IV. *The Effects of Stimulation and Extirpation of the Labyrinth of the Ear, and their Relation to the Motor System.* Part I.—*Experimental.**

By J. Gordon Wilson, *Northwestern University Medical School, Chicago, and* F. H. Pike, *Columbia University, New York.*

Communicated by Dr. F. W. Mott, *F.R.S.*

(Received June 12, 1912.)

[Plates 13–16.]

The expenses of this research were defrayed in part by a grant from the University of Chicago, and all the earlier experiments were done in the Hull Physiological Laboratory of that institution. The later experiments were done in the laboratory of the Otological Department of the Northwestern University at the expense of the Patten Fund, and in the Physiological Laboratory of Columbia University at the expense of this institution.

The object of this investigation may be thus briefly stated:

1. To study the effect of stimulation of the end organ of the vestibular nerve.

2. To study the immediate and remote results of destruction of the labyrinth or of the eighth nerve on one or both sides.

3. To observe the effect of removal of various parts of the brain on phenomena which have been observed to follow stimulation or destruction of the labyrinth.

4. To investigate the paths of connection between the labyrinth and the eye muscles—the vestibular-optic path.

5. To apply the results of the experimental work to a consideration of the phenomena of nystagmus, vertigo, and the sensations of rotation.

Later it is the intention to study anatomically the degenerative processes which have been observed in various parts of the central nervous system, following destruction of the labyrinth and of the eighth nerve.

In order to ascertain the action of the non-acoustic part of the internal ear in mammals it is necessary to ascertain the effect of stimulation of one and then of both labyrinths. Though many investigators have studied this, yet it appears to us that many points must be more clearly defined, especially in regard to deviation of the eyes, if we would successfully attempt to lay down the path along which this action takes place, and seek to contrast the labyrinthine deviation with cerebral and

* A preliminary note appeared in the 'Proceedings of the Society for Experimental Biology and Medicine,' 1911, vol. 9, pp. 9–10.

(297.) Published separately, December 30, 1912.

cerebellar ocular deviations. A number of observations were made, but as they all agreed in the main only one typical experiment will be quoted under each head.

In this paper it is our intention to give but a brief historical summary and a short discussion of our results. We will publish a more complete historical account and a fuller discussion of these results at a later period.

HISTORICAL SUMMARY.

Experimental work on the semicircular canals began with FLOURENS* in 1828, who sectioned the canals of pigeons. He found that injury to these canals caused motor incoördination, and that section of one canal caused a rotatory movement of the head in a plane parallel to that of the injured canal. He described convulsive movements of the eyelids and bulbus oculi as a result of sectioning both horizontal or frontal canals. These early experiments on the pigeon have been repeated by many subsequent workers on pigeons and other animals, with various and conflicting results, some confirming FLOURENS and some reporting negative results. It is, however, possible to trace, in a general way, some points on which two or more observers have obtained consistent positive results and to show, in some degree at least, why certain observers obtained no positive results. FLOURENS, noticing that destruction of the semicircular canals caused disturbances similar in some respects to those following destruction of the cerebellum, suggested that the semicircular canals might also be concerned with co-ordination of movement.

GOLTZ† gave the first clear conception of the mechanism involved. He pointed out that this mechanism consisted of: (1) a central co-ordinating organ; (2) afferent nerves leading from peripheral sensory terminations to the central system; and (3) a set of efferent motor nerves leading from the central system to their terminal organs. The mechanism of stimulation GOLTZ assumed to be the changes in hydrostatic pressure in different parts of the vestibular apparatus with changes in position of the head. GOLTZ showed that FLOURENS' results on pigeons could be duplicated, in a general way, on frogs.

HITZIG‡ discovered galvanic nystagmus, but inclined to refer all the phenomena of vertigo on galvanisation of the head to the brain directly. He showed that galvanic vertigo falls into line with rotation vertigo. He observed that injecting a fine stream of cold water or placing a small piece of ice on the fossa subarcuata caused forced movements of the animal. Both eyes were turned toward the injured side, with nystagmus. Although HITZIG did not apparently recognise the cause of the forced movements when ice was applied to the floor of the fossa subarcuata, there is no question that this experiment was the forerunner of the modern caloric test for disease of the labyrinth so extensively employed by present day clinicians.

* FLOURENS, 'Memoires de l'Académie des Sciences de l'Institut de France,' Paris, 1828, vol. 9, p. 5.

† GOLTZ, 'Archiv für die gesammte Physiologie,' 1870, vol. 3, pp. 172—192.

