

VIII. *On the Descending Degenerations which follow Lesions of the Gyrus Marginalis and Gyrus Fornicatus in Monkeys.*

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[PLATES 27–29.]

INTRODUCTION.

THE following paper contains the record of an investigation into the degenerations which follow lesions of the gyrus marginalis and gyrus fornicatus in Monkeys. The work has been carried on under my direction by Mr. FRANCE, with the aid of a grant from the Government Grant Fund, and represents part of a long investigation into the degenerations which follow artificially produced cerebral lesions, the material for which has been furnished by cases operated upon in conjunction respectively with Professor V. HORSLEY and Dr. SANGER BROWN. These cases and the physiological results of the operations have already been published in the ‘Philosophical Transactions.’* The experiments here dealt with, twelve in number, comprise only the lesions of the gyrus marginalis and gyrus fornicatus, and, with one exception (case 12), are taken from the series of experiments performed in conjunction with Mr. HORSLEY.†

Of the twelve cases, six were of removal, or attempted removal, of the gyrus marginalis, and six of removal, or attempted removal, of the gyrus fornicatus. But in only one or two instances was the lesion, as determined by *post-mortem* examination, exactly limited to the convolution which it was attempted to remove, for in most cases the adjacent gyrus was to a certain extent involved in the injury. This was especially the case when removal of the gyrus fornicatus had been attempted, on account of its deep situation, and the difficulty of getting at it without some manipulation of the superjacent gyrus. Nevertheless, the removal of one or the other

* V. HORSLEY and E. A. SCHÄFER, “A Record of Experiments on the Functions of the Cerebral Cortex,” ‘Phil. Trans,’ B, 1888, pp. 1–45; and SANGER BROWN and E. A. SCHÄFER, ‘Phil. Trans.,’ B, 1888, pp. 303–327.

† In an Appendix, which has been added subsequently, lesions of the external motor cortex are dealt with by Mr. FRANCE.

gyrus was sufficiently complete in all the cases here selected to produce characteristic symptoms and characteristic descending degenerations.

It may be remembered that the symptoms which were found (by HORSLEY and myself) to follow removal of one marginal gyrus indicated paralysis of the trunk muscles and of most of the leg muscles (especially the extensors) of the opposite side of the body; double marginal lesion causing a corresponding bilateral paralysis. This result was in conformity with our earlier experiments, which demonstrated that on electrical excitation of this gyrus movements of the trunk and opposite leg were chiefly produced. It showed conclusively that the gyrus marginalis is to be regarded as part of the so-called motor region of the brain as mapped out by FERRIER. It was, therefore, only to be expected that we should find descending degenerations along the course of the pyramidal tract, as is indeed seen to be the case if the following account of the degenerations and the photographic representations of sections through the spinal cord and medulla are referred to. The chief feature of interest in this part of the investigation is the localisation of the degeneration mainly to the postero-lateral part of the crossed pyramidal tract area of the cord.

With regard to the gyrus fornicatus, the results of electrical excitation were found by us to be negative, so far at least as any movements of muscles were concerned. And we also found that, except such slight paresis as might well have been accounted for by the unavoidable injury to the adjacent marginal convolution, even very extensive removal of the gyrus fornicatus was productive of no muscular paralysis. On the other hand, we obtained well marked deficiency in the general and tactile sensibility of the opposite side of the body, and concluded therefrom that this part of the limbic lobe was probably concerned with the reception of sensory impressions.

If the view which is usually held, viz., that in the central nervous system the direction of conduction and degeneration is the same, be correct, this conclusion of ours would have to be modified, in consideration of the extensive descending degenerations along the whole area of the pyramidal tract which are recorded by Mr. FRANCE as resulting from the lesions of the gyrus fornicatus, for it would be difficult, with these facts before us, to arrive at any conclusion other than that centrifugal nervous impulses emanate from the cells of this gyrus, and pass down along the course of the motor tract.

The question which would then arise is, What is the nature of these centrifugal impulses? The observations already referred to would seem to show that they do not pass to the skeletal muscles, and the idea suggests itself that they are of vaso-motor (? inhibitory) character. Such a supposition is not at variance with the hemi-anæsthetic results obtained on removal of the gyrus fornicatus, for these results might be explained by supposing contraction of cutaneous vessels (and consequent numbness) to result from the removal.

But are we bound to accept the above view regarding conduction and degeneration in the central nervous system? It by no means follows that we are. The only law of

universal applicability (to both central and peripheral nervous system) regarding these phenomena, is the Wallerian, that degeneration supervenes in all nerve fibres which are cut off from their nutrient centres, which in all probability are the cells from which the fibres have originally grown out (His). The nutrient centres for the higher motor tracts lie in the grey matter of the cerebral cortex, and there is nothing intrinsically improbable in the supposition that those for the higher sensory tracts are also to be found there. To decide between these two explanations must be the object of future investigations. [E. A. SCHÄFER.]

ON THE DESCENDING DEGENERATIONS WHICH FOLLOW LESIONS OF THE GYRUS MARGINALIS AND GYRUS FORNICATUS.*

SUMMARY OF THE DEGENERATIONS WHICH FOLLOW MARGINAL LESIONS.

I have examined six cases where a lesion in the marginal convolution was produced. In two cases this injury was strictly confined to the marginal (cases 1 and 4), the gyrus fornicatus being quite uninjured.

In the remaining cases there was some injury to the adjacent external surface of the hemisphere, or to the gyrus fornicatus.

In the *internal capsule* the degeneration has been difficult to detect, and all that I can say, as far as this series is concerned, is that I have not seen degeneration in front of the knee, but have occasionally been able to make out scattered degenerated fibres in the posterior half.

In the *pons* the degeneration is easily seen, scattered, apparently indiscriminately, in the pyramidal bundles. If the cortical lesion had been extensive and the animal had lived for some time (ten weeks or more), a distinct difference in the size of the bundles on the two sides could be seen with the naked eye after hardening.

The *medulla oblongata* also shows degeneration in the pyramids. Here it is more concentrated than in the pons. A shrinking of the pyramid corresponding to the side on which the cortical lesion has been made similar to that in the pons can be seen with the naked eye if the animal has lived long enough for much sclerosis to have been set up (see fig. 2*b*, Plate 28).

In the *spinal cord* the degeneration is continued in the crossed pyramidal tract on the side opposite the lesion, and can be traced in this tract as far as the lower lumbar region.

I have not found degeneration in the direct pyramidal tract in any case. In all cases where the degeneration in the crossed pyramidal tract on the side opposite the lesion is well marked, degeneration in the crossed pyramidal tract on the *same side* as the lesion can also be seen (see fig. 2*d*), occupying a similar position to that on the

* The remainder of the paper is by Mr. E. P. FRANCE.

other side, but very much less in amount. This degeneration has been followed down the cord as far as the lumbar region in some instances.

The shape of the degeneration in the lateral column is sufficiently constant in all cases where there has been considerable injury to the marginal convolution for it to be considered characteristic of this lesion.

In the *cervical region* it is narrowly triangular or claw-shaped, the base being towards the posterior cornu, and the (expanded) apex at the surface of the cord, reaching this at about the middle of the lateral border (see fig. 1c.). One side of the triangle is formed by the line of separation between the crossed pyramidal tract and the direct cerebellar tract. Along this line the degeneration always appears to be most complete, that is to say, the degeneration is chiefly confined to the posterior and outer part of the crossed pyramidal tract; this is noticeable down the whole of the cord. In the cervical region the degeneration spreads out immediately within the circumference of the cord, the direct cerebellar tract appearing as if pushed backwards towards the apex of the posterior cornu, where it occupies an area which is triangular in section, in place of the oblong tract seen in sections lower down.

In the *upper dorsal region* the appearance is much the same as in the cervical region, except that the connection of the degeneration with the circumference of the cord is becoming less extensive, although the whole tract of degeneration has approached a little nearer the circumference, from which it is separated by the now oblong cerebellar tract.

In the *lower dorsal region* the degenerated tract has become less in amount and has approached quite close to the circumference, leaving only a narrow band of healthy fibres in the position of the direct cerebellar tract, and does not extend as far forward, although the apex of the triangle still touches the surface. There are a greater number of healthy fibres to be seen between the grey matter and the degeneration than in the cervical or upper dorsal regions.

In the *lumbar region* the degeneration is very much less marked than higher in the cord, and occupies the angle formed by the posterior root exit and the circumference. In cases where the lesion in the brain had been extensive the degeneration could be traced as far as the fifth lumbar nerve. I have not carried sections below this point.

SUMMARY OF DEGENERATIONS FOLLOWING LESIONS OF THE GYRUS FORNICATUS.

The brains and spinal cords of six Monkeys, in which a part or the whole of the gyrus fornicatus had been removed, were examined.

In most cases the *post-mortem* examination showed that the marginal gyrus had also been injured to a variable extent, owing, no doubt, to the difficulty experienced in exposing and excising a convolution so deeply situated as the gyrus fornicatus without interfering with the adjacent marginal gyrus.

In two instances the removal of the grey matter of the gyrus fornicatus was nearly

complete (Nos. 10 and 11), and with scarcely any injury to the marginal. In these, as well as in all the other cases recorded, there is well marked and extensive degeneration in the crossed pyramidal tract.

In the brains of Nos. 9 and 12 there were lesions other than that of the gyrus fornicatus. In No. 9 a considerable lesion in the hippocampal and under surface of the occipital regions had been effected, and in No. 12 lesions of both temporal lobes.

But the degeneration which passes down into the spinal cord has in all the instances here investigated been confined to one tract—the lateral pyramidal tract—mainly on the side opposite the lesion, and appears to have been in every case produced by the lesion of the gyrus marginalis or of the gyrus fornicatus.* The region of the direct cerebellar tract is encroached upon in some instances (Nos. 2, 6, 7, and 8), but the extent, and even the occurrence, of this encroachment has not appeared to me to bear any constant relation to the amount of lesion of the gyrus fornicatus, occurring, for example, in a case where there was little injury to the gyrus fornicatus, and not occurring in other cases after much more complete removal, although the animals lived three months or more. I conclude, therefore, that the apparent invasion of the direct cerebellar tract is due to some individual variation in the course of the fibres of the crossed pyramidal tract, and not to any degeneration of fibres belonging to the direct cerebellar tract itself. I have not been able to make out with any certainty in my specimens the course of the degeneration in the internal capsule.

In the *mid-brain*, *pons*, and *medulla* (fig. 4*b*) the degeneration has the same appearances as that following marginal lesions, and is found only in the pyramidal bundles on the same side as the lesion.

In the *spinal cord* the degeneration occupies *the whole sectional area of the lateral pyramidal tract*, and in the cervical region is no longer confined to the part bordering on the direct cerebellar tract, as was observed with degenerations following purely marginal lesions (compare fig. 5*c* with fig. 2*d*).

In the *upper dorsal region* the extent and shape of the lesion is similar to that in the cervical region, but about the middle of the dorsal region it begins to diminish in extent, the outer and anterior part of the pyramidal tract assuming its normal appearance first.

At the *lumbar enlargement* it is very much lessened in proportion, but is still distinct, being confined chiefly to the angle formed by the posterior root exit and circumference, as with the marginal degeneration. The degeneration can usually be traced as far as the fifth lumbar nerve, beyond which point I have not carried sections.

Although following the course of the pyramidal tract by no means all the fibres of that tract are degenerated, many remaining normal.

* I have ascertained that lesions of the hippocampal region alone are not followed by any perceptible degenerative changes in the spinal cord.

RECORD OF CASES INVESTIGATED, SHOWING IN EACH CASE THE SITUATION AND EXTENT OF THE CEREBRAL LESION, THE SYMPTOMS OBSERVED DURING LIFE, AND THE DEGENERATIONS WHICH WERE FOUND TO HAVE RESULTED FROM THE LESION.

*Case 1.--No. 11 of First Series.** (Figs. 1*a* to 1*e*, Plates 27 and 28.)

Lesion.—Removal of a longitudinal strip of grey matter from the left side of the brain, along the margin of the longitudinal fissure from the level of the anterior end of the præcentral nearly to the parieto-occipital fissure (fig. 1*a* in surface view, fig. 1*b* in section).

Result.—Some paralysis of both right limbs, which gradually became less evident in the arm; the leg paresis was permanently obvious. This Monkey was killed one year after the operation.

Degenerations Observed.

Pons.—There is a difference in the appearance of the two sides, the pyramidal bundles on the left side being stained with aniline blue-black more darkly than on the right, and appearing smaller.

Medulla.—Here the naked eye appearance of the pyramid of the left side is different from that of the right, being smaller and more deeply stained.

Microscopically, the left pyramid is considerably degenerated and sclerosed, although there are a great many healthy fibres scattered about in it.

Spinal Cord. Cervical Enlargement.—Sections here show degeneration, with sclerosis, in the crossed pyramidal tract on the right side (see fig. 1*c*), extending from the posterior root outwards and forwards till it reaches the circumference at about the middle of the lateral surface. The degeneration is claw-shaped, with the root of the claw at the posterior cornu, the convex side towards the direct cerebellar tract, and the tip at the surface of the cord.

The crossed pyramidal tract is not entirely degenerated, that part only which is adjacent to the direct cerebellar tract being affected, the anterior part having remained healthy. There is some degeneration on the same side as the lesion in a similar position to that on the opposite side.

No degeneration can be seen in the anterior median column on either side either in this case or in any other which has been examined by me.

