PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Experimental Researches into the Functions of the Cerebellum

J. S. Risien Russell

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XVIII. *Experimental Researches into the Functions of the Cerebellum.**

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CONTENTS.

I. INTRODUCTION.

That an apology is necessary for my having undertaken this research after the elaborate investigations which have so recently been published by Luciani, cannot be

* Part of the expenses of this investigation have been defrayed by a grant from the Scientific Grants Committee of the British Medical Association.

more patent to any one than to myself. I feel sure, however, that my apology will be accepted, when it is remembered how far from settled are many of the problems connected with the functions of the cerebellum.

I am prompted to publish the results of my investigations, partly because so many of them are in complete accord with those of LUCIANI, and partly because many of the points which have engaged my attention have not been taken up by him, or, indeed, by any other experimental physiologist, as far as I am aware.

It is once more my pleasant task to express how deeply indebted I am to Professor VICTOR HORSLEY, for his kindness in allowing me to carry out this investigation in the Pathological Laboratory at University College, to thank him for many valuable suggestions, and for the criticisms my results have met with, from to time, at his hands.

To Professor RUBERT BOYCE I owe a debt of gratitude in connection with former researches in which I have been engaged at University College, but at no time has the debt been so great as on the present occasion. He has not only given me the benefit of his criticisms, but has brought to my notice facts, the outcome of his own investigations in the cat, which have had a direct bearing on the problems which have occupied my attention, and have aided in their elucidation.

II. HISTORICAL ACCOUNT OF PREVIOUS EXPERIMENTAL INVESTIGATIONS.

The earliest experimental investigations into the functions of the cerebellum seem to have been those of SAUCEROTTE* who, from experiments on four dogs, concluded that the muscles of the back, neck, and eyes are innervated from the cerebellum, and that the central part of this organ causes acuteness of feeling throughout the body. Forty years later ROLANDO,† after a large number of experiments, attributed to the cerebellum a direct influence on movement, considering it the source of origin of all movements, and its mode of action comparable to that of a voltaic pile, as REIL had previously surmised.

FOVILLE and PINEL-GRANDCHAMP,‡ from clinical observation, and from experiments, concluded that the cerebellum is the seat of sensibility. In 1824 FLOURENS§ advanced a theory with regard to the function of the cerebellum which differed from all previous surmises and from all theories the outcome of former experimentations. His theory was based on experimental observations, and attributed to the cerebellum the power of co-ordinating voluntary movements generated by other parts of the nervous system.

* SAUCEROTTE, 'Prix de l'Académie Royale de Chirurgie,' 1769, vol. 4.

† ROLANDO, 'Saggio sopra la vera struttura del cervello,' &c., Sassari, 1809.

‡ FOVILLE and PINEL-GRANDCHAMP, 'Sur le siège spécial de différentes fonctions du système nerveux,' Paris 1823.

§ FLOURENS, 'Recherches Expér. sur les Prop. et les Fonct. du Syst. Nerv.,' Paris, 1824, p. 36.

MAJENDIE* found that the animal rotated to the side of the lesion when the middle peduncle was divided, but that no rotation occurred when both middle peduncles were divided. The eye on the same side as a unilateral lesion, turned downwards and forwards, while that of the opposite side turned upwards and backwards; but they returned to their normal positions when the opposite peduncle was also divided. On dividing the cerebellum in the middle line, the animal was as if between two opposed forces, and the eyes were in a state of extraordinary agitation.

BOUILLAUD† agreed with FLOURENS that the faculty of co-ordinating the movements of walking, running, flying, &c., resides in the cerebellum; but he could not agree with him in his belief that this organ co-ordinates all voluntary movements. These conclusions were the outcome of a series of experiments on dogs, rabbits, pigeons, and fowls, the cautery being used to inflict various lesions of the cerebellum in these animals, all of whom exhibited disorders of the locomotor functions, and of equilibration.

FLOURENS‡ experimenting on pigeons and other birds, removed successively deeper and deeper layers to the cerebellum, and found that removal of the most superficial layers resulted only in slight feebleness and want of harmony in the movements. As deeper layers were removed, universal agitation, without any sign of convulsion, resulted, all movements being performed abruptly and irregularly. As still deeper layers were removed, the power of springing, flying, walking, and standing upright became more and more altered, and, at last, completely lost. When placed on their backs the birds were unable to get up, and they were in an almost constant state of wild agitation. The will, sensation, and perception were intact; there was no affection of sight and hearing. The possibility of performing combined movements persisted; but the co-ordination of these movements was lost. Similar experiments were performed on certain mammals, and, as in birds, resulted in disharmony of the movements proportional to the amount of the organ removed, and with total ablation of the organ there was complete loss of the faculty of regulating movements. The movements, disordered by the cerebellar lesions, corresponded to all the ordered movements. In birds which flew, it was in the flight that the disorder first appeared; in those that walk, it was in the gait; and in those which swim, in the swimming. FLOURENS accordingly concluded that the cerebellum is the centre for the co-ordination of voluntary movements.

GRATIOLET and LEVEN§ made a very small opening in the bone, and then made a vertical section into the centre of the lateral lobe, by means of a sharp needle. The

* MAJENDIE, 'Journ. de Phys.,' 1824, vol. 4, p. 399.

† BOUILLAUD, 'Arch. Général. de Méd.,' 1827, 15, p. 64.

‡ FLOURENS, 'Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux.' 1842, 2nd. Ed., p. 37.

§ GRATIOLET and LEVEN, 'Comptes Rendus,' 1860, vol. 51, p. 917.

animal instantly rotated towards that side, and the trunk was curved in the same direction; the opposite eyeball was displaced forward aud upward, while that on the same side was displaced downward and backward. There was no sign of hemiplegia, and sensibility was intact. The symptoms were recovered from in a few days.

DALTON* appears to have been the next experimental physiologist whose attention was directed to the cerebellum. He found that pigeons were neither able to stand, walk, or fly after removal of large portions of the cerebellum, and that they were only capable of making confused and ineffectual struggles. He did not consider that any debility or partial paralysis existed; and found that after a time the power of muscular co-ordination was restored. The only abnormal symptom which remained was a moderate general debility, which was only noticeable when the birds made unusual exertion. In fighting, the movements were well directed, though wanting in force. DALTON supposed that the irregularity of motion could only be accounted for by supposing it to be in some way the effect of the sudden injury to the cerebellum as a whole, rather than the simple loss of a part of its substance.

LEVEN and OLLIVIER,† in the following year, published their experimental and other observations on this subject. They passed a well-tempered steel needle through the skulls of guinea pigs, and in one series of experiments wounded the cerebellum alone, while in another series they also injured the bulb. In lesions limited to the cerebellum, the symptoms passed off in a few days. Ordinary sensibility and the organs of special sense were not affected; there was never vomiting or diarrhœa, nor was the appetite impaired, or emaciation observed. The motor phenomena consisted in rotation to the opposite side from the lesion, "circus movements" towards the side the lesion, bending of the head on the trunk, incomplete hemiplegia, slowness of of progression, &c. The trunk was curved, there was general muscular enfeeblement, sometimes a tendency to be drawn towards the opposite side from the lesion, and strabismus with, sometimes, corneal affection of the squinting eye. The second series of experiments, in which the bulb was injured in addition to the cerebellum, does not call for description in this paper, which is intended to deal with uncomplicated cerebellar lesions.

RENZI‡ next experimented on fishes, and concluded that the cerebellum was an organ for co-ordinating spontaneous movements, and that it exercised an undoubted influence over the sense of sight. The next year this observer published the results of a more extended investigation, when he found that partial extirpation of the cerebellum resulted in partial loss of the power of regulating movements, while total ablation caused loss of power of co-ordination, without affecting intelligence, sensory perception and motor power. Lesions of the anterior part of the middle lobe caused a tendency to fall forward, and lesions of the centre or posterior part of this lobe

* DALTON, 'Amer. Journ. of Med. Sc.,' 1861, vol. 41, p. 83.

† LEVEN and OLLIVIER, 'Arch. Gén. de Méd.,' 1862, s. 2, vol. xxv., p. 513; 1863, s. 6, vol. 1, p.68.

‡ RENZI, 'Annal. Univ. d. Med.,' 1863, vol. 185, p. 486; 1864, vol. 187, p. 47.

induced a tendency to fall backward. A lesion of one lateral lobe was followed by reeling to the opposite side, while the head was turned to the side of the lesion, and the rotation was in that direction when a peduncle was its seat. Successive lesions to both peduncles resulted in shaking of the head. These results led Renzi to conclude that the cerebellum is indispensable for the regulation of locomotion, and that it exercises an influence on vision by regulating the co-ordinated voluntary movements.

Dickinson,* in the following year, published the results of a series of investigations. He found that fish lost their balance, became less active, and did not survive total ablation of the cerebellum. Snakes presented failure of lateral balance, and when the lateral connections were left on one side, they twisted into a corkscrew shape and revolved. Frogs showed no appreciable defect, except that when one side connections were divided, the opposite limbs were slightly weaker; and in the toad the only obvious result was a peculiar stilted manner of using the legs. Tortoises walked with a stilted gait, and showed lessened activity; and when the attachment on one side was undivided, the hind leg of the opposite side retained its normal muscular state and activity, while the three other limbs were affected as if the whole organ had been removed. Guinea-pigs and rabbits lost the power of walking, motor power being more impaired in the posterior than in the anterior extremities; they also suffered from giddiness or loss of balance. Pigeons staggered and fell back or to one side at first, and as successive slices were removed, total loss of motor power and eventually death resulted.

Ablation of the cerebrum and cerebellum in snakes resulted in death; but when the cerebrum alone was removed movements of a peculiar kind persisted. The head was no longer held erect, and the head and neck were pushed along by the movements of the trunk. A frog deprived of its cerebrum and cerebellum walked slowly and with difficulty as if the limbs were heavy, especially the fore-legs, and died the same night; while one whose cerebrum alone was removed, lived two days, and walked with considerable vigour, but did not hop. It swam with general and regular movements. The same results were obtained with the water tortoise; if the cerebellar connections were left intact on one side, the movements of the opposite limbs were more free than of those of the same side.

Dickinson concluded that the cerebellum exercised a continuous automatic action, especially on the posterior extremities, producing even and balanced movements. Each lateral half has a bilateral effect, but chiefly a unilateral crossed one; and common sensation, the special senses, the action of involuntary muscles and reflex movements, are unaffected by ablation of the organ.

Vulpian† produced unilateral lesions of the cerebellum in pigeons and rats, which

* Dickinson, 'Brit. and For. Med. Chir. Rev.,' 1865, vol. 36, p. 455; 'Boston M. and S. Jour.,' 1865, 71, p. 237.

† Vulpian, 'Leçons sur la Phys. Gén. et Comp. du Syst. Nerv.,' 1886, p. 603.

caused ataxy of movements. He met with hemiplegia, after such lesions, only exceptionally, and then it was sometimes on the same side as the cerebellar lesion and at other times on the opposite side. Instinct and intelligence remained intact.

Weir Mitchell* irritated the cerebellum, mechanically, by chemical agents and by cold, in pigeons, rabbits, and guinea-pigs. Motor functions alone suffered, and were commonly re-established within a few hours to ten days. Wounds of the deep lateral portions, involving the middle peduncles, caused rotation on the long axis, and, like most deep cerebellar lesions, produced squints, though this was not the case in birds. Mechanical irritation, deep enough to give rise to obvious effects, caused a tendency to move or fall to one side, or a general want of balance, with abruptness and jerkiness of movement, as if weakness and excitation of muscles were combined. Torsion of the neck on the spine was noted, and in grave lesions of the posterior region in birds the head was drawn back. Freezing the superior and posterior regions caused backward movements. Opacity of the cornea was observed in guinea-pigs and rabbits, usually on the side of the most marked squint. There was never loss of sight. This same experimenter succeeded in keeping pigeons alive after destruction of large portions of the cerebellum, sometimes almost the whole of the organ. The only permanent change detected was an incapacity for prolonged exertion; they became tired more readily than normal pigeons. Sensation, emotion, and the generative functions were unaffected. Weir Mitchell considered the cerebellum a great reinforcing organ, capable of being more or less used in voluntary muscular movements.

Ferrier's† researches, which were published seven years later, are too well known in this country to require a detailed description; and, in so far as the majority of them dealt with the results of excitation of different parts of the cerebellum, while my own investigations have been directed towards attempting to elucidate the problems involved when ablation of the organ is performed, allusion will only be made to those cases in which Ferrier destroyed parts of the cerebellum. A red-hot wire was used to destroy the posterior part of the middle lobe in a monkey, which gave rise to a tendency for the animal to fall backwards. In another monkey the surface of the posterior lobule of the left side was similarly destroyed to the depth of a quarter of an inch. The animal tended to fall backward and to the right; "but this movement was sometimes so strong, and combined with spinal rotation, as to cause the animal to roll over on its left side." This author looked on the cerebellum as "a complex arrangement of individually differentiated centres, which in associated action regulate the various muscular adjustments necessary to maintain equilibrium and steadiness of the body; each tendency to the displacement of the equilibrium round a horizontal, vertical, or intermediate axis acting as a stimulus to the special centre, which calls into play the antagonistic or compensatory action."

* Weir Mitchell, 'Amer. Journ. of Med. Sc.,' 1869, p. 320.

† Ferrier, 'The Functions of the Brain,' 2nd Ed., 1886, p. 174; 1st Ed., 1876.

The same year NOTHNAGEL* recorded the result of mechanical excitation of the cerebellum, a needle being used as the excitor, and both the vermis and lateral lobes responding to this mode of stimulation when the pricks were superficial. In the case of one lateral lobe, or half of the vermis, motor phenomena resulted first on the same side of the body and afterwards extended to the opposite side, while excitation of the middle line of the vermis gave rise to motor phenomena on both sides of the body. The greater part of a lobe, and the whole anterior and upper part of the vermis, could be disturbed without the animals betraying any symptom the whole day, while disturbance of a limited part of the vermis gave rise to motor disorders in conformity with the picture drawn by FLOURENS.

LUCIANI† was the first who succeeded in keeping mammals alive for any length of time after ablation of the cerebellum. Symptoms of irritation were noticed during the first few weeks in the dogs operated on, and consisted in contractions and spasms, which afterwards disappeared. Unsteadiness and titubation persisted until death, and although walking was either impossible, or performed very unsteadily, the animals could swim almost like normal dogs. "Heat" was manifested, and when coitus was effected pregnancy followed, and parturition took place in due course. The mental faculties were intact, the emotions were naturally displayed, as were the maternal instincts. One animal was the subject of otitis, conjunctivitis, joint affections, and general marasmus during the latter part of its existence, and eventually died; but another remained in excellent health, gaining weight, and was ultimately killed.

This same observer has more recently added very largely to our knowledge of the functions of the cerebellum by the publication of the results of his extensive investigations in the dog and monkey.‡ He discusses the subject under five headings—(1) phenomena of irritation; (2) phenomena of deficiency; (3) those of compensation; (4) those of degeneration; and (5) trophic phenomena.

Monkeys differ from dogs chiefly in that the symptoms were less severe and more fleeting, and in that tonic flexion of the limbs was present, where, under similar circumstances in the dog, tonic extension was present.

Division of the cerebellum into two lateral halves by a mesial incision, was attended by next to no irritative symptoms, there being, however, some inco-ordination. Tonic extension of the fore limbs existed, but at the autopsy, meningitis was found. Deficiency symptoms consisted in a want of energy and a diminution of muscular tone. Compensation was very complete. The author concluded that the cerebellum is physiologically one organ, whose functions are seriously interfered with if it is divided into two halves.

The middle lobe was destroyed in four dogs and two monkeys, and resulted

* NOTHNAGEL, 'Centralbl. f. d. Med. Wissenschaft.,' 1876, vol. 14, p. 387.

† LUCIANI, 'Lin. gen. del. Fisiol. del Cervel., Prim. Mem.,' Firenze, 1884. See also WORKMAN, 'Alienist, and Neurologist,' July, 1885.