‡ HITZIG, 'Reichert's u. du Bois-Reymond's Archiv,' 1871.

BREUER* referred the phenomena of vertigo to the semicircular canals. In 1888 he (BREUER) was the first to stimulate the semicircular canals in such a way as to show the possibility of getting the specific reactions of single ampulla. He showed that stimulation of one ampulla may cause turning of the head in either of two directions, but that the more intense stimulation caused movement of the head to the opposite side.

EWALD† showed that mechanical stimulation (by the pneumatic hammer) of a particular canal causes movements of the head in the plane of that canal. He found that a pigeon, immediately after removal of one labyrinth, showed oscillating movements of the head, and may fall toward the operated side. In walking, the bird turned toward the injured side. Five to eight days after, the head turned strongly to one side. A few months after the removal of one labyrinth, one could discern nothing abnormal unless with special testing: the pigeon flew, drank, and ran normally (EWALD).‡ Rabbits roll over and over shortly after unilateral labyrinthine extirpation, the limbs of the opposite (uninjured) side are extended and abducted; those of the same (injured) side are flexed and adducted. The animals fall toward the operated side, and roll toward that side because of the mobility of the limbs of the opposite side, and the relative immobility of the limbs of the same side. Dogs exhibit a nystagmus toward the opposite side. This nystagmus is present also after bilateral removal of the labyrinth, but frequently changes in direction. It may persist a few days and then wholly disappear.§ After bilateral removal, the nystagmus may disappear in 20 to 30 hours.

LEE‖ studied in the dog fish (*Mustelis canis*) the results of stimulation of or injury to the various nerve branches or ampullæ. He found that (1) the semicircular canals work in pairs, the anterior canal of one side being paired with the posterior canal of the opposite, the two horizontal canals forming the third pair: (2) stimulation of the ampulla of one anterior canal causes rotatory movements of both eyeballs, with a characteristic movement of the fins, especially the more anterior ones; (3) stimulation of the ampulla of one posterior canal also causes rotatory movements of the eyeballs, the eyeball of the same side rolls upward, that of the opposite side downward; (4) stimulation of the ampulla of one external canal causes the eyeball of the same side to roll straight forward, that of the other side straight backward.

M. BARTELS¶ studied in rabbits the position of the eyes after stimulation of the ear. He registered both the contraction of the eye muscle and the relaxation of its antagonist during the slow phase of nystagmus and the following relaxation and

* BREUER, 'Medicinisches Jahrbuch,' Wien, 1874.

† EWALD, 'Physiol. Untersuch. über des Endorgan des Nervus Octavus,' 1892, pp. 259, 266.

‡ EWALD, *loc. cit.*, p. 26.

§ EWALD, *loc. cit.*, p. 201.

‖ LEE, 'Journ. Physiol.,' 1894, vol. 15, pp. 311–348.

¶ M. BARTELS, "Über Regulierung der Augenstellung durch den Ohrenapparat," 'v. GRAEFE'S Archiv für Ophthal.,' 1911, vol. 80, p. 207.

contraction of the quick phase. In rotation the registered curves showed that the homolateral eye was more affected. The curves from galvanic and thermic stimulation were, as a rule, similar to rotation, though anomalies were noted after unilateral destruction, especially during thermic stimulation. His results led him to believe that the quick phase in nystagmus was not labyrinthine. His conception of the results of vestibular stimulation (based to some extent on TOZER and SHERRINGTON'S* work on the afferent path for the sensory endings in the eye muscles) is that the vestibular stimulation passes to eye muscle nuclei, resulting in a contraction of the corresponding muscles. This contraction stimulates the sensory endings, and a centripetal impulse passes through the motor nerves to the cerebrum by unknown paths. This stimulation of the cerebrum sends stimuli to the eye nuclei for quick relaxation with contraction of the antagonists.

We agree, in the main, with BARTELS' view of the mechanism of nystagmus, and will submit additional evidence in a later communication.

CAMIS† showed by ergographic experiments that, in the frog, the destruction of the labyrinth caused, in addition to the deficiency phenomena, certain transitory irritative processes. These irritative processes were manifested in variations in tone of the skeletal muscles (gastrocnemius). They were homolateral in cases of unilateral labyrinthine extirpation, and bilateral if both labyrinths were destroyed. The local application of cocaine to the injured labyrinth abolished these transitory variations.

