PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

An Experimental Investigation into the Arrangement of the Excitable Fibres of the Internal Capsule of the Bonnet Monkey (Macacus sinicus)

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Phil. Trans. R. Soc. Lond. B 1890 **181**, 49-88
doi: 10.1098/rstb.1890.0003

III. *An Experimental Investigation into the Arrangement of the Excitable Fibres of the Internal Capsule of the Bonnet Monkey* (Macacus Sinicus).*

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Received Dec. 4,—Read Dec. 12, 1889.

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INTRODUCTION.

IN the following paper we propose to give the results of a research on which we have been engaged nearly three years, and by which we hoped to elucidate the arrangement of the motor fibres in the internal capsule.

The fibres which connect the excitable areas in the cortex cerebri with the bulbo-spinal grey matter in the medulla oblongata and spinal cord are commonly spoken of as forming the *pyramidal tract.*

These fibres course downwards between the caudate and lenticular portions of the corpus striatum and the optic thalamus. In passing through this region they enter into the composition of the bundles of white fibres, which received from the older anatomists the unfortunately misleading title of the *internal capsule.* It is obvious

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* The expenses of this investigation have been defrayed by a grant partly from the Royal Society, and partly from the British Medical Association.

that, when the destination and function of these fibres is fully known, this term will be abandoned with great advantage for a specific topographical nomenclature. At present, however, we must use the old expression in default of a better one.

In previous investigations ('Phil. Trans., B., 1887, 1888) we have described the foci* of representation in the cortex cerebri of the Macacque Monkey (*Macacus sinicus*), of the movements of the chief divisions of the body.

It remained for us to see whether there were issuing from such foci bundles of fibres conveying the functional impulses originating in those foci, and whether such fibres were arranged, as has been suggested by one of us ('Lancet,' July, 1884), in an order similar to that which prevails on the surface of the cortex.

From what has been already done in this matter it is evident that the problem can be attacked in two different ways, either by stimulation of the motor fibres of the internal capsule, or by removing different parts of the so-called motor cortex, and tracing downwards the degeneration produced in the motor fibres through the internal capsule and crus cerebri.

In this present paper, we have employed only the former of these two methods, viz., electrical stimulation of the fibres of the internal capsule, as exposed in horizontal section of the hemisphere. Some knowledge of the arrangement of the fibres in the internal capsule has already been gained by experimental and anatomical research, and the facts as known at the present time we will now summarise.

HISTORICAL INTRODUCTION.

Previous writers, on this question, have investigated the subject by several methods in different kinds of animals, viz., Rodents, Carnivora, Monkeys, and Man. The methods employed were for the most part anatomical, or consisted in tracing paths of degeneration. Very rarely has excitation been resorted to. Considering the varied mode in which movement is represented in the cortex of the brain in different animals, we have thought it best to arrange the facts we have deduced from the above researches under the headings of the various species of the animal examined, in the order already given.

Birds.

PITRES† found that in Pigeons and Chickens ablation of a hemisphere produced no descending degeneration.

Mammals.

Rodents.

PITRES† found that in the Guinea Pig and Rabbit destruction of the excitable parts

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* By the term "focus" we mean the point where the movements of any given segment are most intensely represented.

† 'Comptes Rendus de l'Académie des Sciences,' vol. 99, July, 1884, p. 89.

of the cortex produced descending degeneration, which cannot be traced beyond the lower limits of the bulb—*i.e.*, beyond the anterior pyramid of the same side.

NOTHNAGEL[*] never observed motor paralysis to follow either unilateral or bilateral division of the internal capsule in the Rabbit.

MONAKOW[†] removed in the Rabbit the anterior portion of the hemisphere, including part of the excitable zone, and found that this was followed by atrophy of the anterior part of the internal capsule. Removal of the middle zone of the cortex produced atrophy of the third fifth of the capsule, while destruction of the hinder third of the hemisphere (*i.e.*, occipital portion) caused atrophy of the hinder third of the capsule. He further found[‡] that removal of FERRIER's centres 6 and 9 produced respectively atrophy of the hinder and dorsal part, and of the posterior part of the capsule. Finally, the corpus striatum was always normal.

GUDDEN[§] figures (fig. 4, Taf. VIII.) a section of the hemisphere of a Rabbit, the upper third of which, including a thin slice of the corpus striatum, had been removed. The specimen shows marked atrophy of the internal capsule. The same author[||] also removed in young Rabbits the frontal lobe ("stirnhirn") and found that while the corpus striatum remained normal, the "medial part of the peduncle" and the corresponding pyramid and spinal cord were atrophied.

Carnivora.

Several authors have made experiments on the Cat and Dog.

J. BURDON-SANDERSON[¶] excited electrically in the Cat the fibres of the corona radiata, and subsequently the corpus striatum, producing the same movements as he had previously obtained by excitation of the cortex.

CARVILLE and DURET.[**] These authors divided the anterior two-thirds of the internal capsule in the Dog, and thus produced hemiplegia. In a second experiment they found that division of the posterior three-fourths produced also hemiplegia, but accompanied by hemianæsthesia.

VULPIAN,[††] having extirpated the right sigmoid gyrus 183 days previously, the right internal capsule was found, *post mortem*, to be "much thinner" than that of the left side.

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[*] 'Archiv für Pathologische Anatomie und Physiologie und für Klinische Medicin,' vol. 71, 1877, p. 280.

[†] "Weitere Mittheilungen über die Extirpation circumscripter Hirnrindenregionen, &c." 'Archiv für Psychiatrie und Nervenkrankheiten,' vol. 12, 1882, p. 535.

[‡] *Loc. cit.*, p. 141.

[§] 'Archiv für Psychiatrie,' &c., vol. 2, 1870, p. 693.

[||] 'Correspondenzblatt für Schweizer Aertzte,' vol. 2, p. 79.

[¶] Note on the "Excitation of the Surface of the Cerebral Hemispheres by Induced Currents," 'Roy. Soc. Proc.,' vol. 22, p. 368, 1874.

[**] "Sur les Fonctions des Hemisphères Cérébraux," 'Archives de Physiologie, vol. 2, 1875, p. 465.

[††] 'Archives de Physiologie,' vol. 3, 1876, p. 814.

PITRES* found marked descending degeneration in the Dog and Cat, after ablation of the excitable cortex, around the crucial sulcus. The major part of the degeneration ceased at the lower limit of the bulb.

GUDDEN† found that extirpation of the frontal region (stirnhirn) in young Dogs produced atrophy of the "medial part of the peduncle," corresponding pyramid and spinal cord.

LÖWENTHAL‡ found that in the Dog, after removal by Professor HERZEN of the left sigmoid gyrus, some of the lenticulo-striate fibres were atrophied just in front of the genu, and that, of the posterior limb, the fibres composing its anterior third were also atrophied. In a section taken lower down, just above the level of the anterior commissure, the portion of the posterior limb of the internal capsule found to be degenerated proved to be the second and third fifths from before back.

A section through the upper part of the crus showed the inner two-thirds to be degenerated; while in a section lower down—*i.e.*, opposite the exit of the third nerve—the middle third only was degenerated.

FRANCK and PITRES§ obtained, on excitation of the internal capsule in the Dog, the following results:—

Dividing the capsule into motor fasciculi, they found the arrangement from before backwards to be as follows:—

Opening of eyelids and dilatation of pupils;
Movement of opposite fore foot only;
Associated movements of both opposite limbs;
Movement of opposite hind limb only;
Closing eyelids;
Pricking of the opposite ear.

VEYSSIÈRE,‖ by a special instrument, produced hemianæsthesia by a lesion of the posterior third of the hinder limb of the internal capsule.

Quadrumana.

SCHÄFER¶ noted the following facts in a Monkey previously operated on by Professors FERRIER and YEO:—

The parts removed were the ascending frontal gyrus, except a small portion at the

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* 'Comptes Rendus de l'Académie des Sciences,' vol. 99, July, 1884, p. 90.

† *Loc. cit.*

‡ "La Région pyramidale de la Capsule Interne chez le Chien, et la Constitution du Cordon antéro-latéral de la Moelle." 'Revue Médicale de la Suisse Romande,' vol. 6, p. 529, Plates VII. and VIII., 1886.

§ 'Leçons sur les Fonctions Motrices du Cerveau,' &c., par FRANCK. Paris, 1887, pp. 21, 22.

‖ 'Recherches Cliniques et Expérimentales sur l'Hemianæsthésie de Cause Cérébrale,' 1874.

¶ "Report on the Lesions, Primary and Secondary, in the Brain and Spinal Cord of the Macacque Monkey exhibited by Professors FERRIER and YEO." 'Journ. of Physiology,' vol. 4, Nos. 4 and 5, Dec., 1883, p. 323, Plate XII.

upper end next the longitudinal fissure, and except also its lower end, amounting nearly to one-third of the length of the whole gyrus; also the posterior third of the upper division of the anterior portion of the frontal lobe.

Further, the ascending parietal gyrus was removed, except 5 mm. at the upper and 6 mm. at the lower end, and a small piece of the parietal lobule; and, in addition, rather more than half of the ascending limb of the angular and the supra-marginal gyri.

The effects of this lesion were as follows:—

Internal capsule.—Sections of the internal capsule showed in its "central part" a number of bundles mostly degenerated, which were not all closely packed together, but were somewhat scattered, being here and there separated by others which presented a normal appearance. In many of the flattened degenerated bundles there was a thin layer forming a sort of cortical stratum, in which the fibres appear normal.

In a section of the crus cerebri a patch of degeneration was found to be situated in the central part of the crusta, localised near the ventral border as an oval area tapering mesially.

FERRIER[*] found in the Monkey that removal of the præfrontal regions was followed by degeneration of "the lowermost and most internal" fibres in "the transverse sections of the internal capsule and the most median bundles of the foot of the crus cerebri."

Examination of the photographs of the brains shews that in each case the cortical areas for turning of the head and eyes were encroached upon by the lesion.

Man.

TURCK[†] in his original memoir showed that in cases of long-standing hemiplegia the hinder and upper part of the capsule was degenerated, and also the middle segment of the crus.

FLECHSIG[‡] observed in a new-born infant, 44 cm. long, that the internal capsule was white only between the thalamus and lenticular nucleus. At the same time the laminæ medullares of the lenticular nucleus as well as the fibres surrounding their posterior extremities were brighter than the neighbouring parts. In the crus cerebri there was seen on the lower and outer side a sharply bounded bright band 3 mm. broad (pyramidal tract) which was continued up into the internal capsule close to the innermost zone of the lenticular nucleus. In a further paper[§] he shows reason for

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[*] "A record of experiments on the effects of Lesion of different regions of the Cerebral Hemispheres," with GERALD YEO, 'Phil. Trans.,' 1884.—Experiments 22 and 23, p. 528.

[†] 'Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften,' vol. 6, Wien, 1851, p. 300.

[‡] 'Die Leitungsbahnen im Gehirn und Rückenmark des Menschen,' Leipzig, 1876, pp. 27, 28, Taf. II., fig. 3.

[§] 'Archiv für Anat. und Phys. (Anat. Abth.),' 1881, p. 12.

believing that in a horizontal section through the upper border of the middle zone of the lenticular nucleus, the pyramidal tract, including the fibres to the seventh and twelfth nerves, occupies the second, third, and fourth sixths of the posterior limb of the internal capsule.

CHARCOT* sub-divided the capsule according to his well-known plan, as follows :—

The anterior limb he termed the lenticulo-striate bundle. The posterior limb he subdivided into thirds, the two anterior of which he regarded as belonging to the pyramidal tract, while the remaining third was, he believed, limited to the transmission of afferent impressions.

We may remark that, as will subsequently be seen, this description applies only to one sectional level of the capsule.

BRISSAUD† made the most numerous clinical observations on this point. According to him there exist in the crus cerebri four bundles, whose relations from behind forwards may be stated as follows :—

1. A posterior bundle for the transmission of sensory impressions (CHARCOT, MEYNERT).

2. A middle bundle for the innervation of the muscles of the limbs and trunk.

3. A bundle of small size, which he called the geniculate bundle on account of its connection with the genu of the internal capsule. This bundle includes motor fibres, and is distributed to the bulbar nuclei for the movements of the muscles of the face, the tongue (perhaps the soft palate); in fact to all parts of the head and face which can be acted on voluntarily.

4. An internal bundle which ends in like manner in the bulb, and whose degeneration only seems to be coincident with intellectual derangements.

To these four bundles the four following divisions of the internal capsule correspond.

1. To the posterior bundle, the posterior third of the hinder limb corresponds (*i.e.*, the region of hemianæsthesia, CHARCOT, RAYMOND).

2. To the middle bundle, the anterior two-thirds of the hinder limb.

3. The bundle which he called geniculate, corresponds to the genu of the capsule.

4. Finally the whole of the anterior limb of the internal capsule corresponds to the internal bundle of the crus.

Contrary to what certain authors have stated, the crus cerebri cannot become completely degenerated; in other words there is a limit which the degeneration cannot overstep.

This maximum degeneration is recorded by him in observation VII., where the

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* 'Leçons sur les Localisations dans les Maladies du Cerveau et de la Moëlle Épinière,' 1876–1880, pp. 221–224.

† 'Recherches sur la Contracture Permanente des Hemiplégiques,' Paris, 1880, p. 38.

degeneration affected the internal three-fourths of the lower level, and only the posterior fourth escaped. In this case all the frontal lobe, the whole of the parietal lobe and a great part of the occipito-sphenoidal lobe had been destroyed by an extensive superficial softening.

MEYNERT[*] divides the internal capsule into five different kinds of bundles, viz. :—

1. Fibres passing from the cortex, as laminæ medullares, between the zones of the lenticular nucleus.
2. A bundle passing from the frontal region to the optic thalamus, and also forming part of the stratum zonale.
3. Fibres from the nucleus caudatus to the crus cerebri.
4. Fibres from the nucleus lenticularis to crus cerebri.
5. A group of fibres (the most posterior) which pass to the tegmentum.

HUGHES BENNETT[†] and CAMPBELL published a remarkable case in which the left arm was completely paralysed by a hæmorrhage in the internal capsule.

The lesion was found post-mortem and located as nearly as possible to the junction of the most anterior and second fourth of the posterior limb.

DEJÉRINE[‡] reported a case in which a tubercular tumour of the size of a nut, "seated on the internal capsule, between the posterior part of the optic thalamus and the capsule itself," produced paralysis of the right upper limb, together with incomplete right hemianæsthesia.

OBERSTEINER[§] figures an arrangement of the fibres of the capsule and crus similar to that given by BRISSAUD and CHARCOT.

WERNICKE[||] states that the anterior limb of the internal capsule is composed of fibres, which pass partly into the subthalamic region, and partly into the mesial side of the crus, and that the fibres coming from the nucleus caudatus pass circuitously through the laminæ medullares round the two inner zones of the lenticular nucleus.

ANATOMY OF THE INTERNAL CAPSULE.

Definition of the term.—As before said the term *internal capsule* has been given to the descending and ascending fibres of the *corona radiata*, while passing between the basal ganglia ; consequently we assume that the term is only applicable to the fibres so long as they are passing between the two following levels.

The upper of these levels is shown in Plate 11, fig. 2, which is constructed from

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[*] 'Psychiatrie,' Wien, 1884, p. 77.

[†] "Case of Brachial Monoplegia due to Lesion of the Internal Capsule," 'Brain,' vol. 8, p. 78, April, 1885.

[‡] Quoted in article "Encéphale," 'Dictionnaire des Sciences Médicales,' 1887.

[§] 'Anleitung beim Studium des Baues der Nervösen Centralorgane im gesunden und kranken Zustande,' 1888, p. 255.

[||] 'Lehrbuch von den Gehirnkranheiten,' Cassel, 1881, vol. 1, p. 85, fig. 44.

a photograph of a transverse vertical section of a Monkey's (*Macacus sinicus*) right hemisphere. This superior level (black dotted line) is seen to be a plane directed slightly obliquely downwards and outwards, and resting on the upper surfaces of the caudate and lenticular nuclei.

The lower level is scarcely a plane, owing to the configuration of the basal ganglia, as about to be described, but its general direction is roughly represented by a plane inclined upwards and backwards in a line with the upper surface of the optic tract and drawn from the optic chiasma backwards and upwards to the posterior extremity, or the pulvinar, of the optic thalamus.

Of course these levels are purely arbitrary divisions of the fibres of the pyramidal tract, separating a part of them from the centrum ovale above and the crus cerebri below.

The internal capsule may be described as consisting of bundles of fibres, arranged like the rays of a fan, of which the handle if broadened would represent the crus cerebri, while if the fan be considered to be held laterally in a plane parallel to the sagittal section of the hemisphere, the outside rays would correspond respectively with what we shall hereafter term the antero-inferior and postero-superior borders of the internal capsule, this is represented in fig. 3, which is a photograph of a sagittal section of a Monkey's brain (*Macacus sinicus*).

Viewed in horizontal section the capsule is limited by lines drawn at right angles to the anterior and posterior extremities of the lenticular nucleus.

Although this view of the fibres composing the internal capsule is useful to bear in mind, it nevertheless does not express the whole facts of the case. In the first place we have to remember that extending down towards the base of the brain, *i.e.*, towards the basal ganglia and internal capsule, is a large number of fibres converging from all parts of the cortex mantle.

Arranged in order from before back, these fibres may be enumerated as follows, irrespective of the impulses which they are generally considered to convey, classified according to the region of the cortex with which they are apparently connected.

I. Præfrontal.
II. Excitable, Pyramidal, or Fronto-Parietal.
III. Temporal.
IV. Occipito-Temporal.
V. Occipital.

These fibres are shown in their relation to the basal ganglia, anterior commissure, &c., in the accompanying figs. 4, 5, 6. These are drawn from a dissection of a hardened Monkey's (*M. sinicus*) brain in which the large majority of the hemisphere has been cut away, leaving uninjured the nuclei of the corpus striatum. In fig. 4 the ventricular aspect of the mass thus obtained, and also in fig. 6, is seen a dotted line in front, showing how much of the grey matter forming the anterior perforated spot, and part of the amygdaloid nucleus had to be cut away to reveal the anterior commissure (*a.c.*) running under the corpus striatum.

The convergence of the fibres of the capsule is seen in fig. 6, in which the whole of the corona radiata, outer capsule and claustrum, have been removed. It shows the caudate nucleus terminating posteriorly in the surcingle, which ends in the grey matter under the lenticular nucleus.

It is clear that these fibres, when they approach the basal ganglia, either end in these ganglia or pass between them to and from the mesencephalon.

(1) Do any of the fibres descending from the cortex end in the basal ganglia ?

This is a question which will recur, and as its elucidation does not immediately concern us in considering the present point, it may be postponed, see pp. 68, 72.

(2) Do the fibres pass between the basal ganglia to the mesencephalon, and if so which of the classes above enumerated ?

The answer to this question is easier. In the first place the important fibres known as the pyramidal tract pass downwards from the cortex, through the internal capsule into the crus and to the pyramidal region of the mesencephalon. These fibres are universally recognised to be the efferent or motor fibres of the cortex system, and it is the result of the excitation of these fibres which forms the subject of the present communication. In order to make the arrangement of these fibres—as we believe them to exist—more intelligible, we must first refer to the præfrontal class.

I. *Præfrontal.*—The fibres coming from the præfrontal region unquestionably appear in the anterior limb of the internal capsule as horizontal bundles, and compose its antero-inferior border.

Excitation of the præfrontal region of the cortex, as is well-known, has produced no muscular movement except in the hands of MUNK.[*] Ablation of the same region has been stated by Professor FERRIER[†] to have been followed by descending degeneration in the fibres of the anterior limb of the internal capsule. His results, however, judging from the figures he gives of the brains thus operated upon, seem to have included portions of the excitable area for the representation of the movements of the head and eyes.

Anatomical investigation goes to show that the fibres of the anterior limb of the capsule pass to the mesial side of the crus and also to the subthalamic region. Of such fibres our method gave only negative evidence, since in Groups III., VI., VII. (see fig. 1) the anterior limb was practically inexcitable, it is therefore clear that these præfrontal fibres at any rate do not possess efferent motor function.

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[*] MUNK, "Ueber die Stirnlappen des Grosshirns;" 'Sitzungsberichte der k. Preussischen Akademie,' 1882.

[†] 'Functions of the Brain,' 2nd edition, pp. 398, 399.

Whatever be their function it is evident that the fibres entering the anterior limb are arranged much as is indicated in fig. 3, and that, regarding the hemisphere as fixed with its greatest length in a horizontal plane, we may group these fibres, according to their vertical relations to such a plane, into :—

a. Superior and Descending.
b. Horizontal.
c. Inferior and Ascending. See also figs. 3, 5, 6.

But further, on account of the manner in which the grey cortical mantle of the frontal lobe presents, roughly speaking, the form of a cap or segment of a globe, we must, in addition, sub-divide these fibres according to their relative position about the horizontal plane of the hemisphere. Hence we must speak of a middle bundle, viz., those from the tip and anterior part of the lobe; of an internal group, viz., those coming from the mesial surface, *i.e.*, of the anterior third of the marginal and neighbouring gyri; and of an external group, *i.e.*, those coming from the outer part of lower frontal gyri (of course excitable).

Many of these bundles will be referred to under the next heading, and the destination of the remainder, *i.e.*, of the truly præfrontal, we have already discussed.

To sum up then, it is evident that we have excitable fibres coming into the anterior limb from the so-called motor cortex lying on the external aspect of the hemisphere in the opercular region, and these we regard as motor. The mass, however, of the anterior limb is composed of the bundles of fibres coming from the most anterior and mesial surfaces of the frontal lobe, these being non-excitable.