‡ LUCIANA, 'Il Cervelleto; Nuov. Stud. d. Fisiol. Norm. e Patol.,' Firenze, 1891.

in general unsteadiness, strabismus, spasm of the muscles of the neck, tonic extension of the fore limbs in dogs, and tonic flexion in monkeys; all of which persisted about a week. Asthenia, atonia, and astasia, especially of the muscles of the posterior extremities, lasted about a fortnight, and compensation resulted in all cases.

Extirpation of one lateral lobe gave rise to curving of the trunk towards the side of the lesion, tonic extension of the anterior extremity on the same side, rotation on the animal's long axis towards the opposite side; and the globes deviated towards the opposite side. There was asthenia, atonia, and astasia of the muscles of the same side as the lesion. Compensation took place gradually. There was temporary glycosuria in several cases.

Ablation of half the organ was followed by curving of the trunk towards the side of the lesion, rotation on the animal's long axis towards the opposite side, tonic extension in the dog, and flexion in the monkey, of the fore limb of the same side as the lesion, sometimes the hind limb being similarly affected, strabismus and nystagmus. Asthenia, atonia, and astasia of the muscles on the side of the lesion were observed, and compensation was not complete, a certain residuum of these symptoms of deficiency remaining, and pointing to the fact that the other half of the cerebellum is unable to take on the whole of the functions of the half removed. Temporary polyuria and glycosuria existed in two monkeys.

Destruction of one lateral lobe, in animals that had been previously deprived of their middle lobe, evoked symptoms which did not differ materially from those that have just been detailed.

The symptoms which resulted on ablation of the whole organ differed only in degree from those produced by destruction of the middle lobe, being of greater intensity, longer duration, and wider diffusion.

Unilateral, or bilateral, destruction of the sigmoid gyrus, after ablation of the cerebellum, caused the deficiency phenomena to be more pronounced and to persist, the animal being unable to walk without support nearly a year after the operation, so that the author concluded that compensation is brought about by the sensori-motor region of the cerebrum after ablation of the cerebellum.

The chief general conclusions come to by Luciani are that the cerebellum, though an organ of bilateral function, differs from the cerebrum in having a direct and not a crossed action. Its influence is exerted on all voluntary muscles, and not only on those concerned with posture and locomotion; and this influence is of the nature of a sthenic, tonic, and static neuro-muscular process. All parts of the organ have the same function, *i.e.*, it is not composed of centres functionally different from each other and presiding over different groups of muscles. The middle lobe is considered as of no greater functional value than the lateral ones. The organ transmits a direct and indirect trophic action by its efferent paths. The sensorial perturbation consists specially of different forms of vertigo, the motor of various aberrations of movements, which cause inco-ordination; while polyuria, glycosuria, acetonuria, and rapid decrease in weight are expressions of the trophic disturbance.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The cerebellum is looked on as a coadjutor and reinforcer of the great cerebro-spinal system, its action being considered quite different from the action of all other parts of the nervous system. Deficiency of the organ is attended by asthenia, atonia, and astasia, while absolute or partial paralysis of motion and sensation attends similar deficiency of other parts of the nervous system. LUCIANI contends that the difference is due to the fact that the cerebellum forms a small system, relatively independent, defects of which do not interfere with the passage of centripetal and centrifugal impulses passing between the cerebrum and the periphery; and to the other fact, that it does not dominate over any territory exclusively reserved to itself, and not contemporaneously under the influence of the cerebro-spinal system. Lastly, the analogy between the action of the cerebellum and the intervertebral ganglia is insisted on, both the direct and indirect trophic actions being instanced as strikingly the same; and to complete the parallelism, the reinforcing action of the intervertebral ganglia on the anterior roots, and on the muscles they innervate, is insisted on as resembling closely the sthenic, tonic, and static action of the cerebellum.

III. OPERATIVE PROCEDURE.

In all cases in which the animal was to be allowed to live after the operation, the back of the head and neck were first shaved, thoroughly cleansed with soap and water, and finally washed with perchloride of mercury lotion (1-1000). The skin incision adopted in all the later experiments consisted in a single longitudinal cut in the middle line of the back of the head and neck, as this was found perfectly sufficient to allow of complete exposure of the deeper parts, even where the whole cerebellum was to be removed. In my earlier experiments I was in the habit of making an additional incision transversely outward from the upper end of the longitudinal incision, either on one or both sides, according to whether a unilateral or bilateral lesion of the cerebellum was to be subsequently produced, and the skin-flap turned downward and outward on one or both sides, as the case might be. This plan, which was attended with considerably more hæmorrhage, was afterwards discarded for the simpler and quite as effective method of exposing the deeper parts by the single incision.

Whichever of the skin incisions was employed in no way affected the subsequent course of the operation, which differed only according to whether the whole or part of the cerebellum was to be removed. An incision was made along the middle line to the depth of the cervical spines; the muscles were then cut and scraped away from their attachments to the curved lines and adjacent depressions, on one or both sides, as the case might be, then working from the middle line outwards they were torn and scraped away from their attachments to the spines and arches of the upper cervical vertebra. It is very important to work from the middle line outward, as by this means much troublesome hæmorrhage is avoided, as also obtains when very little

cutting is done, tearing and scraping being relied on to free the bony parts of their soft coverings. The unavoidable loss of blood which attends the subsequent stages of the operation makes it necessary that as much hæmorrhage should be avoided as possible in the earlier stages. When I first commenced these operations I was in the habit of trephining the occipital bone with a quarter-inch trephine, over one or other lateral lobe of the cerebellum, and then enlarging the opening, to any extent required, by means of bone forceps; but latterly the trephine was entirely discarded, the bone forceps alone being used to effect an opening into the cranial cavity. Up to this stage in the operation perchloride of mercury lotion (1-1000) was used to wash the wound, and was supplemented from time to time, as occasion required, by hot water (about 100° F.) that had been boiled, with a view to checking any oozing; but from this point nothing but boiled normal saline solution was used to wash out the wound and to arrest bleeding. During the removal of the bone, an aseptic wax was employed to check the bleeding from the sinuses in it. The next step consisted in opening the membranes, and turning aside a flap of the dura mater which covered the part whose extirpation was intended. By means of a sharp, thin-bladed knife, the part to be excised was delimited from the rest of the organ, and was then carefully scooped out by means of a small, sharp spoon. In scooping out the portion of cerebellum, full advantage was taken of the bony tentorium, and every care was taken not to press on or injure the medulla, or the pyramidal tracts a little below this point. All the scraping was done either from below, directly upwards against the bony tentorium, or downwards and outwards, against the base of the posterior fossa, and never either directly downwards or inwards. Syringing out the cavity with hot, normal, salt solution (about 100° F.) was resorted to, both as a means of checking the bleeding and of clearing out all *débris*.

The external wound was then carefully sponged with perchloride of mercury lotion (1-1000), and closed by means of aseptic horsehair sutures, a small portion of the most dependent part of the wound being left open to allow of drainage. The wounds were dressed antiseptically, and seldom failed to unite by primary union.

In the experiments in which the comparative excitability of the two cerebral hemispheres was tested, an opening was effected into the cranial cavity by means of bone forceps, the air-cells being first opened and the bone over the motor areas being subsequently removed with great care, so as to avoid, as far as possible, undue pressure on the cortex.

In those instances in which curves were obtained from the extensor muscles of the fore limbs, the tendons of these muscles were exposed and all included together in one ligature, the tendons being subsequently divided on the distal side of the ligature; the muscles were then freed from their attachments to a considerable distance up the limb, so as to allow them free play.

When absinthe was administered, one or other external jugular vein was exposed in the neck, and varying doses of the essential oil injected into it in the direction of the blood stream, by means of a hypodermic syringe.

The plan adopted in extirpating the labyrinth consisted in making a curved incision, commencing above, passing behind, and ending below the ear. The flap of skin with the pinna was then turned forward, all structures divided and scraped from the bone for a short distance around. The upper and posterior part of the meatus was then enlarged by means of a gouge, and by degrees the middle ear and then the labyrinth were cut into and cleared out.

When the 8th nerve was being exposed, the bulla was more freely denuded of its soft coverings; it was then opened by means of a gouge, after which its inner wall was similarly cut through, until the nerve was exposed. No appreciable length of the nerve could be exposed without lifting up the lateral lobe of the cerebellum, but the nerve could be divided without interfering with this structure. This plan of operation was sometimes followed in extirpating the labyrinth.

In both these methods of operating hæmorrhage was profuse and troublesome, but was checked by the use of aseptic wax.

When the excitability of the cortex cerebri was tested, fine platinum electrodes, attached to the secondary coil of a du Bois-Reymond's inductorium, supplied by a bichromate cell, were employed. In some of the earlier experiments gold wire electrodes, sheathed to their tips with paraffin paper, were substituted for the platinum electrodes.

Ether was the anæsthetic employed in all cases, and the animal was kept profoundly under its influence throughout the whole course of the operation. In some instances, in which the operation was so unusually severe as to suggest the possibility that the animal might be conscious of pain when the effect of the ether had passed off, this anæsthetic was supplemented by a hypodermic injection of morphia while the animal was still under the influence of ether.

IV. OBJECTS AND PLAN OF RESEARCH.

(*a.*) Objects of Research.

The objects of the research were to determine as far as possible the following points:—

1. Whether each lateral half of the cerebellum is capable of acting independently, or whether it is necessary for the connections between the two halves to be intact, in order that the functions of the organ should be properly performed.

2. If impulses pass from one side of the organ to the other before they are transmitted to the cerebrum or spinal cord.

3. What is the nature of the impairment of movement which results when portions of the organ are removed.

4. What relationship exists between one-half of the cerebellum and the cerebral hemisphere of the opposite side, and what is its probable nature.

5. Whether one lateral half of the cerebellum is related mainly to the same side of

the spinal cord, to the opposite side, or to both; and what the nature of the relationship is.

6. Which symptoms resulting from experimental lesions of the cerebellum are most to be relied on for localisation.

7. Whether any, and, if so, which of the symptoms are dependent on interference with the labyrinth or eighth nerve, when experimental lesions of the cerebellum are produced.

(*b.*) Plan of Research.

The following experimental procedures were adopted in attempting to elucidate these various problems:—

1. Median vertical section separating the two lateral halves of the cerebellum from each other.
2. Extirpation of one lateral lobe.
3. Removal of one-half of the organ, *i.e.*, of one lateral lobe together with one lateral half of the middle lobe.
4. One or other of the last two methods of procedure as a preliminary, and subsequent comparative investigation of the excitability of the two cerebral hemispheres.
5. Similar preliminary methods as in the last instance, followed by the administration of the essential oil of absinthe, and comparison of the effect of the resulting convulsions on the muscles of the two sides of the body.
6. Removal of both lateral lobes of the cerebellum.
7. Extirpation of the whole, or half, of the posterior part of the vermis.
8. Ablation of the whole organ.
9. Control experiments on the labyrinth and eighth nerve, which consisted in:—
   - (*a*) Extirpation of the labyrinth.
   - (*b*) Intracranial section of the auditory nerve.
   - (*c*) Chemical irritation of the auditory nerve.

As the large majority of experiments were performed on dogs, and only a few supplementary ones on monkeys, the former animals will alone engage our attention at first, and the results obtained in the monkeys will be reserved for a separate paragraph towards the latter part of the paper.

Part I.—Median Vertical Section separating the two Lateral Halves of the Cerebellum from each other.

So slight were the symptoms which resulted from this lesion to the cerebellum that it was difficult, in fact impossible, to detect anything abnormal about the animal forty-eight hours after the operation, with the exception of the wound which had been produced.

While the animal was under the influence of the anæsthetic, nothing abnormal

could be detected in the way of squint or in alteration of the tendon reflexes; nor could anything abnormal be discovered in these directions when the animal recovered from the effect of the anæsthetic. The only symptom which resulted at all was the very slightest possible inco-ordination, no traces of which could be detected forty-eight hours after the operation. So that although the connections between the two halves of the organ were severed, each half appeared to be able to perform its own functions without the co-operation of the other half, and as far as could be ascertained, no function was in abeyance in consequence of the two halves of the organ being no longer directly united.

In one dog on whom this operation was performed, as soon as it recovered from the ether narcosis it was walking about like a normal dog, there being no more unsteadiness than in any dog so soon after recovery from the effects of a narcotic. No ocular deviation could be detected. Three or four hours after the operation a marked change was observed. The left eye deviated to the left, that side of the head and face was turned up while the right side was of course turned down, and the trunk was arched with its concavity to the right. The left shoulder was raised very high, and the elbow was rotated outwards, the tips of the digits alone touching the ground, and the movements of the limb in progression peculiarly stiff and stilted. Two days later these symptoms were still observed though only in very slight degree, while two days later still, next to no sign of them could be detected. Here it was evident that the symptoms were not due to the primary lesion, but were the result of some secondary trouble, probably a little hæmorrhage into the left half of the middle lobe.

In one dog there was a slight tendency to deviation of the eye downwards, but it was very slight and transitory; beyond this, that particular animal presented nothing abnormal, with the exception, perhaps, of the slightest possible unsteadiness directly after the operation. It fought other dogs for food a few hours after it had recovered from the anæsthetic.

Part II.—Extirpation of one Lateral Lobe. (See fig. 1).

1. Immediate and transitory.
2. Late and permanent.

1. *Immediate Effects.*

These may again be divided into two classes according as they occur (*a*) while the animal is still under the effects of the anæsthetic and (*b*) after the effect of the anæsthetic has passed off.

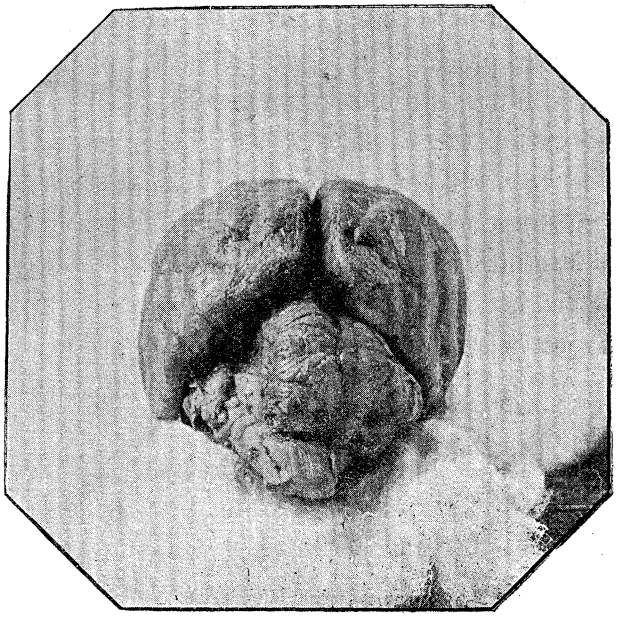
(*a*) *Effects observed while the Animal is under the Influence of the Anæsthetic.*

Ocular deviation was always observed; in some cases both lobes participated, in

which case a "skew deviation" resulted, the globe on the same side as the cerebellar lesion being deviated upwards and outwards, while that on the opposite side was directed downwards and outwards. When only one globe deviated, it was always that on the opposite side to the cerebellar lesion, and the direction assumed was that of a rotation outward, with a varying degree of downward rotation.

I have pointed out elsewhere* that the knee-jerks were altered in a remarkable manner; and this alteration took place in each instance. The knee-jerk on the side corresponding to the cerebellar lesion became very greatly exaggerated, so that a single tap on the patella tendon sufficed to evoke clonus, and even tonus. The effect on the opposite knee-jerk was of an extremely different nature, for instead of

Fig. 1.



Ablation of the Left Lateral Lobe of the Cerebellum in a Dog.

exaggeration there was diminution. That there was actual diminution of the knee-jerk on this side was made more evident by the following experiment:—One cerebral hemisphere was first removed, and as a result of this the knee-jerk on the opposite side became increased. Then the lateral lobe of the cerebellum was removed on the same side as that on which the cerebral hemisphere had been removed; the diminution in the opposite and previously increased knee-jerk was quite distinct. I have also had occasion to call attention to a curious ether effect which was observed in this connection, for whereas the above results were those obtained during ordinary moderate ether narcosis, the very reverse took place when the anæsthetic was pushed to the stage which closely precedes that in which the knee-jerks are abolished by ether.