MAGNUS‡ studied the reflexes arising from the limbs, and showed that the position of a limb has a marked influence on the reflex arising from its stimulation. This effect is due not to the mechanical position of the limb, but to a changed relation which it has with the motor centre in the central nervous system.

In a later communication, appearing since this paper was written, MAGNUS and DE KLEIJN§ showed that (1) the position of the head in space, its position relative to the body remaining unchanged, and (2) the change in the position of the head with reference to the body, produce a change, though to an unequal degree, upon the condition of extensor rigidity in the fore and hind limbs of decerebrated dogs and cats (decerebrate rigidity). The afferent impulses, in the first instance, are of labyrinthine origin; in the second case, they arise in the sensory endings in the muscles, tendons, and vertebral articulations, particularly of the lower and middle regions of the cervical portion of the vertebral column. In certain positions, the two sets of reflex responses may reinforce each other; under other conditions, they may be antagonistic. But the position and condition of extensor rigidity in each limb, under each of the numerous conditions of the position of the head and body, as a whole, in space, and the relative

* TOZER and SHERRINGTON, "Receptors and Afferents of Third, Fourth, and Sixth Cranial Nerves," 'Roy. Soc. Proc.,' London, 1910, vol. 82, pp. 450–457.

† CAMIS, 'Archives italiennes de Biologie,' 1911, vol. 55, pp. 172–179.

‡ MAGNUS, 'Archiv für gesammte Physiol.,' 1909, vol. 130, pp. 219–253.

§ MAGNUS and DE KLEIJN, 'Archiv für gesammte Physiol.,' 1912, vol. 145, pp. 455–548.

position of the head to the body, may be regarded as an expression of the algebraic sum of the two sets of forces, labyrinthine and muscle-tendon-joint, acting upon it.

Hypothesis of the Mechanism of Stimulation of the Semicircular Canals.

GOLTZ's hydrostatic theory mentioned above has been abandoned by most investigators. MACH, BREUER, and BROWN, within a few weeks of each other, proposed a dynamic theory of the stimulation of the nerve endings in the semicircular canals. Although differing slightly in detail, BROWN's* account of the MACH-BREUER-BROWN hypothesis may be taken as giving the points common to all three. GOLTZ held that the semicircular canals gave information as to the *aspect* of the head in space. On the MACH-BREUER-BROWN hypothesis, the semicircular canals gave information of the *change of aspect* of the head in space. BREUER supposed that when the head was rotated in any plane, the fluid in the canals would lag behind because of its inertia, and that the fluid currents thus set up would stimulate the nerve endings in the ampullæ. MACH contended that fluid currents in canals of such fine bore were unthinkable, and that there could be changes of pressure only in the ampullæ. BREUER,† in his later papers, accepts MACH's views, and shows in great detail how changes in pressure may affect the nerve endings in the ampullæ. He emphasizes also the extreme delicacy of the cristæ and the ease with which one may injure them by manipulations of the membranous labyrinth. When the cristæ are swept from their position further experimental procedures on the canals are not attended by normal responses. On the basis of the kinetic theory, the labyrinth gives information not merely of change of aspect of the head, but also of the rate of change. The absolute acceleration of the head is not such a potent stimulus as the angular acceleration.

OPERATIVE PROCEDURE.

The dog is prepared by a bath and by shaving a wide area of the head and neck, varying according to the operation to be done. Occasionally half an hour before operating there is injected subcutaneously from one to two grains of morphia. Ether was the anæsthetic used. When the dog was under the narcotic the part was thoroughly washed and made as aseptic as possible, and the operation was carried out under strict antiseptic precautions.

The method employed to expose and destroy the labyrinth is one which, so far as we know, has not been used before. It has many advantages over the method of EWALD, who exposes the bulla and enters the labyrinth through the middle ear.

* BROWN, 'Nature,' 1878, vol. 18, pp. 633, 657.

† BREUER, 'Sitzungsberichte der kais. Akademie der Wissenschaft zu Wien, Math. physik. classe,' 1903, Abt. iii, Bd. 112, pp. 315–394; 'Zeitschrift für Sinnes-Physiologie,' 1907, Bd. 42, pp. 373–378.

EWALD'S method entails considerable risk from hæmorrhage, takes a considerable time, and necessitates a deep wound in the neck with the accompanying danger from the many important vessels in that neighbourhood. The method we have used is done in a few minutes and is accompanied by little or no hæmorrhage.

Method.

