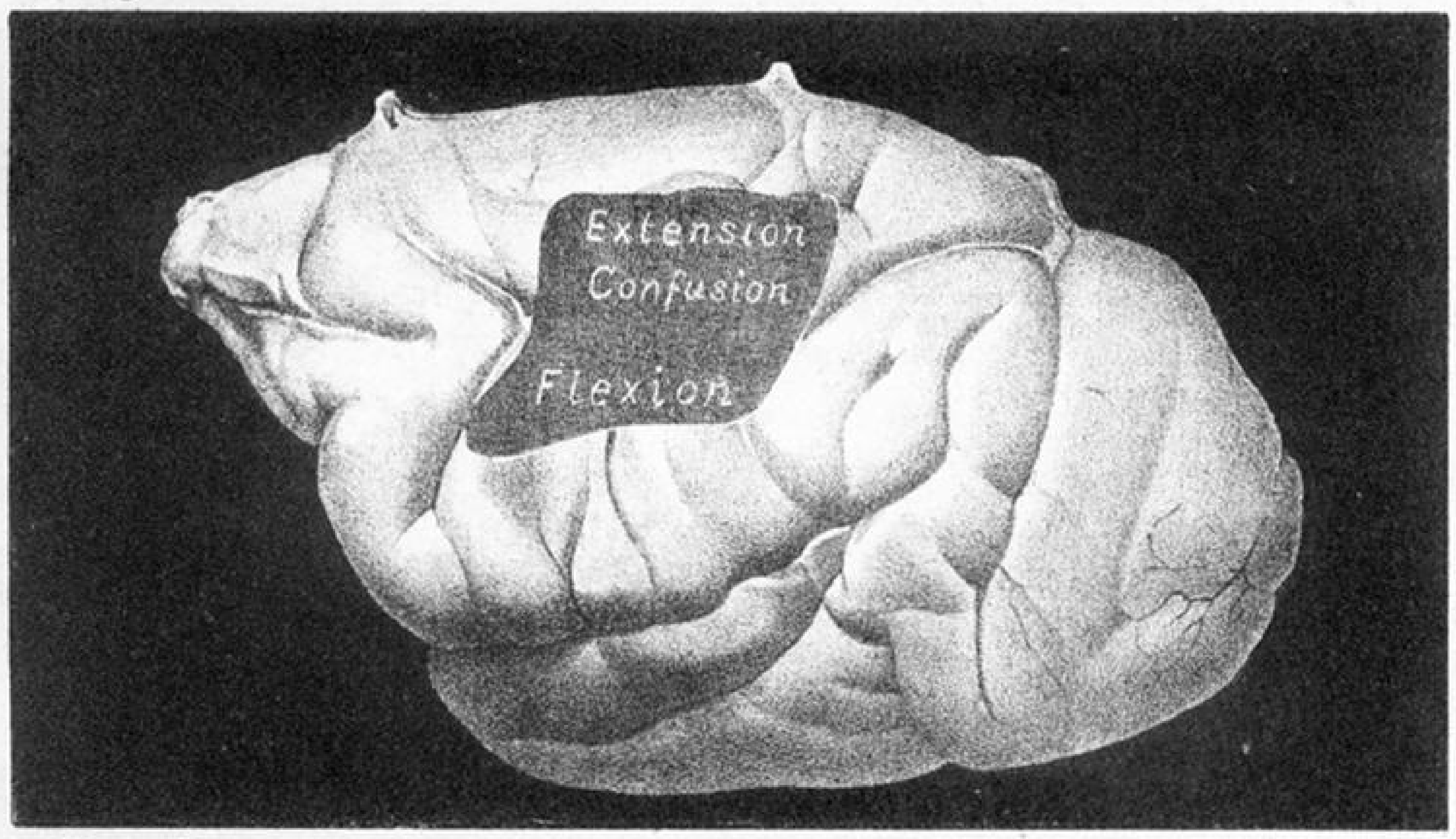

Fig. 3