* 'Roy. Soc. Proc.,' 1893, vol. 53, p. 430.

As this stage was approached, a gradual change took place in the state of the knee-jerks, that on the same side as the cerebellar lesion, which was formerly exalted, became depressed, while that on the opposite side, which was formerly diminished, became exaggerated.

(*b*) *Effects observed after the Animal had recovered from the Influence of the Anæsthetic.*

These varied considerably as to the degree of severity in different cases, and as to the time they persisted.

Ocular Deviation, if observed as of the nature of a "skew deviation" while the animal was unconscious, rarely persisted as such for any length of time after consciousness was restored. The globe on the side corresponding to that of the cerebellar lesion quickly assumed its normal position, so that in a few hours, or at most twenty-four hours, no deviation could be detected. This was, however, not the case with regard to the opposite eye-ball, which continued in its abnormal position for days, but eventually recovered completely.

Nystagmus is more or less constantly met with for a varying time after the operation, sometimes only persisting for a day or two, at other times continuing for a longer period. It was always lateral in direction, and consists in slow jerks towards the side of the cerebellar lesion, which are more marked in the opposite or chiefly deviated eye; *e.g.*, if the left lateral lobe of the cerebellum is removed, the right eye is deviated to the right, and the nystagmoid jerks of both globes are from the right to the left.

Motor Phenomena.—These depend on the extent of the lesion, but in complete removal of one lateral lobe of the cerebellum, the animal is quite unable to stand for the first few days, some animals recovering more rapidly than others. This inability to stand is due to a great extent to a paresis of the posterior extremities, and, to a slighter degree, of the anterior extremity of the same side as the lesion. In attempting to get up, the opposite limbs push the body over to the side of the limbs which are chiefly paresed, and which are unable to support the weight of the animal, and it consequently falls to the same side as the lesion. This has to be carefully distinguished from the cerebellar reel, due to inco-ordination, and which, as will afterwards be shown, is to the opposite side. As the animal recovers, and is able to stand and walk, this paresis of the posterior extremities and of the anterior extremity of the same side as the cerebellar lesion, is obvious. The animal walks on a wide base as if the joints were stiff on that side, the extremities being moved like rigid pins, and as if it were afraid to trust much of its weight to the extremities on the side of the cerebellar lesion. The legs are moved as if they were inflexible, only the pointed digits appear to touch the ground. This mode of progression causes the animal to deviate from a straight course in walking, the deviation being to the opposite side, on the extremities of which its chief weight appears to be thrown. In the earlier

stages when it first begins to walk, and after the animal no longer reels, whenever it falls it is to the same side as the lesion. This is very noticeable in attempts to walk upstairs, when the paresis is rendered very evident. As further proof of this paresis on the side of the lesion, may be instanced the fact that in many cases when the animal first commences to attempt to walk it always tries to get the side of the cerebellar lesion against the wall of the room, or some other form of support, whereas, as will presently be seen, they lie with the opposite side supported at first in order to prevent the movements of rotation which would otherwise occur.

Before leaving this part of the subject it may be well to refer to the condition known as "Circus movements," in which the animal walks round and round with its trunk curved, the concavity being towards the central axis round which it is walking, and its head and tail being thus approximated. This was exceedingly rarely observed as an effect of lesions of the cerebellum, whereas it was a constant feature of lesions of the labyrinth. When it occurred in dogs with cerebellar lesions, it was always in those instances in which only a slight lesion had been effected, such as removal of a small part of one lateral lobe, after which the animals were able to walk about the same day, though with considerable inco-ordination. When it occurred, the animal always walked with the side of the lesion towards the central point around which it was walking, or in other words with the concavity of its arched trunk corresponding to the side from which the portion of cerebellum had been removed.

Inco-ordination.—This is a marked feature of all cerebellar lesions, and its severity depends on the extent of the lesion. After removal of one lateral lobe of the cerebellum, as has already been said, the animal is at first unable to get into the standing posture; but as soon as it can do so, any attempts to walk are attended by reeling to the opposite side, provided the animal be able to walk soon enough after the operation; this reeling is very characteristic, and has to be carefully distinguished from the falling to the same side, as a result of what I take to be paresis, most marked in the extremities of that side. But before the animal is able to stand, inco-ordination shows itself in the movements of the head on the trunk. There is great unsteadiness of the head, and any attempt at voluntary movement increases the unsteadiness. This phenomenon is always aggravated by voluntary acts, such as attempts to lap, or to pick up food, and even when it is not present under ordinary circumstances some unusual excitement will elicit it. Another marked symptom, which is however not always present, is that known as a "rotation fit," in which the animal rotates rapidly on its longitudinal axis towards the opposite side to that from which the cerebellar lobe has been removed. All the animals were not observed to present this symptom spontaneously; but when it occurred it was very striking. On one occasion it was artificially evoked; a dog, who had not as far as I was aware presented any of these movements spontaneously, while being fed with meat, greedily tried to swallow too large a piece; this stuck in his pharynx, and

induced asphyxia, whereupon well-marked rotation movements immediately resulted. With rare exceptions, these rotation movements are only observed during the first day or two after a lesion of the cerebellum; but in one animal in whom they were at first very violent, and oft repeated, they persisted for nearly two weeks. The rule, however, was that they were not observed after the first few days.

Sensory Phenomena.—It is, of course, exceedingly difficult to be certain as to the exact state of sensibility in animals, and in my earlier experiments I could come to no very satisfactory conclusion as to whether the animal had or had not any loss of sensibility, but by degrees it became more and more evident to me that there was anæsthesia and analgesia after ablation of one lateral lobe of the cerebellum, and that while the opposite anterior extremity appeared to escape, the other extremities were all involved, though apparently in different degrees, the posterior extremity on the side of the lesion being that most affected. The tests employed were a wooden clip which exerted very slight pressure, a metal clip which was painful, and cold water. It was always difficult to be certain of the results with the touch clip, but the results with the cold water test were very much more definite, and those with the painful clip most to be relied on. Most of the animals were too lethargic to make it possible for one to come to any conclusion with regard to sensation the first day after the operation; but some that were less lethargic objected to the painful clip on the anterior extremity of the opposite side, while they took no notice of it on any of the other extremities. By the second or third day after the operation this result was evident in most of the dogs, while in some no definite conclusion could be come to even a week after the operation, by which time loss of feeling, if present, was probably being recovered from, so that anæsthesia could not be detected on so many extremities. But, as a rule, no matter how confused may have been the results in the early stage, one thing comes out very clearly later, and that is, that the posterior extremity on the same side as the lesion is the one which is last to recover. The animal may take notice of cold water dropped on to all the other extremities, or the painful clip applied to any of these, and yet take no notice of either of these stimuli when they were directed to the posterior extremity on the same side as the lesion. As regards the order in which the other extremities recovered feeling, as a rule the posterior extremity on the opposite side was the first to recover, but sometimes the anterior extremity of the same side as the lesion appeared to be the first to do so. The time of complete recovery varied in different animals, but in most, sensibility was restored in eight or ten days, though in some it was delayed beyond that time.

Special Senses.—There appeared to be no affection of hearing, sight, or smell.

Considering the close proximity of the eighth nerve and labyrinth, affection of hearing, especially on the side of the cerebellar lesion, might easily result from interference with these adjacent parts, and independently of any defect of the cerebellum, but no affection of hearing could be detected. There was no optic neuritis.

Reflexes.—The animal usually lies with the anterior extremity of the side of the

lesion rigidly extended, while the spasm involves the posterior extremity of the same side to a much less degree, and the posterior extremity of the opposite side only slightly. All attempts at voluntary movements increase the spasm, as does any examination, such as testing the state of the tendon reflexes. Sometimes the irritability is only such as results in clonic spasm in the limb when the "quadriceps" tendon is struck, while at other times tonic spasm follows such a blow. This exaggerated state of the reflexes is undoubtedly most marked on the same side as that from which the lobe of the cerebellum has been removed. As has already been said, when the effects while the animal is under the influence of the anæsthetic were being detailed, the knee jerk shows in a marked manner this exaggeration on the same side as the lesion, and the exaggeration persists as long as the animal is kept under observation, though not to such a marked degree as directly after the operation. The opposite knee jerk behaves somewhat curiously, for whereas, as has already been seen, it is at first greatly diminished, or even absent, by the next day it is exaggerated, and by the second day after the operation it is usually very difficult to say which knee jerk is the more exaggerated, this equality being due to exaggeration of that of the opposite side, and a slight diminution in the excessive irritability of that on the same side as the lesion. When the knee jerks are as nearly as possible equally exaggerated, the triceps and biceps jerks of the anterior extremities still show a marked difference on the two sides, those on the side from which the lateral lobe of the cerebellum has been removed being distinctly exaggerated while those on the opposite side are normal.

The chief effects of removal of one lateral lobe of the cerebellum were, briefly, deviation of the opposite eyeball downwards and outwards, proptosis of both globes, lateral nystagmus, rotation of the neck, so that the side of the head and face corresponding to the lesion turned upwards, curving of the trunk with the concavity to the side of the lesion, motor paresis chiefly of the extremities on the same side as that from which the cerebellar lobe had been removed, blunting of sensibility, rigidity and increased reflexes chiefly in these same extremities, rotation fits to the opposite side, and reeling also in that direction.

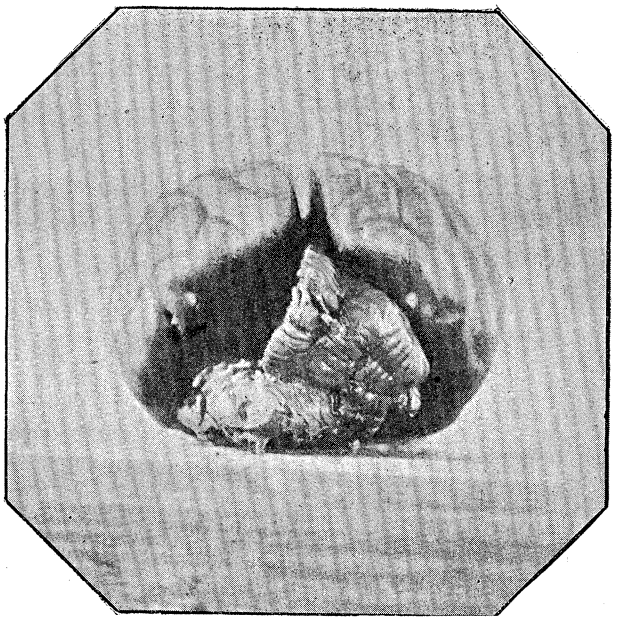
2. *Late and Permanent Effects.*

As a rule compensation was so complete that it was difficult to detect anything abnormal in the animals two or three months after the operation. They were well nourished, and but for the inequality in the condition of the tendon reflexes, those on the side of the lesion being increased, and greater than those on the opposite side, they might well pass as normal dogs. One female animal who had evidently become pregnant just before the operation, gave birth to four healthy pups at the full time, when she seemed none the worse for the process of parturition, was in excellent condition, and showed the natural maternal instincts.

Part III.—Removal of one half of the Organ.

In this series of experiments, instead of removing one lateral lobe alone, an incision was made vertically through the middle lobe of the organ, as nearly as possible in the middle line, and one half of the middle lobe was removed, as well as the lateral lobe on the same side (fig. 2).

Fig. 2.



Ablation of the left half of the Cerebellum in a Dog.

The symptoms which resulted from this lesion were, with one or two exceptions, identical with those which resulted after extirpation of one lateral lobe, except in degree of intensity. With the removal of an increased quantity of the organ there was an intensification of all the symptoms which had been observed after the less severe lesion, and a persistence of them for a greater length of time. So closely did the symptoms agree with those that have already been enumerated, that recapitulation of them here would be needless repetition. One point is worthy of note, however, and that is, that the intensification of the symptoms was out of proportion to the increased amount of the organ which was removed, that is, the increased portion of nervous matter removed was small compared to the great intensification of the symptoms. In other words, the larger mass of the lateral lobe of the cerebellum appears to be of less functional importance than the smaller central lobe.

An animal on whom such an operation had been performed presented in a marked degree the unsteadiness so characteristic of lesions of the cerebellum. Motor power is diminished, sensibility is blunted, and there is rigidity with increased tendon reflexes in exactly the same extremities as are involved in an animal whose lateral

lobe alone has been removed. Instead of such an animal being able to walk within a week after the operation, the first attempts which result in anything resembling a walk do not take place until between two and three weeks after the half of the organ has been removed. Then the animal can only walk with one side of the trunk against the wall of the room, or some other support, and it is always the side corresponding to the lesion which is thus supported. Without such support, its base becomes wider and wider, until the limbs on the side of the lesion (especially the posterior one) give way, and the animal falls to that side.

In such an animal sensibility is blunted to the tests which have always been employed, and which have already been noted, all the limbs being affected with the exception of the anterior extremity on the opposite side from the lesion. As in cases of ablation of one lateral lobe, the posterior extremity on the side of the lesion is the last to recover, and does not do so until three weeks after the operation, as a rule.

Strabismus and nystagmus occur, as in the less severe lesion; but while nystagmus may not persist longer than after the less severe operation, the ocular deviation does.

Such dogs recover so completely, that by the end of two months after the operation, beyond slight stiffness of the extremities on the side of the lesion, and slight unsteadiness evoked on excitement of any kind, little abnormal can be detected on looking at the animal. On examination, the increased deep reflexes, described in connection with the late effects of ablation of one lateral lobe alone, are met with.

So that the symptoms indicative of unilateral ablation of the cerebellum are:—

1. Rotation on the long axis towards the opposite side.
2. Reeling towards the opposite side.
3. The attitude, which consists in a rotation of the cervical spine, so that the side of the face corresponding to the side of the cerebellar lesion is directed upwards, and an arching of the spinal column with its concavity to the side of the lesion.
4. Inco-ordination chiefly in the limbs of the same side.
5. Rigidity, most marked in the extremities of the side of the lesion, and preponderating in the anterior extremity of this side.
6. Exaggeration of the tendon reflexes, most marked on the same side.
7. Motor paresis affecting both extremities on the side of the lesion, and the posterior extremity of the opposite side.
8. Anæthesia and analgesia having the same distribution as the motor paresis.
9. Deviation of the opposite eye-ball downwards and outwards, while that of the same side is only slightly, if at all deviated, except under the influence of the anæsthetic when it looks upwards and to the side of the lesion.
10. Lateral nystagmus, the jerks being from the opposite side towards the side of the lesion.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Part IV.—A Comparison of the Electrical Excitability of the Cerebral Hemispheres after Unilateral Ablation of the Cerebellum.

(a) Immediate effect.
(b) Late effect.

(a) *Immediate Effect.*—An opening was made on each side of the skull, so as to expose both "motor" areas, the air cells being first opened, and every precaution taken not to allow the bone forceps to press on the brain more than could be avoided. An opening was next made over one side of the cerebellum and one lateral half of the organ, or one lateral lobe, was removed in the same manner as has already been described. A flap of dura mater, covering the motor region, was then carefully raised on both sides, and the excitability of the cortex, on the two sides, to the Faradic current, was tested. The chief focus of representation of a certain movement was chosen on each side, and the comparative excitability of the two carefully tested. On thus testing, immediately after the removal of the portion of the cerebellum, the hemispheres appeared to be equally excitable as a rule; but in about ten or fifteen minutes a distinct difference on the two sides could be detected, the opposite cerebral hemisphere being more excitable than that on the same side as the cerebellar ablation. This difference amounted to 200, 300, or even 400 on KRONECKER'S scale. The difference of excitability was detected both in the fore limb representation and also in the representation of the hind limbs.