Dorsal Region.—Here the degeneration is narrower than in the cervical region,

* The series of experiments recorded by HORSLEY and SCHÄFER (*loc. cit.*) will be referred to as the First Series; those recorded by SANGER BROWN and SCHÄFER (*loc. cit.*) as the Second Series. Further illustrations of the extent and depth of the several lesions are to be found in the plates accompanying those papers.

and is nearer the circumference, leaving, however, a band of healthy fibres in the position of the direct cerebellar tract.

Degenerated fibres and slight sclerosis can be seen with the microscope on the same side (left) as the lesion in a similar position.

Lumbar Enlargement.—The degeneration here is less in amount. It occupies the angle between the posterior root and the circumference. A few degenerated fibres can be seen in a similar position on the same side as the lesion.

Case 2.—No. 12 of First Series. (Figs. 2a to 2d, Plates 27 and 28.)

Lesion.—Ablation of the posterior three-fourths of the left marginal convolution and an adjoining strip of the external surface as far as sulcus *x* (fig. 2a). The gyrus fornicatus was also somewhat injured.

Result.—Paralysis of the right side of the trunk and right leg, and partial paralysis of the right arm, which had imperfect power of extension from the shoulder.

This animal was killed six months after the operation.

Degenerations Observed.

The pieces from which sections were cut showed, even with the naked eye, well marked degeneration in the pyramidal bundles in the pons and medulla on the same side as the lesion, and in the spinal cord in the crossed pyramidal tracts of both sides, although much more obviously on the side opposite the lesion.

Medulla.—There is well marked, scattered degeneration in the left pyramid (fig. 2b), with considerable shrinking and sclerosis.

Spinal Cord.—Cervical Region.—There is a marked triangular patch of degeneration in the crossed pyramidal tract on the right side, denser where it borders the direct cerebellar tract, and reaching the circumference near the middle of the lateral border, where it spreads both backwards and forwards, but especially the latter, involving the outer part of the direct cerebellar tract.

In a section at the level of the second cervical nerves (fig. 2c) a band of degeneration is seen close to the circumference, extending from the posterior root exit to where the pyramidal tract degeneration reaches the circumference. On the left side there is a small amount of degeneration, scattered over a similar area, and on both sides there is sclerosis in the degenerated areas.

Dorsal Region.—At the level of the fourth nerves (fig. 2d) the degeneration is very well defined. It extends from the apex of the posterior cornu (right side) outwards and forwards as a diminishing strip, till it reaches the surface about the anterior end of the direct cerebellar tract. There is also a little degeneration along the external border of the direct cerebellar tract, which spreads along the circumference less than in the

cervical region. On the left side there is some degeneration in a similar position to that on the right (see fig. 2*d*).

Eighth Dorsal.—The degeneration here (right side) has much the same position as at the level of the fourth dorsal, although rather less in amount: that is to say, there are more normal fibres in the degenerated patch. The patch is nearer the circumference than higher up. There is a little degeneration to be seen on the left side, having a similar position to that on the right.

Lumbar Region.—The degeneration in the crossed pyramidal tract on the right side comes quite to the circumference, and extends from the posterior root as a small patch outwards and forwards.

A few degenerated fibres can be seen in a similar position on the left side.

Case 3.—No. 14 of First Series.

Lesion.—Removal of the left gyrus marginalis for rather more than the posterior two-thirds, with a small amount of injury to the gyrus fornicatus (see 'Phil. Trans.,' B, 1888, Plate 2, fig. 14).

Result.—Paralysis of the leg and trunk muscles on the right side. The arm was slightly paralysed at first, but soon recovered, and for the first few days there was some loss of reaction to tactile impressions.

This animal died three and a-half weeks after the operation.

Degenerations Observed.

Internal Capsule.—No degeneration can be made out with sufficient distinctness.

Midbrain, Pons, and Medulla.—Scattered degeneration is to be seen in the pyramidal bundles of the left side.

Spinal Cord. Cervical Region.—Scattered degeneration can be seen in the crossed pyramidal tract on the right side, bordering the direct cerebellar tract and gradually approaching the circumference. The greatest amount of degeneration is towards the posterior cornu; it becomes less as it passes forwards and outwards.

The degeneration has a similar position to that seen in No. 2, although it is less distinct and smaller in amount.

A few degenerated fibres can be made out with a higher power (Zeiss, E) in a similar position on the left side.

Dorsal Region.—Degenerated fibres can be seen in a similar position to those in the cervical region, except that they are, on the whole, nearer the circumference.

A few degenerated fibres can be seen on the left side as far as the lower dorsal region.

Lumbar Enlargement.—Degeneration is still to be seen here, on the right side, in the angle between the posterior root and the circumference.

Case 4.—No. 19 of First Series.

Lesion.—Excision of both marginal convolutions : on the left side for the posterior three-fourths of its length, on the right side to a rather less extent.

Frontal sections through the brain show that that part of the gyrus bordering the calloso-marginal fissure, and dipping down into it, was but little injured ; the upper border also was but little injured (see ‘Phil. Trans.,’ B, 1888, Plate 2, figs. 19R and 19L).

Result.—Almost complete paralysis of the leg and trunk muscles, but there is some ability to move, especially to flex, the legs, particularly the left leg.

This animal died on the ninth day after the operation.

Degenerations Observed.

No degeneration could be seen with the naked eye.

Microscopic. Pons.—A few degenerated fibres are to be seen in the pyramidal bundles of both sides.

Medulla.—Scattered degeneration can be seen in the pyramids on both sides, more distinctly than in the pons.

Spinal Cord. Cervical Enlargement.—Degenerated fibres can be seen on both sides scattered about the crossed pyramidal tracts, chiefly occupying the part which borders on the direct cerebellar tract, and extending outwards and forwards from the apex of the posterior cornu.

Dorsal Region.—The patch of degeneration is more concentrated, although smaller in extent. In the lower dorsal region especially it lies closer to the circumference of the cord. It is more marked on the right than on the left side.

Lumbar Region.—In the lumbar region the degeneration can still be seen on both sides, occupying the angles between the posterior root and the circumference.

The degeneration consists of swollen fibres with axis cylinders in various stages of breaking down.

Case 5.—No. 21 of First Series.

Lesion.—Removal of the posterior three-fourths of both marginal gyri at one operation. Frontal sections through the brain show that the removal was complete except along the calloso-marginal fissure (see ‘Phil. Trans.,’ B, 1888, Plate 3, figs. 21A to 21D).

Result.—Paralysis of the trunk and legs.

This animal died on the twenty-seventh day after the operation.

Degenerations Observed.

There was a slightly marked appearance of degeneration to be seen with the naked eye in both crossed pyramidal tracts all down the cord.

Microscopic. Pons.—Scattered degeneration can be seen in the pyramidal bundles of both sides.

Medulla.—Scattered degeneration can be seen in both anterior pyramids.

Spinal Cord. Cervical Region.—The degeneration occupies that part of the crossed pyramidal tracts which borders on the direct cerebellar tract, and extends from the posterior cornua towards the circumference on both sides. It is not very well marked, but occupies a similar position to that of all the other marginal cases.

Dorsal Region.—In the dorsal region it is relatively less in amount, closer to the circumference, and does not extend as far forwards.

Lumbar Enlargement.—It is much less in amount here, and lies in the angles formed by the posterior cornua and the circumference of the cord.

Case 6.—No. 22 of First Series.

Lesion.—Removal of both marginal convolutions at two operations.

Frontal sections through the brain show that the convolutions were completely removed, except a small strip of grey matter at the deepest part of the callosomarginal fissure on the left side. The adjoining external surface was also injured.

Result.—The first operation on the left side produced the usual paralysis of the opposite hind limb and of the trunk. The second operation (right side) produced paralysis of the trunk and legs of the opposite side, except that the knee and hip can be feebly flexed.

The animal died three months after the first operation.

Degenerations Observed.

Very well marked degeneration is visible to the naked eye on both sides in the crossed pyramidal tracts.

Pons and Medulla.—Under the microscope sections show scattered degeneration in the pyramidal bundles and pyramids.

Spinal Cord. Cervical Enlargement.—There is degeneration on both sides, extending over a large portion of the crossed pyramidal tracts, and involving part of the region of the direct cerebellar tracts.

The degeneration in the crossed pyramidal tracts is like that observed in the spinal cords of the other animals after similar lesions, although more extensive than in most cases. The region of the direct cerebellar tract* is also greatly involved on both sides. A small triangular patch of healthy fibres represents this tract, close to the posterior root exit.

Dorsal Region.—The degeneration is well marked and rather more defined than in the cervical region. The parts in the direct cerebellar tracts noticed to be free from degeneration in the cervical region are still seen, and appear rather larger.

* Probably the portion of the pyramidal tract which encroaches on the cerebellar tract.

Here the sclerosis has the shape and position characteristic of degeneration following marginal lesions, being claw or wedge shaped, with the base towards the posterior cornu, and the apex extending forwards and outwards until it reaches the circumference about the middle of the lateral column, where it spreads out, and joins posteriorly the degeneration which occupies the superficial part of the direct cerebellar tract region. The degeneration is relatively less in amount than in the cervical region.

Lumbar Enlargement.—The degeneration is small in amount, and lies on each side close to the circumference of the sections, in the angle formed by the posterior root.

Case 7.—No. 36 of First Series.

Lesion.—Removal of a considerable part of the left gyrus fornicatus. The marginal convolution was found to be injured in the greater part of its extent ('Phil. Trans.,' B, 1888, Plate 6, fig. 36).

Result.—The whole of the right side of the body, as far as the iliac crest, was almost completely insensible to touch, prick of a pin, and to a jet of cold water suddenly applied. There was loss of sensibility over the right arm. The right leg, although not anæsthetic, was far less sensitive than the left. The arm, leg, and trunk are paresed, although they are still used. There was incomplete recovery from the paresis.

The animal died seven weeks after the operation.

Degenerations Observed.

Midbrain and Pons.—Extensive scattered degeneration can be seen in the pyramidal bundles of the left side.

Medulla.—The degeneration in the pyramids is very extensive on the left side, more so than in simple marginal lesions.

Spinal Cord. Cervical Enlargement.—On the right side there is extensive scattered degeneration in the crossed pyramidal tract, involving the greater part of the area occupied by this tract. The degeneration forms a broad triangular patch, extending from the posterior cornu outwards and forwards, reaching the circumference a little behind the middle of the lateral surface (corresponding with the area of the crossed pyramidal tract).

From the postero-lateral groove there extends, close to the circumference, a narrow band of degeneration in the outer part of the direct cerebellar tract region, which joins, as it passes forwards, the anterior and external end of the degeneration in the crossed pyramidal tract; so that this latter degeneration and that extending along the circumference enclose between them a band of healthy fibres of the direct cerebellar tract.

There are a few degenerated fibres to be seen in a similar position on the opposite side of the cord (left).

Dorsal Region.—The degeneration here is more triangular than in cases of simple marginal lesion, and more extensive. It does not reach quite so far forward as in the cervical region, but is nearer the circumference of the cord; so that in this part (middle dorsal) there is only a narrow and irregular band of healthy fibres left in the position of the direct cerebellar tract. The degeneration seen in the cervical region, extending along the circumference of the cord, here disappears.

Lumbar Enlargement.—The degeneration is confined to the angle formed by the posterior cornu and the circumference; it is much smaller than in the dorsal region, but more extensive than with simple marginal lesions.

Case 8.—*No. 37 of First Series.* (Figs. 3*a*, Plate 27, and 3*b*, Plate 28. See also 'Phil. Trans.,' B, 1888, Plate 6, figs. 37*B* to 37*E*.)

Lesion 1.—The anterior part of the left gyrus fornicatus was removed.

Result.—The external ear of the opposite side gave no reaction to tactile impressions producing pain elsewhere; it could not be determined whether any other parts were completely insensible.

Lesion 2.—A week after the first operation, the greater part of the remainder of the convolution was cut away (see fig. 3*a*).

Frontal sections through the marginal convolution and gyrus fornicatus show that that part of the gyrus fornicatus which borders on the corpus callosum has remained almost uninjured, whilst, on the other hand, that part of the marginal convolution which borders on the calloso-marginal fissure is injured in two places (anteriorly and posteriorly).

Result.—Great diminution of sensibility over the right side; tactile impressions produced no reaction; painful impressions were slowly perceived, and not localised. This "allochiria" began to be exhibited about a week after the second operation; it afterwards disappeared. No paresis was observed.

The animal was killed three months after the first operation.

Degenerations Observed.

Degeneration is distinctly seen with the naked eye in the pons and medulla (pyramid) on the left side, and in the spinal cord, as far as the lower lumbar region in the crossed pyramidal tract, on the right side, involving also the direct cerebellar tract on the same side to a considerable extent.

Midbrain and Pons.—In the pyramidal bundles of the left side scattered degeneration is visible with the microscope; it is not so great in amount as in the pons of No. 6, but, on the other hand, the cerebral lesion in this case is not so extensive.

Medulla.—Scattered degeneration is distinctly to be seen in the left pyramid. There is well-marked sclerosis, besides degenerated nerve fibres.