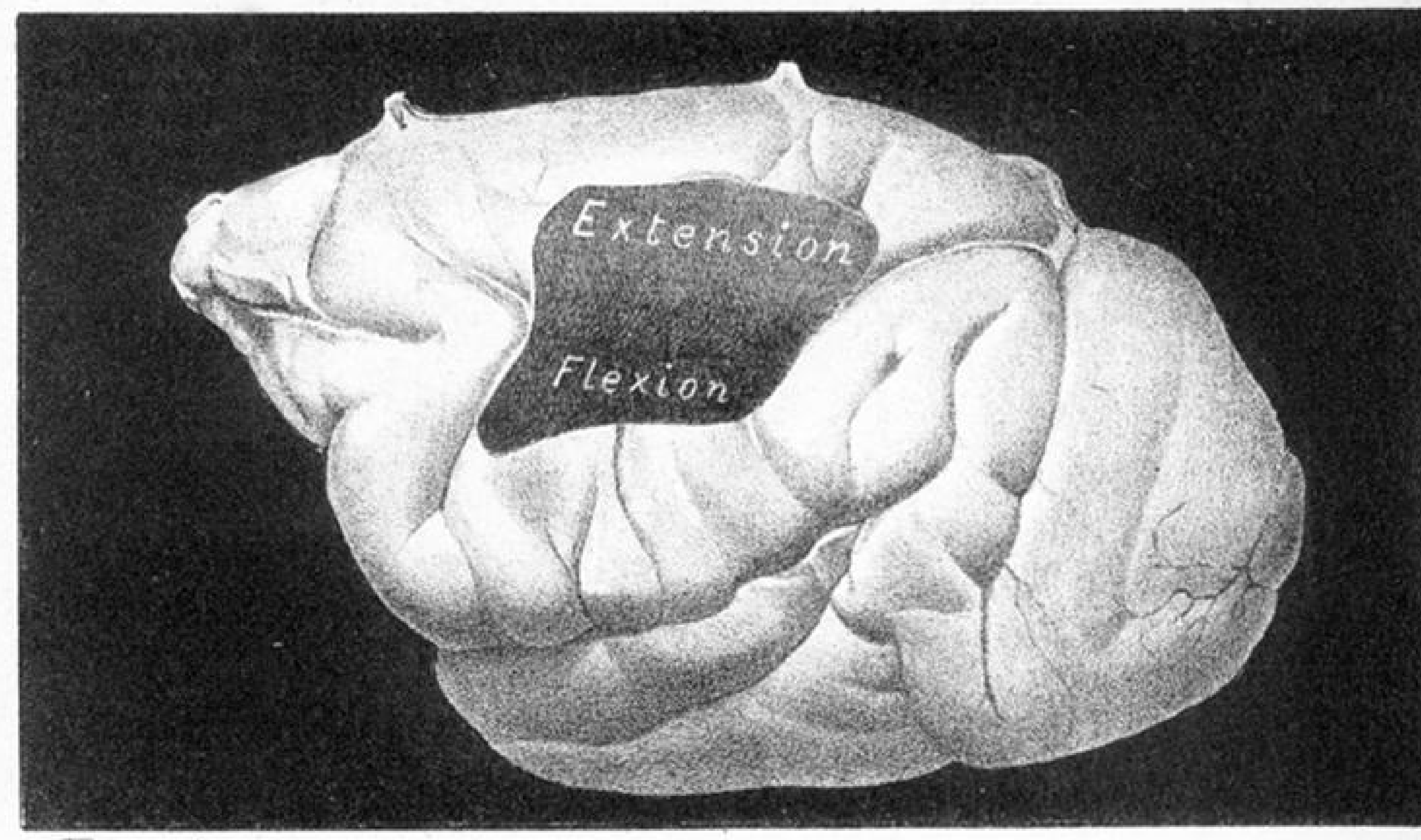

Fig. 4