Looked at in their sagittal arrangement, we find that the excitability diminishes from above down, or, in other words, the pyramidal portion decreases and the præfrontal and non-excitable increases.

II. *Excitable or Pyramidal, Fronto-Parietal.*—This is the collection of fibres commonly known as the pyramidal tract, and which on being stimulated produce movement in a distinctive manner. Strictly speaking, the term pyramidal tract should apply only to those fibres contained in the pyramids, *i.e.*, those for the muscles of the limbs and trunk. In fact, many authors divide the "motor" capsular fibres into two groups, one devoted to the cerebral nerves, and the other termed the pyramidal fibres. This distinction we consider fair, but the term pyramidal tract has been so extended as to include these two groups of so-called motor fibres. But, while we agree in general to this distinction, it must not be forgotten that these two sets of fibres are not in utterly distinct compartments, but that the area of each overlaps.

We would prefer, therefore, to employ the term excitable to express the whole number of fibres possessing "efferent" or "motor" function.

These fibres we presume come from most of the excitable portions of the cortex.

We say *most* of the excitable region, because the recent investigations of SCHÄFER[*] show that on excitation of the occipital and angular gyri certain movements of the eyes are evoked, which, by reason of their greater latency of production, seem to be a result of secondary stimulation of the area for such movements situated in the frontal region.[†] Consequently, although this point is still greatly *sub judice*, it seems probable that the excitable fibres of the internal capsule only come from the fronto-parietal region. The course they take to reach the various points in the capsule will be determined by the anatomical relations of the cortical mantle to the basal ganglia, the exact lines of such courses, though not yet determined anatomically, may be theoretically imagined.

We have ascertained the anterior and posterior limits respectively of the excitable fibres in each experiment, and have constructed the following outlines, see fig. 1 (twice the natural size), showing the delimitation of these fibres in each group, the position of each point being determined by the averages given in Table I., see next page.

III., IV., V. *The Temporal, Occipito-Temporal, and Occipital Fibres.*—The delimitation of these fibres we have only in the present research ascertained by the process of exclusion, *i.e.*, by their non-excitability. We believe that they have for the most part to do with the general and special senses, but the method of the present research does not throw any fresh light on the subject.

It is, however, worthy of note that even in the narcotised state, when the scalpel divided these fibres at the hinder end of the capsule, there frequently occurred a marked general reflex movement. Excitation of the peripheral ends of these cut fibres produced, of course, no effect.

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[*] 'Roy. Soc. Proc.,' vol. 43, 1888, p. 411.

[†] *Cf.* also SHERRINGTON'S very valuable anatomical confirmation of SCHÄFER'S statements. 'Proceedings of the Physiological Society,' March, 1889.

TABLE I.*

Group I.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Tongue protruded	7	..	24	15
Mouth opens	13	..	51	32
Eyes turn	22	..	60	41
Opening eyes	24	..	55	39
Head and eyes turn (simultaneously)	41	..	54	47
Head turns	42	..	50	64
Retract angle of mouth	58	..	64	82
Shoulder	61	..	71	66
Elbow	62	..	87	74
Fingers	67	..	80	73
Abdomen	70	..	88	79
Wrist	75	..	81	78
Thumb	76	..	83	79
Hip	76	..	94	85
Small toes	78	81	98	88
Hallux	80	..	96	88
Knee	81	..	93	87
Ankle	86	..	95	90

Length of capsule, 100.

Group II.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes turn	25	50	68	47
Opening eyes	37	..	61	49
Head turns	42	62	71	56
Mouth opens	43	..	57	..
Retract angle of mouth	48	55	83	65
Shoulder	55	..	88	71
Tongue protruded	57	..	61	59
Fingers	58	75	86	72
Elbow	58	81	87	72
Wrist	60	..	71	65
Abdomen	60	..	80	70
Thumb	73	81	90	81
Hip	75	..	86	80
Knee	79	..	85	82
Small toes	82	88	91	86
Ankle	84	..	96	90
Head and eyes turn	..	84	..	84
Hallux	92	93	100	96

Length of capsule, 100.

[*] See also p. 71.

Group III.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Opening eyes	41	54	62	50
Eyes turn	48	49	60	54
Head and eyes turn (simultaneously)	53	..	60	56
Head turns	56	..	70	63
Mouth opens	57	..	71	64
Retract angle of mouth	58	71	79	68
Tongue protruded	62	..	72	67
Elbow	66	73	88	77
Thumb	69	..	84	77
Fingers	69	73	84	77
Shoulder	69	70	84	77
Wrist	70	74	88	79
Hip	79	..	84	82
Abdomen	80	..	86	83
Knee	80	..	86	83
Ankle	83	..	89	86
Hallux	84	..	91	87
Small toes	85	..	91	87

Length of Capsule, 100.

Group IV.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes turn	23	..	57	40
Opening eyes	30	45	60	45
Head turns	34	55	65	55
Mouth opens	40	..	62	51
Shoulder	50	..	65	57
Retract angle of mouth	50	65	85	65
Fingers	52	..	80	66
Head and eyes turn (simultaneously)	55	..	..	55
Wrist	55	..	75	65
Elbow	55	..	80	67
Tongue	55	..	82	72
Thumb	62	..	82	72
Ankle	72	..	85	78
Abdomen	75	..	85	80
Hip	75	..	85	80
Knee	75	..	85	80
Small toes	75	..	90	82
Hallux	75	..	90	82

Length of Capsule, 100.

Group V.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes open	38	47	54	46
Eyes turn	38	48	59	48
Head turns	41	..	58	49
Mouth opens	44	..	48	46
Head and eyes turn (simultaneously)	53	..	60	56
Angle of mouth retracted	54	76	80	67
Tongue protruded	55	..	76	65
Elbow	57	..	82	69
Fingers	57	..	84	70
Shoulder	58	..	81	69
Abdomen	58	66	85	71
Wrist	62	80	82	72
Thumb	64	..	79	71
Hip	68	..	80	74
Knee	74	..	77	75
Hallux	77	..	84	80
Small toes	79	..	85	82
Ankle	80	..	88	84

Length of capsule, 100.

Group VI.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes open	40	..	64	52
Eyes turn	42	..	60	51
Head turns	47	61	66	56
Elbow	48	..	75	61
Angle of mouth retracted	51	..	78	64
Tongue protruded	55	..	..	55
Mouth open	55	..	63	59
Shoulder	57	..	69	63
Fingers	59	..	77	68
Thumb	60	..	72	66
Wrist	62	..	72	67
Hip	69	..	77	73
Ankle	71	72	82	79
Knee	76	..	82	79
Abdomen	77	..	83	80
Small toes	78	..	82	80
Hallux	78	..	82	80

Length of capsule, 100.

Group VII.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes open	5	..	51	28
Eyes turn	5	..	51	28
Head turns	22	..	45	33
Head and eyes turn	29	..	35	32
Tongue protruded	35	..	52	43
Abdomen	41	52	58	49
Angle of mouth retracted	45	55	65	55
Shoulder	45	..	65	55
Wrist	48	..	62	55
Elbow	51	..	65	58
Thumb	55	..	61	58
Hip	56	..	65	60
Fingers	57	..	62	59
Hallux	61	..	72	66
Ankle	64	..	..	64
Knee	66	..	..	66
Small toes	66	..	72	69

Length of capsule, 100.

Group VIII.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes turn	8	..	41	24
Eyes open	16	..	41	28
Angle of mouth retracted	16	28	50	33
Elbow	16	41	62	39
Shoulder	20	58	66	43
Head turns	33	41	66	48
Fingers	37	..	62	49
Wrist	41	..	62	51
Small toes	49	..	66	57
Ankle	49	..	75	62
Abdomen	50	..	..	50
Hallux	53	..	66	59
Thumb	48	..	66	62

Length of capsule, 100.

The Configuration of the Basal Ganglia.

It is now necessary to consider in detail the shapes and relative positions of the three chief divisions of basal grey matter, to the fibres of the internal capsule.

We think we may best accomplish this by describing in succession from above down the sections typical of each group of experiments (see p. 65). The position of the genu, which, as will be seen in fig. 1, gradually moves backwards and inwards, as we pass down the capsule to near the base, *i.e.*, until the posterior limb, as seen in these sections, changes from an oblique antero-posterior direction to an almost transverse position. This is strikingly exhibited in Table II., calculated from the observed dimensions of the capsule in each experiment.

TABLE II.

Group.	Average total length of capsule.	Length of Anterior Limb.	Length of Posterior Limb.
	m.m.	m.m.	m.m.
I.	18·2	7	11·2
II.	17	6	11
III.	18	7	11
IV.	20	9	11
V.	21	10	11
VI.	20	9	11
VII.	17	2	15
VIII.	12	0	12

The genu is of course the point of junction of the two limbs, and it will be seen at once that while the length of the posterior limb remains remarkably constant until its axis finally changes direction, the anterior limb on the other hand increases in size from above down, lying in the notch between the caudate and lenticular nuclei (see figs. 1, 2, and 5), until the section approaching the grey matter of the base of the brain, it rapidly disappears (as in Group VIII.), see fig. 1.

It will be convenient next to consider two angles; firstly that which the anterior limb makes with the posterior limb in forming the genu, and secondly the angle of inclination of the long axis of the posterior limb to the middle line. By subtraction of these two from 180° we naturally obtain at once the inclination of the anterior limb to the mesial plane.

Since the angle of the genu is correlated with that of the inclination of the anterior limb, we set both out in the following Table III. (The angles we measured with a goniometer on photographs of the specimens made just after each experiment.)

Each of the angles typical of the several groups was found by taking the average of all the angles of the capsules contained in each group.

TABLE III.

Group.	Angle of genu.	Angle of inclination of axis of posterior limb to mesial line.	Angle of inclination of axis of anterior limb to mesial line.
	°	°	°
I.	134·5	15·8	29·7
II.	123·3	20·3	36·4
III.	118·9	30·8	30·3
IV.	105·1	36·2	38·7
V.	97·1	44·8	38·1
VI.	87·9	55	37·1
VII.	Not ascertainable	40*	. .
VIII.	No genu	57·5	. .

From this Table it is clear how, while the posterior limb is constantly altering its inclination to the mesial plane, the anterior limb moves comparatively slightly from the same plane in the middle three-fifths of the depth of the capsule. In other words, the caudate wall of the groove separating the anterior ends of the striate nuclei is practically vertical, though slanting outwards rapidly above, more slowly below, as is seen to be the case, when a frontal section is made of the anterior limb. (See fig. 2.)

It is necessary now to give what we have regarded as the defining points of difference between the several groups of capsules experimented on. (See fig. 1.)

Group I. (the highest).—Genu forms a widely open angle (134·5°) so that the capsule is almost a segment of a circle. Of the lenticular nucleus only the outer zone or putamen appears, and it has a bi-convex outline. (See typical photograph, Plate 10, Experiment 35 of our series, and fig. 1.)

Group II.—The genu is distinct and less obtuse, being 123·3°. The second zone of the lenticular nucleus has not yet appeared, though the caudate reaches backward to a point a little posterior to the genu (the anterior part of the surcingle). (See typical photograph, Experiment 67.)

The outline of the lenticular is now becoming triangular.

Group III.—The angle of the genu is becoming still smaller, averaging 118·9°. The second zone of the lenticular nucleus is not yet visible though nearly exposed. The caudate nucleus reaches posteriorly to the genu. The lenticular nucleus is becoming more triangular. In the large majority of sections the pulvinar is evidently free in the ventricle. (See typical photograph, Experiment 42.)

Group IV.—This group is easily marked, since in it we have with the main features given under Group III., the first appearance of the second or middle zone of the lenticular nucleus. (See typical photograph, Experiment 31.)

Group V.—The second zone is more marked, the white interzonal or lamellar fibres

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* Probably this figure is unexpectedly low, owing to (1) the crescentic shape of the capsule, (2) the number of observations being few, viz., two.

separating this zone from the putamen are in this section extended backwards almost to the end of the lenticular nucleus. The angle of the genu is nearly a right angle, and the limbs of the capsule are approximately equal in length. (See typical photograph, Experiment 69.)

Group VI.—This group is the same as Group V., from which, as the individual capsules show, it can only be separated by the smaller angle of the genu and by the axis of the posterior limb, becoming more transverse to the longitudinal axis of the hemisphere. (See typical photograph, Experiment 50.)

Group VII.—This group is very definite since it shows sections of all three zones of the lenticular nucleus, and since the level is below the capsular groove between the two nuclei in the corpus striatum, it passes through the basal grey matter of the floor of the lateral ventricle. The anterior commissure appears near the middle line; the part seen corresponds to the highest point of the arch it forms. Since this section is cut along the line of the Fissure of SYLVIUS, it necessarily is wholly below the frontal lobes. As will be seen, there is a slight anterior limb in this section, see fig. 1. (See typical photograph, Plate 11, Experiment 81.)

Group VIII.—This section just above the crus closely resembles Group VII., save that the anterior limb is no longer represented, and the two innermost zones of the lenticular nucleus cannot now be separated. (See typical photograph, Experiment 79.)

Notes on Groups VII. and VIII.—In these groups the basal ganglia and capsule, as divided by these sections, present a very constant figure; thus the posterior limb of the internal capsule makes an angle with the middle line of about 60°, its posterior border being formed by the optic thalamus, while anteriorly there are ranged along its front the respective ends of the three grey zones of the lenticular nucleus. If the section pass just above the Fissure of SYLVIUS the three zones will be seen, if lower, the two innermost zones are found to be confused into one grey mass and cannot be separated.

In the *highest sections* (*i.e.*, those in which the three zones are distinct) of these groups, there are the remains of the anterior limb of the capsule lying to the inner side of the innermost zone of the lenticular nucleus. This remnant of the anterior limb is (in the highest sections), about 3 mm. long in the antero-posterior direction. This bundle of white fibres is not in immediate contact with the anterior commissure, but is separated from it by some of the grey matter of the lenticular nucleus. This delimitation of what we consequently call the anterior limb can be easily seen, and it is from this point that in this group of sections we have commenced the measurement of the capsule, continuing the same as before along its outer margin, *i.e.*, contiguous to the lenticular nucleus, as far as the hinder end of the outer zone of that nucleus (see fig. 1).

The remnant of the anterior limb above described is bounded on its inner aspect, *i.e.*, along the middle line of the cerebrum by a narrow (1–2 mm. wide) strip of inexcitable tissue. (? Septum lucidum and anterior perforated spot; grey matter.)

Summary and Application of the Anatomical Facts.

It remains to connect these anatomical data with the facts observed upon excitation.

In the first place discrimination must be made between the effects of exciting fibres in their continuity and on their transverse section respectively, since it is plain that the identity of result might otherwise lead to an undesirably extended view of the limits of the efferent tract.

Reference to fig. 1 and to Table I. shows that some of the efferent excitable fibres which partly compose the anterior limb in Group I. are rapidly concentrated in the posterior limb as we descend to Group III. These fibres are those for the movements of opening the mouth and protrusion of the tongue, as is shown by a glance at fig. 1, C and F.

At Group IV., fig. 1, it is evident that a further change now occurs Apparently owing to the appearance of the second or middle zone of the lenticular nucleus, that part of the anterior limb which is opposite this second zone is found to be excitable, whereas the rest, which really exactly corresponds with the whole anterior limb of Group III., is inexcitable as in that Group.

It is to be observed (fig. 1) that this excitability of the posterior part of the anterior limb again diminishes until we arrive at Group VII., where, upon the further appearance of the third or innermost zone, the hinder end of this limb is seen to be excitable.

To speak next of the inexcitable fibres of the anterior limb, we have in the foregoing pages referred to the views of those who have treated the subject, and we only would express our belief that these fibres of the anterior limb are for the most part horizontal, and that they pass backwards through the genu to the thalamic region.

A point of equal interest is the arrangement of excitable and inexcitable fibres in the posterior limb of the capsule.

In Groups I. and II., fig. 1, the posterior limb is excitable in its whole length, but, in Group III., the hindermost part (*i.e.*, for the last $\frac{9}{100}$ths) is inexcitable. This inexcitable portion steadily increases as we pass downwards (see fig. 1), so that in Groups VI., VII., and VIII., the excitable part terminates posteriorly at the hinder limit of the middle zone.

The classical dictum,* that the sensory fibres are contained in the posterior *third* of the hinder limb of the capsule only holds good for the lowest levels. The gradual character of the development of this inexcitable (afferent) part of the capsule is interesting by way of contrast with the variable arrangement of the excitable fibres in the anterior limb just discussed.

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* CARVILLE and DURET, CHARCOT, *loc. cit.*

Genu.—Hitherto we have only indirectly spoken of the genu and its relation to the surrounding parts. To determine its position exactly at the different levels of the capsule, we first, by means of successive horizontal sections parallel to the longest antero-posterior diameter of the hemisphere, exposed the level of our Group I. We then inserted (vertically) a long needle at right angles to the plane of the section just at the genu immediately in front of the most anterior extremity of the optic thalamus. Each successive horizontal (parallel) section of the hemisphere contained, consequently, the position of the genu as in the highest section (the upper level, Group I.).

From these data we found that the position of the genu in its antero-posterior relations varied extraordinarily little, but that the position of the entering angle of the inner border was gradually transferred to that of the outer border, and, finally, in the last three groups, the puncture revealed the fact that the position of the genu, as seen in the highest section and now projected upon the lowest, had moved about 2 mm. in front of, and outside the angle of the outer border of the capsule, or 4 mm. from its original site. In other words, the genu had moved backwards and inwards, and this change of position was more rapidly developed in the lower than the upper sections.

Of course, the inward and backward direction of the efferent tracts is also seen (especially the former) in frontal sections of the capsule.

Laminæ Medullares.—The white fibres, which in horizontal sections of the hemisphere, appear as lamellæ to separate the zones of the lenticular nucleus, but which, in vertical frontal sections, appear to run into and connect the zones, we have repeatedly excited without any result. We, therefore, are led to conclude that these fibres, whatever be their function, do not belong to the great excitable cortico-efferent system.

OBERSTEINER[*] gives a schematic diagram, in which he figures fibres passing down from the cortex through the laminæ medullares to end in the subthalamic region.

WERNICKE[†] suggests that these interzonular, or lamellary fibres, are in part derived from the nucleus caudatus, and are passing down to the crus.

MEYNERT[‡] believes that such fibres are derived from the cortex rather than from the nucleus caudatus.

METHOD OF INVESTIGATION IN THE PRESENT RESEARCH.

Animal Employed.—The Bonnet Monkey (*Macacus sinicus*), *i.e.*, the smaller variety of that species of Monkey, was the animal which we have invariably used.

In all we have performed 45 experiments, and in every case the animal was com-

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[*] *Loc. cit.*, p. 334

[†] *Loc. cit.*

[‡] *Loc. cit.*

pletely under the influence of ether, and was killed before it recovered from the anæsthetic.

With few exceptions the left hemisphere was the one used for the examination, and, as a rule, the cortex had just before been minutely explored. It was found most convenient to remove the vault of the cranium for about 1 cm. to the other side of the middle line, and laterally as low as the zygoma in front, and behind to a corresponding level.

The dura mater was reflected over the area thus exposed, care being taken not to injure the longitudinal sinus; the hemisphere was then drawn towards the middle line so as to allow of the middle cerebral artery being ligatured soon after its origin, this was easily done by passing a fine thread beneath the vessel through the contiguous portions of the orbital and temporo-sphenoidal lobes.

A horizontal incision was then made with a long sharp scalpel through the substance of the hemisphere, from the outer surface towards the middle line, but stopping short 1 or 2 mm. of the mesial plane. In this way section of all arteries, save the branches of the ligatured middle cerebral was avoided, and, hence, hæmorrhage was in a great measure prevented. The only vessel which gave much trouble was the lenticulo-striate artery running vertically through the outer zone of the lenticular nucleus. In the first two experiments, we sought to arrest this hæmorrhage by a fine point of an actual cautery, but we found, to our surprise, that although the area touched was extremely small, yet the cut ends of the fibres of the adjacent internal capsule were so damaged (by the radiant heat of the cautery) as to be inexcitable; moreover, we speedily found that all hæmorrhage could be easily arrested by placing on the bleeding point a small cube of amadou.

When the hæmorrhage had thus been controlled the upper portion of the hemisphere which, as described above, had not been completely separated, but merely raised like the lid of a box, was replaced, and preparations were made for recording the results of the stimulation.

The plan of recording which appeared to us likely to afford the most accurate results, and, at the same time, not to involve so much delay in exposing the capsule as to cause the death of the fibres, was as follows:—

Upon paper, on which fine lines were engraved by an engine with mathematical accuracy so as to cover the surface with squares of 1 mm. side, we drew by means of compasses the exact outline of the basal ganglia as exposed by the section.

In this way we obtained at once the cut surface of the internal capsule correctly projected on paper, divided into squares of 1 mm.; these squares we then numbered from the front of the anterior limb of the capsule to the posterior end of the lenticular nucleus. Finally, we stimulated each of these bundles of fibres thus obtained of 1 square mm. area, and recorded the effect produced.

Mode of Stimulation.—The electrodes used were two fine platinum points, 1 mm. apart, so that the excitation should be exactly limited to each square excited. The exciting current was an interrupted induced current obtained from the secondary coil of a Du Bois Reymond inductorium, supplied by a 1 litre bichromate cell. The distance of the secondary coil from the zero point of completely covering the primary was such as to give a minimal stimulus, and this was usually about 10 cm.

After the experiment was completed the animal was killed by excess of chloroform, the hemisphere removed, washed in salt solution and the surface photographed.

Upon the photograph thus obtained, the numbers representing the different bundles of fibres (1 mm. square) were transferred by compasses from the plan originally drawn on the ruled paper.