Spinal Cord. Cervical Region.—There is degeneration in the crossed pyramidal

tract on the right side, similar in shape and position to that seen after lesions of the motor areas, being triangular in shape, with a broad base towards the posterior cornu, but becoming narrower as it extends forwards and outwards till it reaches the circumference, about the middle of the lateral surface. Here it spreads out a little, joining a tract of degeneration which passes forwards in the direct cerebellar tract close to the circumference, from near the posterior root. There is a band of healthy fibres belonging to the cerebellar tract, between the degeneration at the surface of the direct cerebellar tract and that in the main part of the crossed pyramidal tract.

Dorsal Region (fig. 3*b*).—The degeneration comes nearer to the circumference, leaving a narrower band of healthy fibres in the position of the direct cerebellar tract. It extends over the whole area of the pyramidal tract.

Lumbar Enlargement.—The degeneration is considerably less on the right side, and on the left there is none to be seen. It extends from near the posterior root exit a short distance forwards close to the circumference, and lies chiefly in the angle formed by the posterior cornu and the circumference, although it does not come quite close to the posterior cornu.

Fourth Lumbar Nerve.—A small amount of degeneration can still be seen on the right side, in a similar position to that noted above, but not quite so near the root exit.

Case 9.—No. 39 of First Series.

Lesion 1.—Incomplete removal of the gyrus fornicatus and considerable injury to the middle of the marginal convolution (see 'Phil. Trans.,' B, 1888, Plate 7, fig. 39).

Lesion 2.—Removal of that part of the limbic lobe which bends round the splenium of the corpus callosum.

Lesion 3.—A fortnight later the posterior part of the hippocampal convolution was scooped away.

Result.—Anæsthesia, and distinct muscular paresis of both right limbs.

This animal was killed about five months after the first operation.

Degenerations Observed.

Degeneration could be seen with the naked eye in the pyramidal bundles in the midbrain, pons, and medulla. After hardening, these parts look paler and smaller than those of the opposite side.

In the spinal cord a patch of degeneration is to be seen occupying the crossed pyramidal tract as far down as the third lumbar nerve.

Microscopically, degeneration can be seen, scattered in the pyramidal bundles of the *midbrain* and *pons* of the left side.

The *medulla oblongata* shows considerable degeneration and sclerosis (apparently more than in the pons) in the left pyramid.

Spinal Cord. Cervical Region.—There is a patch of degeneration in the crossed

pyramidal tract on the right side, triangular in shape, extending from the cornu outwards and forwards till it reaches the surface near the middle of the lateral border. The degeneration is most marked in that part which borders the direct cerebellar tract; there are many degenerated fibres and considerable sclerosis. The direct cerebellar tract is encroached upon at its anterior end by the crossed pyramidal tract degeneration, which spreads out, backwards and forwards, a little way along the circumference of the cord.

Dorsal Region (fourth dorsal nerve).—The lateral tract degeneration comes nearer the circumference of the cord, and is altogether situated more posteriorly than in the cervical region.

The degeneration does not invade the direct cerebellar tract in this region.

On the opposite side there are a few degenerated fibres and some sclerosis in a corresponding area.

Eighth Dorsal Nerve.—The degeneration here is less in amount than at the fourth dorsal; it occupies a similar position, except that it comes altogether to the surface.

Lumbar Enlargement.—The degeneration here is small in amount and lies in the angle formed by the circumference of the cord and the tip of the posterior cornu. Degeneration can still be seen on the other side.

Case 10.—*No. 40 of First Series*. (Figs. 4*a*, Plate 27, 4*b* and 4*c*, Plate 28. See also 'Phil. Trans.,' B, 1888, Plate 7, fig. 40*B*.)

Lesion.—Removal of the right gyrus fornicatus, with injury to the marginal gyrus (fig. 4*a*, Plate 27).

Frontal sections through the brain show that the gyrus fornicatus was completely removed, and that the lower border of the marginal, especially at the front, was much undermined, and thus partly cut off from the corona radiata. There were also one or two small patches of softening on the external surface.

Result.—There was, at first, some paresis of the limbs and of the facial muscles on the left side.

For ten days there was entire loss of reaction to tactile and painful impressions on the left side. There was gradual, but only partial, recovery of sensation.

The animal died ten weeks after the operation.

Degenerations Observed.

Degeneration and shrinking could be seen with the naked eye in the pyramidal bundles of the pons and medulla on the right side, and in the crossed pyramidal tract on the left side, down the whole length of the cord.

Pons.—Microscopically there is distinct scattered degeneration in the pyramidal bundles of the pons.

Medulla.—The right pyramid shows extensive degeneration and sclerosis (fig. 4*b*).

Spinal Cord. Cervical Enlargement.—There is a well defined patch of degeneration involving the whole crossed pyramidal tract on the left side, triangular in shape, with the base towards the posterior cornu and the apex at the middle of the lateral surface of the cord. The apex spreads out along the circumference posteriorly, and encroaches for a short distance upon the cerebellar tract. The degeneration extends far forwards, as in most of the other similar lesions; the mesial part of the degeneration (the part towards the grey matter) is less concentrated than the part bordering the direct cerebellar tract. There is a little sclerosis.

On the right side (side of the lesion) there is a small amount of degeneration and sclerosis, scattered over a similar area.

Dorsal Region (fig. 4c).—The degeneration occupies the whole area of the crossed pyramidal tract, and appears even to extend in advance of that tract.

It is more concentrated than higher up, as is the case in all dorsal sections. In the lower dorsal region the degeneration has much the same appearance, except that it is altogether nearer the circumference of the cord, and does not extend as far forwards.

There is a very small amount of degeneration in a similar position on the opposite side.

Lumbar Enlargement.—The degeneration here is irregularly oblong in shape, and extends from the postero-lateral groove along the circumference for about one-fourth the distance from that groove to the anterior median fissure.

It does not touch the posterior cornu, except near the root exit.

No degeneration can be seen on the right side (side of the lesion).

Case 11.—No. 42 of First Series. (Figs. 6a, 6b, and 6c.)

Lesion 1.—Removal of the anterior two-thirds of the left gyrus fornicatus (see fig. 6a, Plate 27). Frontal sections through the brain show that only that part of the gyrus fornicatus which is seen on the mesial aspect was completely removed, those portions of the gyrus which lie next the corpus callosum and at the bottom of the calloso-marginal fissure having remained practically intact.*

Result.—Great diminution of sensibility over the right side of the body, which gradually, but only partially, passed off. Some muscular paresis on the right side, especially of the leg.

Lesion 2.—Eleven weeks after the operation, the right gyrus was exposed and injured by scratching with a needle. The permanent injury caused by the needle was so slight as hardly to be perceptible. No result was observed during life.

The animal was killed thirteen weeks after the first operation.

* It is especially to be noted that in this case there was no perceptible injury of any region, excitation of which has been proved to produce muscular movements.

Degenerations Observed.

Degeneration could be seen *with the naked eye* in the crossed pyramidal tracts on the right side, in the whole length of the spinal cord.

Internal Capsule.—There are many degenerated fibres to be seen with the microscope, in a horizontal section, scattered about posterior to the knee.

(The *midbrain*, *pons*, and *medulla* of this brain were lost.)

Spinal Cord. Cervical Enlargement (fig. 6*b*, Plate 29).—Scattered degeneration, with considerable sclerosis, can be seen in the crossed pyramidal tract on the right side, having a shape like that seen in the other cases recorded; it is triangular, with the base at the posterior cornu, and extends outwards and forwards, becoming narrower till it reaches the surface, where it tends to spread out.

On the left side there is a little sclerosis, scattered over a similar area. There are also some recently degenerated fibres in the same area, the result, no doubt, of the needle operation on the right gyrus fornicatus.

Dorsal Region.—At the level of the fourth dorsal nerve (fig. 6*c*) the degeneration on the right side does not extend as far forward as in the cervical region, but it covers a relatively greater area.

On the left side there is also some degeneration, but the difference on the two sides is very marked.

At the level of the *eighth dorsal nerve* the degeneration is less in amount on both sides; it lies close to the surface of the cord, and does not extend as far forwards as at the level of the fourth dorsal.

Lumbar Region.—The degeneration in the crossed pyramidal tract is close to the surface, and lies in the angle formed by the posterior cornu and circumference of the cord. It is much less in amount on the right side than in the dorsal region, and on the left can hardly be seen.

*Case 12.** (Figs. 5*a*, 5*b*, and 5*c*.)

Lesion.—Removal of the right gyrus fornicatus (fig. 5*a*, Plate 27), with some injury to the marginal convolution.

Result.—Anæsthesia over the whole left side of the body, partial in some places, complete in others. The left forearm retained its sensibility; the rest of the arm, the trunk, and the leg had very little, if any, sensibility. This condition continued for seven weeks, with slight and gradual improvement. The leg was slightly paresed.

At subsequent operations the greater part of the temporal lobe was removed on the right side, and the superior temporal gyrus on the left (see SANGER BROWN and SCHÄFER, 'Phil. Trans.,' B, 1888, p. 312, Monkey, No. VII.).

The animal was killed more than eight months after the first operation.

* This case of lesion of the gyrus fornicatus is mentioned in a paper by Professor SCHÄFER ("On Sensory Localisations in the Cerebral Cortex") in 'Brain,' April, 1888.

Post mortem, it was found that the middle part of the gyrus fornicatus was destroyed, and that the corresponding part of the marginal convolution was somewhat injured and depressed (fig. 5*a*). Besides the lesion of the temporal lobes above mentioned, the surface of the brain just above and in front of the Sylvian fissure was also found to be slightly injured.

Degenerations Observed.

In the midbrain, pons, and medulla the shrinking of the pyramidal bundles on the right side, as compared with those of the left, is very distinctly visible to the naked eye. They are also more deeply stained with aniline blue-black on the right than on the left side.

Microscopically, a number of degenerated fibres can be seen on the right side. In the medulla there is also some sclerosis.

Spinal Cord.—Level of second cervical nerve. Degeneration could be seen, even with the naked eye, in the lateral pyramidal tract on the left side (fig. 5*b*). There is a little degeneration in the pyramidal tract on the same side as the lesion (right), although less than after an extensive marginal or other motor lesion.

Level of sixth cervical nerve.—The degeneration has much the same appearance here as at the second cervical, except that it is rather better defined.

Level of fifth dorsal nerve.—The patch of degeneration is smaller than in the cervical region, but denser; it lies somewhat closer to the surface, especially nearer the posterior root exit (fig. 5*c*).

At the level of the eighth dorsal the patch is perceptibly smaller than at the fifth.

Lumbar Region.—At the level of the first nerve the degeneration is less extensive. It lies along the circumference of the cord near the apex of the posterior cornu.

At the level of the fifth lumbar the degeneration can still be made out without difficulty.

That the degeneration in this case had nothing to do with the lesions in the temporal lobes has been ascertained by carefully investigating other cords in which there were lesions in those lobes only.

Methods Employed in Preparing the Tissues for Microscopic Examination.

The brain and spinal cord of each animal, immediately after removal from the body, were placed in MÜLLER'S fluid, or bichromate of potash (2 per cent. solution), and hardened in this for not less than a month, the fluid being repeatedly changed. After hardening, they were first rinsed with water, or placed directly into methylated spirit without washing, and allowed to remain in this until cut up.

For staining by WEIGERT'S or PAL'S method, I have obtained better results if the brain has not been allowed to remain in spirit for more than a week, although the

length of time it has been kept in spirit does not seem to affect the staining with carmine or aniline blue-black.

For cutting sections the freezing method has chiefly been used. I have employed the celloidin method for particular purposes, but the wrinkling which occurs on passing large sections through xylol has been found a drawback to the use of this method.

The following have been used for staining the sections, viz., aniline blue-black,* lithium-carmine, WEIGERT'S and PAL'S processes. Aniline blue-black has given, on the whole, the best results in my hands, for I have been able to detect early degeneration better than by either WEIGERT'S or PAL'S methods, and sclerosis equally well. It is also better for photographic purposes than any of the others, except PAL'S.

I have found it better to stain individual sections than to stain in bulk, and, if the sections are passed through acidulated water after staining with aniline blue-black, the colour and differentiation are improved.

Lithium-carminet† has given good results when used to stain in bulk, the piece being kept in the solution for not less than a month. An objection to this stain is that it is trying to the eyesight to examine a long series of sections.

* Aniline blue-black . . .	2 gm.
Methylated alcohol . . .	60 c.c.
Distilled water	40 c.c.

† Lithium carbonate (sat. sol.)	100 c.c.
Carmine	5 gm.

APPENDIX.

Received April 22,—Read May 16, 1889.

On the Degenerations which follow the Removal of the External Motor Cortex, and of the whole Motor Cortex of One Hemisphere in Monkeys as compared with those which follow Lesions of the Gyrus Marginalis alone.

Since sending in the foregoing paper I have investigated the following cases:—

A.—Three of removal of the external motor surface of the brain in which the animals lived for a considerable time (from two to four months) after the operation.* The lesions were so much alike, and the resulting degenerations are so similar, that it would be superfluous to describe each case separately.

Sections were cut through the brain obliquely downwards and forwards perpendicular to the fibres of the crusta, and transverse sections of the pons, medulla, and of the three regions of the spinal cord were made.

Degenerations Observed.

In the *internal capsule* the degeneration is well-marked and constant, occupying the side next the lenticular nucleus. The inner side next the thalamus is almost entirely normal. The degeneration is greatest in amount about the angle, extending over the middle third.

Crusta.—The degeneration occupies the middle third and is clearly defined, the dorsal part being less completely degenerated than the ventral.

Pons.—The degeneration extends over the whole pyramidal bundles of the same side, almost all the fibres being degenerated.