The following experiment will serve as an example: on October 16, 1893, the bone over the "motor" areas on both sides was removed, but the dura mater left intact. The bone covering the left half of the cerebellum was next removed, and the membranes left untouched. A flap of dura mater was then carefully raised on both sides, so as to expose the "motor" areas on the two sides, and as the opening in the bone had been made on the left side first, the right flap of dura mater was that first raised, so as to place the hemispheres, as far as possible, under similar circumstances. Both hemispheres were then tested, and found to respond equally to the Faradic current. The left lateral lobe of the cerebellum was then extirpated, and the excitability of the two hemispheres tested immediately afterwards, when they were found to be still equal; but about ten minutes later, the right cerebral hemisphere was more excitable than the left. Flexion of the elbow was elicited with a current of 300 on KRONECKER'S scale, while it required a current of 500 to elicit the same movement from the left hemisphere; and a current of 200 elicited no movement on either side.

About twenty minutes after the removal of the left lateral lobe of the cerebellum, flexion at the hip was elicited on excitation of the right cortex cerebri with a current of 400 on KRONECKER'S scale, while it required a current of 800 to evoke the same movement on excitation of the left hemisphere. Neither hemisphere responded to a current of 300.

Ten minutes later, or half-an-hour from the commencement of the experiment, flexion at the elbow was evoked by excitation of the right hemisphere with a current of 200, whereas a current of 500 failed to elicit the same movement from the left hemisphere.

In a dog, the left lateral lobe of whose cerebellum was removed three months before the excitability of the two cerebral hemispheres was tested, I found that the right cortex responded to a weaker current than the left, the difference in the strength of current required to evoke contraction of the extensor muscles of the wrist on the two sides amounting to as much as 400 on KRONECKER'S scale. The fore limbs of the animal were fixed to the table, the extensor tendons divided at the wrist, the muscles separated from the bones to a considerable distance up the fore arm, and their tendons attached, by means of cords, to two FICK'S spring myographs, whose springs had been equally calibrated. In this way, records were obtained, on a blackened surface, of the contraction of the extensors of the wrist and digits on each side, when the corresponding "motor" area was stimulated. The extent of the contraction diminished on both sides as the strength of the current was reduced, the result obtained from the right extensor muscles was always considerably less than that obtained from those on the right side, and a strength of current which still obtained a good response on excitation of the right hemisphere, failed to evoke any response from the left.

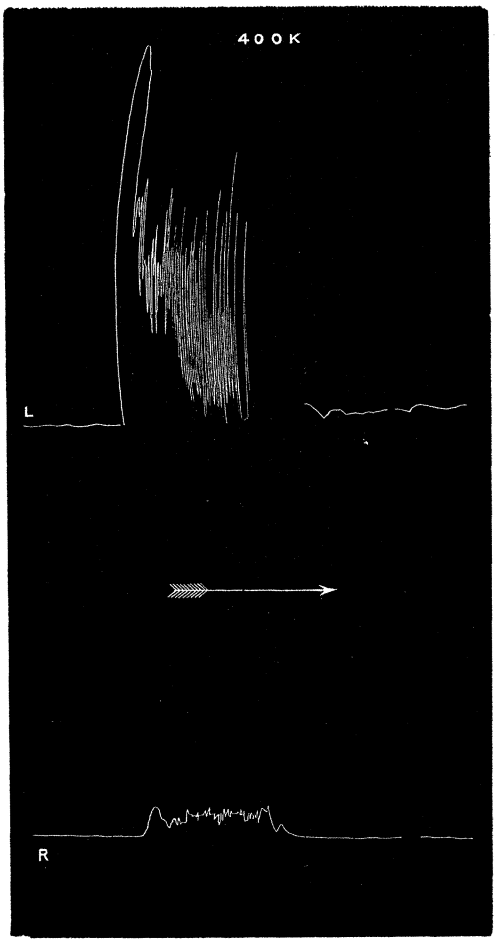
I next used such strengths of current as would evoke a series of unilateral cortical discharges. With a current of 800 on KRONECKER'S scale, excitation of the left hemisphere evoked a feeble discharge, while the same strength of current resulted in a well-marked discharge being obtained from the right hemisphere. The results obtained with a current of 1000 applied to each hemisphere, and one of 1500 to the left, also showed a marked inequality on the two sides. With a current of 400, I could induce no discharge from the left hemisphere, while the right responded in the manner shown in fig. 3. A current of 600 was the smallest with which I was able to induce a series of discharges from the left hemisphere, whereas, from the right, I obtained well-marked discharges with a current of 300.

Part V.—The Effect of Absinthe in cases of Unilateral Ablation of the Cerebellum.

The results of electrical excitation of the cerebral hemispheres were very definite, and left no doubt in my mind as to their being genuine, and consequent on the unilateral ablation of the cerebellum; nevertheless, it seemed advisable to probe the matter still further, and instead of stimulating given foci of each hemisphere, to evoke a general discharge of both hemispheres, and obtain graphic records of the convulsions on the two sides, for comparison. As has been already said, the plan of exciting given foci is open to certain objections, which have been detailed, and although the chance of error has been reduced to a minimum by the precautions which have been taken, yet no test could be more free from fallacy than that of evoking general

convulsions, and obtaining graphic records of these convulsions on the two sides of the body. Accordingly, I performed a series of experiments, in which general convulsions were evoked by means of intravenous injections of the essential oil of absinthe, after one lateral lobe, or one lateral half, of the cerebellum had been removed, and graphic records of the convulsions on the two sides were obtained from the extensor muscles of the fore limbs. The extensor tendons were first exposed, and included in

Fig. 3.



Curve from extensor muscles of anterior extremity of a Dog on excitation of the Right Cortex with the Faradic current three months after ablation of the left Lateral Lobe of the Cerebellum. No response on excitation of Left Cortex with same strength of current.

a common ligature, after which they were divided on the distal side of the ligature; the muscles were then freed from their attachments to the bones of the fore arm and their fascial coverings, for a considerable and equal distance on the two sides. The cerebellum was next exposed in the usual manner, and one lateral lobe, or half of the organ, extirpated. One or other external jugular vein was exposed in the neck; and then both fore limbs were immovably fixed to the board on which the animal was

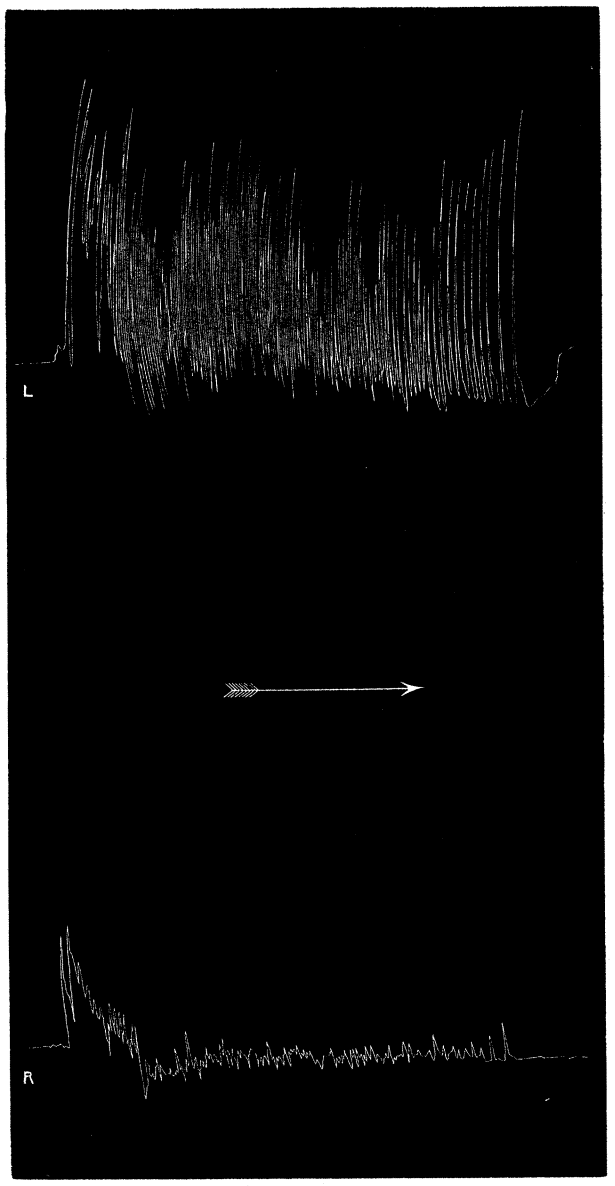
placed, and the board, in its turn, firmly fixed to the table. The ligatures, which included the extensor tendons, were attached to two of FICK's spring myographs, whose springs were equally calibrated, and the writing points of which recorded on the blackened surface of papers stretched over two cylinders a considerable distance apart, which were kept in motion by means of a clock. Every precaution was taken to have as nearly as possible the same amount of tension on the strings which connected the levers with the extensor muscles, and at the same time to have the arms of the recording levers of the same length. Having thus placed matters on the two sides as nearly as possible equal, and having ascertained that the ether narcosis was not too profound, three minims of the essential oil of absinthe were injected into the external jugular vein of one side. After the effect of the first dose of absinthe passed off, the same or increased doses were given, as occasion demanded.

The results of these experiments were very striking and demonstrated, in the clearest manner possible, that while convulsions occurred on both sides, those of the muscles of the fore limb, on the side from which the half of the cerebellum had been removed, greatly preponderated over those of the opposite side (see fig. 4). So great was the difference in the records of the convulsions on the two sides, that it seemed more than probable that it was due to some error in the recording apparatus; I therefore reversed the attachments to the myographs, connecting the string formerly attached to the one myograph to the other, and *vice versâ*. The result of this manœuvre showed clearly that there had been no error of record before, for the reversal of the myographs, or, what comes to the same thing, the reversal of the limbs, simply reversed the picture on the recording apparatus. It is thus beyond dispute that in general convulsions evoked by intravenous injections of the essential oil of absinthe, the convulsions on the same side as that from which the half of the cerebellum has been removed are greater than those of the opposite side. Such were the results when the convulsions were evoked about half-an-hour after the unilateral ablation of the cerebellum, and the question next arose as to whether this effect is an immediate one, or whether, like the results of comparative electrical excitation of the two cerebral hemispheres, it takes a little time to become evident. Therefore, in another series of experiments, I prepared everything first of all, and only extirpated the half of the cerebellum just before the absinthe was injected into the jugular vein. This procedure is by no means instantaneous in itself, in addition to which a variable amount of time elapses between the injection of the absinthe and the appearance of the convulsions, in spite of which the records of the convulsions on the two sides may at first be as nearly as possible equal, while subsequent ones show the preponderance of those on the same side as that from which the half of the cerebellum has been removed.

The fact that the convulsions were unequal on the two sides, that those on the side of the cerebellar defect were greater than those on the opposite side, needed no further confirmation, the fact was incontestable; but, in attempting to interpret the

nature of the phenomenon, it became evident that several points required careful consideration. The first of these appeared to be the necessity of carefully distinguishing whether the effect was to be ascribed to an irritative lesion of the cerebellum, or

Fig. 4.



Curves from the Extensor Muscles of the anterior Extremity of a Dog four weeks after removal of the left Lateral Lobe of the Cerebellum. Convulsions evoked by Absinthe.

whether it was a result of absence of the influence normally exerted by the half of the cerebellum that had been removed. In order to settle this question, I repeated these experiments in animals which had been deprived of one lateral lobe of the cerebellum for one, two, three, and five months. In all of these the results obtained with

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

absinthe were the same as those obtained when the lobe was removed, at the time that, or soon before, the drug was administered; the convulsions on the same side as that from which the cerebellar lobe was removed being greatly in excess of those on the opposite side, as evidenced by the curves obtained from the extensor muscles of the fore limbs (see fig. 4). As in the former experiments, so in these, the myographs were reversed in order to exclude the possibility of fallacy from some error of the instrument, that first connected with the right extremity being now connected with the left, and *vice versâ*, the result in each instance being that the curves were reversed on the recording apparatus, the greater curve taking the position of the lesser, and the lesser the position of the greater.

Quite apart from the evidence of the curves, there was no difficulty in detecting on direct observation of the extensor muscles of the fore limbs, that those on the side from which the lateral lobe of the cerebellum had been removed were in very much more vigorous action than were those of the opposite side.

Another point observed was that in cases in which a series of convulsions were obtained, in quick succession, by means of the intravenous injection of absinthe, the centres, on whose discharge the convulsions depend, showed signs of exhaustion on the opposite side, in some cases, while those dominating over the muscles of the side of the cerebellar ablation were in vigorous activity.

Two points seem worthy of notice in connection with the curves from the dog, the left lateral lobe of whose cerebellum was removed three months before the convulsions were evoked, the tonus of the second stage of the convulsions on the left side seems to assert itself slightly more than was the case a month after ablation of the lateral lobe, and the convulsions on the right side are more pronounced than they were then.

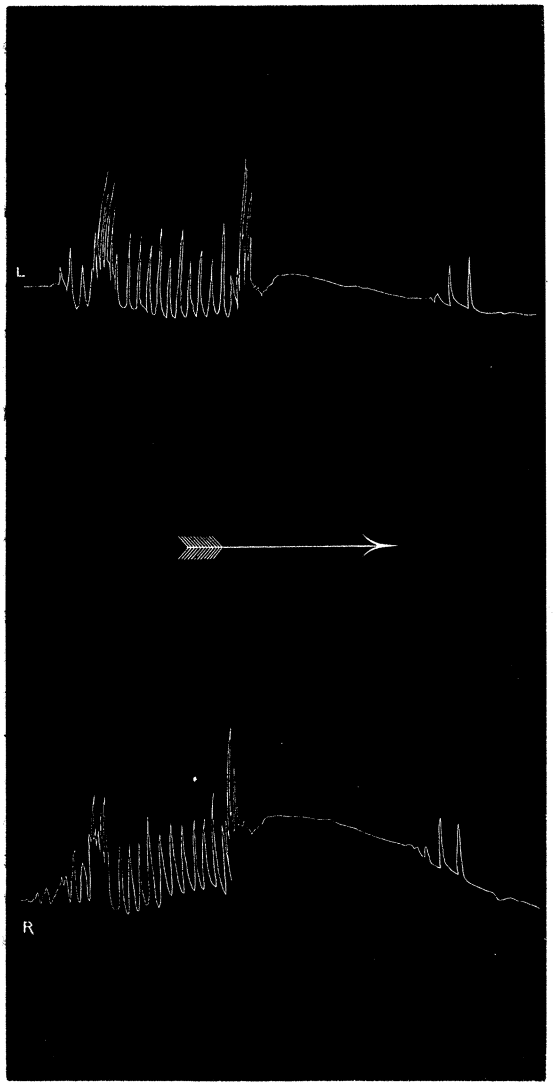
In order, if possible, to have a clear conception of the exact alterations of the curve from the normal, absinthe was administered to dogs whose central and peripheral nervous systems were intact, and curves obtained from the extensor muscles of the fore limbs during the convulsions which resulted (see fig. 5).

As may be seen from the figure, the curves are as nearly as possible equal and identical on the two sides, and each series of convulsions, which constitutes a fit, is made up of three stages, the first and third of which are characterised by clonic convulsions, while the second, or intermediate stage, is characterised by tonic spasm. On comparing these curves with those obtained in animals one lateral lobe or half of whose cerebellum had been extirpated, it became evident that the curves on both sides were altered in the animals whose cerebellum was defective, the degree of alteration depending, up to a certain point, on the length of time which elapsed between the time that the unilateral ablation of the cerebellum was effected and that when the convulsions were evoked. The curves obtained almost immediately after the removal of the portion of the cerebellum show little alteration in character from

the normal on either side, but in those obtained later the alteration of the curves on both sides was distinct.

As has already been said, the curves of the convulsions on the side of the cerebellar lesion are greater than those of the opposite side, and of the alteration in the character of the curve there could be no possible doubt. It was the intermediate or

Fig. 5.



Absinthe Convulsions in a Dog whose Central Nervous System was intact. Curves from the Extensor Muscles of both anterior extremities.

tonic stage which was chiefly altered, as a glance at figs. 4 and 5 will show. This tonus either had clonic convulsions superimposed, or it was poorly marked, or altogether absent, the two clonic stages merging into each other. The alteration of the curve representing the convulsions on the opposite side was unquestionably

one of degree, slightly of nature. This curve was diminished in extent, as compared with the normal curve, in all its stages, and in addition to this, a slight degree of clonus was, in most cases, superimposed on the tonus (see fig. 4).