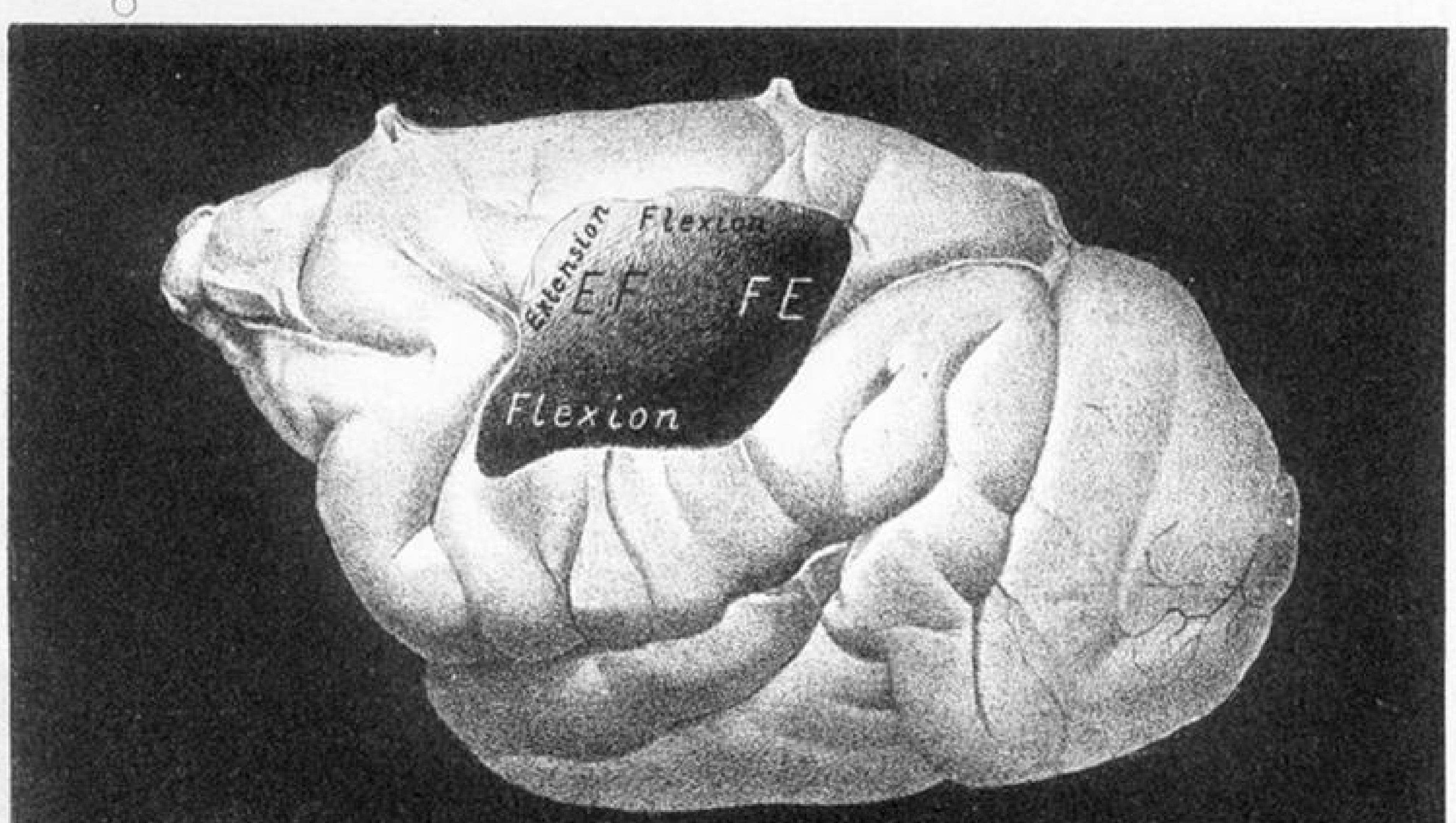

Fig. 5