Medulla.—The whole pyramid on the same side is degenerated, except a narrow portion towards the posterior and mesial border, which is less degenerated than the rest of the tract.

Spinal cord.—In the *upper cervical region* the whole extent of the crossed pyramidal tract is degenerated, that part bordering the direct cerebellar tract less completely than the rest. The degeneration extends along the circumference, backwards towards the posterior root exit, as a gradually narrowing band enclosing the direct cerebellar tract, which has an elongated wedge shape.

In the *dorsal region* the degenerated tract is entirely separated from the circumference by the direct cerebellar tract. It can be followed down the cord as far as the *lower lumbar region* where it is seen as a few degenerated fibres close to the circumference and a little external to the posterior root exit.

* For an account of the symptoms observed during life see "A Record of Experiments upon the Functions of the Cerebral Cortex," Cases 4, 5, and 8, by Professors SCHÄFER and HORSLEY, 'Phil. Trans.,' B, Vol. 179 (1888), pp. 1-45.

B.—Four cases of removal of the entire motor surface from one hemisphere in monkeys.

The symptoms observed during life, and the degeneration found after death were almost exactly alike in all these cases; but in the two which only lived one week the degeneration was not so easy to follow out as in the other two.

These animals lived for periods varying from one week to five months after the operation.*

Degenerations Observed.

In the internal capsule the degeneration is similar to that following lesions of the external motor cortex, but in addition to this, the inner side of the capsule is degenerated.

In the *crusta* and *pons* but little difference can be made out, the degeneration in the pyramidal tract being, perhaps, somewhat more complete.

In the *medulla* the pyramid of the same side is entirely degenerated.

In the *spinal cord* the whole crossed pyramidal tract is degenerated, the part bordering on the direct cerebellar tract as completely as the rest. The degeneration gradually diminishes as it descends, but can still be seen at the level of the 3rd and 4th lumbar nerves.

Summary of Results obtained by the Study of Degeneration following Lesions of the Motor Cortical Area.

Removal of the grey matter of the motor area of the brain, exclusive of the marginal gyrus, produces degeneration which becomes collected in the internal capsule, and thence downwards follows a regular and definite course as has already been abundantly shown by previous observers.

Diagram 1.



Horizontal section through one hemisphere showing the position of degeneration in the internal capsule following removal of the *external* motor surface (exclusive of gyrus marginalis).

In the *internal capsule*, as seen in a horizontal section, it occupies the middle third extending farther behind the knee than in front (diagr. 1), but quite distinct for a short distance in front of the knee. The degeneration does not involve the whole breadth of the internal capsule, but leaves the inner border almost entirely free.

* For an account of the symptoms observed during life and the exact extent of cerebral surface removed, see "A Record of Experiments upon the Functions of the Cerebral Cortex," *loc. cit.*, Cases 15, 16, 17, and 18.

The part of the capsule along the inner border is occupied by the fibres from the gyrus marginalis (diagr. 2), as is proved by the fact that when the entire motor area (including the gyrus marginalis) is removed, the whole width of the internal capsule is degenerated (diagr. 3), although the inner border never appears so completely degenerated as the outer.

Diagram 2.



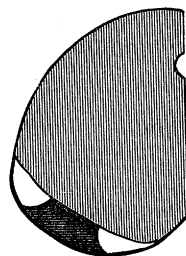
Horizontal section through one hemisphere showing the position of degeneration following removal of the gyrus marginalis.

Diagram 3.



Frontal section through brain, showing diagrammatically the course, through internal capsule, taken by degeneration following lesions in both the outer and mesial motor surface.*

Diagram 4.



Diagrammatic representation of the degeneration in the crusta.

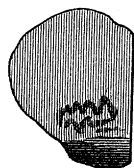
In the crusta, the degeneration occupies the middle third (diagr. 4), and little difference in appearance can be seen between that following an external motor (exclusive of gyrus marginalis), and that following a complete motor lesion; except that after removal of the external motor area only, the degeneration is not so great along the dorsal as along the ventral border of the crusta.

In the medulla the whole area of the pyramid is degenerated in those cases where

* The course of the fibres from the mesial surface is represented by darker shading than that of those from the external motor surface.

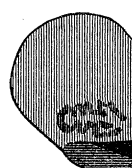
the whole motor area was removed; whilst in those where only the external motor area was involved a part along the posterior mesial border appears less completely degenerated than the rest (diagrams 5 and 6).

Diagram 5.



Degeneration in the pyramid of the medulla following lesions of the external motor area.

Diagram 6.



Degeneration following lesions of the entire motor area.

In the spinal cord the degeneration occupies the whole extent of the crossed pyramidal tract in those cases where the whole motor area was removed; but where only the external motor area was involved, that part of the pyramidal tract bordering on the direct cerebellar tract is less degenerated, though never quite free from degeneration.

This fits in with what I have said of the degeneration following marginal lesions, which chiefly occupies the part bordering on the direct cerebellar tract.

In the cervical region, the degeneration besides occupying a position corresponding to that seen in the dorsal region, also extends as a narrow band along the circumference towards the posterior root exit (diagr. 7), but there is always a well-marked tract of healthy fibres (direct cerebellar tract) close to the posterior root exit, extending into and separating the degeneration in the crossed pyramidal tract proper from the band extending along the circumference.

Diagram 7.



The degeneration as seen in the upper cervical region showing the direct cerebellar tract enclosed by degenerated crossed pyramidal tract.

Diagram 8.



Showing the degeneration at the level of the sixth dorsal nerve.

In the dorsal (diagr. 8) and lumbar regions no constant difference in shape and position can be made out between the degeneration following removal of the external motor surface, and removal of the entire motor area.

It gradually diminishes as it descends, but can be seen in the lumbar region (at the level of the 3rd or 4th nerve) as an oval patch close to the circumference and near the posterior root exit.

I have never in any case in the Monkey observed degeneration in the anterior columns of the spinal cord, and conclude, therefore, that in these animals the pyramidal decussation in the medulla oblongata is complete.

DESCRIPTION OF PLATES 27-29.

Case 1 (Figs. 1a to 1e).

- Fig. 1a (Plate 27).* View of the brain showing the extent of the lesion.
 Fig. 1b (Plate 28). Transverse vertical section through the brain showing the depth of the lesion.
 Fig. 1c (Plate 28). Transverse section of the spinal cord in the cervical region.
 Fig. 1d (Plate 28). Transverse section of the spinal cord in the middle dorsal region.
 Fig. 1e (Plate 28). Transverse section of the spinal cord at the lumbar enlargement.

Case 2 (Figs. 2a to 2d).

- Fig. 2a (Plate 27).* View of the brain showing lesion.
 Fig. 2b (Plate 28). Transverse section of the medulla.
 Fig. 2c (Plate 28). Transverse section of the cord at the level of the second cervical nerve.
 Fig. 2d (Plate 28). Transverse section at the level of the fourth dorsal nerve.

Case 8 (Figs. 3a and 3b).

- Fig. 3a (Plate 27).* View of the left side of the brain showing the lesion in the gyrus fornicatus.
 Fig. 3b (Plate 28). Transverse section of the spinal cord in the cervical region.

Case 10 (Figs. 4a to 4c).

- Fig. 4a (Plate 27).* View of the right side of the brain showing the lesion in the gyrus fornicatus.
 Fig. 4b (Plate 28). Transverse section of the upper part of the medulla.
 Fig. 4c (Plate 28). Section of the dorsal cord.

Case 12 (Figs. 5a to 5c).

- Fig. 5a (Plate 27). View of the left side of the brain showing the lesion in the gyrus fornicatus.
 Fig. 5b (Plate 29). Transverse section of the spinal cord in the cervical region.
 Fig. 5c (Plate 29). Transverse section from the middle dorsal region of the cord.

* Figures marked with an asterisk are taken from the paper by HORSLEY and SCHÄFER. The others are from photographs.

Case 11 (Figs. 6a, 6b, 6c).

Fig. 6*a* (Plate 27). View of mesial surface of left hemisphere showing lesion in gyrus fornicatus.

Fig. 6*b* (Plate 29). Cervical cord showing degeneration in right pyramidal tract.

Fig. 6*c* (Plate 29). Dorsal cord.

Fig. 7 (Plate 29). Transverse section from the upper dorsal region of the spinal cord of a Monkey, in which nearly the whole of the motor cortex of one side of the brain was removed some months previously.

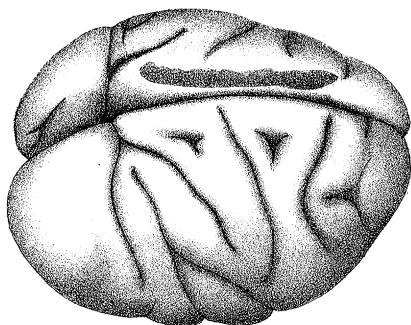
Figs. 8, 9, and 10 (Plate 29). Photographs of spinal cord degeneration under a high power.

Fig. 8. One month after production of lesion in brain. At the upper and right hand part of the figure are seen normal fibres belonging to the direct cerebellar tract.

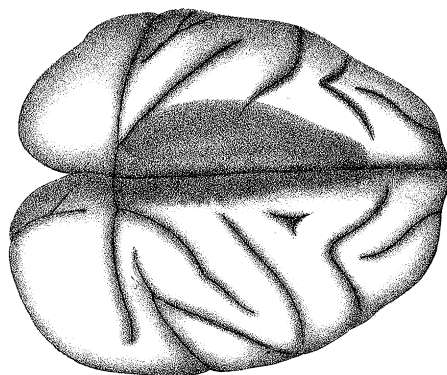
Fig. 9. Three months after production of lesion in brain. At the lower and right hand part of the figure are seen normal fibres belonging to an adjacent tract.

Fig. 10. Six months after production of lesion in brain.

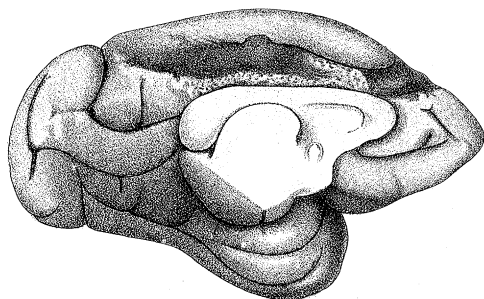
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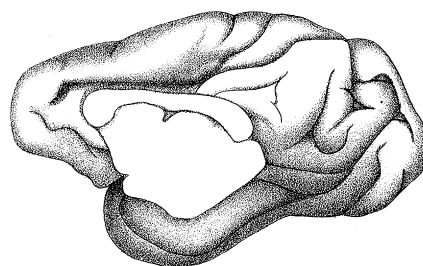
2a



3a



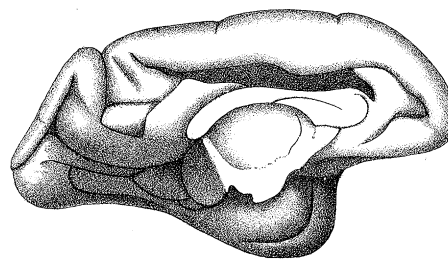
4a



5a



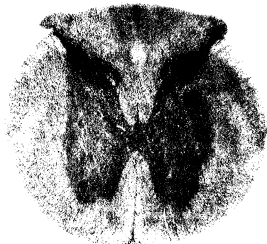
6a



1.b.



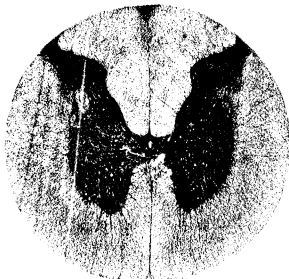
1.c.