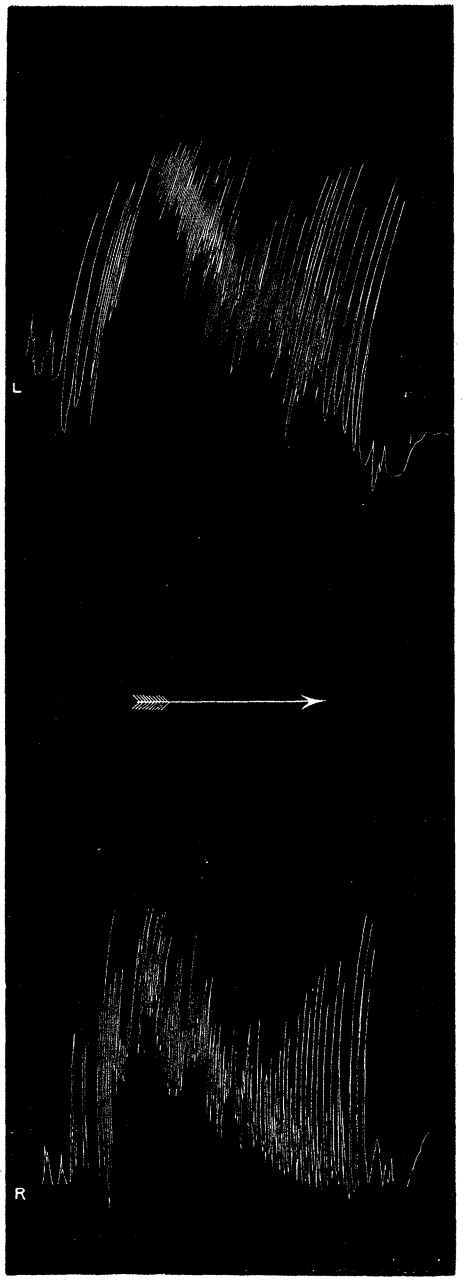
When the whole of the cerebellum was removed, the convulsions subsequently evoked, by means of intravenous injections of absinthe, were equal on the two sides, and the curves obtained from the extensor muscles of the fore limbs presented the same characters as those obtained from the extensor muscles of the anterior extremity on the same side as that from which one lateral half of the cerebellum had been removed (see fig. 6). Instead of the complete discharge being made up of a tonic stage interposed between two clonic ones, there was either no sign of the tonic stage, or very little of it, the whole discharge being composed of a series of clonic convulsions.

The results of this experiment make it evident that the removal of one half of the cerebellum has a direct influence on the opposite cerebral hemisphere; while the effect on the hemisphere of the same side must in some way be brought about indirectly, possibly through the agency of the opposite cerebral hemisphere, which as we have seen is evidently influenced in a very marked manner by the absence of the influence of the half of the cerebellum which has been removed. But these results may have another interpretation which will be discussed later.

When convulsions were evoked by means of intravenous injections of absinthe, unilateral ablation of the cerebellum subsequently performed, and then a further series of convulsions induced with absinthe, the phenomena observed when one lateral half of the cerebellum was removed before any discharge was induced, and the absinthe injected at some subsequent period, did not result. Instead of the records of the convulsions showing the marked inequality on the two sides observed in the former series of experiments, the curves obtained from the extensor muscles of the anterior extremities were as nearly as possible equal on the two sides, and presented the same characters in other respects. The characters of the curves differed little, if at all, from the normal curves obtained when the whole of the central nervous system was intact, there was a well-marked clonic stage, then a tonic and finally a short clonic stage. If, however, the animal was kept under the influence of ether, without any more absinthe being administered until a period of from half to three-quarters of an hour had elapsed, the records of convulsions then evoked, while being possibly still quite, or nearly, equal on the two sides, showed that the curve corresponding to the extensor muscles of the anterior extremity of the side from which the half of the cerebellum was removed, differed from that of the opposite side in that a condition of slight clonus was, as it were, superimposed on the tonus in the second stage of the discharge. Instead of the line connecting the representation of the two clonic stages being a fairly uniform one, it is made up of a series of short up and down strokes, which represent a certain amount of clonic spasm, but the general contour of the curve was preserved. This slight clonus superimposed on the tonus is sometimes met

with in normal dogs, but is then on both sides. In some instances where convulsions had been evoked by absinthe before half of the cerebellum was removed, and when

Fig. 6.



Absinthe Convulsions in a Dog after Ablation of the whole Cerebellum. Curves from the anterior extremities' Extensor Muscles.

convulsions were afterwards obtained on further administering absinthe, it sometimes happened that after a series of convulsions, some inequality on the two sides began to

show itself on the tracing, the curve corresponding to the side from which the half of the cerebellum was removed being greater than that representing the convulsions on the opposite side; but there was still an absence of the marked clonic character of the discharge which replaced the tonic element of the second stage of those discharges obtained on the side of the lesion when the unilateral ablation of the cerebellum was performed prior to the administration of absinthe, only a slight amount of clonus being as it were superadded to the tonus.

Part VI.—Removal of Both Lateral Lobes of the Cerebellum.

The animals subjected to this operation were only kept under observation for short periods, as there seemed no special object to be gained by keeping them alive longer than was necessary to be certain of the exact symptoms which attended such lesions, and as it was always soon evident that the same process of recovery was going on in them as in all the other dogs with cerebellar lesions.

Ocular Deviation consisted in downward rotation of both globes, which were also deviated outward to a variable extent. As in other cases of strabismus, the result of cerebellar lesions, the globes returned to their normal positions in the course of a few days.

Nystagmus was upward in direction with a tendency to rotation of the upper segment of each globe outward at first. The spontaneous nystagmus was replaced by nystagmus only on movement of the eyeballs, and that in the direction in which the eyes were directed; and in the course of two or three days there was no longer any nystagmus.

Motor Phenomena.—The animal was unable to stand, owing to the combination of circumstances I have already detailed in connection with unilateral ablation of the cerebellum. All four extremities were affected, and the motor paresis was considerably more marked in the posterior extremities than in the anterior.

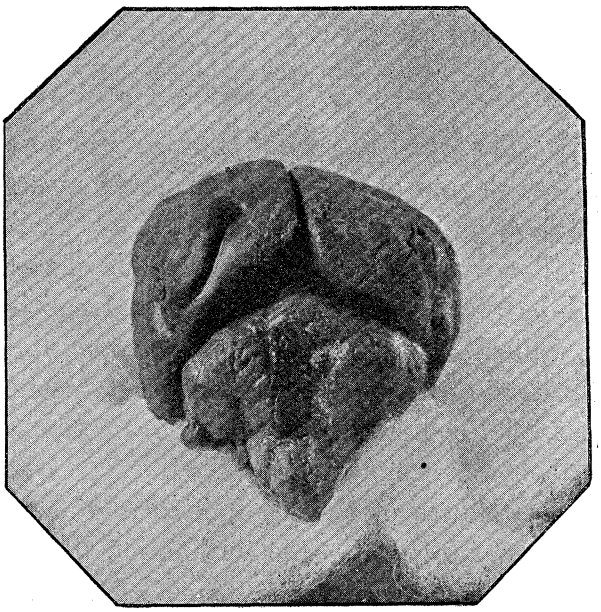
Inco-ordination showed itself in general unsteadiness, but no rotation movements were ever observed in these animals in which a bilateral lesion of the cerebellum had been produced. The unsteadiness was, as in other cases, increased, or evoked, by voluntary efforts, excitement, &c.

Sensory Phenomena.—There were anæsthesia and analgesia, as tested by cold water and the clips, of all the extremities, which cleared up on the anterior extremities before the posterior, except in those instances in which more of one lateral lobe of the cerebellum had been removed than of the other, in which case the posterior extremity on the same side as the lesser lesion sometimes recovered before the opposite anterior extremity, and, of course, also before the opposite posterior extremity.

Reflexes.—Extensor spasm was marked in both anterior extremities, which were rigidly extended at right angles to the trunk at first. Rigidity of the posterior

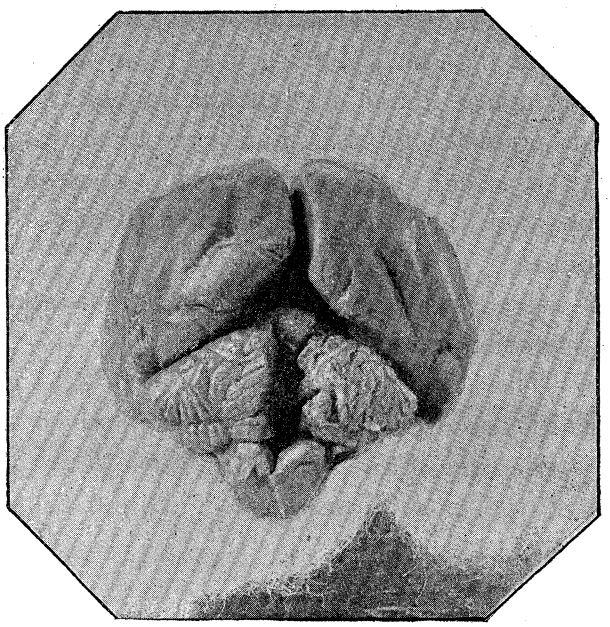
extremities was very much less marked. All the tendon reflexes on both sides were increased. There was no deviation of the head or arching of the trunk, such as was observed in unilateral ablation of the organ.

Fig. 7.



Ablation of the Pyramid and Declive of the middle Lobe of the Cerebellum of a Dog.

Fig. 8.



Ablation of the Pyramid, Declive and part of the Monticulus of the middle Lobe of the Cerebellum of a Dog.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Part VII.—Extirpation of the Posterior Part of the Middle Lobe, or of one Lateral Half of it.

1. *Extirpation of the Posterior Part of the Middle Lobe* (see figs. 7, and 8).

(a) Immediate and transitory effect.

(b) Late and permanent effect.

(a) *Immediate Effect.*

Ocular Phenomena.—Both eye-balls were slightly proptosed, and were rotated downwards and to a less degree outwards. Whenever nystagmus was detected it was vertical or of a rotatory and irregular character.

Motor Phenomena.—There was always distinct paresis of the posterior extremities, while, as far as could be ascertained, the anterior extremities were only slightly affected. The animal walked on a widened base, as far as the posterior extremities were concerned, and, instead of resting on the pads of its posterior paws, it rested on the whole of that part of the limb included between the ankle and digits, and scraped the hind legs along the ground as it walked.

Inco-ordination.—Unsteadiness of the head, increased on attempts at voluntary movements of all kinds, was present. Inco-ordination did not show itself in any lateral reeling, as in the case of unilateral lesions of the cerebellum, but, as the animal made attempts to walk, each succeeding step taken with the fore limbs resulted in their being raised higher and higher from the ground, and one step followed another before the limb had reached the ground, the animal as it were attempting to find solidity in mid air, at an increasingly elevated level, until the fore part of its body is raised so high that the dog falls backwards. When the animal is going through this performance, it reminds one much more of a performing horse at a circus than of a normal dog walking on its hind limbs alone, owing to the fact that so great a part of the posterior limb rests on the ground, whereas a normal dog walking on its hind legs alone rests on the pads of its paws, without touching the ground with any other part of its limbs.

Rotation movements were not observed, except in one instance, when they occurred a few hours after the operation, and were slight.

Sensory Phenomena.—There is blunting of sensibility of all the extremities at first, but the anterior extremities recover before the posterior, which, however, usually show no sign of anæsthesia at the end of a week.

Reflexes.—Rigidity of the extremities was slight, and the tendon reflexes were slightly increased.

(b) *Late Effect.*

All the symptoms that have just been detailed passed off within a variable period, depending on the amount of the lobe removed, usually three or four weeks, or less.

All that remained, if anything, of the former symptoms, was possibly some slight defect in the movements of the posterior extremities, which was scarcely detectable. The animals could stand on their hind limbs alone like normal dogs, and could jump, in their attempts to reach food held above them, quite as well as normal dogs. In some it was difficult to be sure that any alteration in the state of the tendon reflexes persisted, while in others there seemed to be still a slight increase of the knee-jerk.

When the greater part of the middle lobe of the cerebellum was extirpated, which included the whole of the posterior half and some of the anterior :—

1. The tendency to fall backwards, if present, was only slight, as compared with when the posterior portion of this lobe alone was removed.
2. Inco-ordination chiefly in the posterior extremities.
3. Rigidity was present in all the extremities, but more in the anterior.
4. All the tendon reflexes were exaggerated.
5. Motor paresis involved all the extremities, but the anterior only to a minor degree, the greater part of the defect being noticed in the posterior extremities.
6. Anæsthesia and analgesia affecting all the extremities, but less marked in the anterior than in the posterior.
7. Divergence and rotation downwards of both eyeballs.
8. Nystagmus was vertical or of an irregular rotatory character.

When only the posterior part of the vermis is removed the same symptoms are present, though to a less degree, with the exception of the tendency to fall backwards, which is very much more marked.

2. *Extirpation of half of the Posterior Part of the Middle Lobe* (see fig. 9).

(a) Immediate and transitory effect.
(b) Late and permanent effect.

(a) *Immediate Effect.*

Ocular Phenomena.—The eyeball, on the same side as the cerebellar lesion, was rotated downwards and to the side of the lesion, that is outwards. No deviation of the opposite eyeball could be detected. There was nystagmus of both globes to the opposite side and slightly upwards.

Motor Phenomena.—There was only slight evidence of any impairment of the movements of the limbs. This slight paresis was in both posterior extremities and in the anterior extremity of the side of the lesion; but it was scarcely evident in some animals except in the posterior extremity of the side of the lesion.

Inco-ordination.—The slightest possible unsteadiness existed at first, but so slight and transitory was this symptom that it might well have been an effect of the anæsthetic, and in no way directly dependent on the cerebellar lesion.

Reflexes.—There was slight increase of the tendon reflexes on the same side as the cerebellar lesion; less than after removal of the whole of the posterior part of the

middle lobe, and of course in no way comparable to the great exaggeration which followed removal of one lateral lobe of the cerebellum. The knee-jerk on the opposite side did not participate in the slight increase of its fellow, nor did it appear to be at all diminished.

As far as could be ascertained, no other symptoms were present.

(b) *Late Effect.*

So exceedingly transitory were the symptoms just alluded to, that they cleared off in the course of a few days, and certainly by the end of a week nothing abnormal could be detected, unless it were some slight doubt as to whether the ocular globes were quite parallel, or whether the knee-jerk was a shade brisker than that on the opposite side or not.

Ablation of one lateral half of the posterior portion of the vermis is therefore characterised by :—

1. Slight inco-ordination of the extremities of the same side.
2. Slight rigidity in the extremities of the same side.
3. Slight increase in the tendon reflexes of that side.
4. Evidence of motor paresis chiefly detectable in the posterior extremity of the same side.
5. Deviation of the eyeball on the same side outwards and downwards.
6. Nystagmus from that side towards the opposite side, and slightly upwards.

Part VIII.—Ablation of the Whole Cerebellum (see fig. 10).