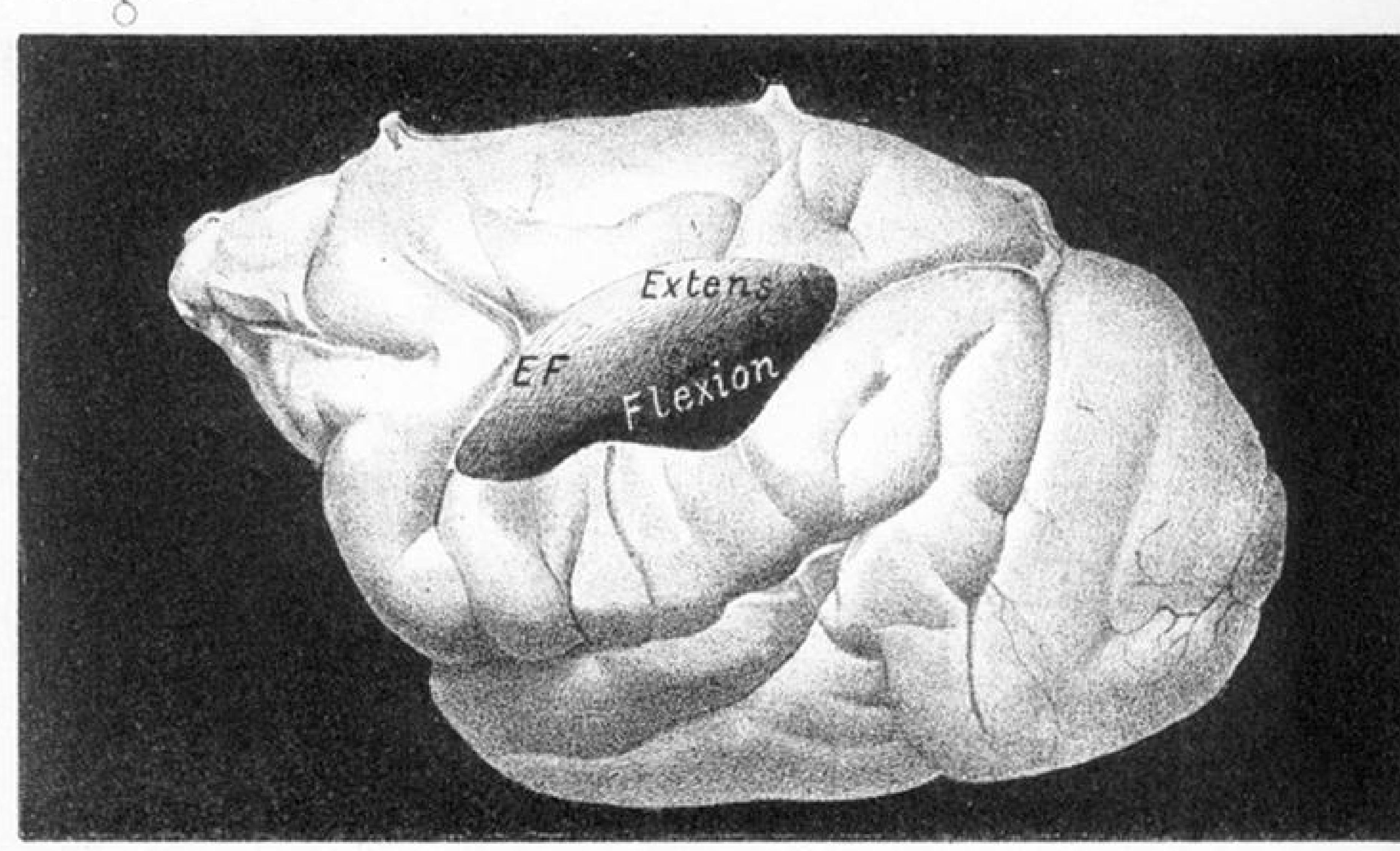

Fig. 6