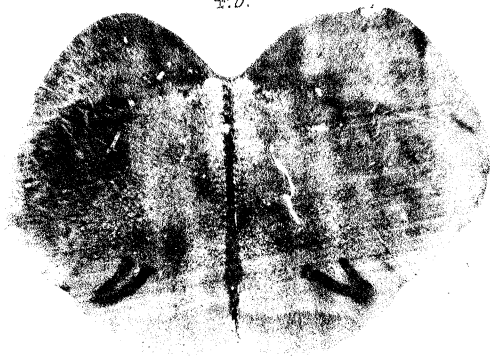
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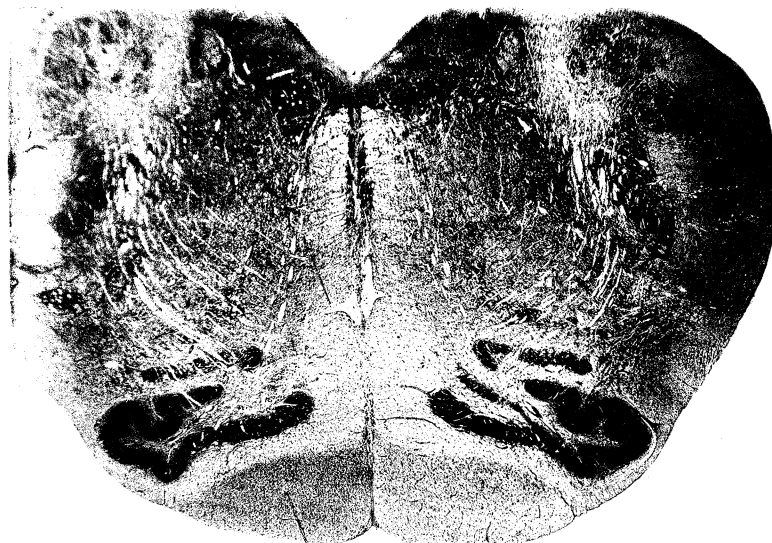
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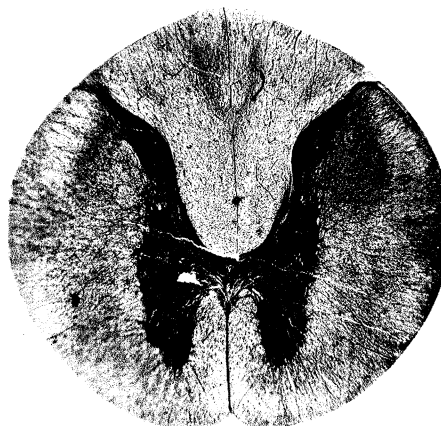
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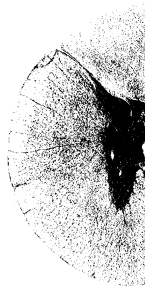
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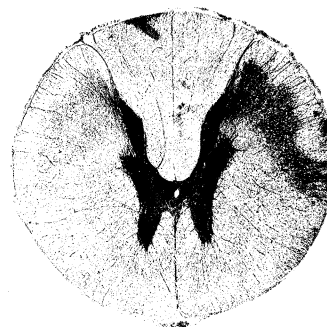
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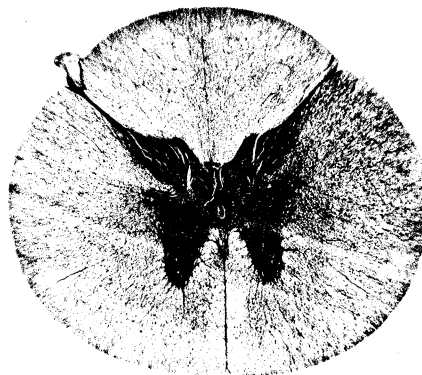
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2.d.



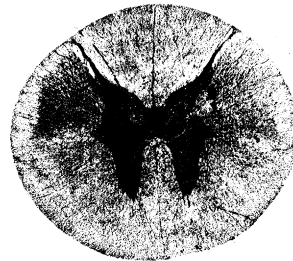
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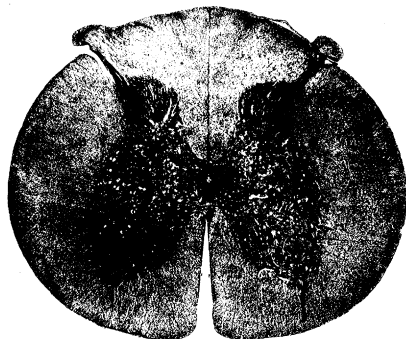
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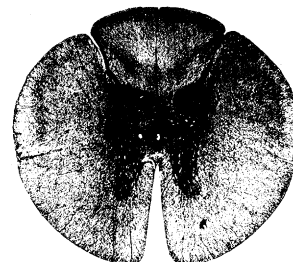
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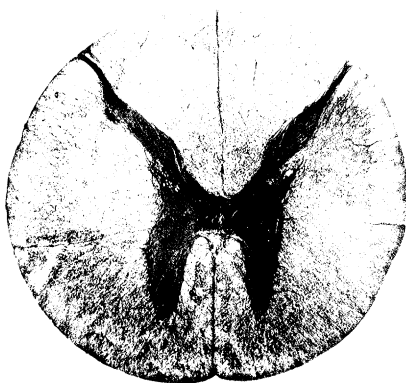
6.b



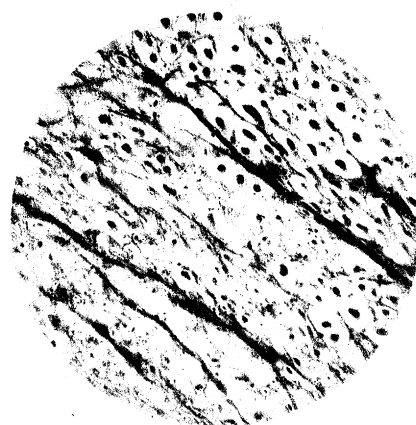
6.c



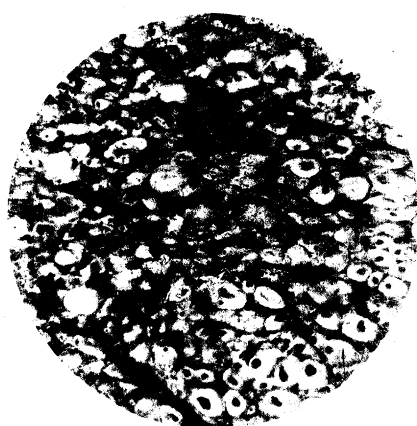
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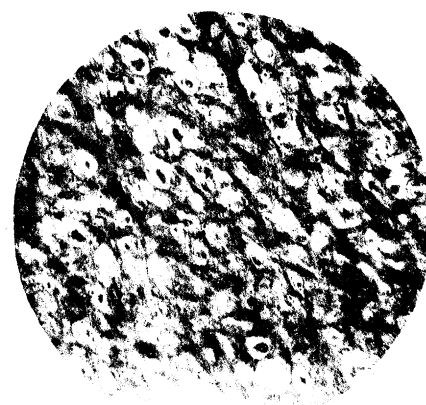
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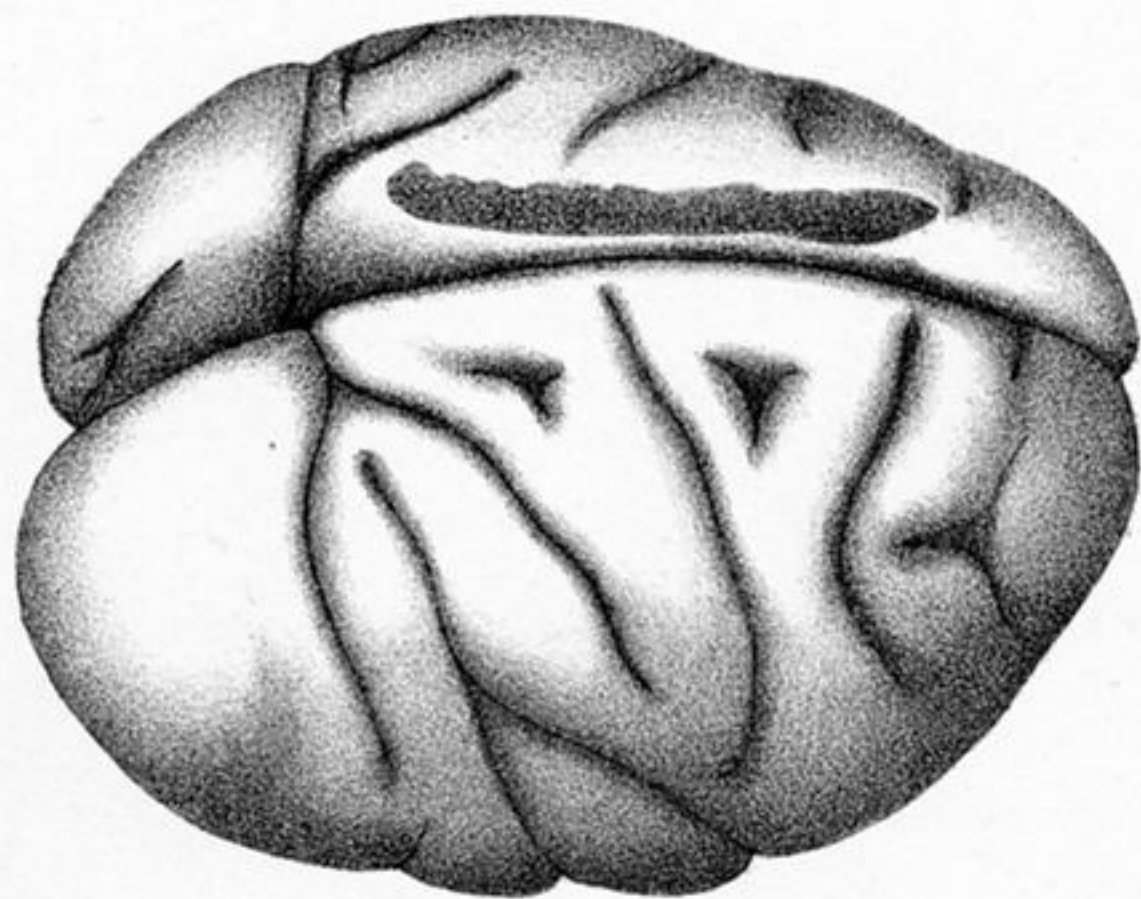
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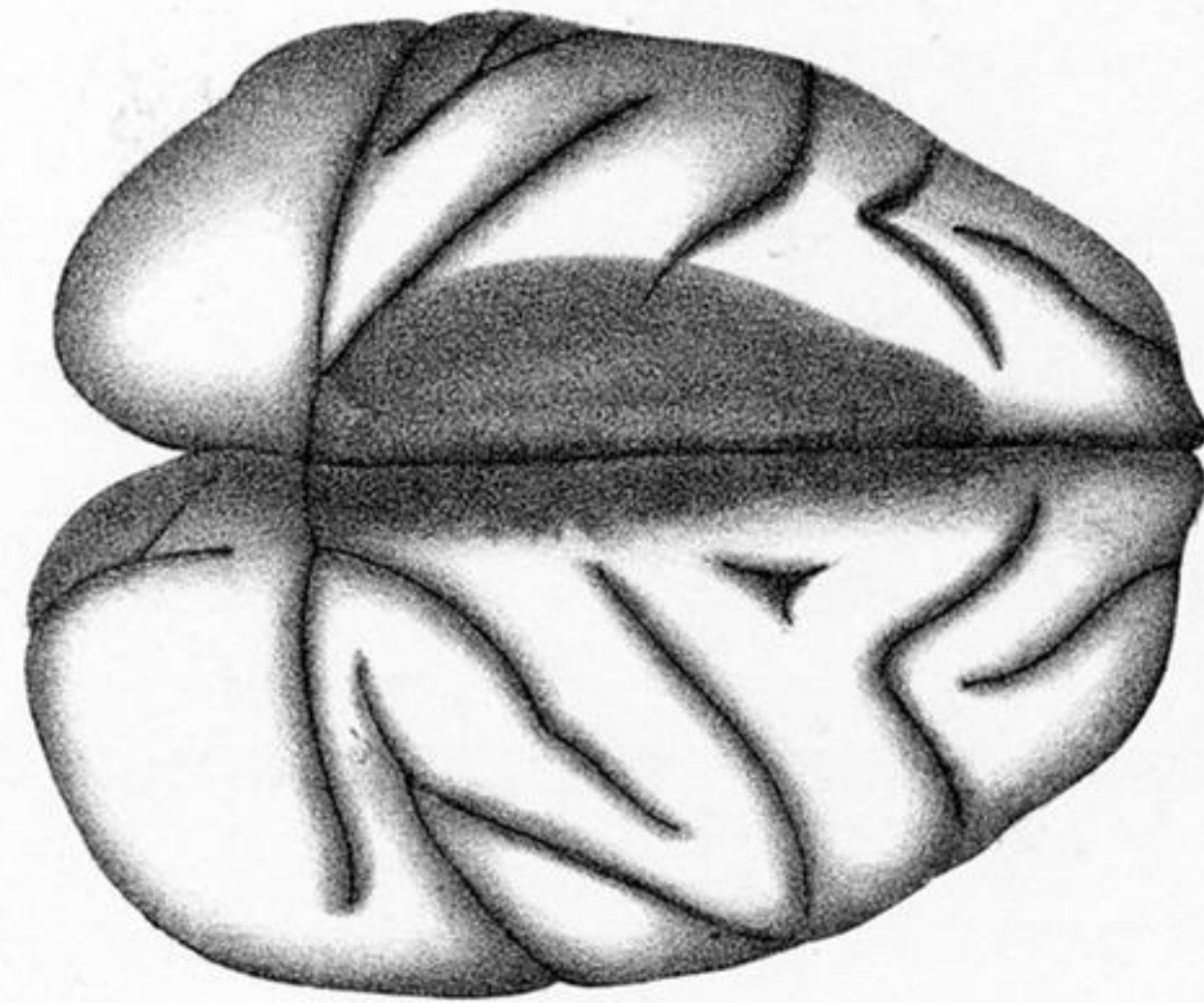
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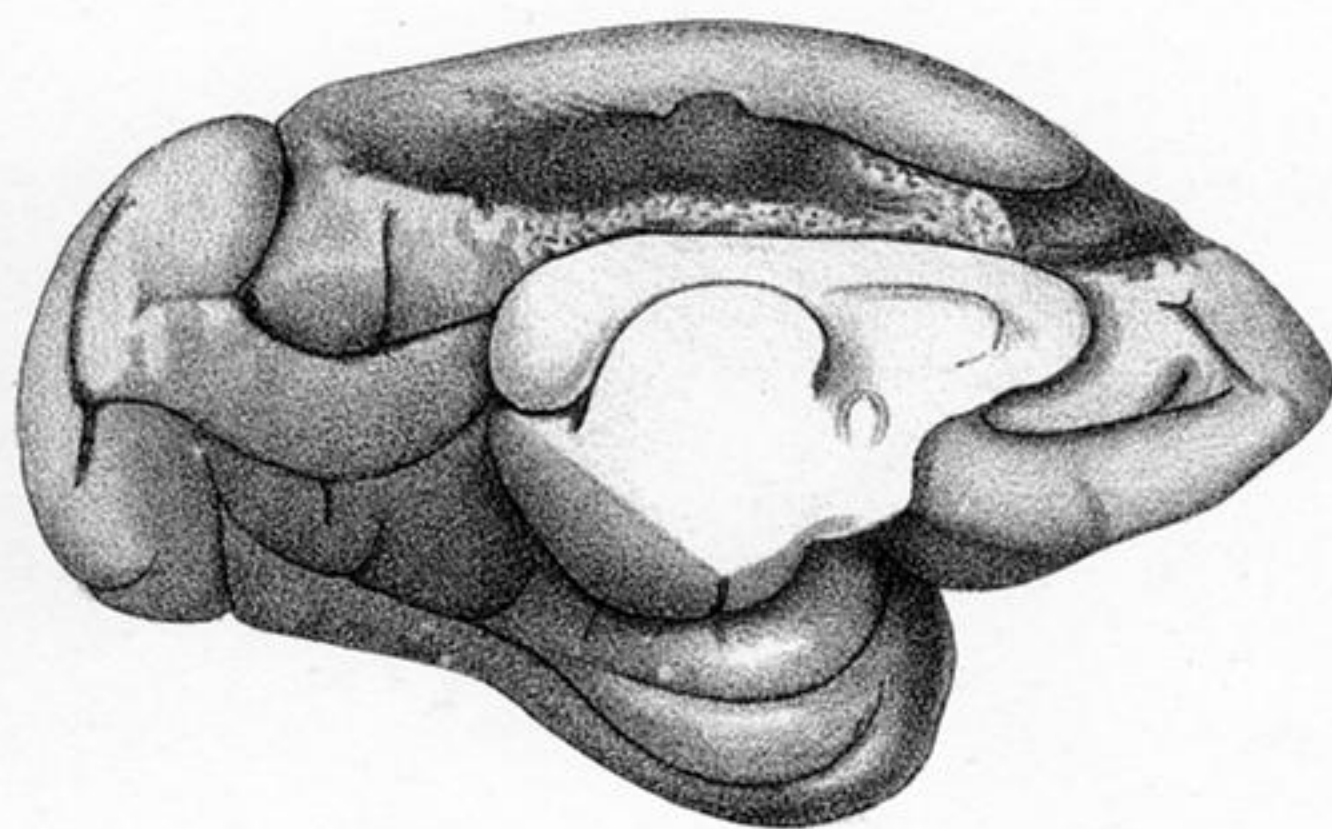
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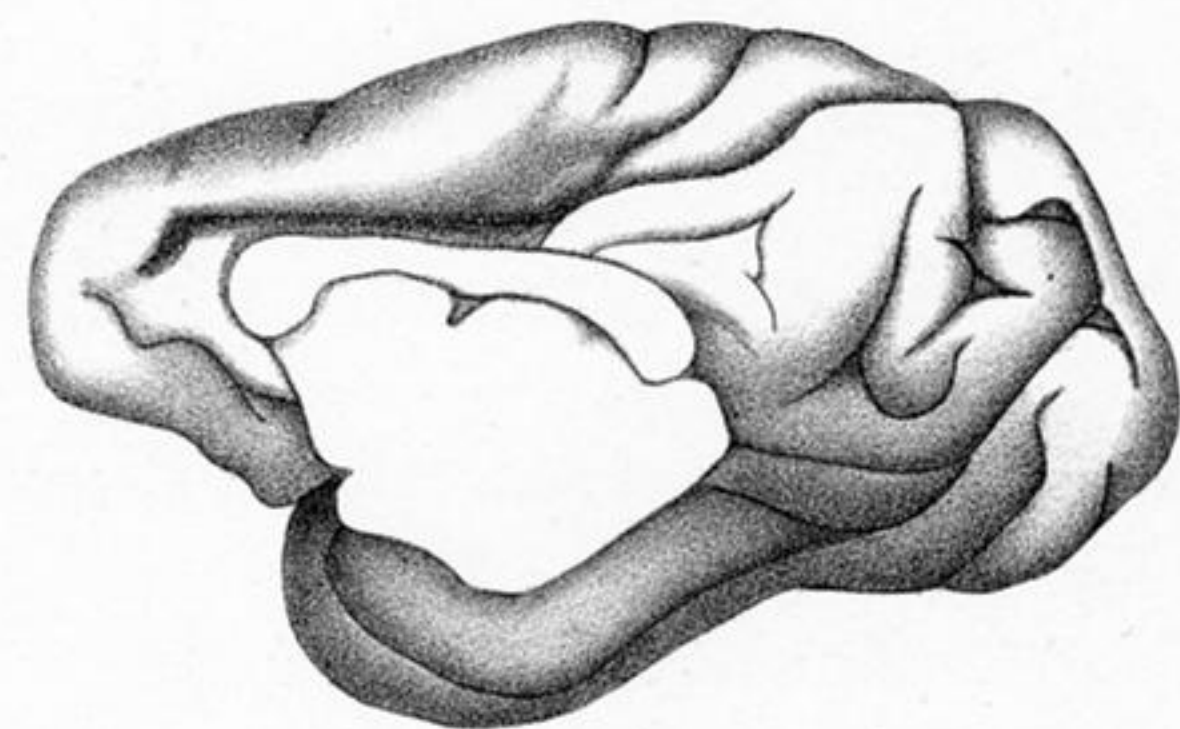
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3a