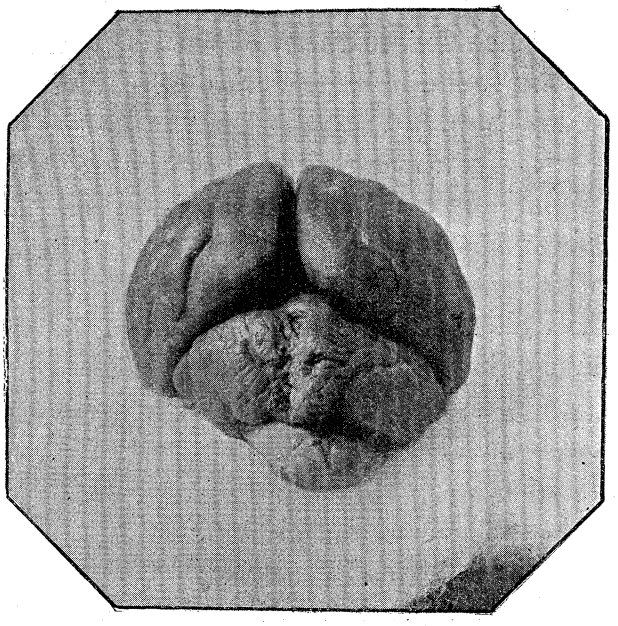
In four instances in which total extirpation of the cerebellum was attempted the animals died the same night after the operation, and the autopsies revealed nothing which would have accounted for their death, which was consequently ascribed, rightly or wrongly, to shock. I have, however, been able to get dogs to survive by performing the operation in two stages, removing one half of the organ on one occasion, and two or three weeks later, when the animals had sufficiently recovered from the effects of the first operation, removing the remaining half. In addition to this I have twice succeeded in getting dogs to recover when the whole organ was removed at one operation. The most noteworthy symptoms which attended ablation of the whole organ were the following :—

Ocular Deviation took the form of a varying degree of downward rotation of both globes, which displacement was a variable time in being recovered from.

Nystagmus was not spontaneous; it only occurred on movement of the globes, and then the jerks were in the direction in which the eyes were turned.

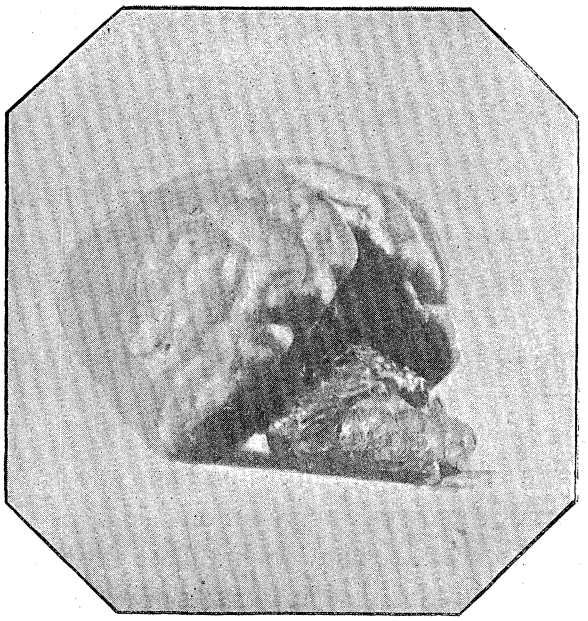
Motor Phenomena.—The animal was unable to sit up or stand. Paresis affected all the extremities, but the posterior to a greater extent than the anterior; and the latter recovered before the former.

Fig. 9.



Unilateral Ablation of the Posterior Part of the middle Lobe of the Cerebellum in a Dog.

Fig. 10.



Ablation of the Cerebellum in a Dog.

Inco-ordination.—No rotation phenomena were ever observed; but general unsteadiness, having the characters which have been already described in connection with other lesions of the cerebellum, was present. On attempting to get up, the animal fell indiscriminately to one or other side.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Sensory Phenomena.—As in those dogs in which both lateral lobes of the cerebellum were removed, there was anæsthesia and analgesia of all the extremities, which though persisting for a much longer time, cleared up in the same order as those bilateral lesions, viz., the anterior extremities were first to recover, while the posterior extremities did so later.

Reflexes.—Extensor spasm of the anterior extremities was a feature of this lesion also, the limbs being rigidly extended at right angles to the trunk, as a rule; and when this was not present spontaneously, it was evoked whenever the animal was disturbed. Rigidity of the posterior extremities was less marked than in the case of the anterior ones. The tendon reflexes were increased on both sides. There was no rotation of the neck, or curving of the trunk, such as was met with when only one lateral half of the organ was removed. Therefore the symptoms which characterise total ablation of the cerebellum are :—

1. General inco-ordination.
2. Rigidity most marked in the anterior extremities.
3. Exaggeration of tendon reflexes.
4. Motor paresis affecting all the extremities, but the posterior more than the anterior.
5. Anæsthesia and analgesia of similar distribution.
6. Deviation of the eye-balls slightly downwards.
7. Nystagmus in whatever direction the globes are directed.

*Part IX.—Control Experiments on the Labyrinth and Eighth Nerve.**

As I explained in a former paper,† Professor Victor Horsley kindly suggested to me that, as the auditory nerve and labyrinth are in such close proximity to the cerebellum, it was necessary to institute control experiments, with a view to excluding the possibility of the effects being wholly or partly due to interference with one or other, or both, of these structures. The following experiments were consequently performed as controls :—

(1) Extirpation of the labyrinth on one side.
(2) Intercranial division of the eighth nerve on one side.
(3) Chemical irritation of the eighth nerve on one side.

As all these procedures were attended with almost identical results, they will be considered together; but, before doing so, it is necessary for me to explain that, owing to the impossibility of exposing a sufficient length of the eighth nerve to apply an irritant to it without lifting up the lateral lobe of the cerebellum, the irritant was placed on the end of the nerve as it entered the labyrinth. Crystals of chloride of

* *Cf.* Flourens, Cyon, Brewer, Högyes, Bechterew, Sewall, &c.
† *Loc. cit.*

sodium were packed around the stump of the nerve, and kept in position by means of a plug of aseptic wool introduced into the labyrinth.

The symptoms which resulted from these lesions of the labyrinth and eighth nerve were characteristic, and perfectly distinct from those which have been detailed in connection with lesions of the cerebellum, as will be immediately seen.

Vertigo, as evidenced by reeling, was a constant feature of these lesions, but varied in the degree of its intensity in different animals, and according to the time that the observation was made after the operation. It was always most marked at first, and gradually became less later. In only one animal did it reach the degree of severity necessary to produce rotation movements such as were observed in unilateral lesions of the cerebellum, and in this case the rotation movements were violent, and took place on the dog's long axis towards the side of the lesion, and not towards the opposite side, as was invariably the case in unilateral ablation of the cerebellum. Reeling was sometimes very marked, and the animal always fell towards the side of the lesion; at other times it was less marked, so that the animal would be preserving a fairly straight course, in walking, when it would suddenly reel and fall to the side of the lesion.

Another constant feature of the labyrinthine disturbance was the condition known as "circus movements," in which the animal walked round a central axis, which was on the side of the lesion. The circumference of the circle performed is a relatively small one, so that the trunk is curved with its concavity to the side of the lesion when these movements are taking place, the tail and head being approximated. There is no spasm of the trunk muscles producing this curving of the animal; it simply walks round and round in so small a circle that it is necessary for it to bend its body in order to do so.

Ocular deviation was present, and consisted in a rotation of the globe on the side of the lesion downwards and sometimes in addition inwards. The extent of the latter factor varied, and sometimes it appeared to be replaced by a slight outward tendency, as described by Bechterew.* Like this observer, I find that the opposite globe turns inwards, but I have not met with the upward rotation of this globe described by him.

Nystagmus was always well marked, differed in character on the two sides, and varied according to the time after the operation that the observation was made. Directly after the operation there was usually upward nystagmus of the globe on the same side as the lesion, with a varying amount of the inward element; while that of the opposite side was the subject of lateral nystagmus, the jerks being outward. Two or three hours after the operation the same animal would present well-marked rotatory nystagmus of both globes, the upper segment of the eyeball on the side of the lesion turning inward, while the same segment of the opposite globe rotated outward.

* Bechterew, 'Pflüger's Archiv,' 1883, vol. 30. p. 312.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Motor power was not impaired, sensibility was intact, there was no rigidity, and the tendon reflexes were not altered.

V. CERTAIN GENERAL CONSIDERATIONS.

I wish to allude briefly to the following points before concluding this paper :—

1. The trophic influence supposed to be exerted by the cerebellum.
2. How cerebellar lesions in monkeys differ from similar lesions in dogs.
3. Congenital deficiency of the cerebellum in a cat.

1. The Trophic Influence Supposed to be Exerted by the Cerebellum.

That nerve fibres derived from the cerebellum degenerate both downwards into the medulla and also upwards into the cerebrum there is no question. That is, fibres do degenerate downwards chiefly on the same side of the medulla as the cerebellar lesion, occupying the lateral region ; and fibres degenerate upwards, cross in the superior decussation and go chiefly to the opposite basal ganglia. More than this I am not prepared to say at present, but I hope before long to be able to publish a detailed account of my investigations in this direction.

For the first few days, and in some cases for a week or two, my dogs certainly wasted rapidly ; but after this they gained flesh as rapidly as they had lost it, and eventually became very much better nourished than they were before the operation. In some cases, when the animal was kept a long time, they became exceedingly well nourished and fat. Whether the wasting at first was due to any direct trophic effect lost with the part of the cerebellum removed, I am not prepared to say. I think that it is far more likely that it was due to the fact that the animals, as a rule, would not attempt to take food at first, and could only be got to swallow a limited quantity of milk syringed into the back of their mouths. Those animals which took their food well from the beginning did not waste ; but then in them the part of the cerebellum removed had been trivial.

Conjunctivitis was sometimes met with, and even corneal opacities resulted in a few rare instances ; but I should be sorry to commit myself to any view that they are trophic results of the cerebellar lesion. I am more inclined to believe that possibly perchloride of mercury lotion, or the vapour of ether, get into the eyes and set up this irritation. Certainly, whereas several of the dogs first operated on presented conjunctival irritation, those operated on later, after I had taken strict precautions to prevent the entrance of these agents into the eyes, very rarely presented even slight conjunctivitis. But even without these irritating substances to account for it, it is not surprising that with so much proptosis of the globes, as was so often present, there should have been some irritation of the conjunctiva.

It was the rarest thing to see any sores on the dogs, and if they had sores before

the operation, these seemed to heal, without being made in any way worse by the operation. One animal alone developed a sore, which might have been the result of the loss of some trophic influence of the cerebellum. The whole cerebellum had been removed, and the animal would always lie on the same side, and was often wet owing to lying in its own urine, under which unfavourable circumstances a sore developed on one shoulder, in consequence of which the animal was killed by an overdose of chloroform.

2. How Cerebellar Lesions in Monkeys Differ from Similar Lesions in Dogs.

All the symptoms, with the exception of motor paresis and blunting of sensibility, were much less intense in monkeys than in dogs. In the limited number of monkeys I operated on, ocular deviations were not marked, and I detected no nystagmus. General unsteadiness, so marked in certain lesions of the cerebellum in dogs, was very slight in similar lesions in monkeys.

Rotation movements were never observed. Motor paresis was always very pronounced, as was blunting of sensibility; both of which affected the same limbs as in similar lesions in dogs. The paresis on the same side as a unilateral ablation of the cerebellum was well marked; and the general paresis, with inability to sit up, owing to weakness of the trunk muscles, was most striking after ablation of the whole organ.

There was an absence of the extensor spasm of the fore limbs so characteristic of cerebellar lesions in dogs; and the tendon reflexes did not show nearly the same excessive degree of excitability.

3. Congenital Deficiency of the Cerebellum in a Cat (see fig. 11).

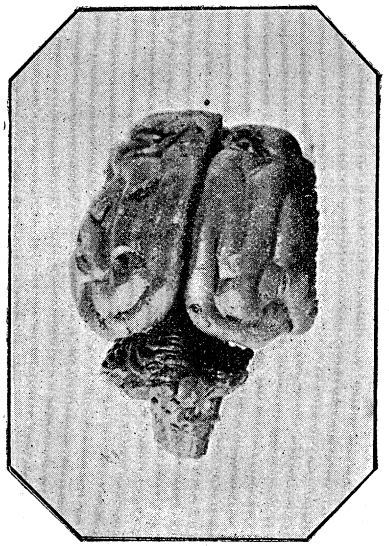
Owing to the extreme kindness and courtesy of Dr. S. W. Carruthers, I had an opportunity of examining a cat which he showed at the Neurological Society of London, and which presented distinct paresis of both the extremities on the right side, but more in the posterior, and a slight amount in the left posterior extremity. Dr. Carruthers had recognised, in this cat, the picture presented by my dogs with unilateral ablation of the cerebellum, and handed it over to me for examination. There was marked defective development of the cerebellum, and the right lobe was scarcely half the size of the left (see fig. 11). This was what we expected to find, from the symptoms presented by the cat during life.

VI. Conclusions, and their Discussion.

The first conclusion warranted is based on the results of mesial section of the cerebellum, and points to one lateral half of the organ as in no great measure

depending on the co-operation of the other half for the proper performance of its functions; a conclusion opposed to LUCIANI'S view, though his own results of mesial section of the cerebellum appear to me to support my conclusion. If the organ is physiologically one, the most grave disturbances of function ought to result from severance of its two lateral halves, whereas the reverse obtains. Further, unilateral ablation of it ought to be followed by general peripheral defects, instead of defects the majority of which are unilateral. Similarly, the effect of such unilateral ablation ought to have the same effect on both cerebral hemispheres, instead of an effect so widely different on each. The results of mesial section, and of unilateral ablation of the cerebellum, make it clear that the bulk of the impulses pass from the one half of the organ to the cerebrum or spinal cord directly, and do not traverse the opposite half of the organ before reaching their destinations.

Fig. 11.



Congenital defect of the Cerebellum in a Cat. Right half much smaller than left.

The phenomena observed after destructive lesions of this organ prove that instead of assigning to it one special function, distinct from those subserved by other parts of the central nervous system, it would be more correct to look on the cerebellum as a part of that great system having many functions in common with other parts of it, and that whereas one cerebral hemisphere is functionally related to the opposite half of the body, the influence of the cerebellum is exerted on the same side of the body, *i.e.*, it has a direct action, as opposed to the crossed action of the cerebrum.

Formerly inco-ordination has been held to account for the impairment of movement met with after lesions of the cerebellum. LUCIANI recognises three factors as responsible for the defect, asthenia, astasia, and atonia; and my own results point to inco-ordination, rigidity, and motor paresis as accounting for it. What I wish chiefly

to urge is that one of the factors on which the impaired movements depend is as truly a "motor" paresis as that which results from ablation of the "sensori-motor" cortex of the cerebrum. True motor paresis, the result of experimental ablation of parts of the cerebellum, has been described by others;* but it has been of the opposite side of the body, and not the same side as the cerebellar lesion. Without a microscope examination of the spinal cord demonstrating the absence of any injury to the pyramid on the side of the cerebellar lesion, such results are without value, for the pyramid is extremely easily injured above the decussation, in any operation on the lateral lobe of the cerebellum. No such microscopic examination has been made in any of the cases in which paresis of the opposite side of the body is said to have been met with after ablation of one lateral half of the cerebellum.

The case of defective development of the cerebellum in a cat in which the right lateral lobe was very much smaller than the left, and in which there was paresis of the right extremities, and to a slight extent of the posterior extremity of the left side, supports my view. So, too, cases of lesion of one side of the cerebellum, in the human subject, have been recorded in which there was motor paresis on the same side of the body.

It seemed possible that the cerebellum might influence motor power indirectly through the agency of the motor cortex of the opposite side, owing to the crossed relationship which exists between one half of the cerebellum and the opposite cerebral hemisphere. But we have seen that the effect of removal of the cerebellar influence from the cerebral cortex is to cause increased rather than diminished excitability of the cortical cells, so that we are justified in assuming that the motor influence exerted on the muscles, by the cerebellum, is a direct one through the spinal centres, rather than one acting indirectly through the opposite cerebral cortex.

Contrary to the views of previous observers, I look on the ocular deviations which occur after destructive lesion of the cerebellum as paralytic, and not irritative phenomena. That is, the removal of the cerebellar influence from some of the ocular muscles, allows of the production of abnormal deviations of the globes being brought about by the unantagonized muscles.

As to nystagmus, I think two kinds must be distinguished; one which is spontaneous and due to some uncontrolled action, and the other which is only evoked on movement of the globes in any direction, and which is attributable to weakness of the ocular muscles rather than to any over-action of them.