An incision is made behind the ear in the well-marked posterior auricular groove between the head and the neck muscles. The centre of the incision is over the most prominent anterior part of the processus mastoideus, which can be easily felt through the skin at the point where the linea nuchæ superior turns forward toward the processus zygomaticus. Separating the tissue between the head and neck muscles, the latter part of the nuchal ridge and the anterior inferior border of the pars mastoidea are exposed. The attachments of the neck muscles (splenius, longissimus capitis, semi-spinalis capitis, obliq. capit. super.) so far as necessary are cut close to the bone, and by means of a periosteal elevator are stripped back so as to expose the pars mastoidea. There is no hæmorrhage to delay the operation, and, as a rule, no vessel requiring ligating ; should the animal be small, in order to get sufficient space it may be necessary to expose and ligate the posterior meningeal artery as it enters its foramen in the occipital mastoid suture.

The muscles are now held aside by retractors. A small trephine opening is made in the mastoid bone and a plug varying in diameter from about $\frac{1}{4}$ inch upwards is removed (fig. 1). This comes away easily because the external layer of the mastoid is here separated from the otic bone by spongy diploic bone. This spongy part can be further removed with a small chisel or curette till the white shining hard otic bone is clearly seen. (See Plate 13, figs. 1*a* and 1*b*.)

The canals, especially the horizontal and posterior, come so close to the exposed capsule of the otic bone that when stimulation of the labyrinth is desired no more need be done. Should it be desired to destroy the labyrinth the following points have to be noted : In the centre of the trephine wound and separated from it by a thin plate of bone lies the deepest part of the fossa subarcuata. This part may often, especially in young dogs, be observed as a small area less shining in colour and less hard, so that one can push a dissecting probe through into the fossa. With this point as a guide it is easy to locate and open the canals and vestibule and destroy the eighth nerve. The external canal lies along the floor of the opening in the bone, and, slowly removing the bone with a small chisel, the canal is exposed. Then working more medial-ward than lateral-ward one exposes the posterior canal, and then the vestibule. The advantage of working in this direction is that there is no danger of opening into the lateral sinus. By means of a small sharp excavator the parts can be well cleaned out and the opening extended into the internal auditory meatus. Owing to its position the cochlea is not directly injured. The wound is closed with sutures and a dressing applied.

To cut the eighth nerve intracranially the same incision is made as to expose the labyrinth. The posterior meningeal artery is ligatured and the bone carefully removed between its foramen and the pars mastoidea. Into this opening a probe flattened at the end is inserted, and the dura is carefully elevated in a downward and inward direction until twitching of the face indicates that the seventh nerve is reached. A special probe is now used, bent so as to enter the internal auditory meatus. By means of it the seventh and eighth nerves are destroyed. The hæmorrhage is often very considerable.

The semicircular canals of the cat are more superficial than in the dog, and are easily accessible by operative procedures. After shaving a considerable area of skin around the ear, the lambdoidal ridge of the occipital bone and the bulla of the temporal bone are located with the fingers and an incision made in the skin, beginning about halfway between the external ear and the median line of the skull and extending down over the bulla tympani. The temporal muscle is freed from its attachments at the lower part of the lambdoidal ridge and along the posterior part of the posterior root of the zygoma.* A small trephine opening, a few millimetres deep, in the temporal bone immediately in front of the lambdoidal ridge and just above the posterior root of the zygoma will expose the hard otic bone in which the semicircular canals are embedded. They are easily destroyed with a chisel and a sharp excavator. If care is taken to avoid the sinuses just posterior to the wound the hæmorrhage is very slight. If stimulation of the semicircular canals is all that is desired, they lie so close to the surface that no excavation need be done. So sensitive are they to changes of temperature that simply removing the temporal muscle from that portion of the bone in a room that is only moderately warm will be followed by a deviation of the eyes to the exposed side. In all our experiments our operative results were verified by *post-mortem* examination.

As the animal during part of the investigation is under an anæsthetic the question of the position of the eyes under a narcotic is important. In these experiments the narcotic was pushed so far as to avoid two main sources of error.

1. Voluntary movement of the eyes in light narcosis.

2. Involuntary movements which are apt to occur at different stages of narcosis in the dog.†

This possible error was guarded against by frequent observations, by observing both eyes, and by experimenting only when the animal was perfectly at rest and remained so under the stimulation.

Errors from voluntary movement are easily avoided, but not from involuntary. It not infrequently happens that such a stimulant as hot water or the electric current may so vary the depth of narcosis as to produce movements usually turbulent and irregular, especially of the eyes. This can be avoided by attaining such a depth of

* JAYNE, 'Mammalian Anatomy,' Philadelphia and London, 1898, Part I, fig. 125.