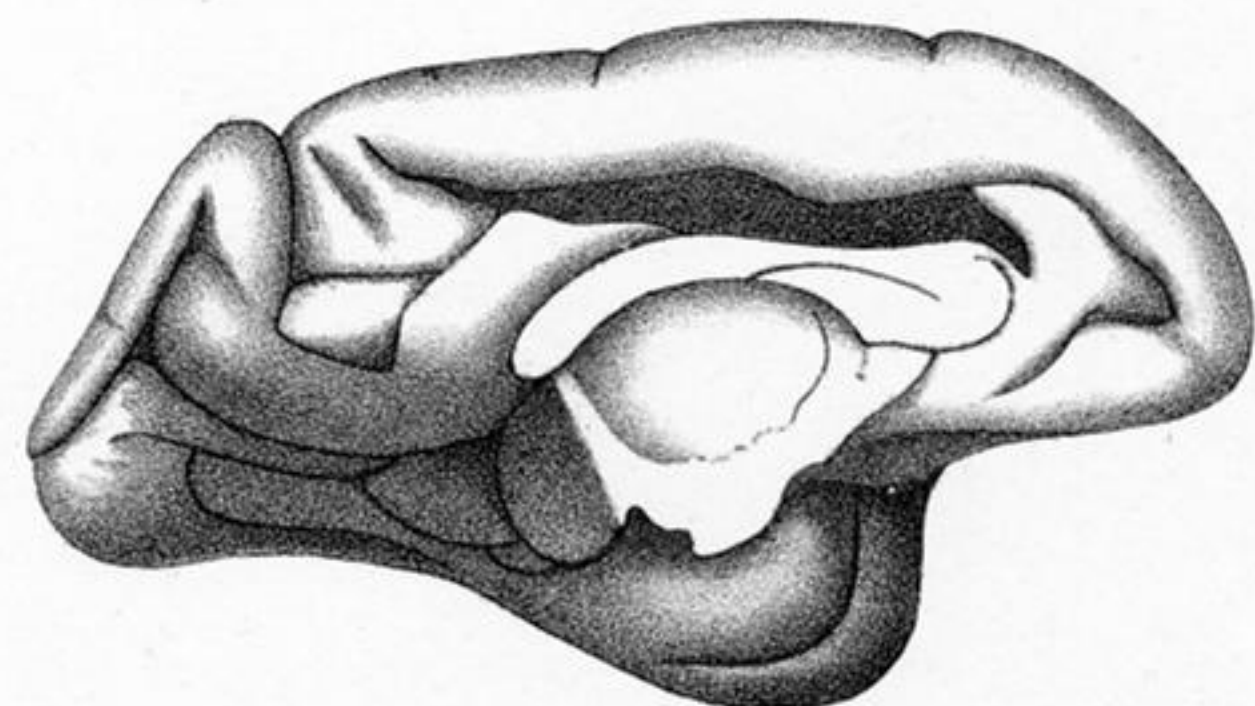
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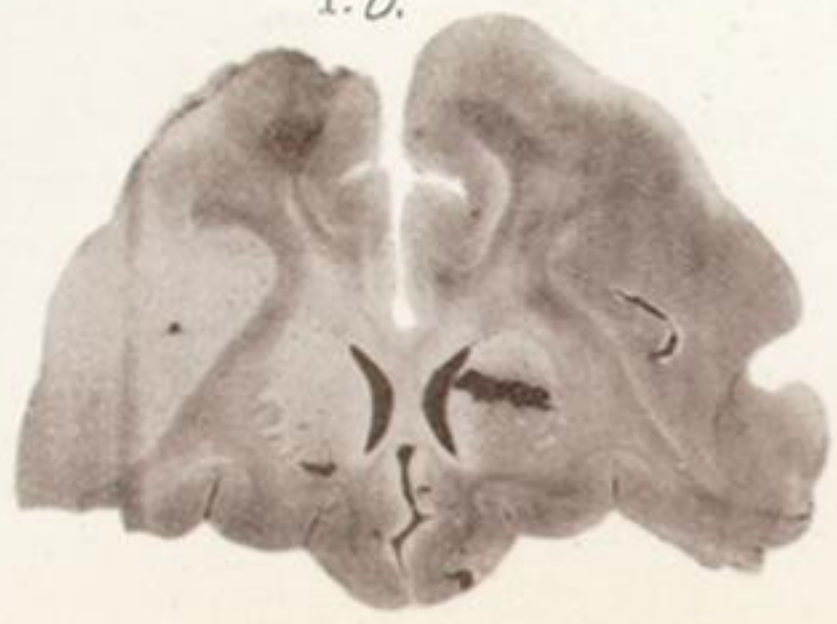
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6a