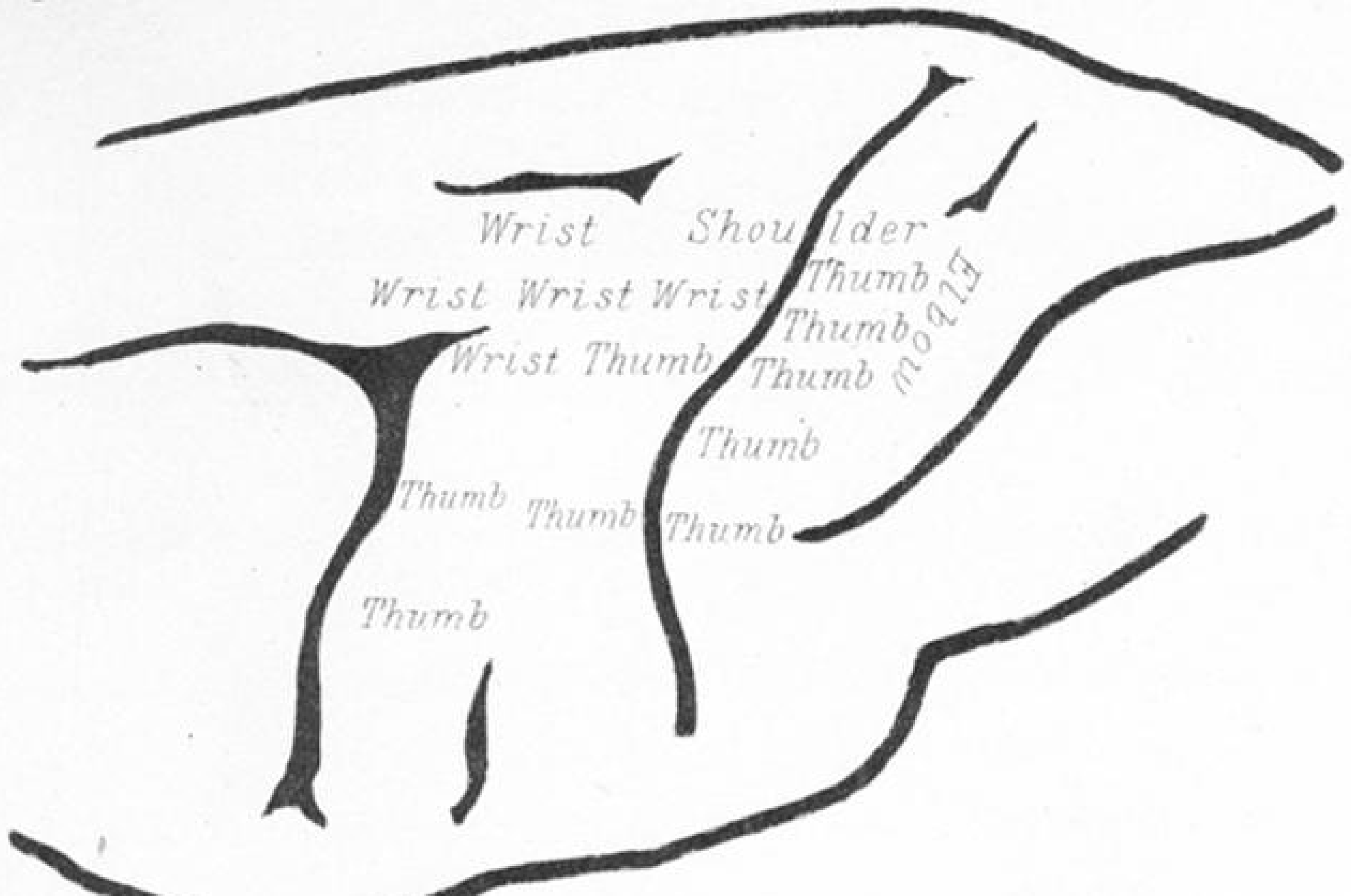

Fig. 7