Mode of Enumeration and Recording Results.—We have just said that we numbered the millimetre squares of the internal capsule in order from before back; we adopted this plan for the reason that as the anterior limit of the excitable portion of the capsule varies in position, *i.e.*, retreats as the section descends (*cf.* fig. 1.), it was necessary to express the position of the fibres having the same function by some means which should bear an absolute value in relation to the rest of the capsule. By this means we have been enabled to trace the bundles having the same function through their various changes of direction as they pass down through the different sections of the capsule to reach the crus.

Inasmuch as the capsule is divided into millimetre squares by the above method, each figure denoting any bundle of fibres represents at the same time the distance of that bundle from the front end of the anterior limb.

In plotting out the plan of the capsule during an experiment we arranged it so that the more important posterior limb should be drawn parallel to one direction of the rows of squares on the ruled paper; consequently, as the anterior limb forms an obtuse angle with the posterior limb, the squares dividing it were necessarily échelonned. This, however, afforded no real difficulty, and the more so since in the most important sections very little of the anterior limb is excitable. We, therefore, expressed each square or bundle of fibres by a fraction, the numerator of which denoted the distance that it was situated from the anterior end of the capsule, while the denominator gave the total length of the capsule in that particular section; in this wise one fraction, or, in other words, the position of one bundle of fibres in one section, is strictly comparable with that in another section.

In order to bring all the fractions thus obtained together, and to find the average position of the representation of any given movement in each group, we converted all the fractions into decimals to two places. We took two places as adequately accurate, since any error beyond would only amount to $\frac{1}{1000}$th of the length of the capsule, and as this actually amounts, on the average, to not more than ·02 mm., it is a length which is far too small to be considered among the errors of the experimental method.

The decimals thus obtained, denoting the squares indicating the localisation of each movement elicited, were next added together in the several groups, and the average taken.

Since these decimals were taken to two places, each capsule in every group becomes divided into a hundred parts, and if we drop the decimal point, we may regard the figure as a whole number, taking the whole capsule to be 100. For example, the movement of "protrusion of the tongue" was observed in Group II. to occur in two experiments, the length of the capsule being respectively in each case 12 mm. and 17 mm., the average therefore being 14 mm. The movement was observed to follow excitation of the first millimetre in each case, and to end at the third millimetre in the one case and at the fourth in the other. Consequently the movement began at $\frac{1}{12}$th and $\frac{1}{17}$th of the actual length of the respective capsules, and was last obtained at $\frac{3}{12}$ths and $\frac{4}{17}$ths.

On converting these fractions into decimals they become respectively ·08 and ·06 for the anterior limit and ·25 and ·23 for the posterior limit, and on taking the averages of these we obtain ·07 and ·24.

Now that we have the situations of the fibres expressed in terms of the average length of the capsules of each group, we need not keep the decimal point if we regard the capsule as divided into a hundred parts, and then take the figure as a whole number, so that in Table I. the limits of the representation of the protrusion of the tongue become 7 and 24, *i.e.*, $\frac{7}{100}$ and $\frac{24}{100}$.

This mode of treating the figures has this great advantage, that whatever the length of the different capsules may be in any group, we can compare the function of the fibres in similar parts.

At the same time this mode of extending the differentiation of the capsule has this disadvantage, viz., that, although taken absolutely, as is represented by the fraction $\frac{1}{14}$, we obtained the movement from the most anterior millimetre of the capsule, yet in converting $\frac{1}{14}$ into a decimal to two places, we necessarily obtain $\frac{1}{14} = {\cdot}07$, and then, in regarding the capsule for purposes of relative comparison as divided into 100 parts (dropping the decimal point), we thus obtain the figure 7, meaning the first seven-hundredths, as representing the first portion at which the movement occurred.

In fact, in attempting to analyse and to compare the results of each experiment, *i.e.*, the fractions, we found it impossible to employ the method of a common denominator, and therefore selected, at Mr. GOTCH's suggestion, the two places of decimals. We were obliged to take two places of decimals, since, as a glance at Table I.* shows, one place of decimals would not have given the differentiation we have discovered to exist, though at the same time it was clear to us that two places would so extend our subdivisions of the capsule as to make it difficult to convey the absolute expression of the amount (*i.e.*, extent) of representation.

These averages are set out in the last column in Table I., in which the movements are also arranged in their order from before back.

In Table I. the first column gives the names of the movements observed, and, as just stated, in the order in which they occur from before back. The first column of figures denotes the distance from the anterior extremity of the capsule of the first

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[*] See p. 60.

bundle of fibres, excitation of which produced the movement. The third column gives the most posterior point or bundle of fibres at which the movement of a part could be elicited, so that the distance between the figures in these two columns gives the total or absolute extent of the fibres from which that movement of a part could be obtained.

The intermediate or second column gives, in those cases where it was most marked, the point of maximal representation, *i.e.*, of greatest intensity.

Further, it is seen at once that the distribution of the fibres for any one part is not allocated to one small point in the capsule, but spread over it for a certain distance, so that the overlapping seen on the cortex occurs here, though to a larger extent.

To further elucdiate the arrangement of the fibres and to facilitate future reference, we have constructed a series of diagrams (fig. 1, A–R.) on exactly the same scale as fig. 1 (*i.e.*, twice the natural size), on which we have marked the extent of representation in the different groups of sections of each segment observed. In each figure the shaded part represents the fibres, excitation of which produces movement of the given segment. The limits of these fibres were obtained from the numbers of Table I. As we have already drawn attention in describing fig. 1, we would remark on the extraordinary diminution of the fibres before the successive appearance of the zones of the lenticular nucleus, and the equally striking increase of the fibres when these zones become visible, *e.g.*, Groups IV. and VII.

Good examples of this are to be seen in the diagrams for the turning of the eyes, the small toes and hallux (fig. 1, B, Q, R).

Physiological Relations of the Basal Ganglia to the Internal Capsule.

Although the ventricular surface of the caudate nucleus has been asserted to be excitable by Carville and Duret,[*] Ferrier,[†] and Minor,[‡] we have failed to obtain the slightest movement by exciting the sectional surfaces of either of the basal ganglia. We do not advance these observations as of special value, considering that we removed the ventricular surface, but the contrast between the absence of any result when the ganglia were excited and the marked spasm which immediately followed the application of the electrodes to the capsule is in harmony with the observations of Franck and Pitres,[§] and with whose general deductions on this point we fully agree.

To finally elucidate this important point, we have also excited the intra-ventricular surfaces of the basal ganglia, but without any positive result.

Consequently on review of the experimental evidence, it seems to us most likely that the basal ganglia are really inexcitable.

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[*] *Loc. cit.*

[†] Ferrier, *loc. cit.*, p. 264.

[‡] 'Neurologisches Centralblatt,' June, 1883.

[§] *Loc. cit.*

Analysis of Results.

On pp. 60–63 we give, in Table I., the order of arrangement of the representation of different parts of the body. We cannot well separate the consideration of this arrangement from that of the order in which the different characters of the movements are placed, hence we will reserve to p. 79 the discussion of the facts set out in Table I.

We will, however, proceed to discuss certain points of general interest upon which a clear opinion must be formed before the main results of this research can be given at length. Of such points we take first, as the most important, the phenomenon of bilateral movement.

Movements of Muscles of the same side as that stimulated.

The phenomenon of bilateral movement occurring upon excitation of one hemisphere has often been approached from its theoretical, experimental, and clinical aspects. It has been assumed by BROADBENT* that this is effected by the impulses passing from the sound hemisphere across commissural fibres postulated to exist between the lower (*i.e.*, bulbo-spinal) centres of the two sides, and he explained the common mode of recovery from hæmorrhagic compression and destruction of the internal capsule by this theory. This theory has been favourably received by neurologists as an explanation of the phenomenon of bilateral movement, but we submit that the subject can only profitably be treated upon experimental facts as a basis.

Before any satisfactory conclusions can be arrived at, we must obviously first determine exactly how much bilateral representation of movement exists in the cortex of a normal uninjured nervous system, and, in this case, of the Bonnet Monkey. Further we must understand clearly what we mean by bilateral representation.

Beginning with this last, we mean that the same movement of symmetrical parts of both sides of the body is represented in one point of the cortex of both hemispheres, *i.e.*, that excitation of such a point evokes simultaneous and identical movement in the same part of both sides of the body.

In attempting to classify "bilateral movements" it is necessary to point out first that movements such as conjugate deviation of the eyes are not, strictly speaking, examples of bilateral representation. For while it is true both eyeballs move, nevertheless one is rotated out, the other rotated in, and since this conjugate deviation occurs as the result of a single idea, the movement of both eyeballs really corresponds to that of one limb, and this is more especially the case since, as just said, the muscles employed on each side are different. A final confirmation of this view lies in the fact that excitation of one hemisphere produces conjugate deviation in one direction only, while excitation of the other evokes an exactly opposite movement.

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* 'British Medical Journal,' vol. 1, 1876, pp. 333, 371, 401.

To this point we shall subsequently return. We may now mention the movements which are credited with being bilaterally represented, and we shall arrange them in classes, the justification for which will subsequently appear.

Credited as Bilateral.

Movements of Trunk Muscles (*i.e.*, Rectus, abdominis, &c.)		Class I. Not bilateral, *vid. inf.*
Movements of Tongue		
Conjugate deviation of Eyes		
Turning of Head		
Retraction of Angle of Mouth		Class II. Imperfectly bilateral.
Pursing of Lips		
Opening of Eyelids	Identical movement	
Closing of Eyelids		
Pouting of Lips		Class III. Truly bilateral.
Mastication		
Swallowing (*i.e.*, movements of soft palate)		
Adduction of vocal cords		

Class—I. *Movements asserted to be bilateral, but not actually so.*

Movements of the Trunk Muscles.—The muscles of the trunk have above all others in the body been commonly supposed to be bilaterally associated in action. This is, however, quite contrary to observed fact. We have never seen any movement of both recti or oblique abdominis follow excitation of the fibres for the trunk muscles in the capsule, although we invariably saw movement restricted to the muscles of the opposite side, notably the rectus. We have observed this to be the case clinically, and believe that the statements made in the opposite direction rest upon imperfect examination. Further confirmation is to hand in the description given by Professor SCHÄFER* and one of us, of the results of excitation and ablation respectively of the "trunk areas" in the marginal gyrus, from which it appears that the same unilateral representation was discovered to exist.

Movements of the Tongue.—As we are specially investigating the cortical representation of these movements, we desire to defer the detailed observation of the capsular fibres subserving the same, until the former is completed.

Conjugate Deviation of the Eyes and Turning of the Head.—We have already mentioned the movements of the eyeballs, and we now intend to strengthen what is said on p. 73.

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* HORSLEY and SCHÄFER, 'Phil. Trans.,' B, vol. 179, 1888, pp. 10 and 14.

We there showed that the deviation of the eyes was a combined movement of opposed muscles (*internal* rectus with *external* rectus) of both sides of the body to produce one effect, and that the opposite hemisphere, when excited, produced exactly the opposite effect.

Further, considering that the visual field is hemiopic, and that the two eyes always have their axes parallel (when not accommodated for near objects), we may look upon the two eyes as acting like one, and we may also regard their movements to be of the same kind as those of the head.

Stimulation of the left cortex produces movement of the head and also of the eyes to the right, and, conversely, when the right cortex is irritated these parts move to the left. Movement to the same side is never observed, hence these movements we regard as distinctly unilateral.

Class II.—Imperfectly Bilateral Movements.

(a.) *Opening of Eyelids.*—In 'Phil. Trans.,' B., 1888, p. 241, we describe how we observed in one Monkey that there were two millimetre-squares on the cortex, excitation of which caused opening of the opposite eyelids to occur before those of the same side. In the present research we have obtained the same result from the internal capsule in one case (Monkey No. 69), at points 50–55 (whole capsule, 100), the movement being also stronger.

The extreme rarity of this phenomenon—occurring, as it does, only twice in about seventy different experiments in the same variety of Macacus—makes it clear that the movement of *opening* the eyelids is practically bilaterally represented. However, the phenomenon is not without interest in discussing the evolution of function in the "motor" cortex.

(b.) *Closure of Eyelids.*—In contradistinction to what we find with regard to opening of one eye before the other, we have obtained closure of the opposite eyelids, not only taking place before those of the same side, but even independently of the eyelids of the same side.

We drew attention for the first time to this differentiation of cortical representation of the eyelids in our second paper just referred to, where we described the opening of one eye before the other. Since writing that paper, we have been engaged in investigating the cortical representation of closure of the eyes, and we have found that there is a nearly horizontal zonular strip of the cortex just below and slightly overlapping the lower border of the upper limb area of representation, in which the single movement of closure of the opposite eyelids is represented.

In some cases this is imperfect, *i.e.*, the eyelids of the side stimulated closed as well as those of the opposite side. It is clear, therefore, that this movement is only imperfectly bilateral, a fact of the greatest importance, as is evidenced by the fact that we have been able with this observation to correctly diagnose that the homologous portion of the cortex in man was the seat of an irritative lesion.

Hence we were not surprised to find that in the internal capsule there were fibres, excitation of which produced closure of the opposite eyelids only.

(c.) *Pursing of the Lips.*—This is another imperfectly bilateral movement, it being most marked always on the opposite side.

(d.) *Retraction of the Angle of the Mouth.*—Rarely have we observed truly bilateral, *i.e.*, symmetrical, retraction of the angle of the mouth, this being the exception to the rule of retraction to the opposite side.

Class III.

(a.) *Pouting of the Lips.*—This eversion of the lips appears to be truly a bilateral movement.

(b.) *Mastication.*—So far as we have been able to observe, this complex movement is mainly bilateral, but we are compelled to postpone its detailed consideration until our analysis of its cortical representation is complete.

(c.) *Swallowing, including movements of the Soft Palate.*—This in our experience of the capsule has always been bilateral on excitation.

(d.) *Adduction of the Vocal Cords* has been shown [*] to be perfectly bilaterally represented.

(e.) *Bilateral Movement of both Elbows.*—This (as flexion) we have found to occur four times altogether in our experiments, when the internal capsule of one side has been excited. The occasions, however, on which this was observed were so few, and the movement so slight and limited that we cannot regard it to be a proof of bilateral representation of this segment of the upper limb in one hemisphere. Moreover, during a long series of experiments upon the cortex this was never observed.

The explanation of this phenomenon we prefer to postpone until further knowledge makes its discussion profitable.

It occurred at point 57, and only in the central [†] Groups, Nos. IV., V., VI.

To sum up, therefore, we consider the following movements to be alone truly bilaterally represented.

Pouting of Lips.
Mastication.
Swallowing.
Adduction of the Vocal Cords.

It will now be expedient to describe the general results obtained by the various groups of experiments.

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[*] KRAUSE, in the Dog; SEMON and HORSLEY, in the Monkey. This is denied by MASINI, and by GAREL and DOR.

[†] *I.e.*, opposite the middle level of the capsule.

Lateral Arrangement of the Excitable Fibres in the Internal Capsule.

We now introduce a new branch of this subject, namely, the relations in lateral juxtaposition of the efferent fibres.

So far we have described the antero-posterior arrangement of these fibres, but we have postponed the consideration of the results obtained by exciting the capsule in individual points of its breadth.

As the capsule varied in width from 1 to 3 mm., and as the part of the sections involving the inner zones of the lenticular nucleus was also constituted of white fibres in and around those zones, we have sometimes found five rows of excitable points (each 1 mm. square). The result obtained from these points we shall now analyse. Altogether we were able to obtain two or more rows of 1 mm. squares in 26 experiments.

Anatomically speaking, in horizontal transverse section we may regard the fibres of the internal capsule as falling into three groups, viz. :—(*a*) those in the mid line; (*b*) those next the lenticular nucleus, and (*c*) those on the inner side next the optic thalamus, &c.

Of the 26 cases above-mentioned, in seven the excitability appeared to be equally distributed throughout the breadth of the capsule. However, besides these seven, we found that in 15 the most excitable part was that next the lenticular nucleus, this gradually decreasing towards the optic thalamus, but in the remaining four the capsule was most excitable alongside of the thalamus. Considering the anatomical arrangement of the cortex mantle to the position of the basal ganglia and internal capsule, it is not at all improbable that these results may be referable to the fibres entering the capsule from above in an oblique direction, and hence in a horizontal section, they will offer for excitation not only a transversely cut end alongside the lenticular nucleus, but also longitudinal surfaces, which are progressively less and less exposed to excitation as we move across the capsule from the lenticular nucleus to the optic thalamus.

If correct, this view would postulate the theory that the fibres forming the part of the capsule nearest the middle line are inexcitable. This, at any rate, is evidently strongly suggested by the experiments. Moreover, in a frontal microscopic section of the region, the fibres which emerge from the gyrus fornicatus on reaching the capsule, are seen to occupy the most internal position therein, and excitation of the gyrus fornicatus has always failed to elicit movement.

To sum up this question, it is self-evident that, the lateral arrangement of the fibres is infinitely less important than that of the antero-posterior direction, and principally because the function of each point in any given transverse row of squares is the same in character though diminishing in intensity, as we pass from the outer to the inner side of the capsule.

TABLE IV.

Groups.																		
I.	Tongue	Mouth opens	Eyes turn	Eyes open	Head and Eyes turn	Head turns	Angle of Mouth	Shoulder	Fingers	Elbow	Wrist	Trunk	Thumb	Hip	Knee	Small toes	Hallux	Ankle
II.	Eyes turn	Eyes open	Mouth opens	Head turns	Tongue	Wrist	Angle of Mouth	Trunk	Shoulder	Fingers	Elbow	Hip	Thumb	Knee	Small toes	Head and Eyes turn	Ankle	Hallux
III.	Eyes open	Eyes turn	Head and Eyes turn	Head turns	Mouth opens	Tongue	Angle of Mouth	Elbow	Shoulder	Thumb	Fingers	Wrist	Hip	Trunk	Knee	Ankle	Hallux	Small toes
IV.	Eyes turn	Eyes open	Mouth opens	Head turns	Head and Eyes turn	Shoulder	Angle of Mouth	Wrist	Fingers	Elbow	Tongue	Thumb	Ankle	Trunk	Hip	Knee	Hallux	Small toes
V.	Eyes open	Mouth opens	Eyes turn	Head turns	Head and Eyes turn	Tongue	Angle of Mouth	Elbow	Shoulder	Fingers	Trunk	Thumb	Wrist	Hip	Knee	Hallux	Small toes	Ankle
VI.	Eyes turn	Eyes open	Tongue	Head turns	Mouth opens	Elbow	Shoulder	Angle of Mouth	Thumb	Wrist	Fingers	Hip	Ankle	Knee	Trunk	Hallux	Small toes	
VII.	Eyes turn	Eyes open	Head and Eyes turn	Head turns	Tongue	Trunk	Angle of Mouth	Shoulder	Wrist	Elbow	Thumb	Fingers	Hip	Ankle	Hallux	Knee	Small toes	
VIII.	Eyes turn	Eyes open	Angle of Mouth	Elbow	Shoulder	Head turns	Fingers	Trunk	Wrist	Small toes	Hullux	Ankle	Thumb					

Character of the Movements of the Parts Represented in the Fibres of the Internal Capsule.

We have given at pp. 60–63 the antero-posterior arrangement in the capsule of the movements of the different parts of the body (see Table), we now furnish two tables (see Tables IV. and V.) in the latter of which again taking the whole capsule as 100, the extent of representation of each kind of movement of the several parts of the body is given.

We wish first to review the Table IV., given on p. 78, in detail, to see how far the order of arrangement of representation of parts, *i.e.*, independently of the character of the movement of such parts in the capsule, agrees or disagrees with the arrangement which we have shown to exist in the cortex.

The accompanying diagram (fig. 7) the details of which we have partly published in the 'Philosophical Transactions,' 1887–88, the remainder being in course of publication, gives in bare outline the relative positions of the points of chiefest representation as we have found them, by minimal excitation, to exist in the cortex of the Bonnet Monkey (*Macacus sinicus*).

With this outline before us we would suggest that the main axes of the fibres of the internal capsule correspond as far as antero-posterior arrangement goes with lines drawn at right angles to the direction of the upper two-thirds of the fissure of ROLANDO. It also remains to be seen whether there is any relation between the arrangement in the cortex in the horizontal antero-posterior division and the order of fibres in the capsule.

Table IV. contains the antero-posterior arrangement of the average position of the representation in the capsule of the various parts of the body, set out horizontally. Although each observation is placed vertically under each other, this is not necessarily true of their anatomical position, as we have already shown.

It substantiates our view that the oblique lines over the "motor" cortex described above give truly the order of representation in the capsule. For while the movements of opening the eyelids and of the eyes are seen to occur in front in both cortex and capsule, those of the toes are equally the most posterior. Hence placed in order from before back we have eye movements, head movements, upper limb movements, trunk and lower limb movements.

Or stating in further detail the order of the representation as given in the foregoing table in the average position of each segment in each part of the body, the following general order of representation is arrived at, viz. :—

Summary of averages :—

44	Eyes open	Eye movements
42	Eyes turn	
50	Mouth opens	
50	Head and eyes turn	Head movements
52	Head turns	
53	Tongue	
60	Angle of mouth	
62	Shoulder	Upper limb movements
64	Elbow	
66	Wrist	
66	Fingers	
70	Thumb	
70	Trunk	
76	Hip	Lower limb movements
77	Ankle	
78	Knee	
78	Hallux	
80	Toes	

Further, if we state for each of these their relative positions to the whole of the capsule, we obtain figures which give the relative positions absolutely as above shown by the numbers placed at the left hand side of the column.

We draw attention by brackets to the association of parts in movement as already shown to occur in the cortex.

Nothing, we believe, shows more distinctly the truth of our position that the arrangement in the capsule is but an imitation of that on the cortex, which in its turn is but a peripheric projection of the order of the metameres of the whole body.