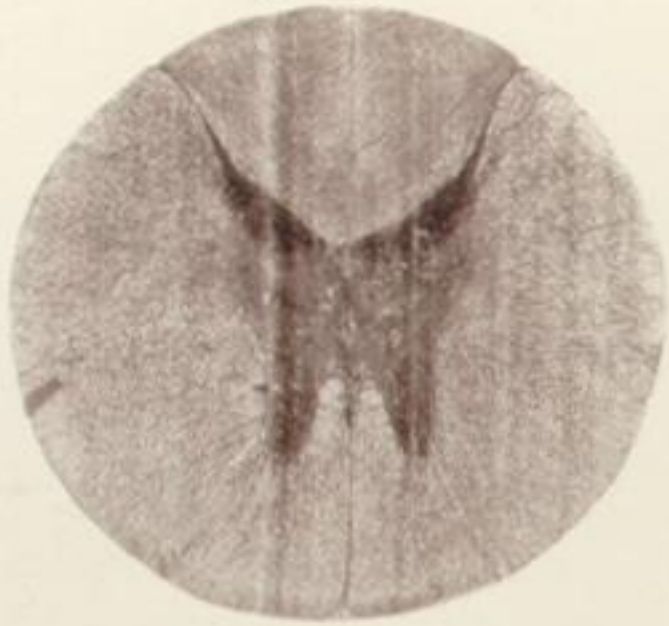
1. *b.*



1. *c.*



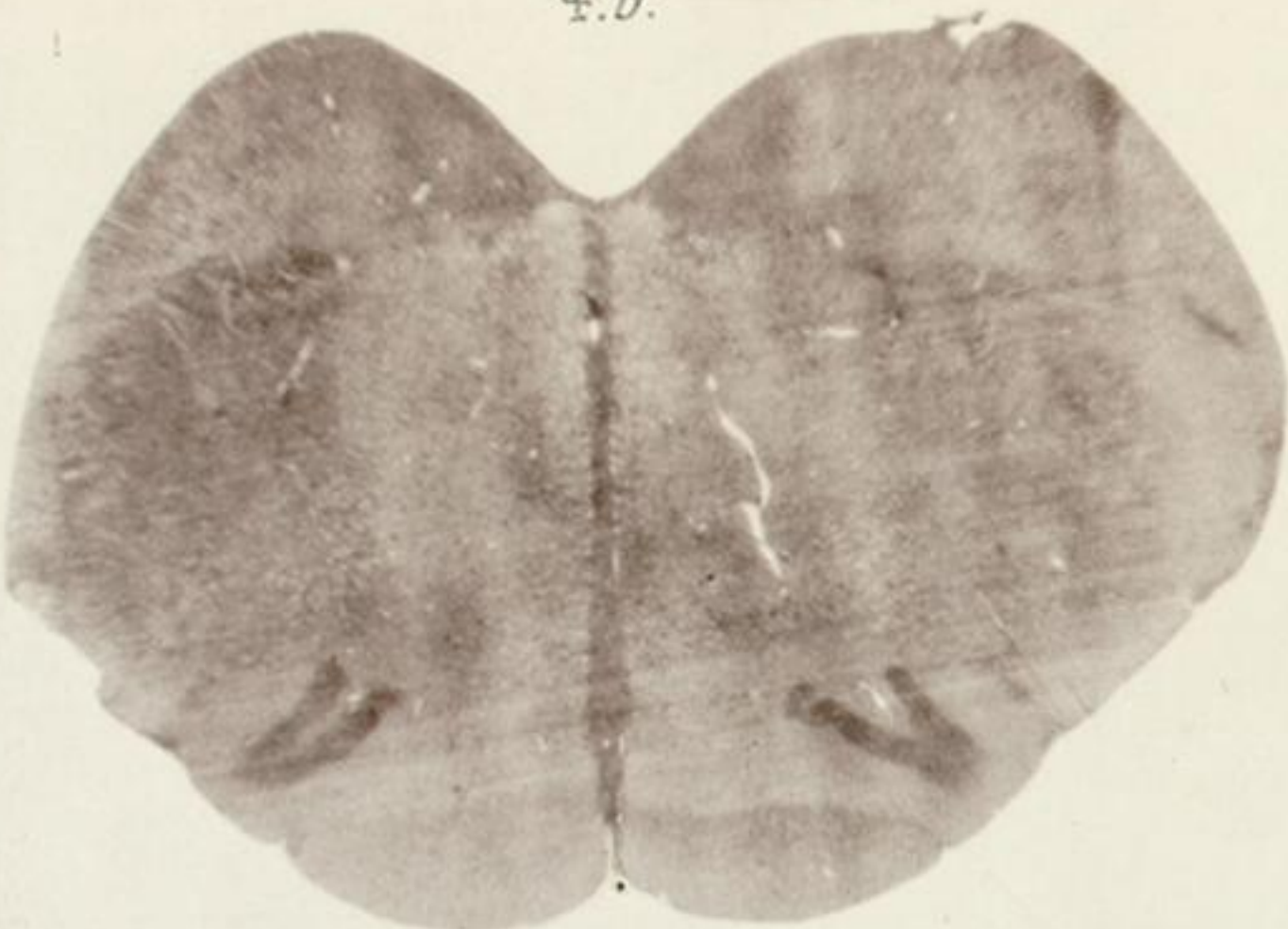
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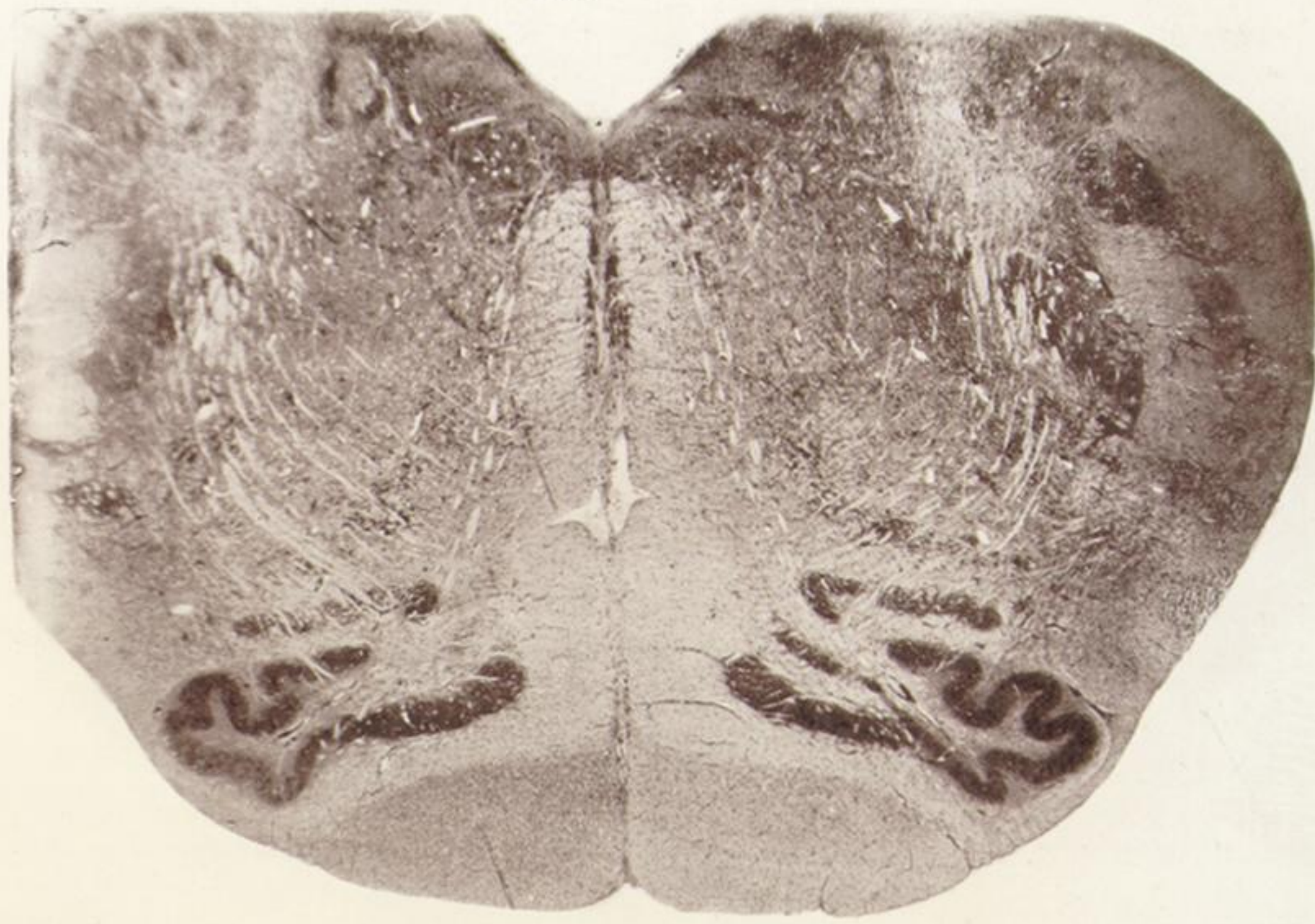
1. *e.*



4. *b.*



2. *b.*



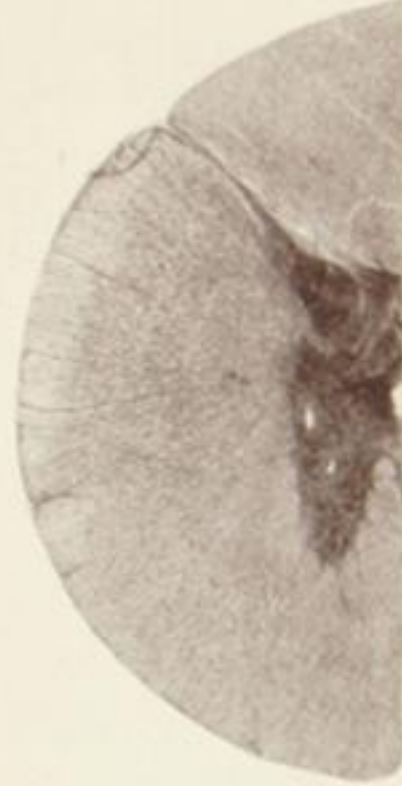
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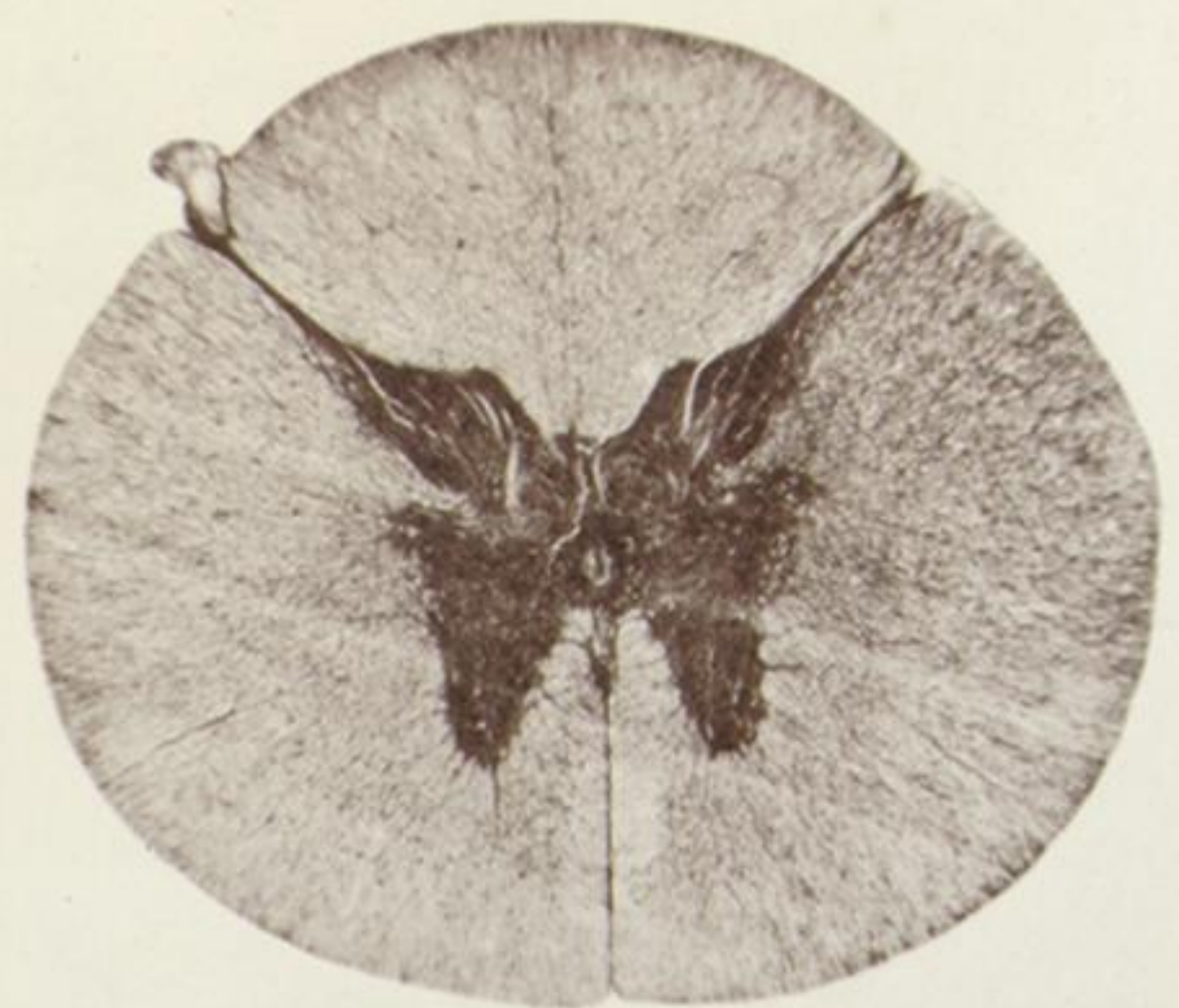
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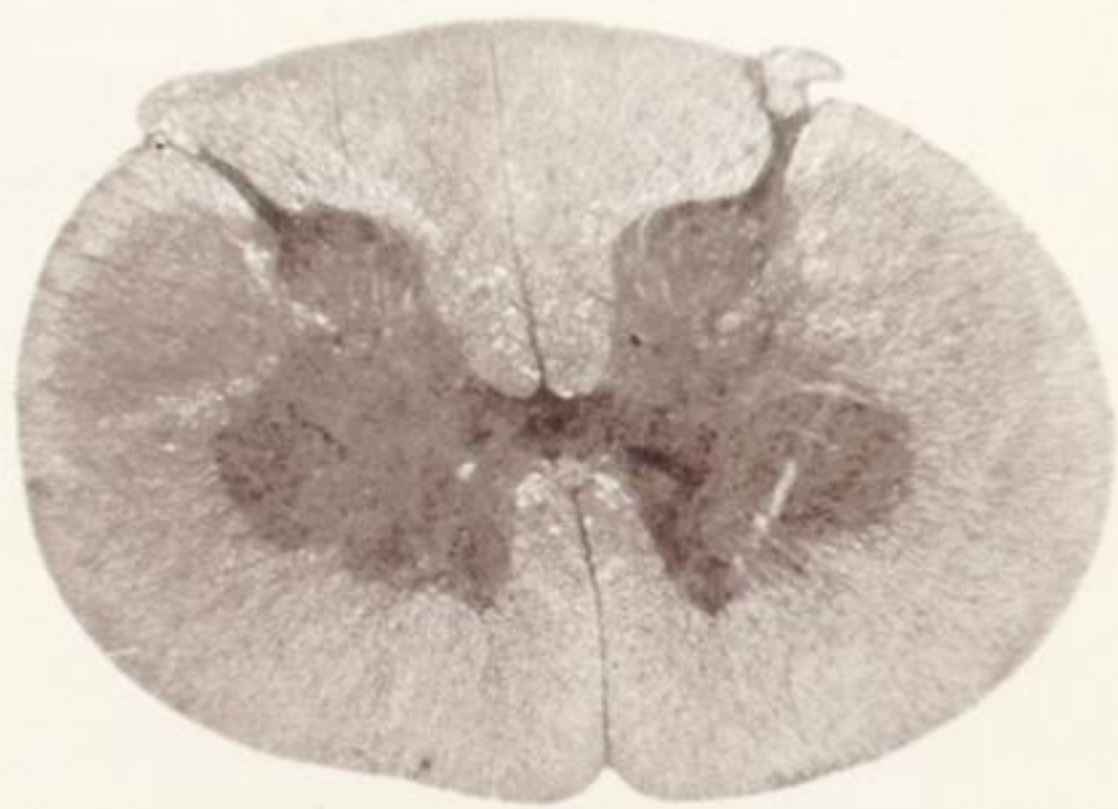
4. *c.*