The rigidity and exalted condition of the tendon reflexes on the side of the lesion also point to a direct influence of the cerebellum on the spinal centres, as has been stated in a former paper.† I regard this influence as one of control, which, when taken off from the centres in the spinal cord, allows of their over-action. The facts appear to warrant this view, and there is, I venture to think, no necessity to call to our aid

* *Cf.* Serres, Dickinson, &c.

† *Loc. cit.*

the theory advanced by Dr. Hughlings Jackson,* which supposes that the cerebral and cerebellar influences antagonize each other normally, so that when one or other influence is removed, not only does paralysis result as a direct effect of the lesion, but the paralyzed parts become rigid owing to their invasion by the unantagonized influence from the intact organ. Indeed, this view was negatived by my former results, in which the activity of the knee-jerk consequent on removal of one cerebral hemisphere was further increased by ablation of one lateral lobe of the cerebellum.

The attitude so characteristic of ablation of one lateral lobe, or half of the cerebellum, is, I believe, due to spasm in the paresed trunk muscles on the side of the lesion, and this is in keeping with what we find in the limbs, for those paresed are those in which there is spasm.

With regard to inco-ordination, I incline most strongly to the views of Dr. Hughlings Jackson,† who supposes that the disorders of locomotion are brought about primarily by the over-action of muscles which are attempting to compensate for others which are paralysed. This explanation holds good as far as the unsteadiness and irregular movements are concerned, but there are other symptoms included under the term inco-ordination which cannot be accounted for in this way. Rotation movements and reeling in some particular direction, are, I take it, the results of subjective sensations of loss of balance, which however result in objective phenomena directly due to over-action. It is a significant fact that rotation movements only occur in unilateral lesions of the cerebellum, and that they do not occur when both lateral lobes, or the whole organ is removed. Possibly the reason why the animal rotates to the same side after section of one middle peduncle,‡ and to the opposite side after removal of one lateral lobe of the cerebellum, as found by Luciani and myself, is because the excitation involved in section of the peduncle generates in excess the very impressions which are lost when the lateral lobe is absent. Or it may be that the auditory nerve was injured in those experiments in which the middle peduncle was divided, in which case, as we have seen, if rotation occurs, it is to the side of the lesion.

Anæsthesia and analgesia after destruction of parts of the cerebellum point to this organ as exercising sensory as well as motor functions, and it is interesting to note that the limbs paresed are those in which there is blunting of sensibility—another fact pointing to the resemblance of the cerebellum to the "sensori-motor" cortex of the cerebrum.

The crossed influence of one half of the cerebellum on the opposite cortex appears to be one of control (as was theoretically surmised by Dr. Gowers §) owing to the fact that the discharge from the opposite cerebral hemisphere evoked by the induced current, or by absinthe, is greater than normal, after unilateral ablation of the cere-

* Hughlings Jackson, 'Med. Times and Gaz.,' 1878, vol. 2, p. 485.

† *Loc. cit.*

‡ *C.f.* Majendie, Hitzig, &c.

§ Gowers, 'Lancet,' 1890, vol. 1, p. 955.

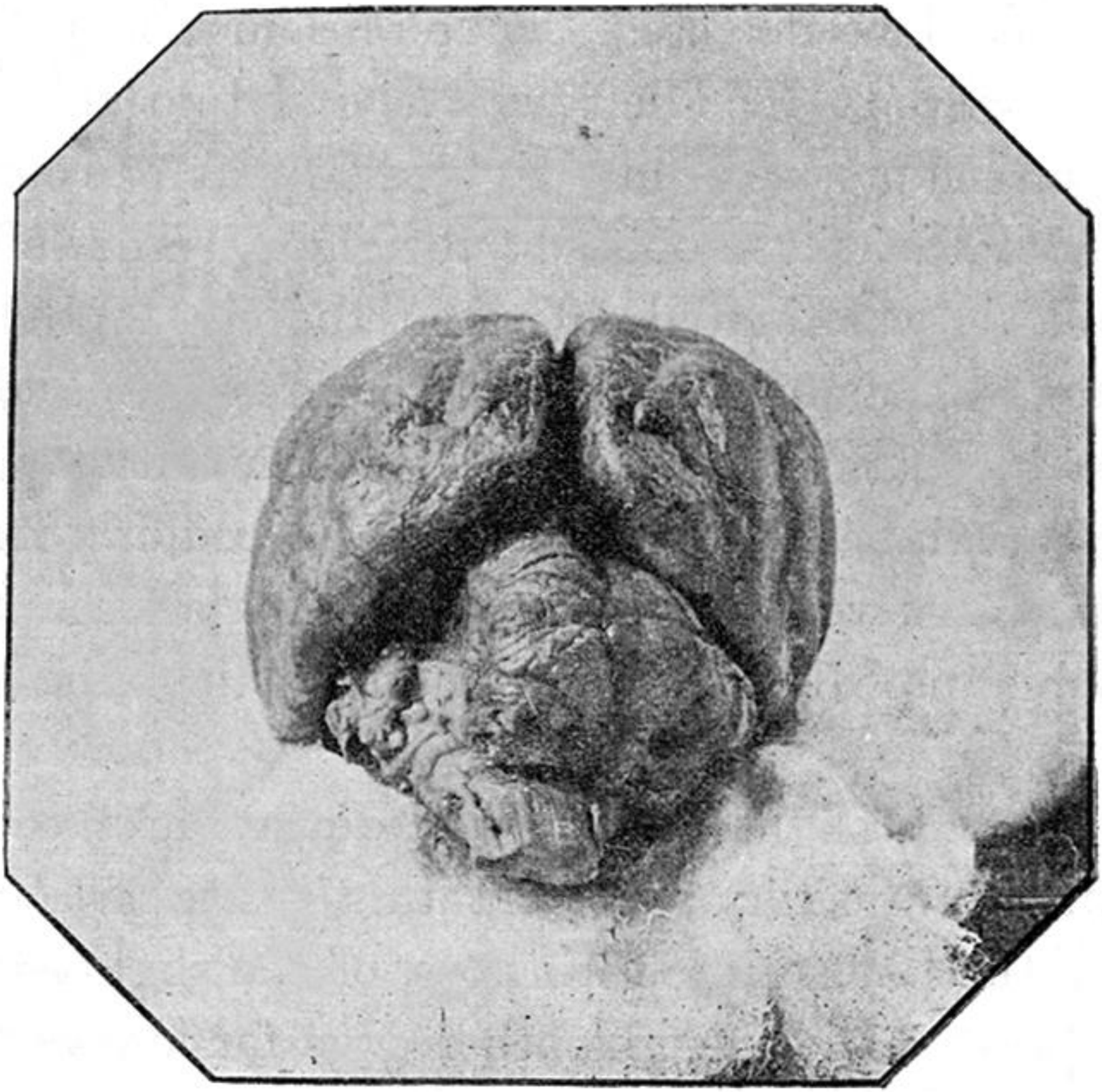
bellum. LUCIANI has shown that compensation is brought about by the "sensori-motor" cortex of the cerebrum after ablation of parts of the cerebellum; and I am strongly tempted to believe that this increased activity of the cells of the opposite cerebral hemisphere, after unilateral destruction of the cerebellum, is a provision for compensation, and accounts for the rapid and almost complete recovery which takes place after such a lesion.

How to account for the diminished discharge from the cerebral hemisphere on the same side as the cerebellar lesion, under similar conditions, must, for the present, remain an open question. It may mean that one half of the cerebellum inhibits the other half under normal circumstances, or that the cerebral hemisphere whose excitability is increased inhibits its fellow, or that the half of the cerebellum itself no longer inhibits the anterior horn cells of the same side of the spinal cord.

Finally, it is evident that the effects obtained on ablation of different parts of the cerebellum do not depend on any disturbance of the auditory nerve or the labyrinth. As unilateral ablation of the cerebellum is the most likely lesion to be attended with any disturbance of these structures, it will suffice if we contrast its effects with those which attended the operations on the labyrinth and eighth nerve.

	Cerebellum.	Labyrinth, &c.
Strabismus	Opposite eye down and out, eye of same side little if at all deviated	Opposite eye deviated inwards. Eye on same side deviated downwards chiefly
Nystagmus	Lateral jerks of both globes towards the side of the lesion	Direction different on the two sides, and different at different intervals after the operation
Motor Phenomena	Paresis chiefly affecting limbs of same side	No affection of motor power
Inco-ordination	Rotation and reeling to opposite side	Rotation rare and to same side as lesion. Reeling in same direction
Sensory Phenomena	Blunting of sensibility chiefly of limbs on same side	No blunting of sensibility
Reflexes	Increased chiefly on the same side as lesion	Unaltered

Fig. 1.



blation of the Left Lateral Lobe of the Cerebellum in a Dog.

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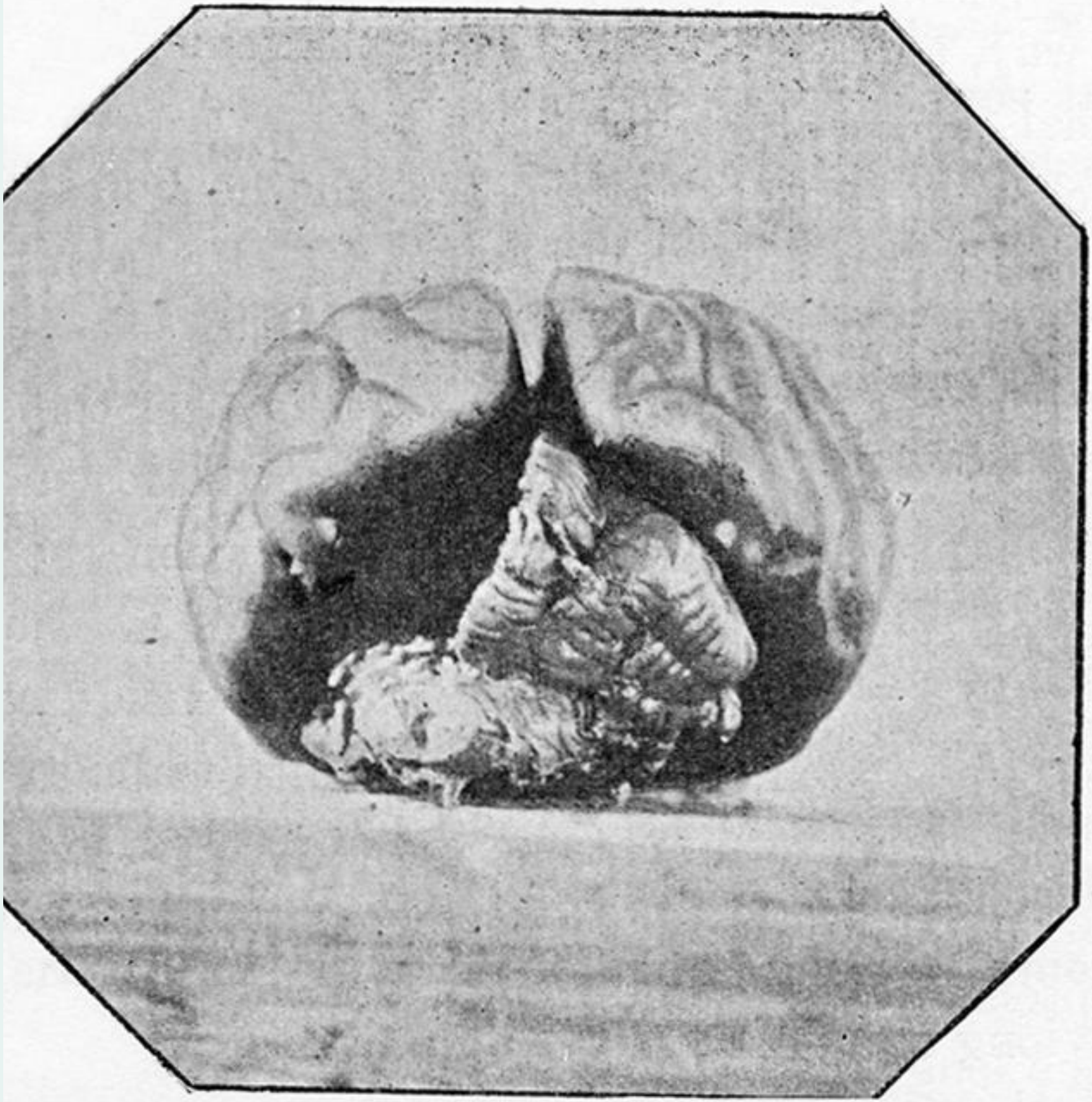
Fig. 2.



Ablation of the left half of the Cerebellum in a Dog.

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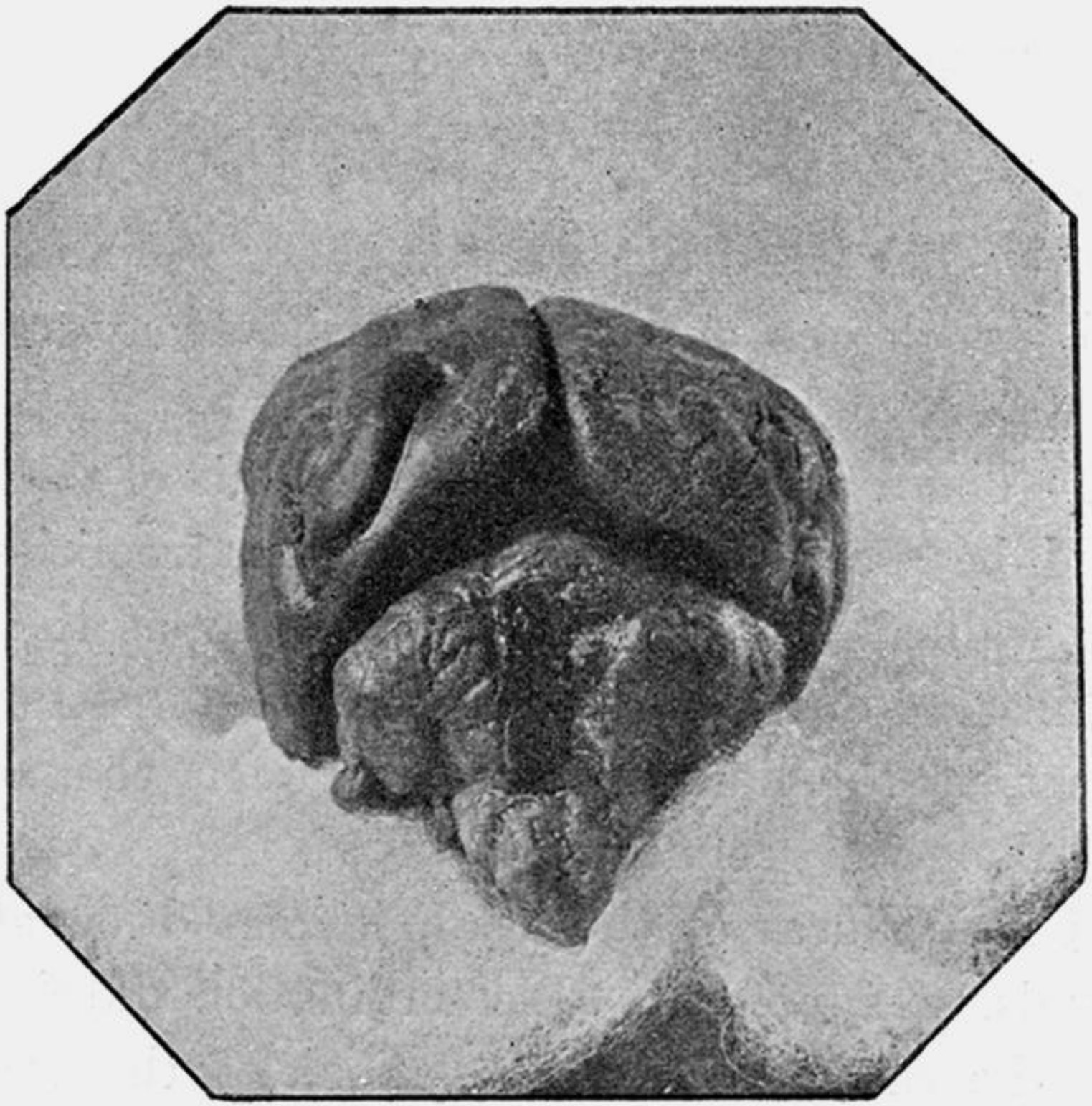
Fig. 7.