The accuracy of this general view is borne out by an analysis of the representation of the segments of one, the lower limb. In both the cortex and capsule the hip is most represented in front, the small toes hindermost (*i.e.*, posterior to the hallux), and the other joints intermediately. Similarly, in accordance with the view of SCHÄFER and HORSLEY* that the trunk muscles are represented mediately in the "motor" region, we find that in the capsule the representation of this part is, as a rule, between the upper limb and lower limb regions.

For the upper limb the arrangement in the capsule is analogous to that for the lower limb, namely, the largest joint, the shoulder, is most anterior, and the smallest, the most specialised, the thumb, is most posterior. By dropping verticals in fig. 7, on p. 81, this is evidently the cortical arrangement projected below.

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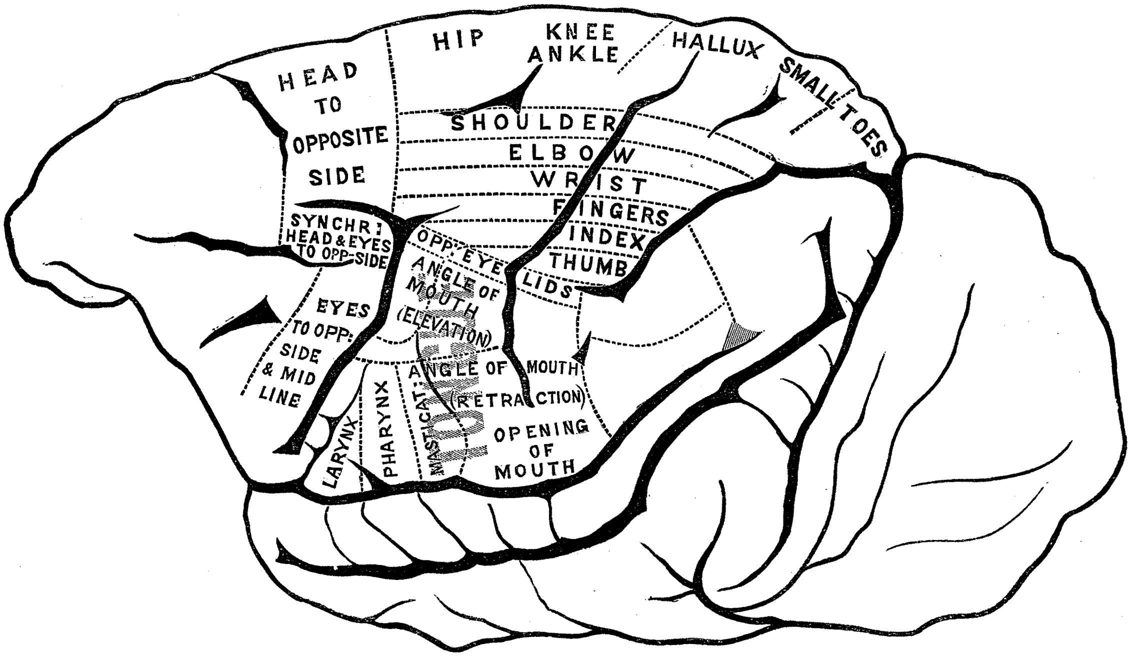
* 'Phil. Trans.,' B, 1888, p. 9; 'Roy. Soc. Proc.,' vol. 36, 1884, p. 437.

Fig. 7.



Eyes open
Eyes turn
Mouth opens
Head and eyes turn
Head turns
Tongue
Angle of mouth
Shoulder
Elbow
Wrist
Fingers
Thumb
Trunk
Hip
Ankle
Knee
Hallux
Toes

Arrangement of excitable fibres in the internal capsule.

Drawn from a photograph (magnified twice) of the outer surface of a Monkey's (*Macacus sinicus*) left hemisphere.

TABLE V.—(Length of Capsule = 100.)

Kind of Movement.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Eyelids, both sides open	24–25	37–61	41–62	30–60	38–54	40–64	5–51	16–41
,, opposite side more than same side	..	..	..	..	50–55			
,, both sides close	..	..	..	66–75	100 (1 observ.)	..	33	
,, opposite side alone closes	..	..	67–77	..	60–65	64	60–62	75 (1 observ.)
Eyeballs become parallel	..	..	..	49–51	40	..	33	
,, turn to opposite side	22–60	25–68	48–60	23–57	38–59	42–60	5–51	8–41
,, turn to opposite side and downwards	8–16	..	..	..	25–60			
,, turn up and to opposite side	..	..	..	..	..	..	5	
Pupils dilate	..	..	..	42	45	..	..	16–25
Head and eyes turn synchronously to opposite side	41–54	..	53–60	55	53–60	..	29–35	
Head turns to opposite side	42–64	42–71	56–70	34–65	41–58	47–66	22–45	33–66
,, turns, muzzle up	52							
,, retracted	..	..	75	65–90 (1 observ.)				
Lips, depression of opposite lower	..	..	..	..	54–68			
,, pouting of both	..	56	..	..	..	..	..	41–50
,, pursing of both, but especially on opposite side	..	..	..	65	..	63		
Angle of mouth,* opposite retracted	58–82	48–83	58–79	50–85	54–80	51–78	45–65	16–50
,, both sides retracted	..	..	58	..	..	63		
Mouth opens	13–51	43–57	57–71	40–62	44–48			
,, shuts	..	25–37	73 (1 observ.)					
,, opens and shuts (as in mastication)	14–69	44–47	77	45–47	61–63	88–94 (1 observ.)	45	
Tongue protruded straight	7–24	57–61	47	52–69	64–65	55		
,, ,, to opposite side	..	..	..	66–83	57–62	..	35–47	
,, ,, to same side								
,, ,, to same side (concave to opposite side)	..	..	73					
,, narrowed	..	..	78	..	75–80			
,, retracted, heaped up posteriorly	..	..	52	63	76			

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* We have not in this paper differentiated between elevation and retraction of the angles of the mouth.

TABLE V.—continued.

Kind of Movement.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Tongue retracted, tip retracted	..	..	..	77	64–69	..	52	
" " and protruded	..	50						
(1) to same side	..	50						
(2) to opposite side	..	..	77					
" heaped behind, rolled, and protruded to same side	..	..	68	61–72	65–72			
Swallowing	..	..	..	65				
Barking	..	..	36					
Shoulder, advancing	62–76	..	74–82	62–63	66–79			
" retract	..	..	75	80	59	55		
" adduction	..	68–86	75–83	60–83	66–80	65–89	45–62	49–66
" abduction	..	..	77	40	..	..	..	16–25
" rotation in	..	56	..	77	65	..	66	41–58
" rotation out	67–70	63–70	67	59	55–71	..	51–54	16–50
Elbow, extension	70	58–62	66–73	60	57–59	55–61	41	17
" confusion	75–91	68–74	75–80	58	70–76	57–67		
" flexion	60–91	69–86	70–87	57–83	66–79	57–77	51–65	33–62
Wrist, extension	75–100	63–73	75–90	58–74	65–76	68–72		
" flexion	..	..	64–73	60	78	..	62	
" pronation	80	..	89–100	45–72	67–71	65–69	70	62
" supination	..	..	..	55–63	68	..	41–64	41–50
" ulnar adduction	..	..	..	..	..	69	..	50
" confusion	..	..	..	..	..	60		
Index finger, flexion	..	..	..	..	..	60–69		
" flexion, extension	..	..	..	..	..	65		
Fingers, extension	..	61–72	65	62–68	67–71	57–61	50	
" extension, flexion	66	..	83					
" interosseal flexion	91–100 (1 observ.)	..	84–90	..	50			
" flexion	65–77	65–86	75–82	62–79	63–85	68–82	62	37–62
" confusion	..	77						
Thumb, extension	..	61	..	70 (1 observ.)	79	65	55	
" extend, flexion	..	..	94 (1 observ.)					

TABLE V.—continued.

Kind of Movement.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Thumb, interosseal flexion	83–87	..	82–88	..	76			
,, flexion	71–76	79–88	78–87	65–81	68–80	62–73	61	62
,, flexion, extension	..	..	..	..	..	65		
,, abduction	..	..	..	45–50				
Trunk, opisthotonus	70–76							
,, rotation to opposite side	..	61–72						
,, arching to opposite side	..	..	60					
Abdomen, opposite rectus	70–88	60–80	80–86	80	58–85	77–83	41–58	
Tail, adduction or flexion to opposite side	..	..	87					
,, extension to opposite side	..	..	84	..	..	77–88		
Hip, extension	100	83	88	..	52–71			
,, confusion	..	77	81–87					
,, flexion	62–71	85–90	74–85	74–91	72–76	68–79	65	
,, adduction	..	75	88	..	85–90			
,, rotation out	85–89	..	..	85–90	68–70			
,, rotation in	..	68–81	..	83	75–85	69		
Knee, extension	100	..	78–82	..	75			
,, confusion	..	77	84					
,, flexion	79–83	81–93	84–86	76–88	74–77	76–82	66	
,, rotation in	..	..	78					
Ankle, dorso flexion	78–81	92–96	83–89	73–82	83–88	72–85	64	58–78
,, plantar extension	100	83	88–90	66	73	83	..	41
,, eversion	88–94	..	77–94	..	78–82	69		
,, inversion	..	87–93	78	85–90	71	77		
Small Toes, extension	91–95	84–94	86–92	76–94	82–86	82–88	61–72	58–66
,, interosseal flexion	..	..	88–100					
,, flexion	71	83	86	72–80	82	69	..	41–66
,, flexion, extension	70–76							
Hallux, extension	82–88	92–98	84–91	79–92	72–83	82–88	..	66
,, flexion	73	..	86–95	72–86	78–86	69	..	41–66
,, flexion, extension	70–76							

We are now in a position to point out the chief facts of interest to be noted in Table V., and which illustrate the relation between the localisation of motor or efferent function in the cortex and that in the capsule. Under the drawing, fig. 7, we have inscribed in their accurate relative positions the arrangement of the capsular fibres. If lines be laid obliquely as stated on p. 79, the exact correspondence of the cortical capsular representation will be readily seen.

Movements of Eyelids.

The most striking among these is that of closure of the opposite eyelids only (or in an incompletely evolved cortex accompanied by slight movement of the same side). The cortical localisation of this movement we give in fig. 7, and a line drawn vertically shows it to be relatively far behind the area for the other movements of the lids.

So in the capsule it is found fully one-tenth to one-fifth of the length of the capsule further back, and thus comes into relation with the representation of the upper limb and angle of the mouth. No closer correspondence between the representation in the cortex and that in the capsule could well be imagined.

In passing on to the next feature of special interest we would mention that we only observed the minuter changes in the movements of the lips, mouth, tongue, and jaws towards the end of this work, since our analysis of the facial region (not yet published) has only been carried on during the last fifteen months. Hence our account of these movements is necessarily brief.

Upper Limb Movements.

Elbow.—In describing* the analysis of the upper limb cortical representation we have shown that extension of the elbow is represented most anteriorly and superiorly, and flexion most inferiorly and posteriorly, while confusion of these movements is localised between their foci of most intense representation. This is most clearly found to be also the case in the capsule. The elbow, being a simple hinge joint and allowing only of extension, flexion and confusion, affords a ready means for this comparison between the cortex and capsule, and therefore it is interesting to note that in every group of sections this close similarity of representation was established.

Fingers.—So also the hinge joints of the fingers show that extension is represented anteriorly and flexion posteriorly in the capsule, this difference being, as seen in Table V., present in every group.

Thumb.—The same also prevails for the thumb.

Lower Limb Movements.

Since the cortical representation of the movements of the lower limb was shown by our analysis to be relatively imperfect, it was to be expected that with the mingling

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* 'Phil. Trans.,' B., 1887–88.

of fibres in the capsules, still less differentiation would be found. This is obviously shown in Table V., but on inspection, the representation of even flexion of the *small toes* is consistently (every group) in front of that of extension. To a minor degree and with less consistency (4 of 6 groups) the same holds for the hallux.

Relative Amount or Degree of Representation of Extension compared to Flexion.

This subject may not be without interest to those who have, from excitation experiments, attempted to gauge the relative amount of functional activity in the cortex.

The facts bearing upon this point obtained from the records of hinge joint movements are so clear and unmistakable that they are of value.

The following are the proportional rates of frequency as observed in the capsule.

	Flexion.	Extension.	Remarks.
Elbow	38	16	Joints whose usual movement is powerful flexion
Fingers	38	17	
Thumb	22	9	Joint the flexion of which is usually carefully regulated by extension
Small toes	15	26	Joints very frequently spread in extension for standing
Hallux	16	17	Joint used as a thumb as well as for support

The bearing of these facts obviously requires no further comment, and the more so as they are but confirmatory of the results we obtained in our analysis of the cortical representation of these parts.

CONCLUSIONS.

As the foregoing paper is but a collection of detailed facts we can only offer as conclusions a few bare statements.

1. The fibres of the excitable portion of the internal capsule are arranged from before back, in the same order as the foci of representation in the excitable part of the cortex, taken along lines drawn at right angles to the direction of the fissure of ROLANDO.

2. This applies to the great divisions of the body, *i.e.*, head, upper limb, &c.

3. The arrangement of the fibres for the different segments of each great division is likewise that which prevails in the cortex.

4. Similarly the character of each movement is represented in the capsule as in the cortex.

Description of Plates.

PLATES 5.–9.

Fig. 1. This figure consists of a number of drawings of the internal capsule and basal ganglia of the left side in horizontal section, corresponding to the eight different levels into which we have grouped our observations, and enlarged twice the natural size.

a. = Anterior commissure.
C. = Caudate nucleus.
F. = The point of fusion of the lenticular and caudate nuclei in the basal grey matter.
i. = Inner zone of the lenticular nucleus.
l. = Middle zone of lenticular nucleus.
L. = Outer zone of lenticular nucleus or putamen.
O. = Optic thalamus.

Figs. 1, A.–R., give on tracings of the outlines of fig. 1, the limitation of the fibres, excitation of which produced a particular movement, the character of which is indicated in the margin.

Figs. 4, 5, 6 (on Plate 6). Views of a dissection of the hardened brain of a *Macacus sinicus*, in which almost the whole of the hemisphere has been cut away, leaving only the basal ganglia to show their relations to each other and to the internal capsule. Fig. 4 is viewed from the inner or ventricular side, fig. 5 from below, and fig. 6 from the outer side.

A.a. = Anterior and ascending division of præfrontal fibres, lying in the deep groove between the caudate and lenticular nuclei.
a.c. = Anterior commissure.
Ch. = Optic chiasma.
Cb. = Cerebellum.
H. = Horizontal fibres of præfrontal portion of capsule.
Hi. = Hippocampus major.
Gy.Hi. = Gyrus hippocampi.
C.q. = Corpus quadrigeminum.
l.m. = Outermost lamina medullaris.
s.d. = Superior and descending division of præfrontal fibres.
Ca. = Caudate nucleus.
Pu. = Putamen or outer zone of lenticular nucleus.
P.F. = Excitable (“motor”) or fronto-parietal fibres.
L. = Posterior limit of excitable fibres.

Note change of direction at this point opposite middle zone (*m*) of lenticular nucleus, the fibres forming the internal capsule behind and below (*m*) are respectively occipital, occipito-temporal, and temporal.

M.C. = Middle commissure.

III., V., and VI. denote the third, fifth, and sixth cranial nerves.

PLATE 10.

Groups I.–VI. These are photographs typical of each level at which we have excited the capsule, corresponding to the first six groups of our observations.

Ca. = Caudate nucleus.
Le. = Lenticular nucleus.
O.Th. = Optic thalamus.

PLATE 11.

Groups VII. and VIII. These are photographs of our last two levels and follow on Plate X.

NOTE.—Group VIII. has been reversed in the reproduction.

The section is taken from the left hemisphere, except in Groups IV. and VIII., which are taken from the right side.

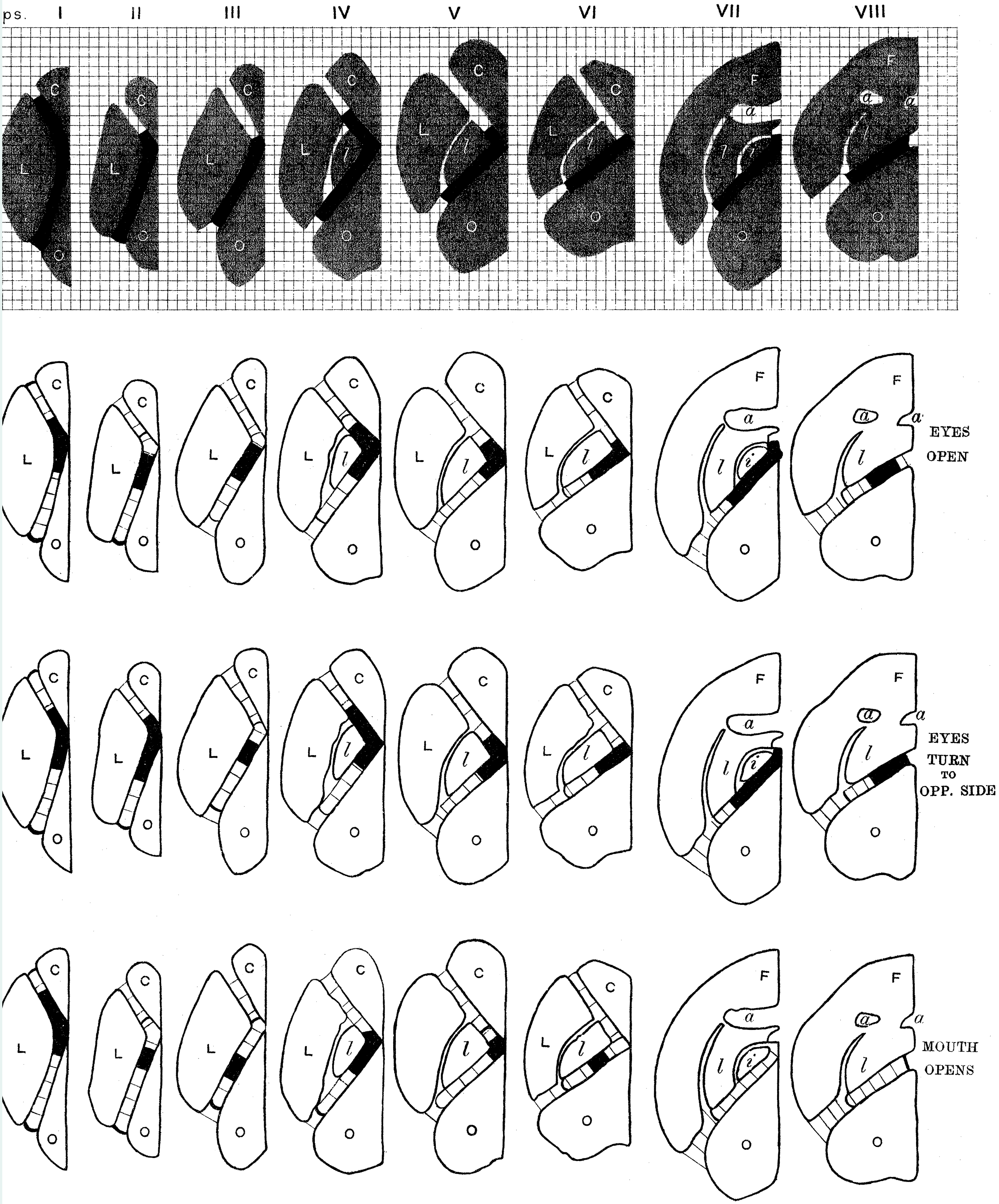
Fig. 2. A photograph of a transverse vertical section of the right hemisphere of *Macacus sinicus*, showing the limits of the capsule and the direction of its anterior limb in frontal section.

Ca. = Caudate nucleus.
C.c. = Corpus callosum.
Le. = Lenticular nucleus.
S.l. = Septum lucidum.

Fig. 3. This figure is a photograph of a sagittal section of the hemisphere of a *Macacus sinicus* stained by PAL'S method and mounted in balsam. The medullated fibres are consequently stained black, the grey matter being of a lighter greyish tint.

A.a. = Anterior or ascending fibres of præfrontal division of capsule.
H. = Horizontal fibres of the same.
S.d. = Superior or descending fibres of the same.
P.f. = Pyramidal fibres (excitable).
P. = Fibres entering the posterior limb of the capsule.
Ca. = Caudate nucleus.
Le. = Lenticular nucleus.
O.th. = Optic thalamus.
A.c. = Anterior commissure.

Fig. I



Lith.& Imp. Camb. Sci. Inst. Co.

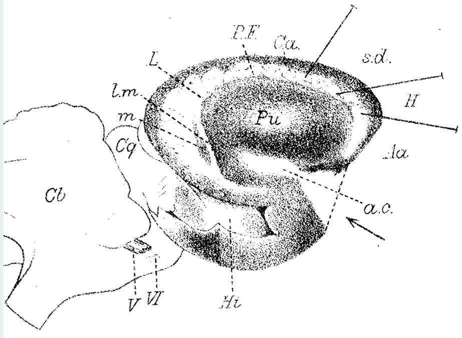


Fig. 6.

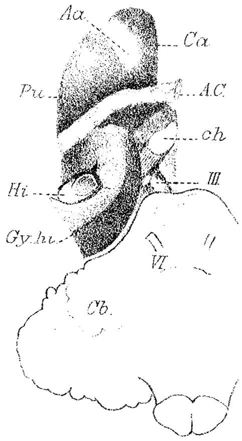


Fig. 5.