3. *b.*



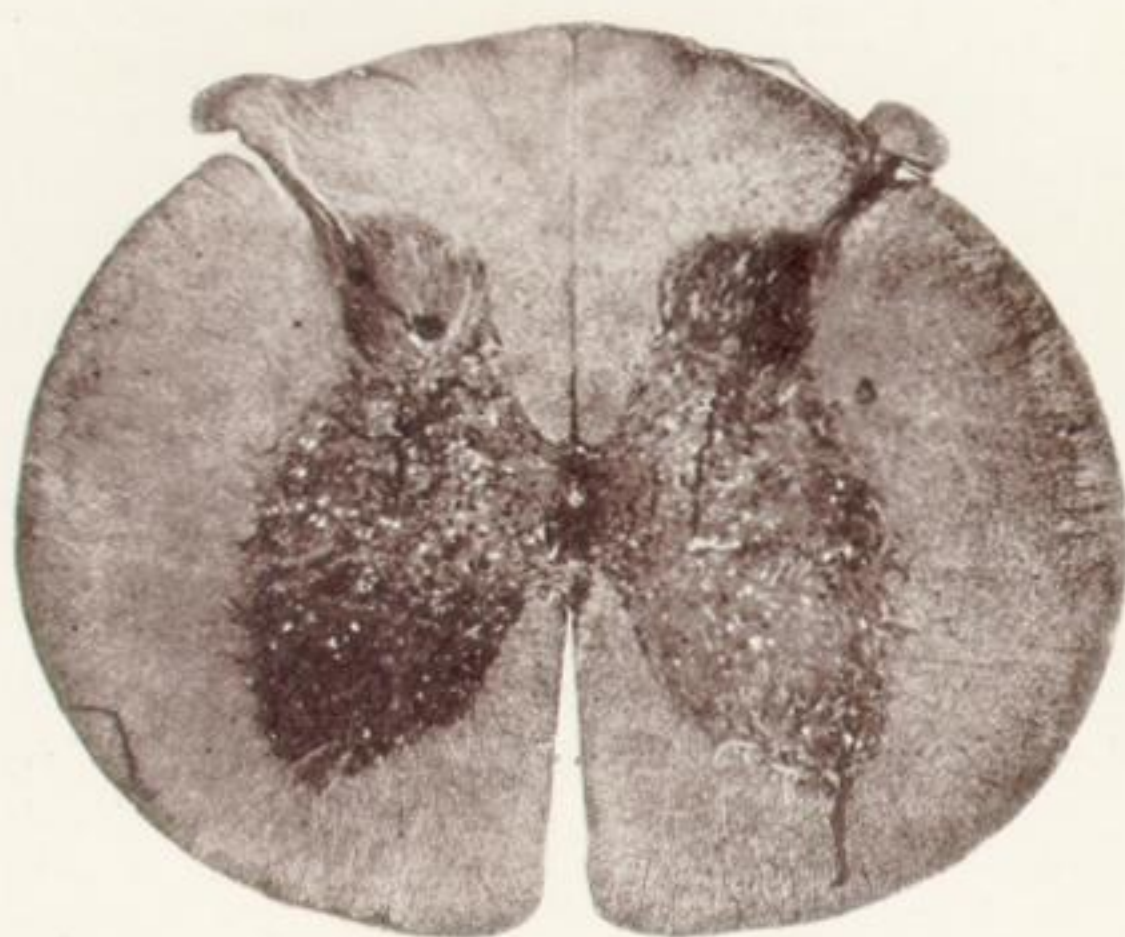
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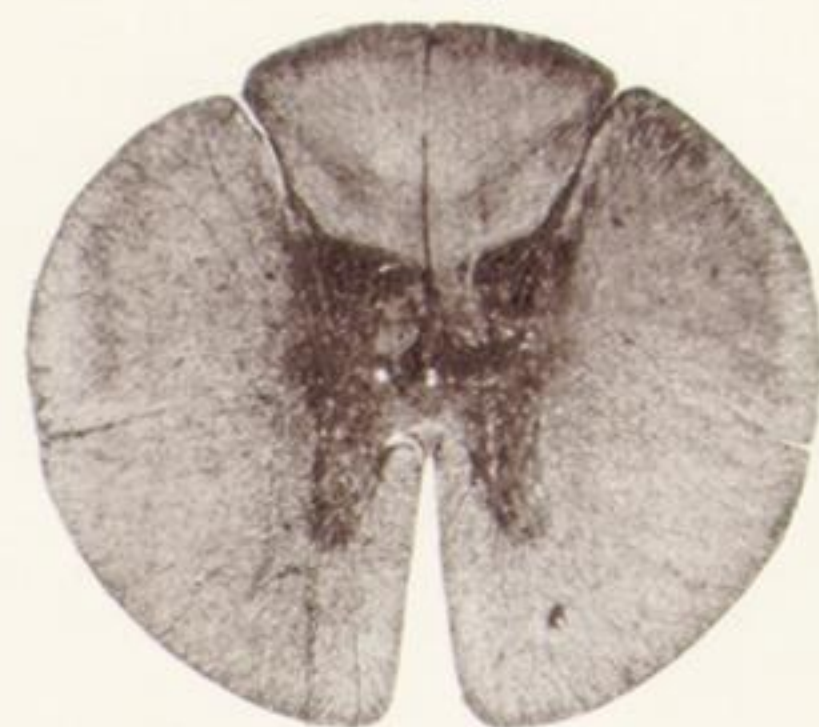
5. c



6. b



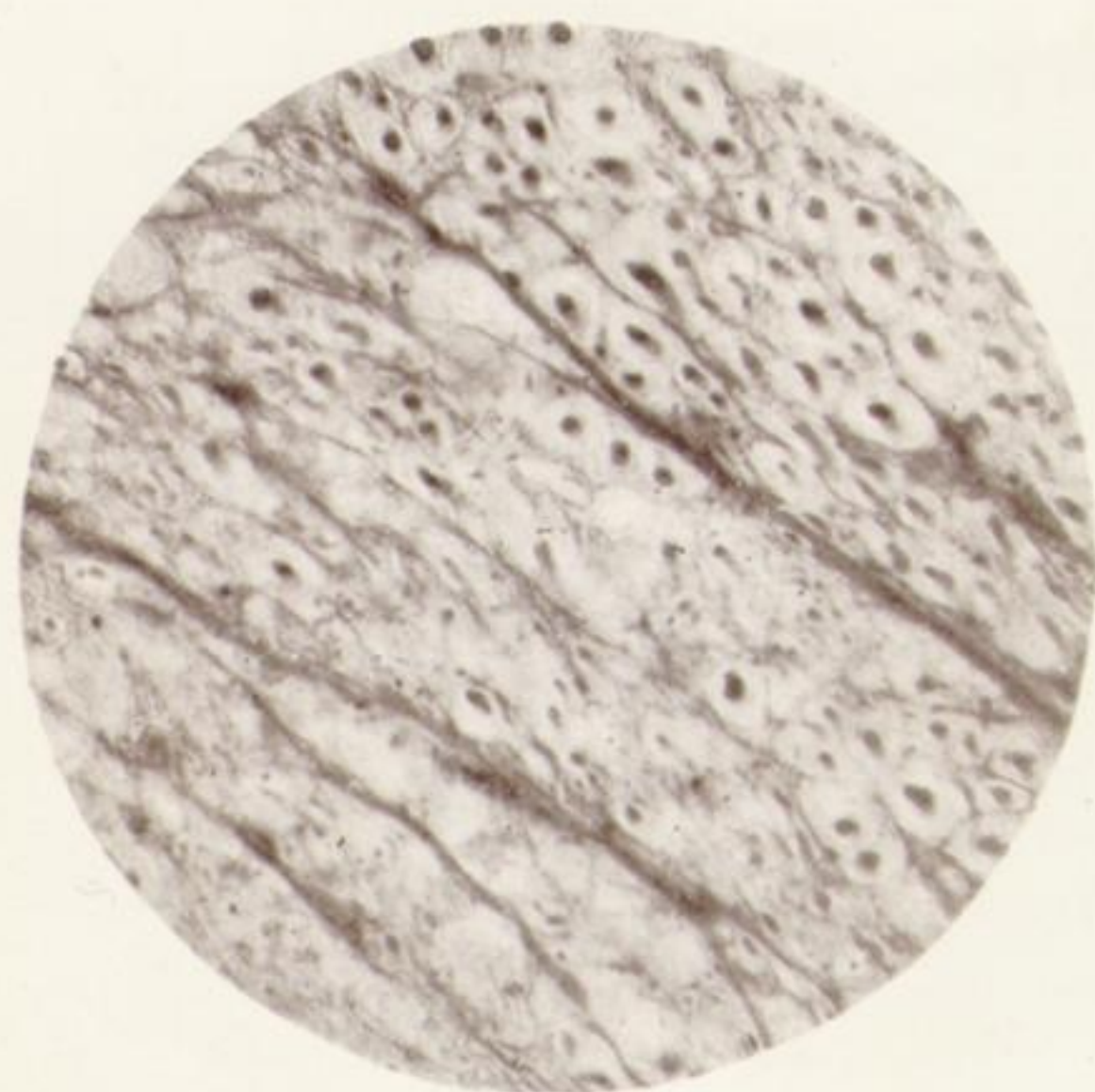
6. c



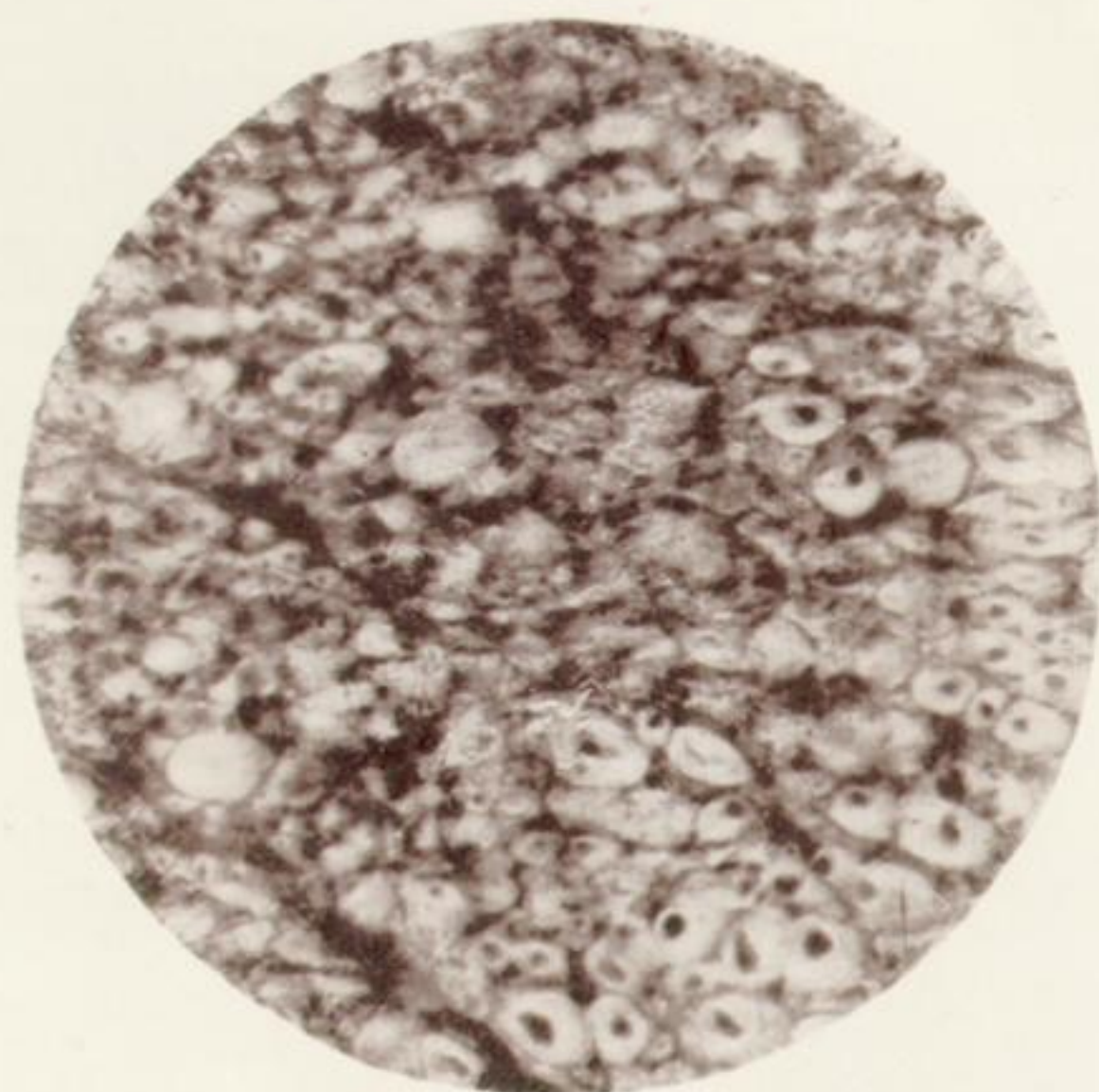
7.



8.



9.



10.