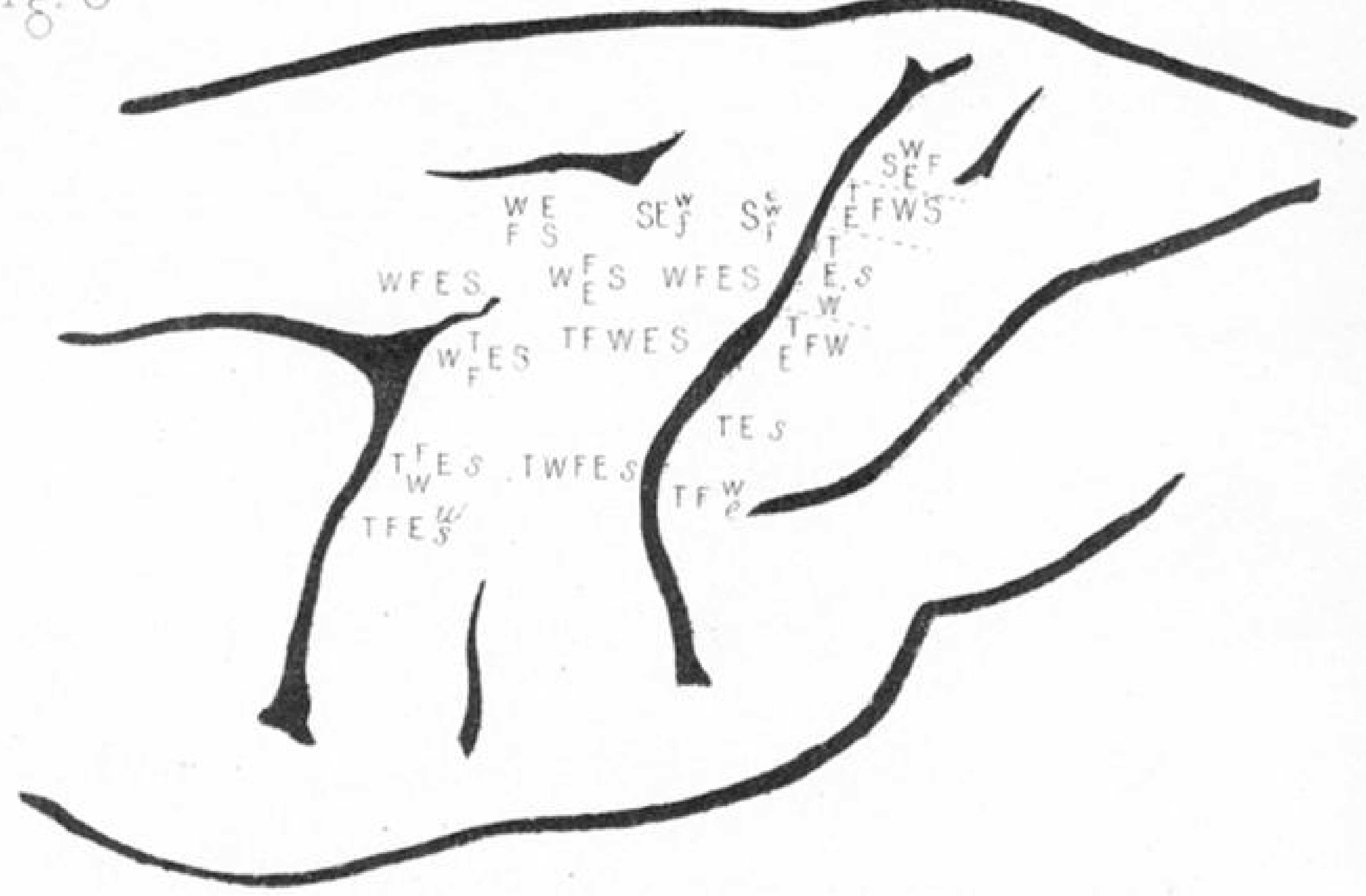

Fig. 8