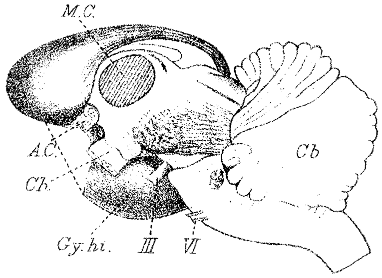
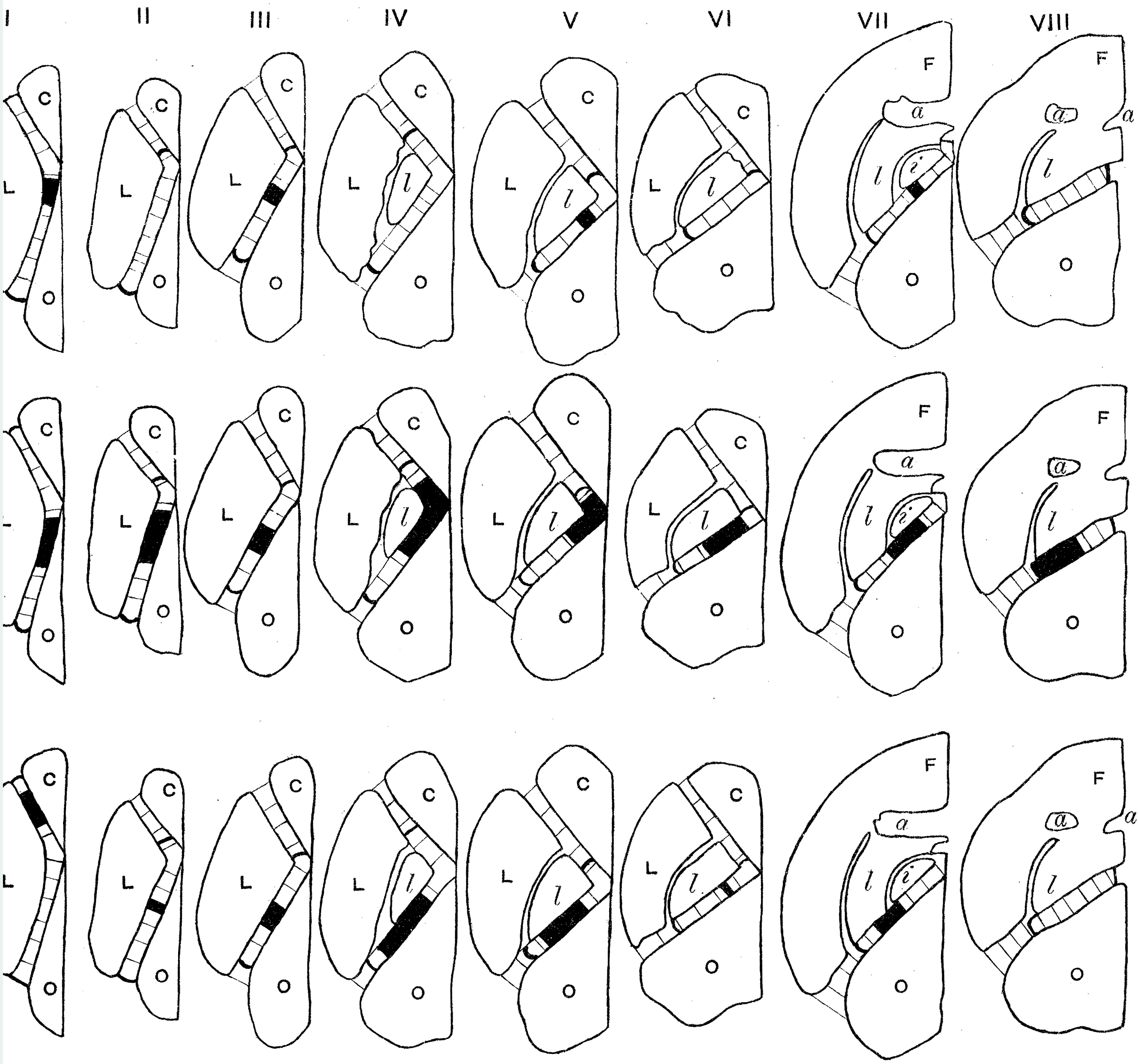


Fig. 4

Contd.



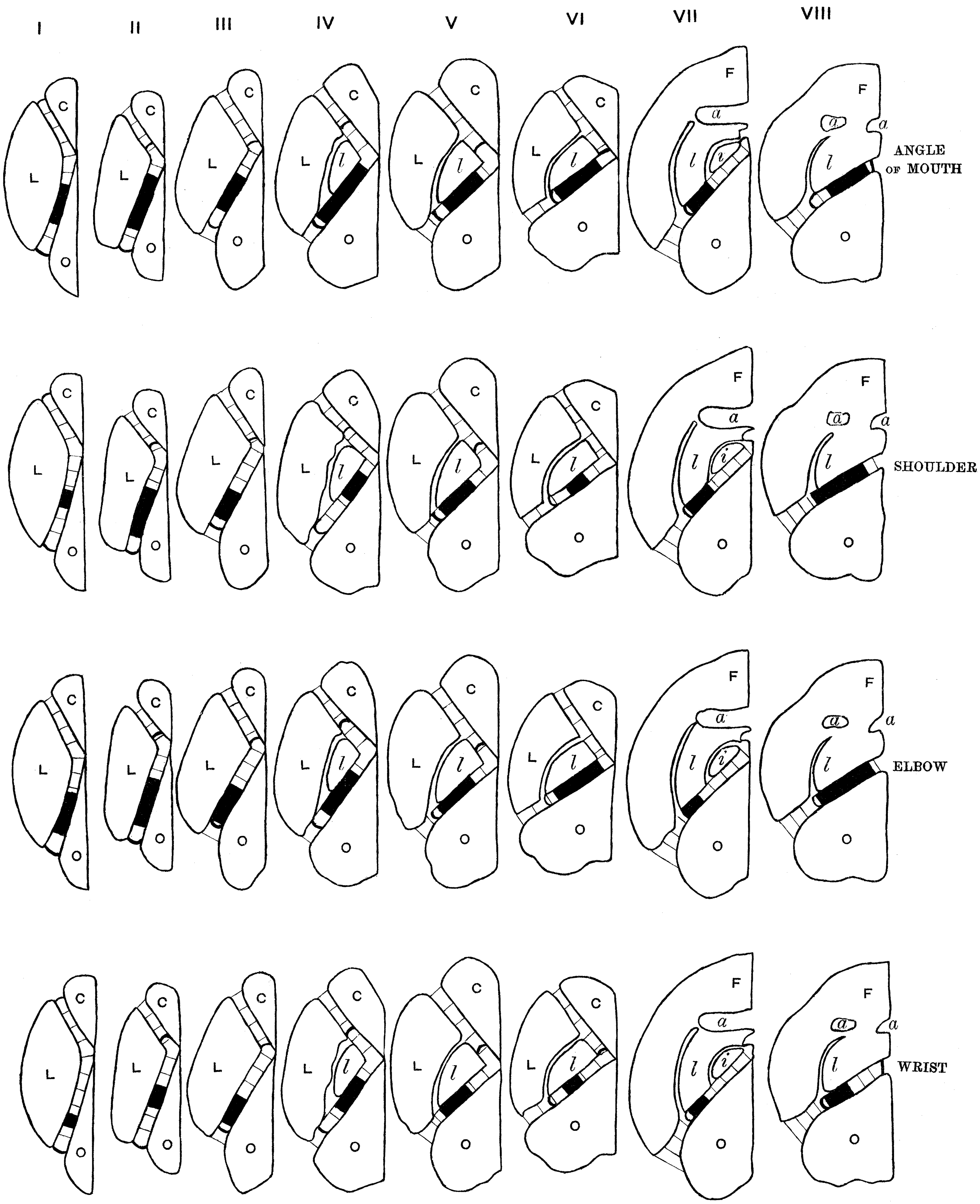
HEAD AND EYES SIMULTANEOUSLY TURN TO OPP. SIDE

HEAD TURNS TO OPP. SIDE

TONGUE

Lith.& Imp. Camb. Sci. Inst. Co.

Beevor & Horsley. *Phil. Trans.* 1890. B. *Plate* 7.



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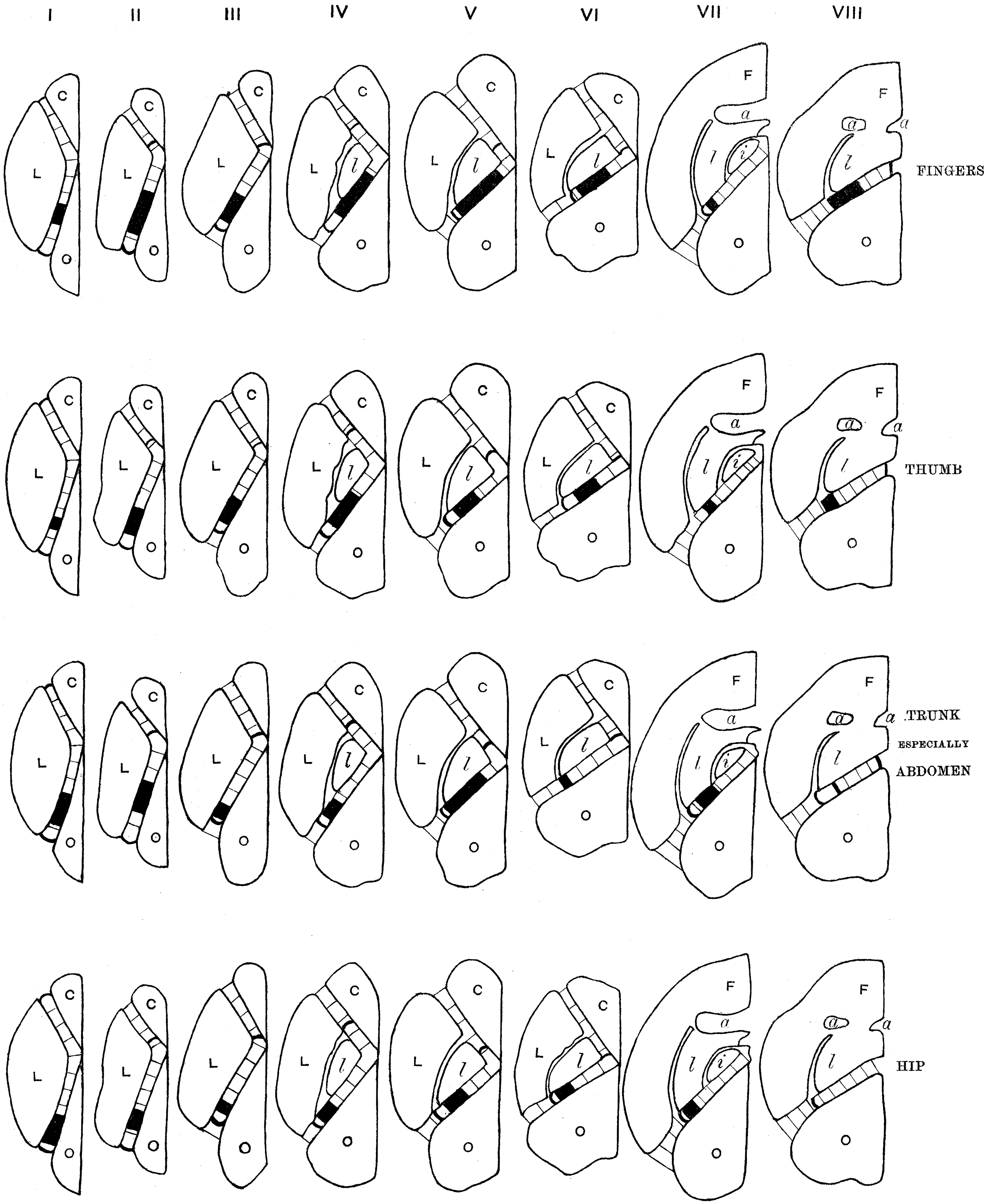

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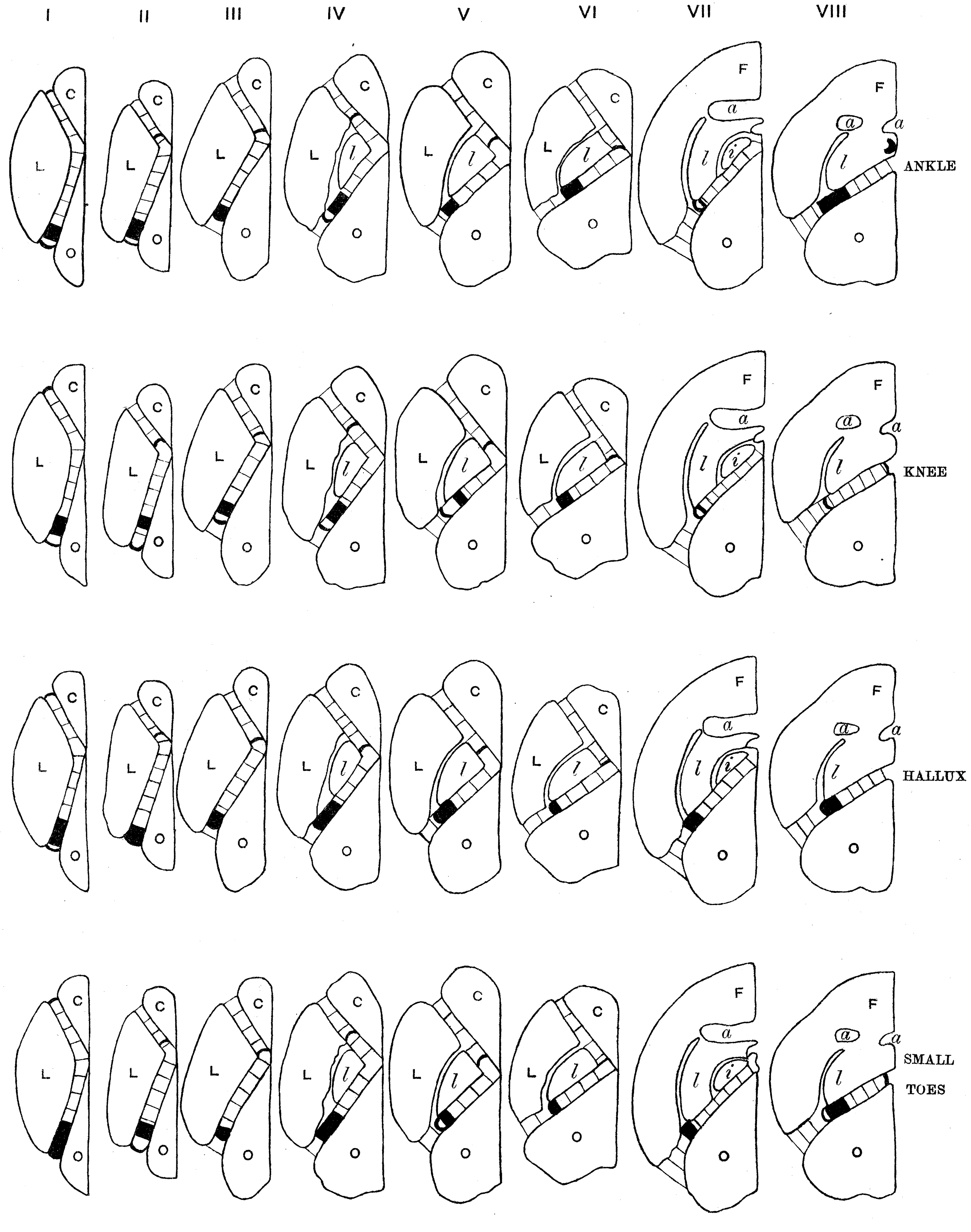

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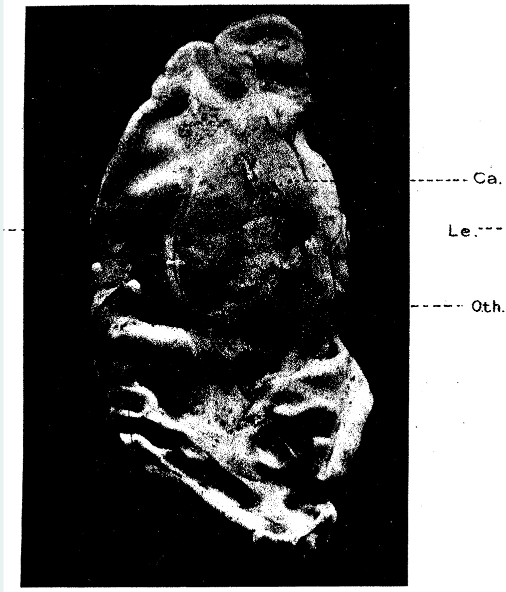
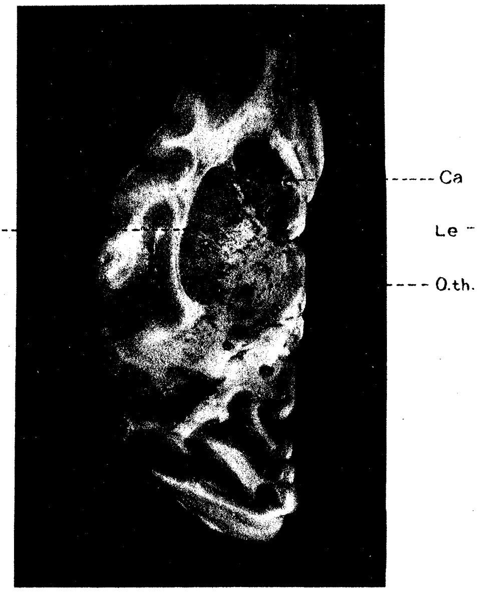


Group I.



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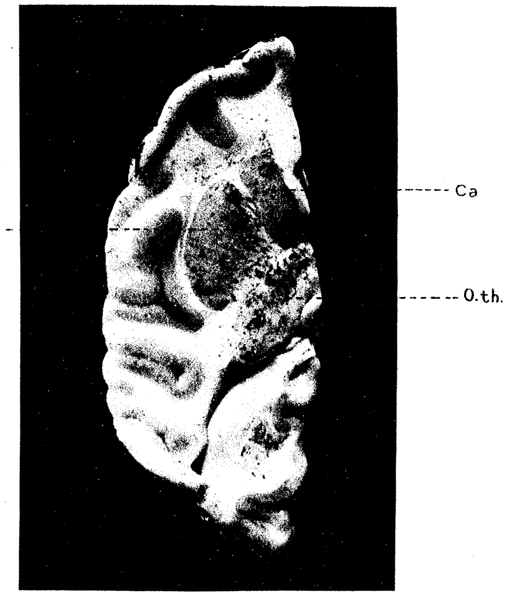
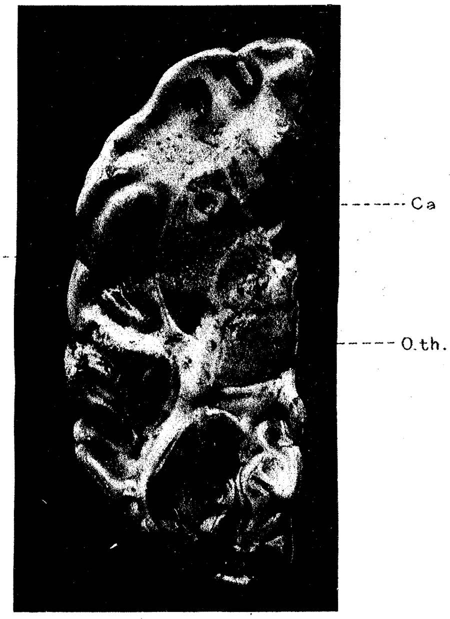


Group III.

Group V.



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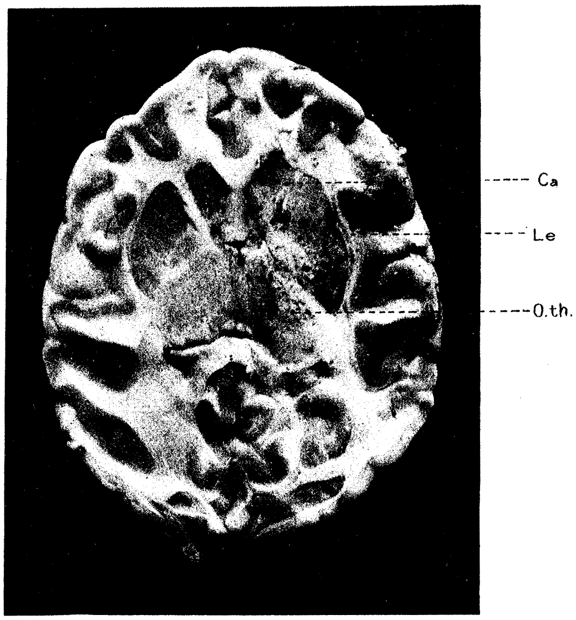

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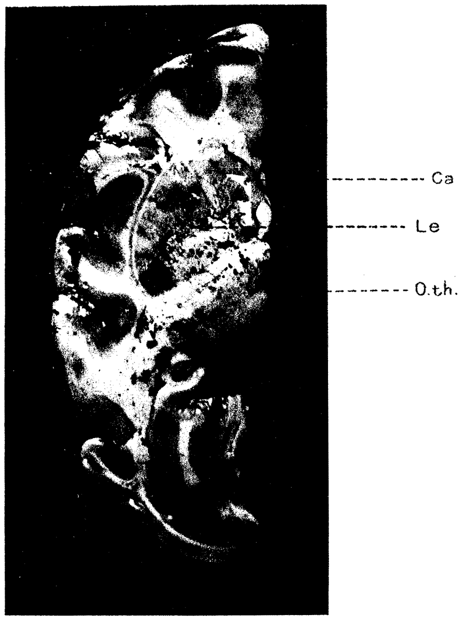


PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Danielsson & C°, Photo-print.