Ablation of the Pyramid and Declive of the middle Lobe of the Cerebellum of a Dog.

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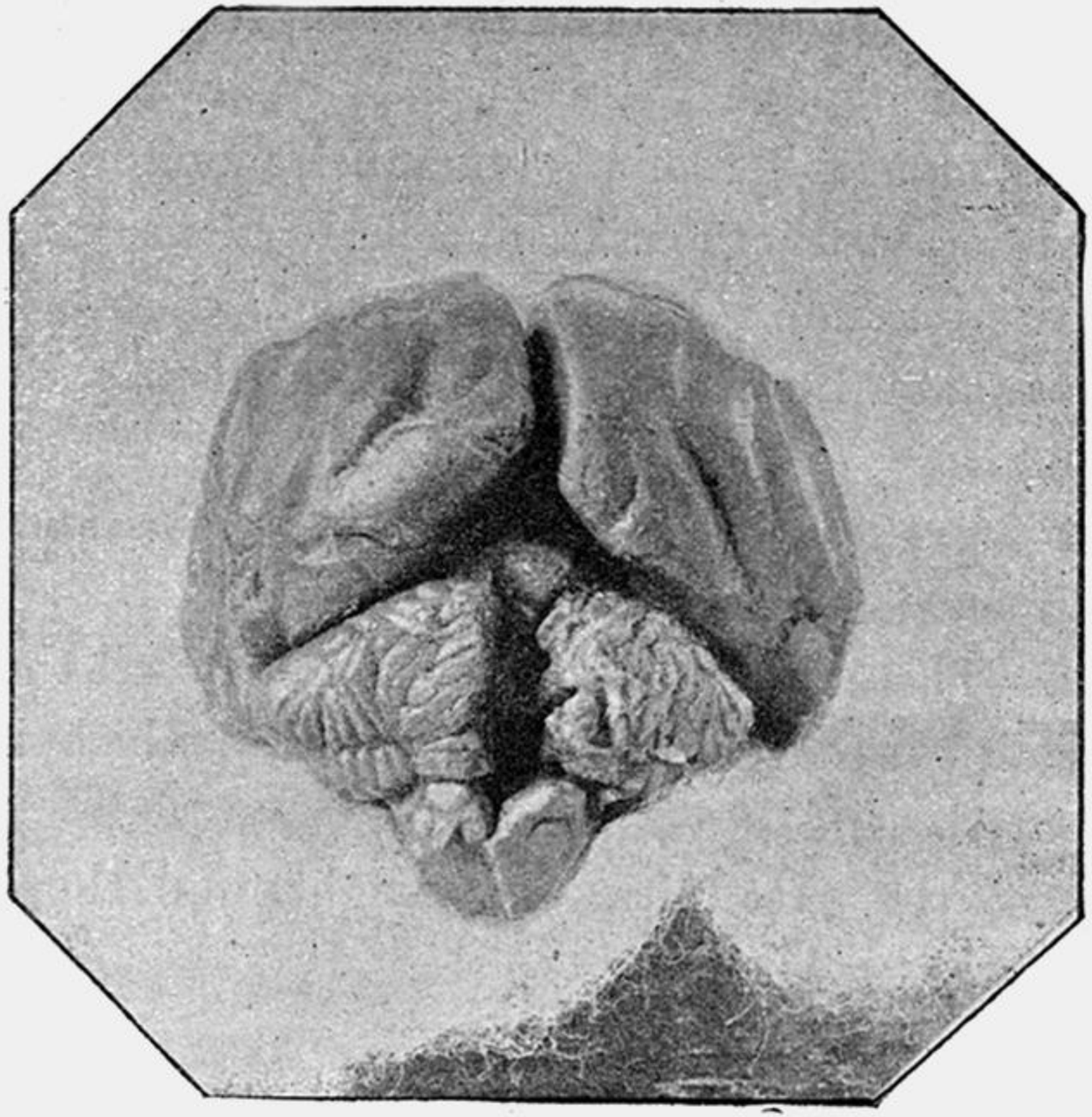
Fig. 8.



Ablation of the Pyramid, Declive and part of the Monticulus of the middle Lobe of the Cerebellum of a Dog.

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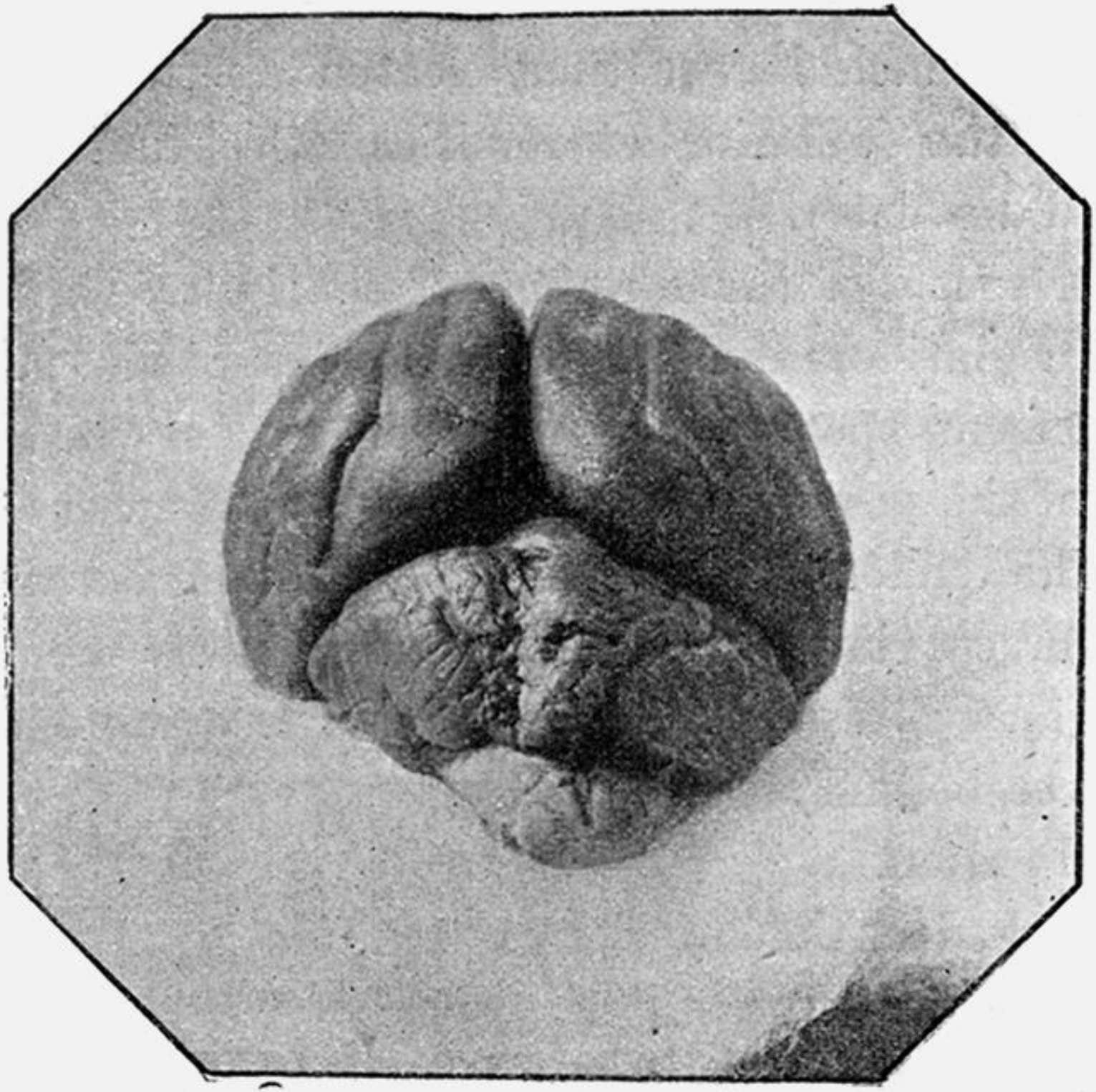
Fig. 9.



Unilateral Ablation of the Posterior Part of the middle Lobe of the Cerebellum in a Dog.

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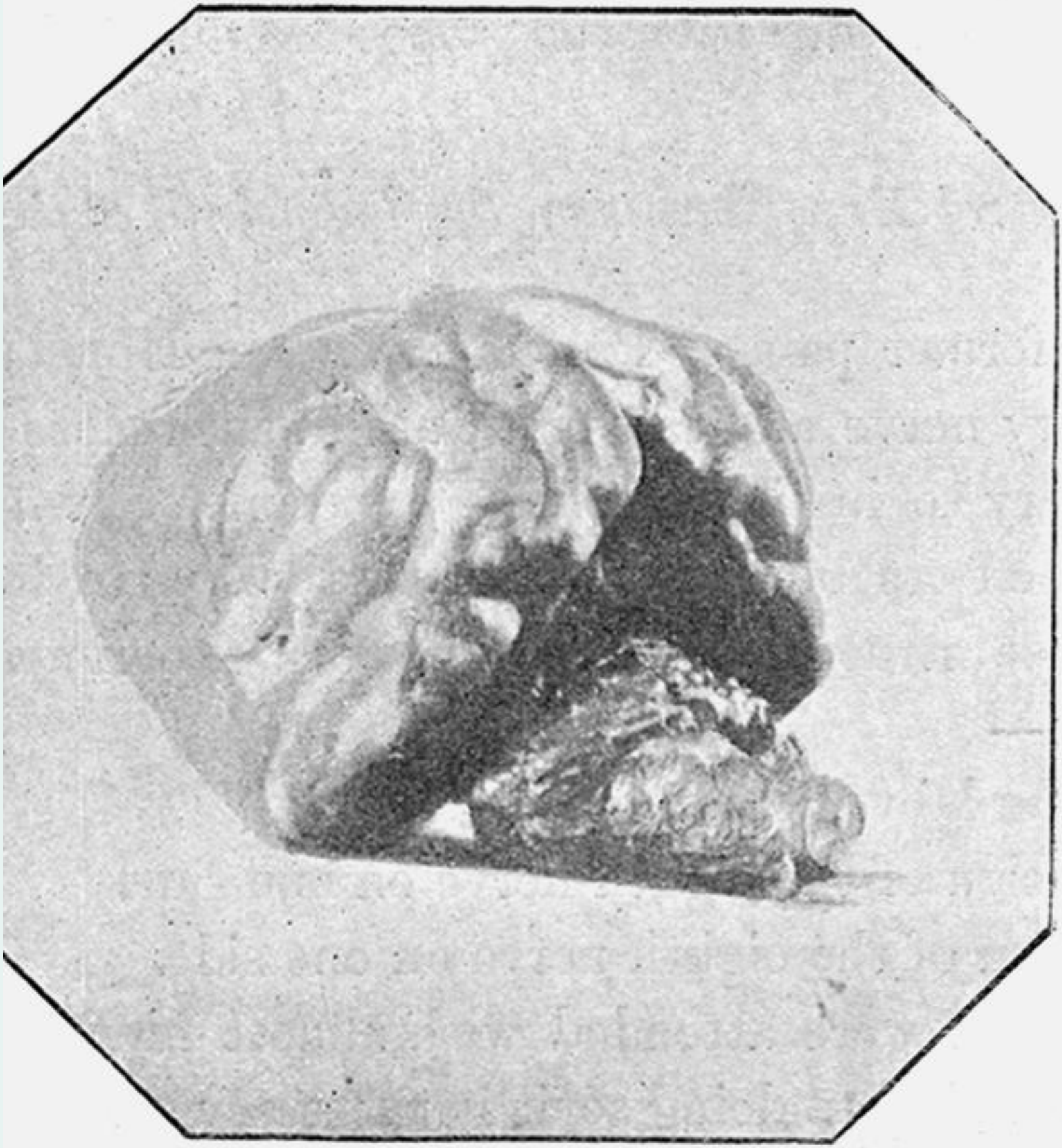
Fig. 10.



Ablation of the Cerebellum in a Dog.

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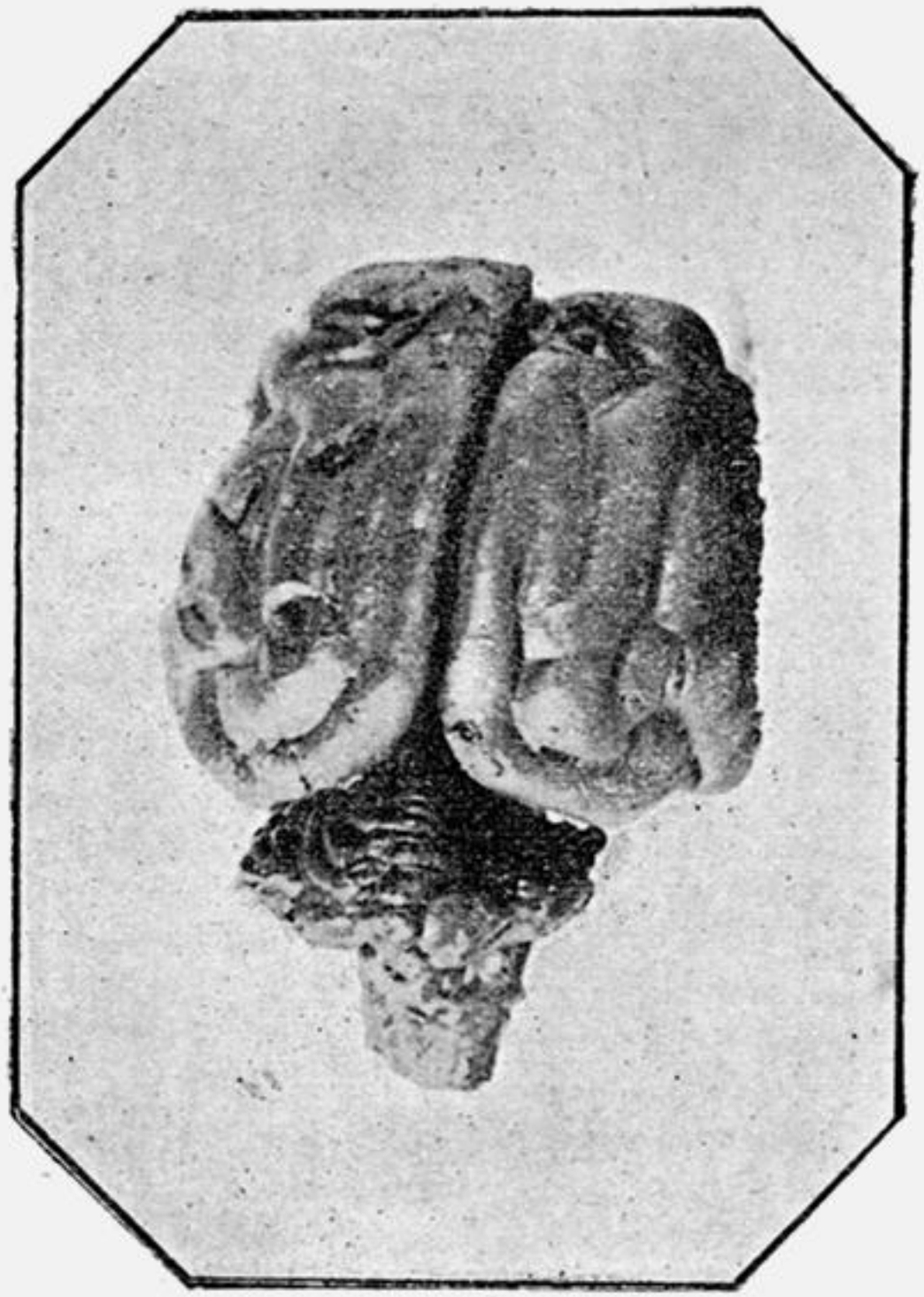
Fig. 11.



ongenital defect of the Cerebellum in a Cat. Right half much smaller than left.

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