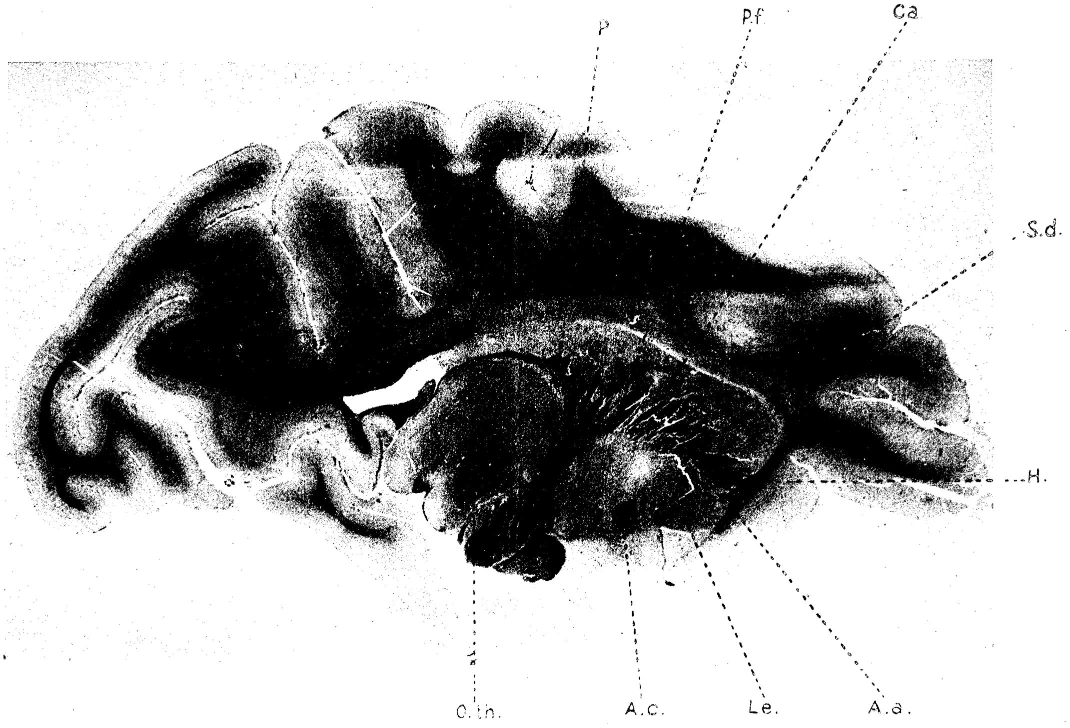
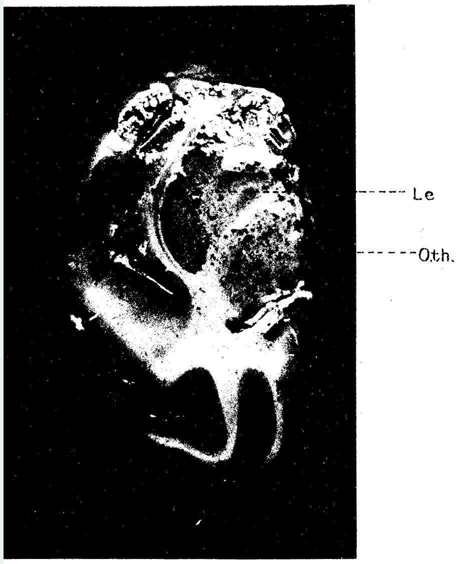


Fig 3.

Group VII.



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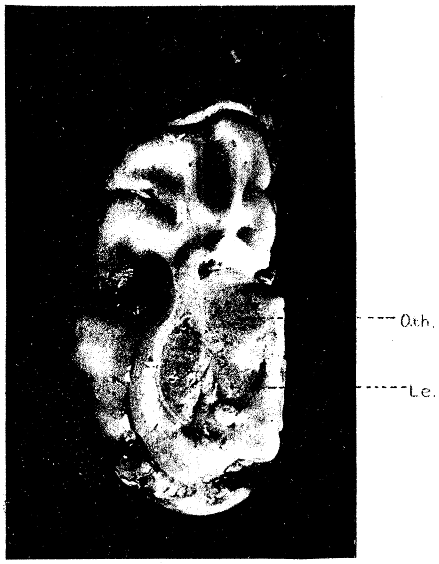
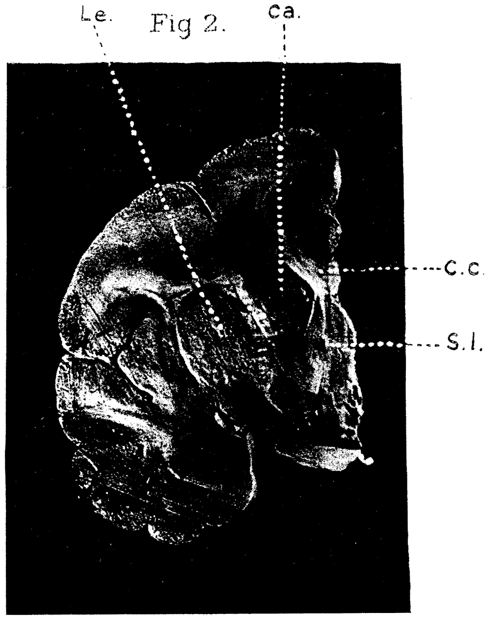


Fig 2.



Danielsson & C°. Photo-print.

Fig. 1.

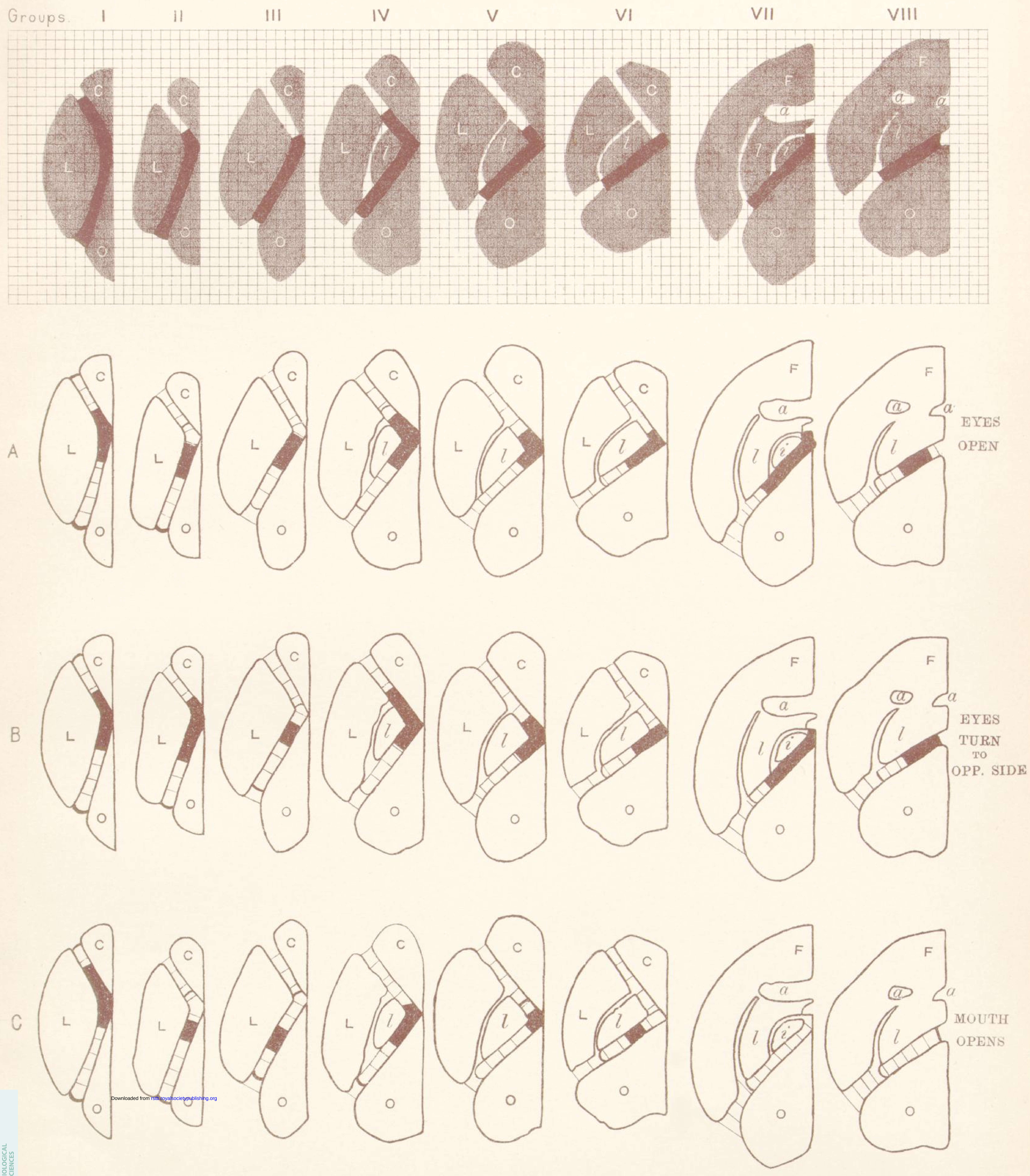


Fig. 1. This figure consists of a number of drawings of the internal capsule and basal ganglia of the left side in horizontal section, corresponding to the eight different levels into which we have grouped our observations, and enlarged twice the natural size.

a. = Anterior commissure.
C. = Caudate nucleus.
F. = The point of fusion of the lenticular and caudate nuclei in the basal grey matter.
i. = Inner zone of the lenticular nucleus.
l. = Middle zone of lenticular nucleus.
L. = Outer zone of lenticular nucleus or putamen.
O. = Optic thalamus.

Figs. 1, A.–R., give on tracings of the outlines of fig. 1, the limitation of the fibres, excitation of which produced a particular movement, the character of which is indicated in the margin.

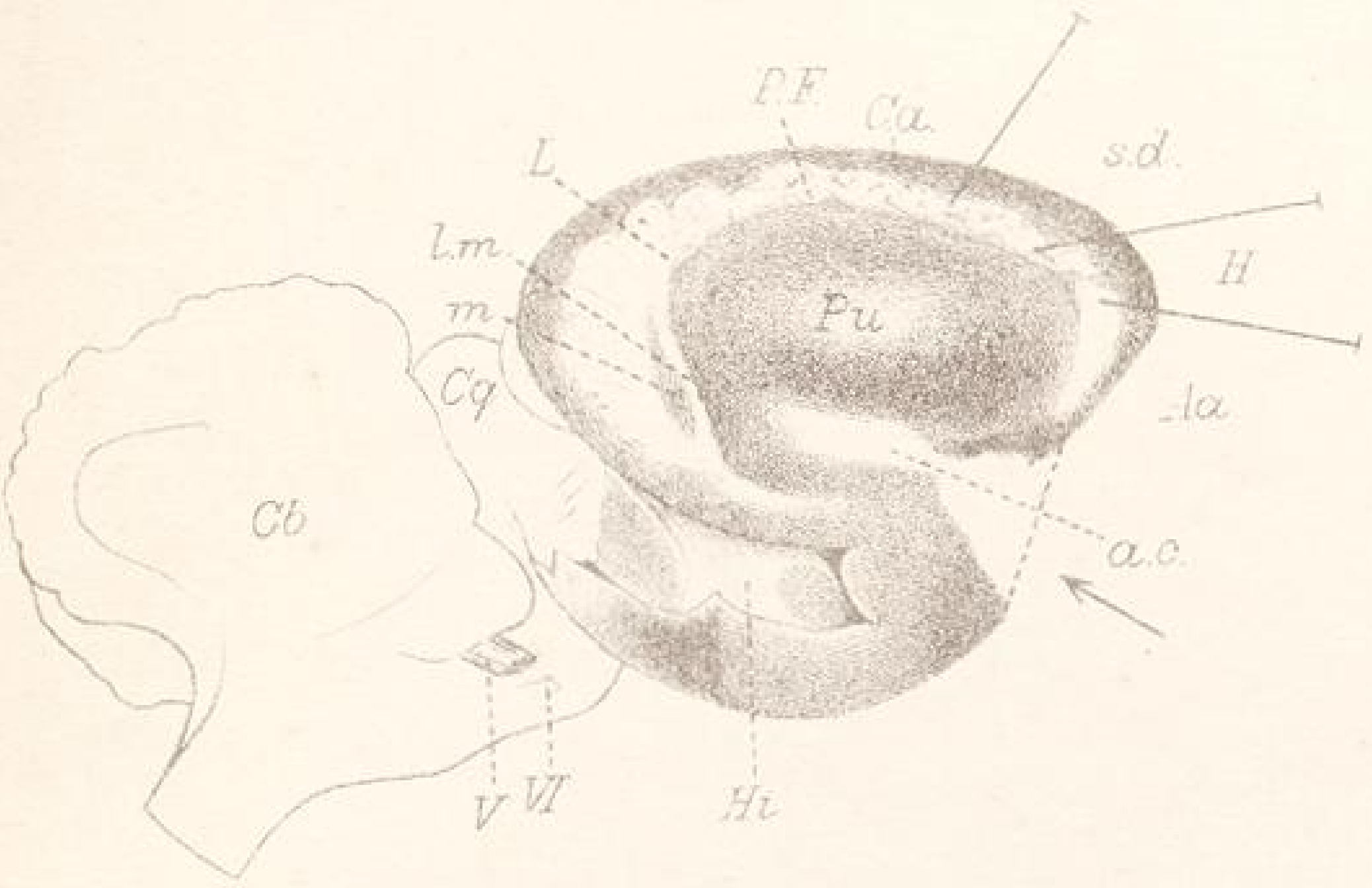


Fig. 6

Fig. 5.

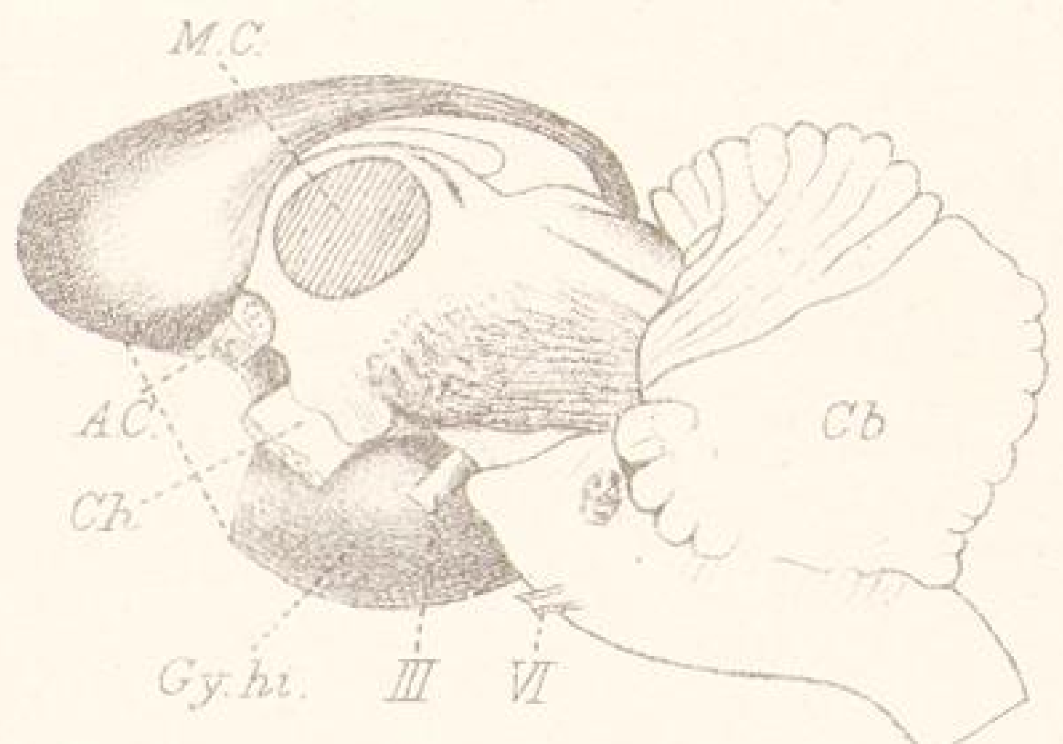
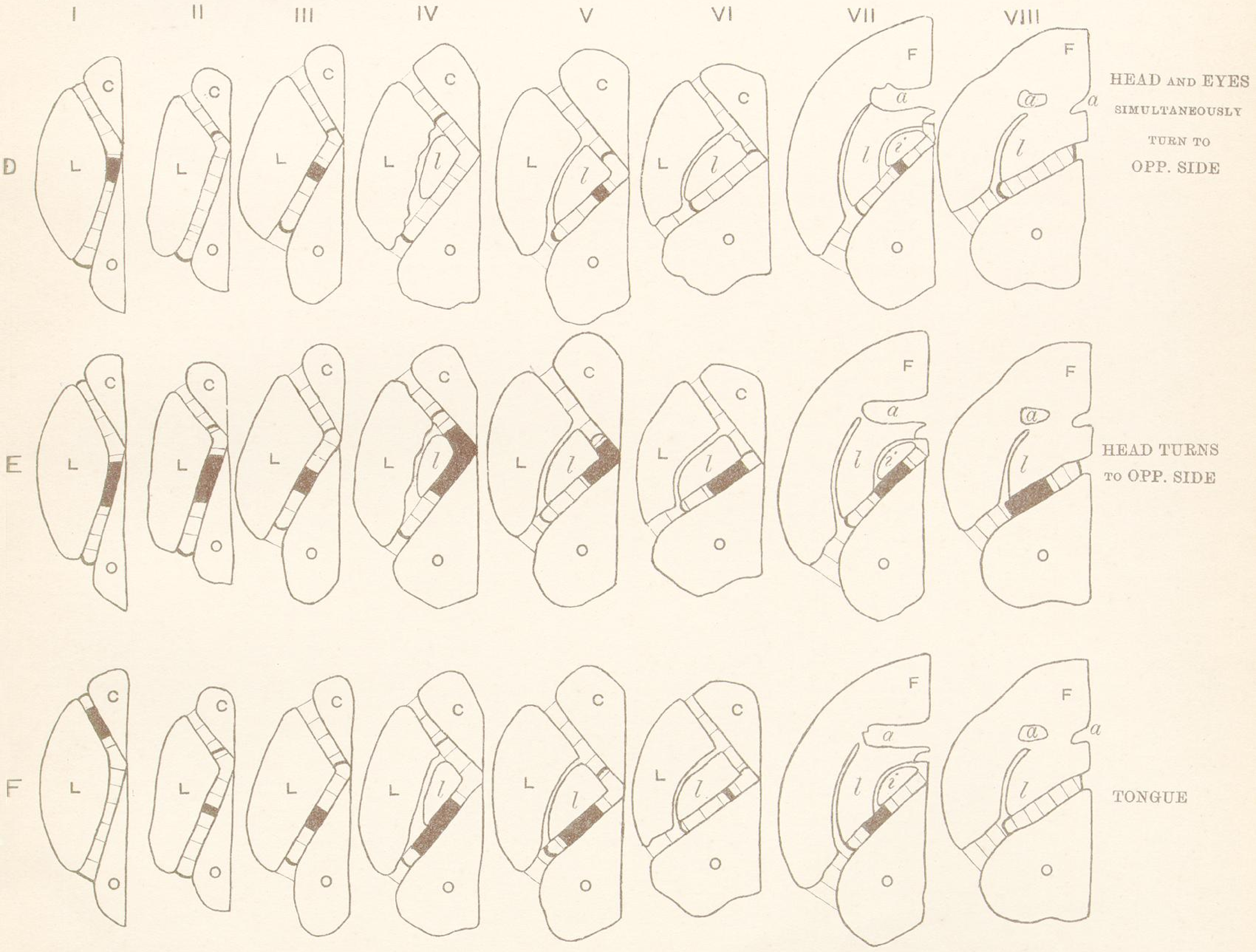


Fig. 4

Fig. I. Contd



Figs. 4, 5, 6 (on Plate 6). Views of a dissection of the hardened brain of a *Macacus sinicus*, in which almost the whole of the hemisphere has been cut away, leaving only the basal ganglia to show their relations to each other and to the internal capsule. Fig. 4 is viewed from the inner or ventricular side, fig. 5 from below, and fig. 6 from the outer side.

A.a. = Anterior and ascending division of præfrontal fibres, lying in the deep groove between the caudate and lenticular nuclei.
a.c. = Anterior commissure.
Ch. = Optic chiasma.
Cb. = Cerebellum.
H. = Horizontal fibres of præfrontal portion of capsule.
Hi. = Hippocampus major.
Gy.Hi. = Gyrus hippocampi.
C.q. = Corpus quadrigeminum.
l.m. = Outermost lamina medullaris.
s.d. = Superior and descending division of præfrontal fibres.
Ca. = Caudate nucleus.
Pu. = Putamen or outer zone of lenticular nucleus.
P.F. = Excitable ("motor") or fronto-parietal fibres.
L. = Posterior limit of excitable fibres.

Note change of direction at this point opposite middle zone (*m*) of lenticular nucleus, the fibres forming the internal capsule behind and below (*m*) are respectively occipital, occipito-temporal, and temporal.

M.C. = Middle commissure.

III., V., and VI. denote the third, fifth, and sixth cranial nerves.


I
II
III
IV
V
VI
VII
VIII
G
ANGLE OF MOUTH
H
SHOULDER
I
ELBOW
J
WRIST
C
L
O
l
i
a
F


I
II
III
IV
V
VI
VII
VIII
K
L
FINGERS
THUMB
TRUNK
ESPECIALLY
ABDOMEN
HIP
C
L
l
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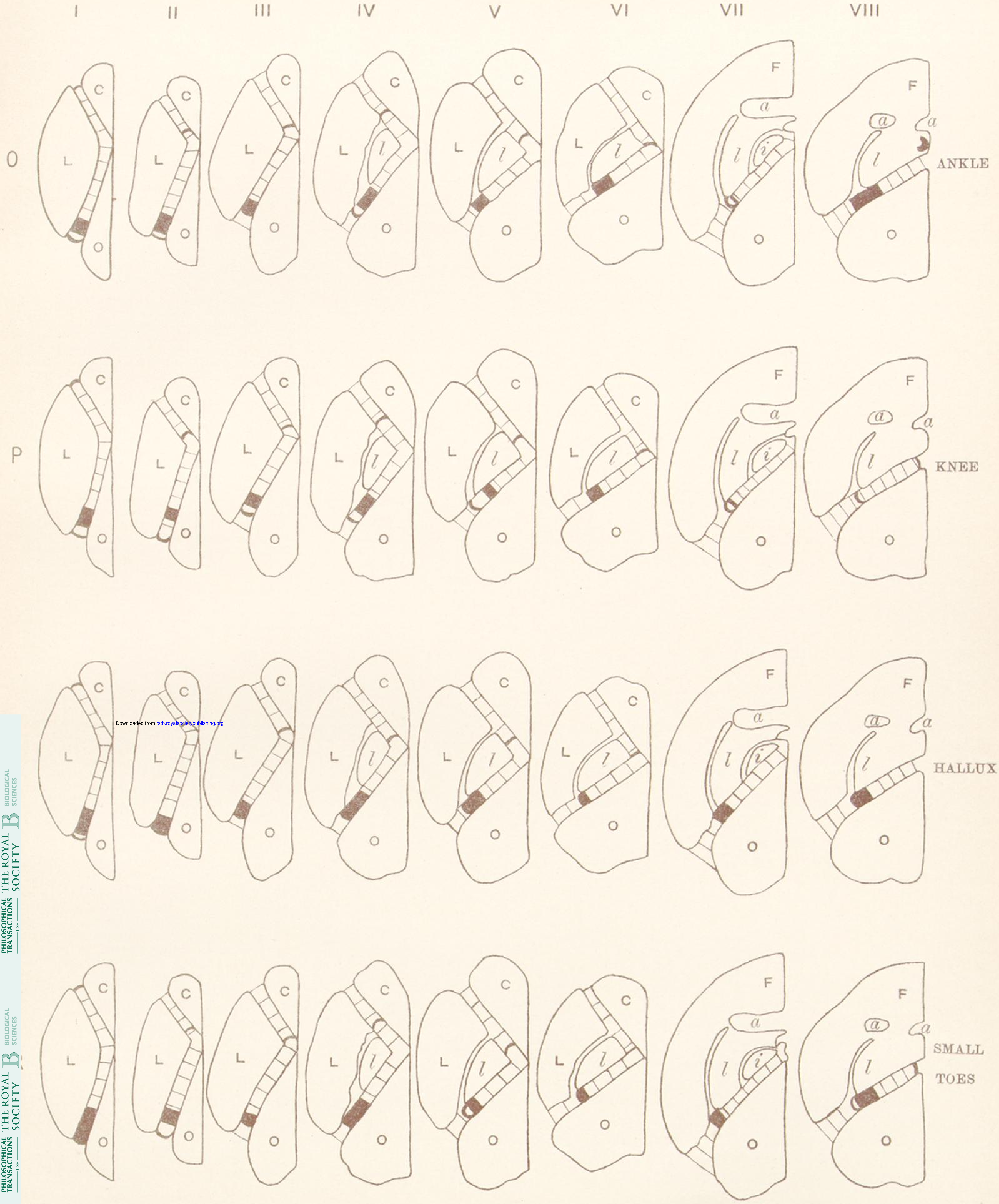
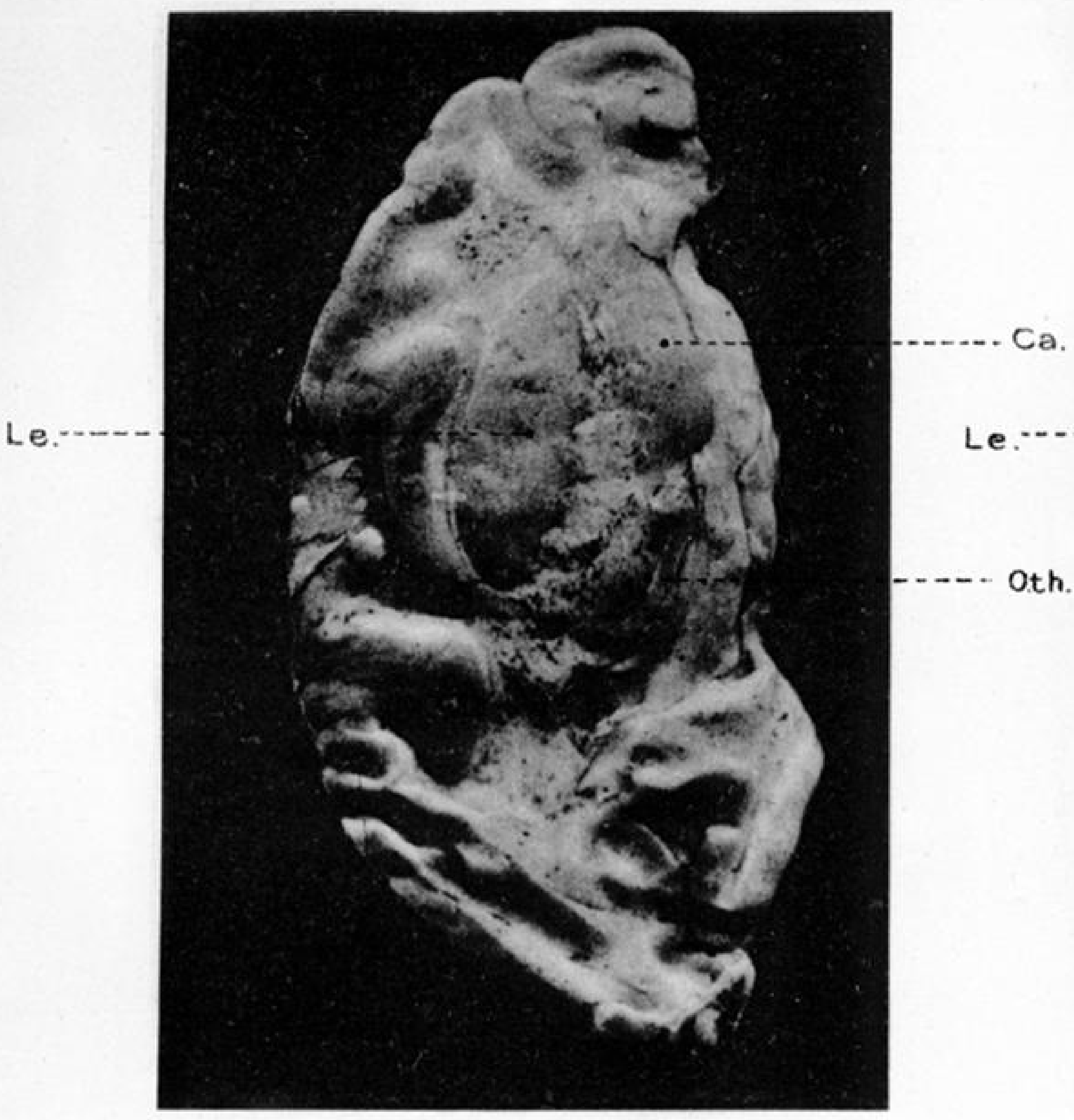
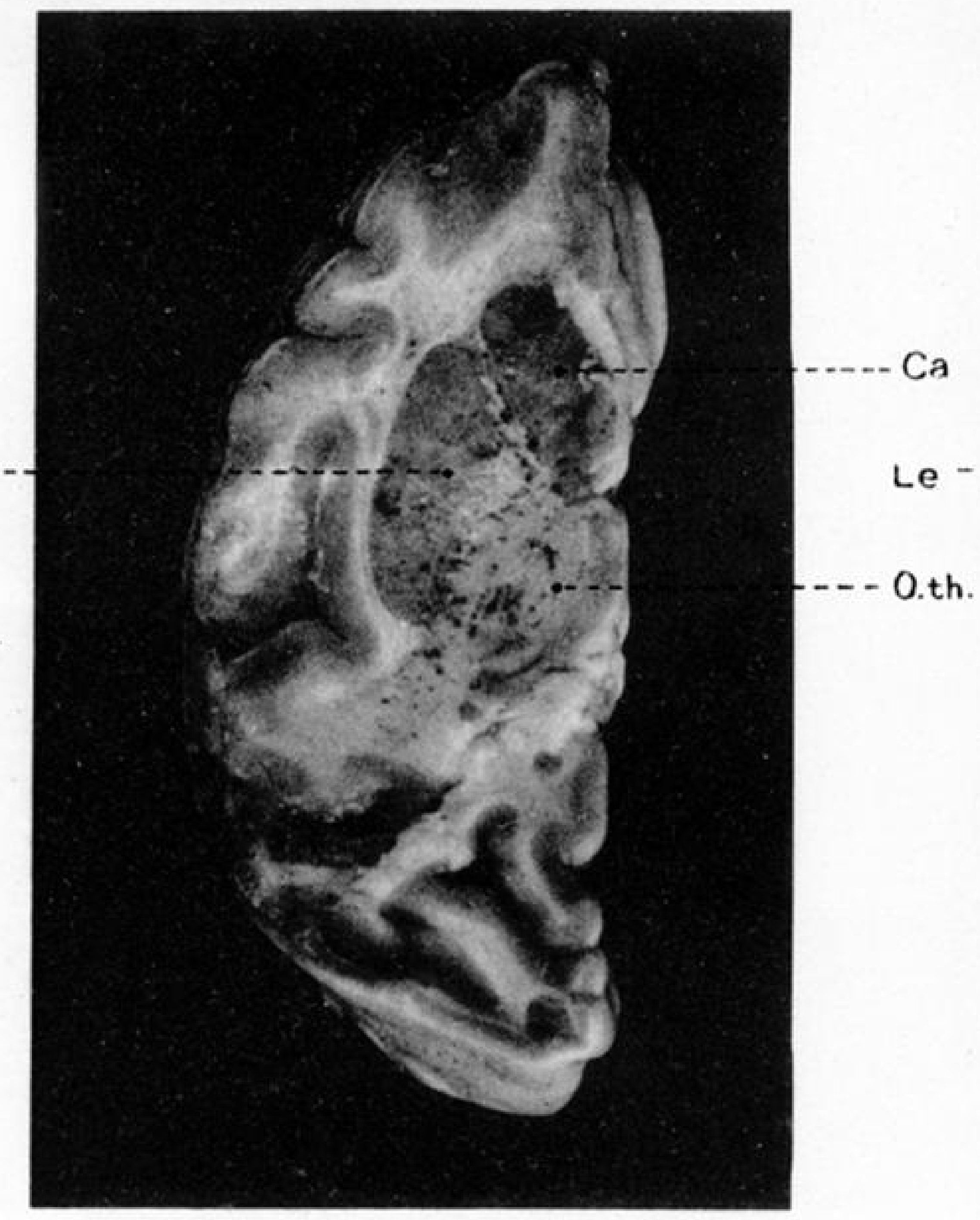
a
i

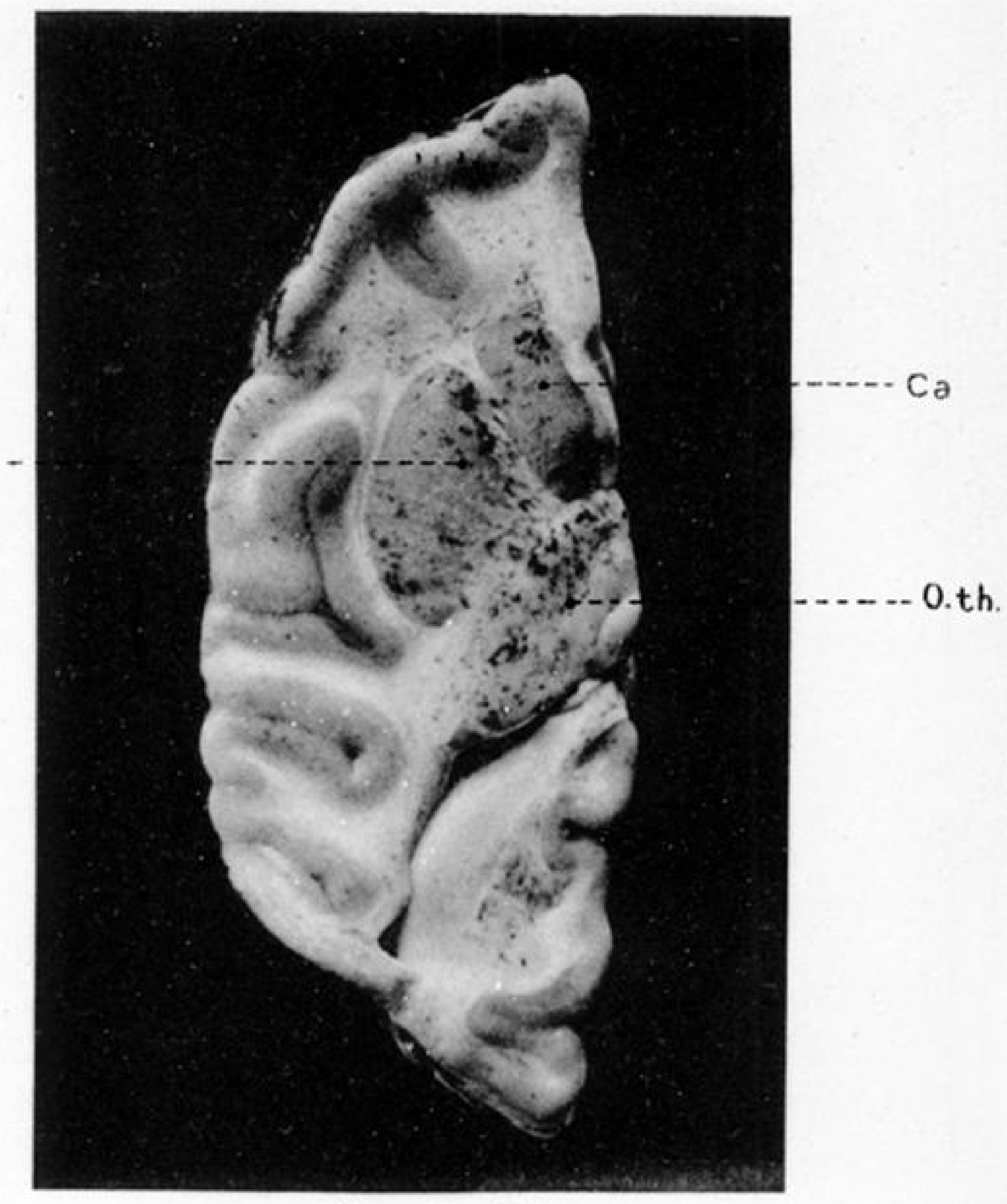

I
II
III
IV
V
VI
VII
VIII
O
P
ANKLE
KNEE
HALLUX
SMALL
TOES
C
L
l
i
a
F
O



Group I.

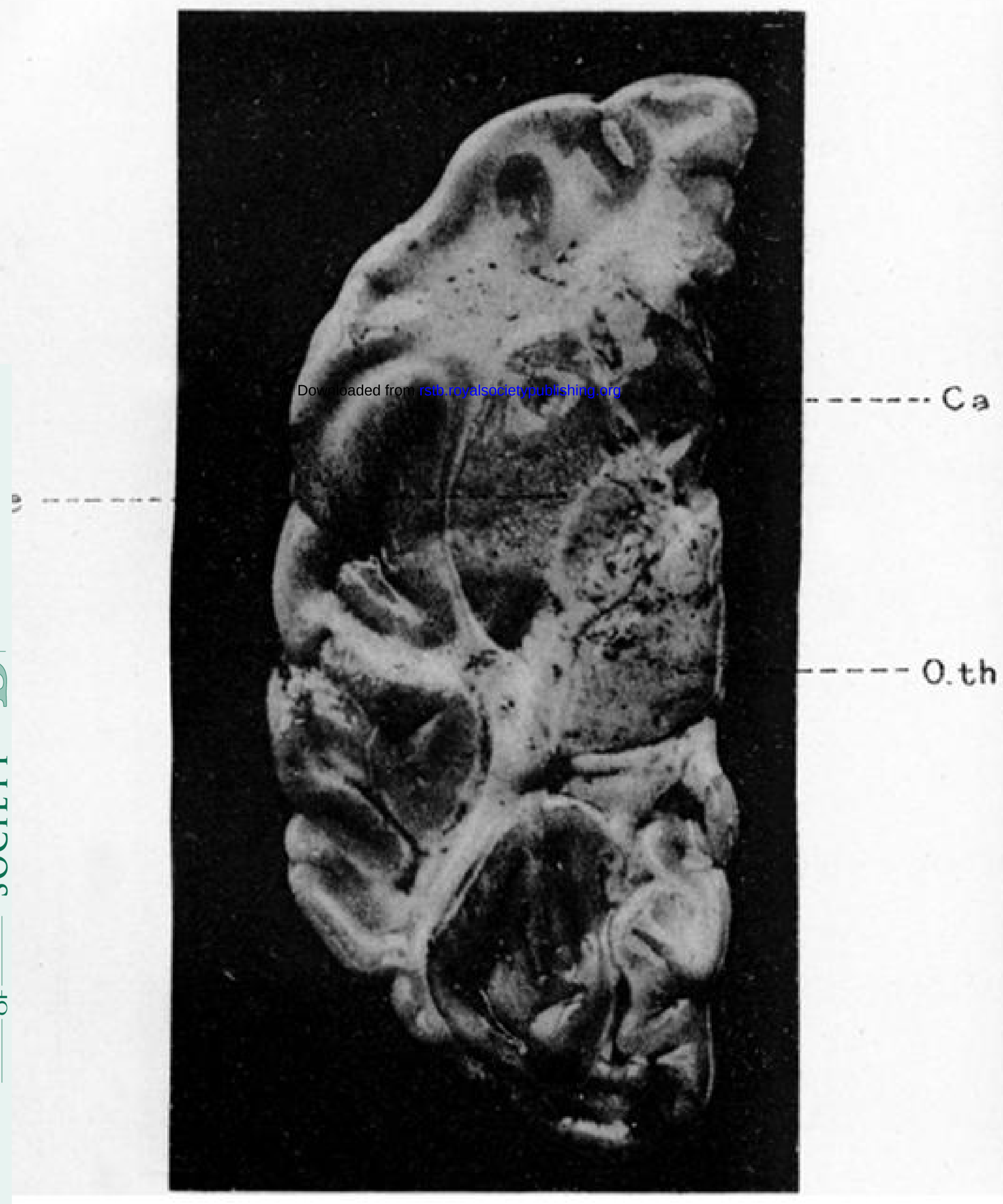


Group II.

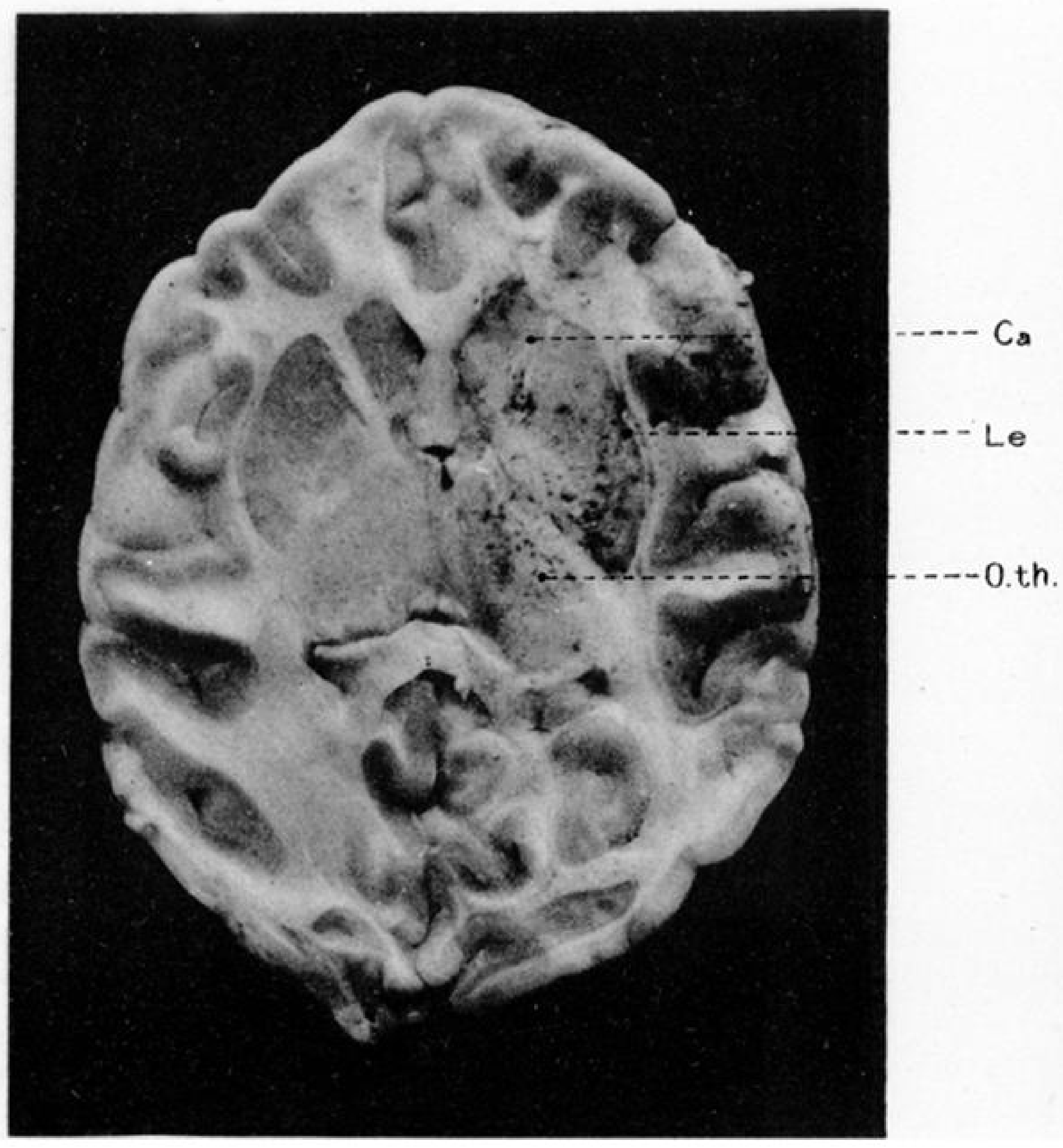


Group III.

Group V.



Group IV.



Group VI.

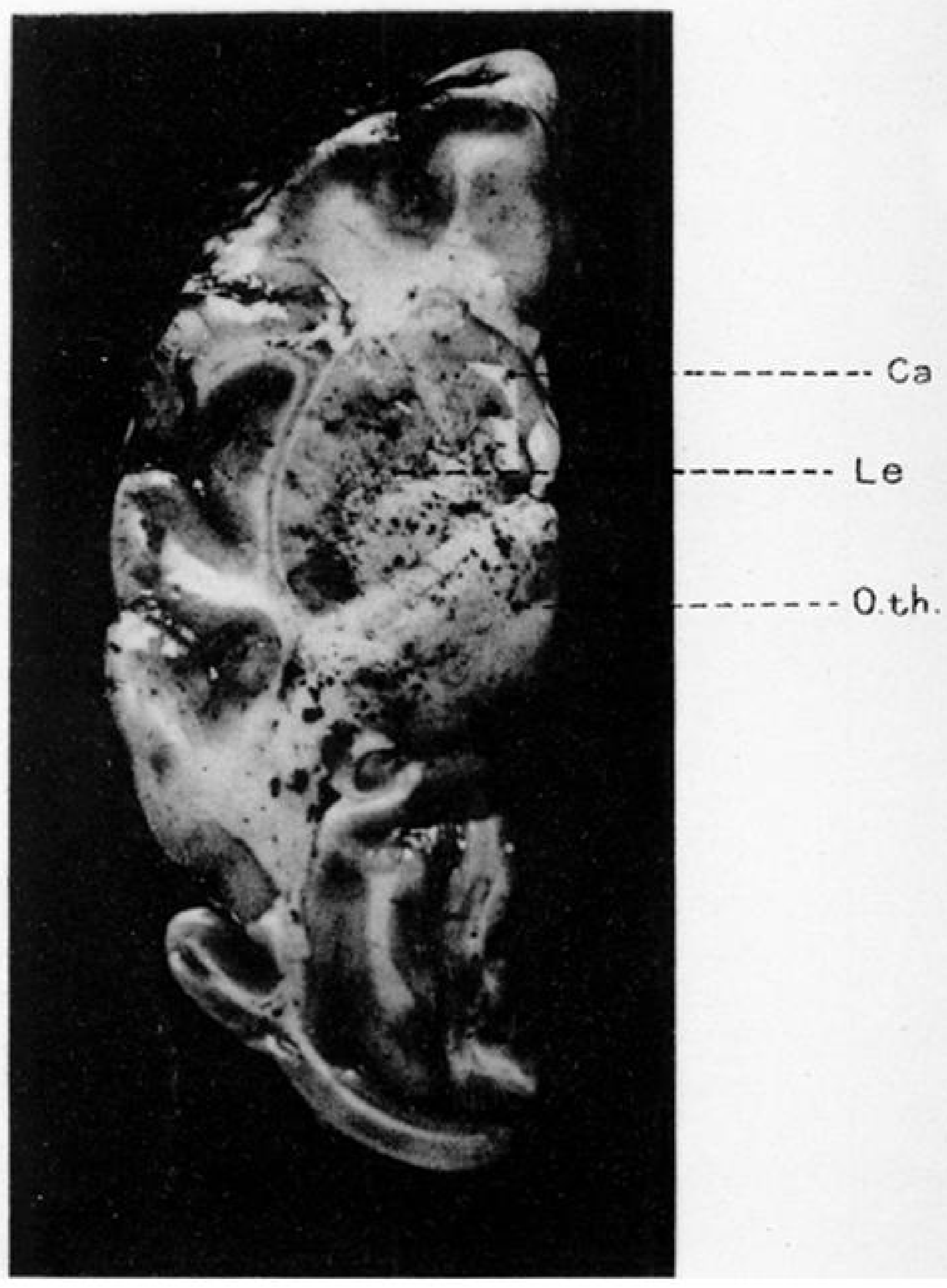


PLATE 10.

Groups I.–VI. These are photographs typical of each level at which we have excited the capsule, corresponding to the first six groups of our observations.

Ca. = Caudate nucleus.
Le. = Lenticular nucleus.
O.Th. = Optic thalamus.

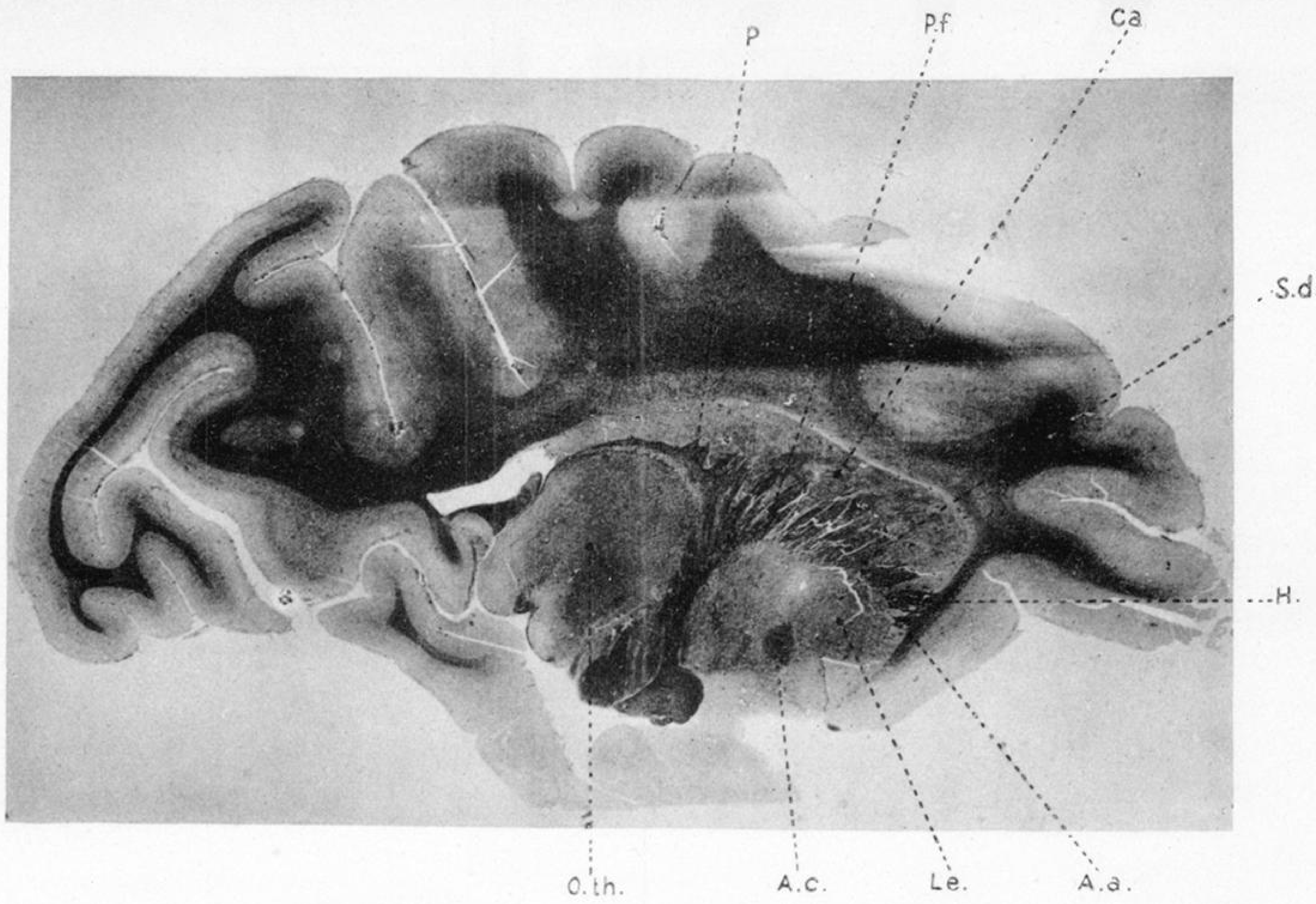
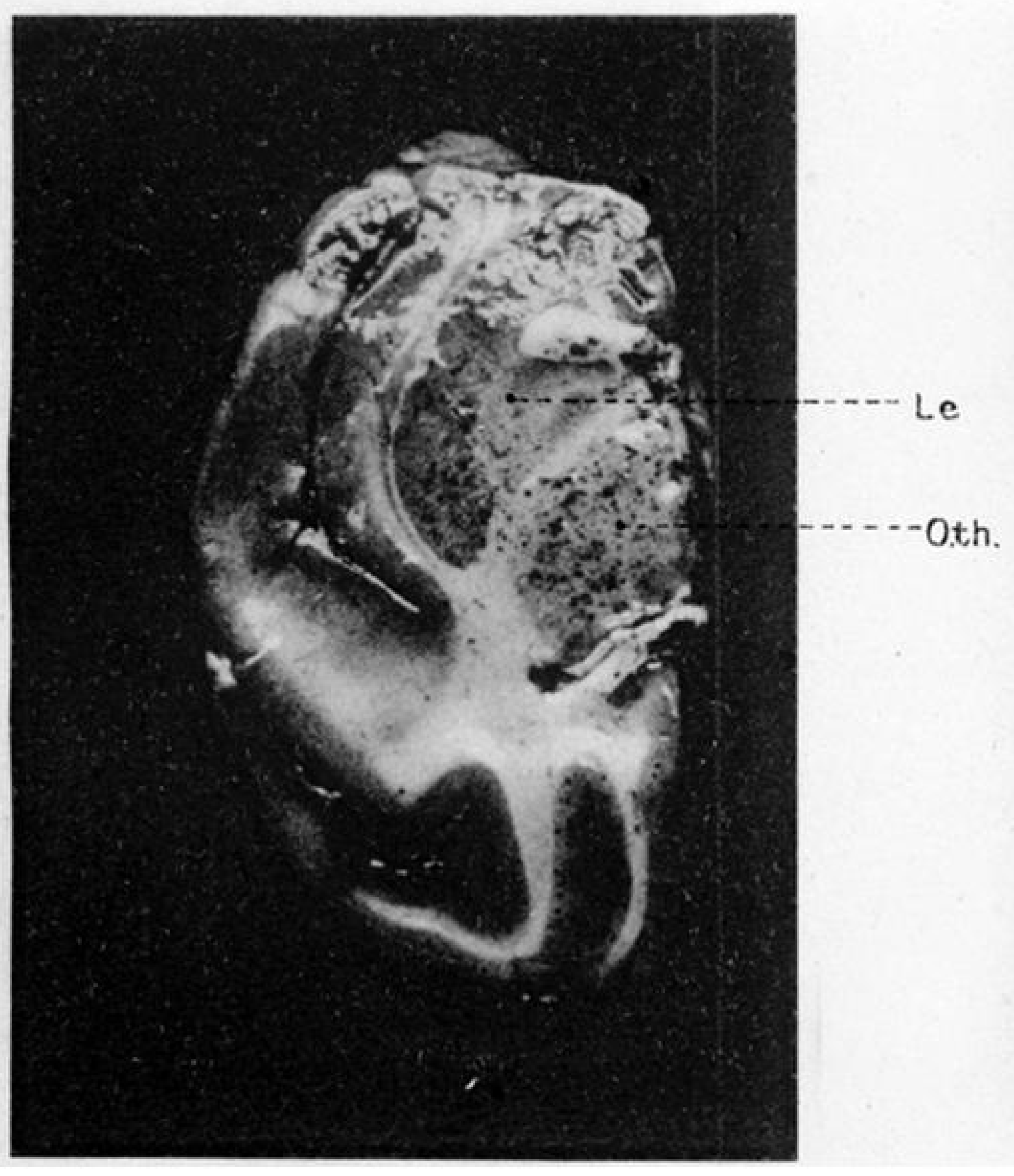


Fig 3.

Group VII.



Group VIII.

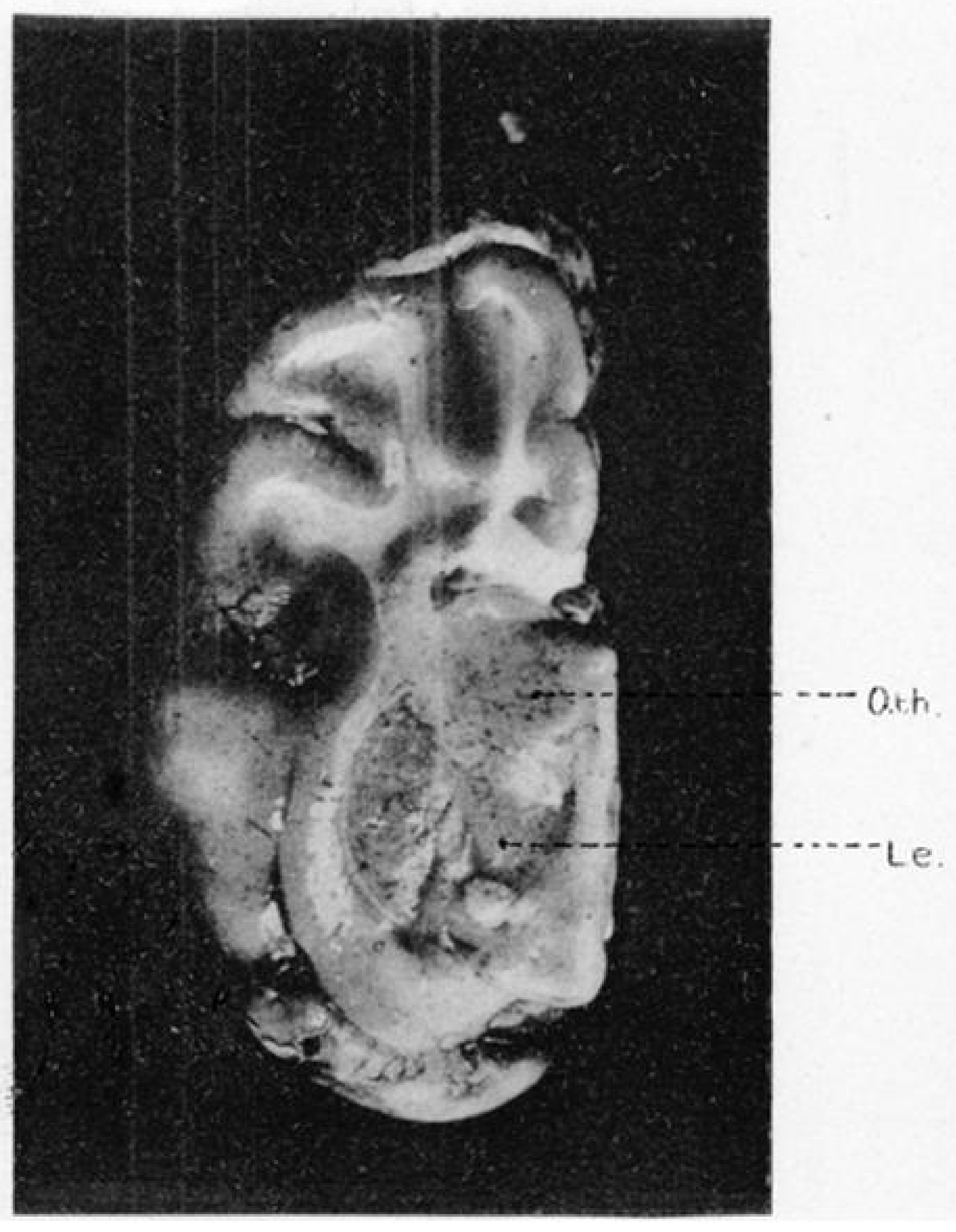


Fig 2.

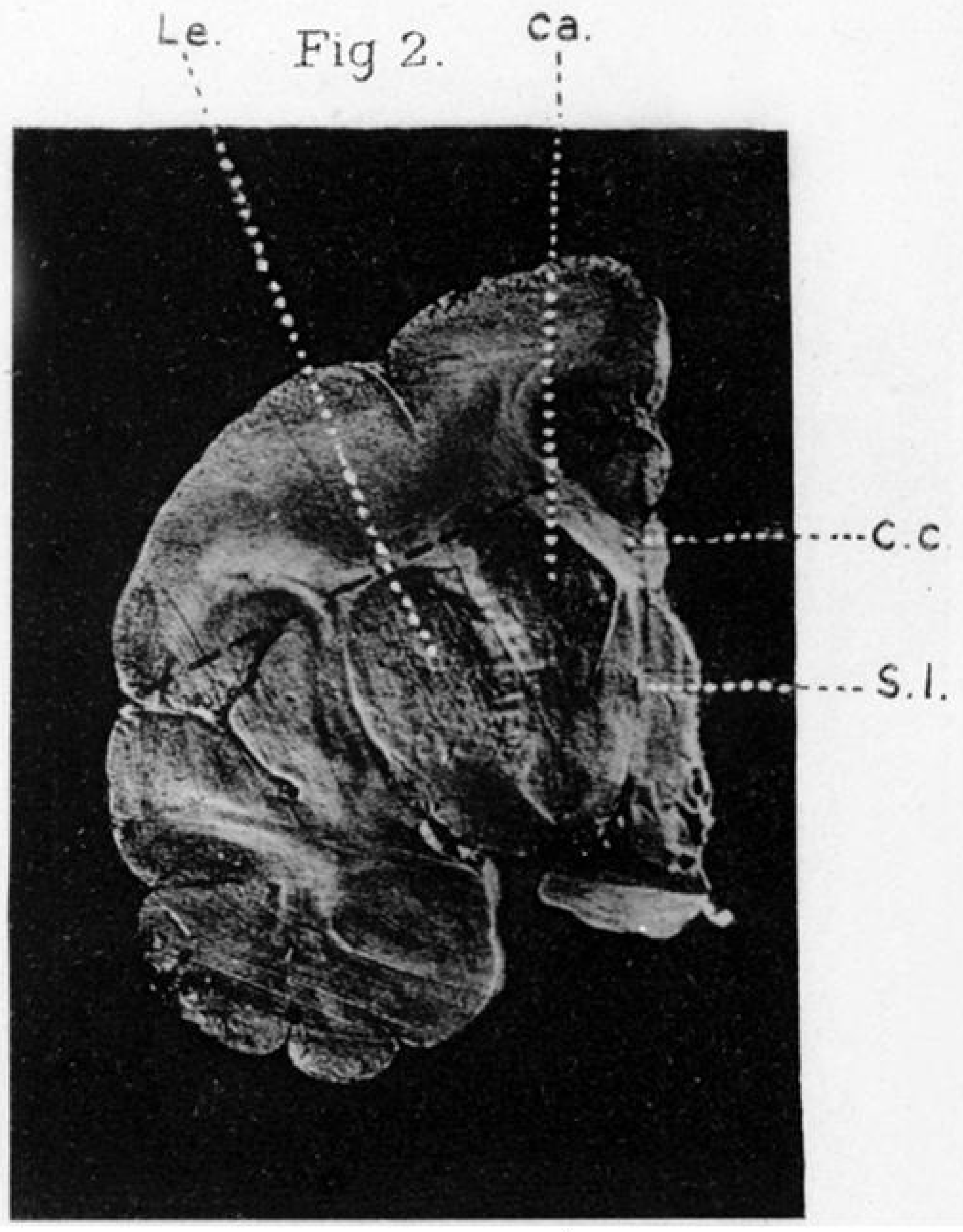


PLATE 11.

Groups VII. and VIII. These are photographs of our last two levels and follow on Plate X.

NOTE.—Group VIII. has been reversed in the reproduction.

The section is taken from the left hemisphere, except in Groups IV. and VIII., which are taken from the right side.

Fig. 2. A photograph of a transverse vertical section of the right hemisphere of *Macacus sinicus*, showing the limits of the capsule and the direction of its anterior limb in frontal section.

Ca. = Caudate nucleus.
C.c. = Corpus callosum.
Le. = Lenticular nucleus.
S.l. = Septum lucidum.

Fig. 3. This figure is a photograph of a sagittal section of the hemisphere of a *Macacus sinicus* stained by PAL's method and mounted in balsam. The medullated fibres are consequently stained black, the grey matter being of a lighter greyish tint.

A.a. = Anterior or ascending fibres of præfrontal division of capsule.
H. = Horizontal fibres of the same.
S.d. = Superior or descending fibres of the same.
P.f. = Pyramidal fibres (excitable).
P. = Fibres entering the posterior limb of the capsule.
Ca. = Caudate nucleus.
Le. = Lenticular nucleus.
O.th. = Optic thalamus.
A.c. = Anterior commissure.