† RUSSELL, RISIEN, 'Journ. Physiol.,' 1894–5, vol. 17, p. 11.

narcosis as to deaden all pain reflexes, a stage which lies about the limit of the abolition of the eye reflexes. Especially is the attainment of this stage required in stimulations following removal of a part or the whole of the cerebrum.

The deviation and nystagmus were usually observed by means of Chinese white placed in the centre of the cornea of each eye.

It will be noted that the forms of stimulation used were :—

1. Mechanical or physical stimuli—pressure, heat, cold.
2. Electrical—we chiefly used the constant current.

Stimulation of One and of Both Labyrinths.

April 29, 1911.—Brown male dog. Exposure of periotic capsules in both ears.

Left labyrinth exposed first. Canals intact. Before stimulation right eye was deviated strongly downward and slightly outward. When ice was applied, *right* eye moved *upward* and to the *left*; while *left* eye moved *downward* and to the *left*. Observation repeated.

Hot water applied to left otic bone gave slow deviation of both eyes to right. Ether removed for a few minutes. Ice now caused nystagmus, with slow upward movement to left and a very slight quick downward movement to the right. Ether again given and both eyes are deviated to the left. Hot water following ice caused strong downward deviation and then deviation to right—slow movement to right in both eyes.

Electrical stimulation with constant current (two dry cells). When *carbon pole* (+) was in trephine opening, and zinc pole (−) placed on the muscles of the neck, there was deviation of left eye to left and downward; movement somewhat jerky, but tendency was distinctly toward left and downward. Rapid return of eye to normal (or at least former) position after cessation of current. Right eye in about normal position during flow of current, but was deviated downward and to right after current ceased to flow. Experiment repeated: Left eye moved slowly downward and outward (to left) during flow of current; right eye moved upward and inward (to left). When current was stopped left eye moved upward and inward (to right); right eye moved downward and outward (to right).

Zinc (−) *pole* was now placed in trephine hole and carbon (+) pole on muscles. Left eye moved upward and inward (to right); right eye moved downward and outward (to right). Movement more rapid than when + pole is in trephine hole. Observation repeated.

Right labyrinth now exposed; canals intact. Both eyes, right and left, were now looking straight ahead. *Hot* water; both eyes go to left and downward; movement slower in left eye than in right. *Ice* following hot water; both eyes moved upward and to right; movement more marked on left eye.

Hot water on both sides at once. Right eye deviated downward and to right. Left eye deviated downward and to the left. *Ice on both sides* at once. Both eyes turned upward.

Electrical stimulation of right labyrinth. Zinc (−) pole over right periotic bone turned left eye quickly downward and to left; returned slowly when current was stopped. Right eye moved *slowly* upward and to left; returned to right and downward quickly when current stopped. Carbon (+) pole over otic bone, left eye moved downward and to right; right eye, downward and to right.

Both sides simultaneously (three dry cells in each set). Zinc (−) of one set of batteries over right otic bone, carbon (+) of other set over left, other + and − on muscles at back of the neck, both eyes turned downward and to left. Then carbon (+) over right otic bone, zinc (−) over left, both eyes turned downward and to right. If both carbon (+) poles were connected with otic bones, and both zincs applied to muscles in neck, there was no result. If both zinc (−) poles were placed over the bones and both carbons (+) applied to the muscle, there was no result.

Left labyrinth now opened with chisel. Pressure of gauze on end of forceps caused both eyes to turn upward and to right.

Dog killed.

TABLE of Results. Dog, April 29, 1911.

Stimulation of left labyrinth.	Left eye (deviation).	Right eye (deviation).
Before stimulation	Normal	To right and down.
Ice	Down and to left	Comes back to normal.
Hot water	To right	To right.
Ice	To left	Up and to left.
Hot water	Down, to right	Down, to right.
Electrical (+) carbon *on*	Slow, to left, down	To left, up.
,, ,, *off*	Rapid, return to normal	To right, down.
,, (−) zinc *on*	Up, to right	Down, to right.
Pressure	Up, to right	Up, to right.

Stimulation of right labyrinth.	Left eye (deviation).	Right eye (deviation).
Before stimulation	Normal	Normal.
Ice	No movement	Up, to right.
No stimulation	No movement	Returns to normal.
Hot water	Down, to left; movement slower in left eye	Down, to left.
Ice	Up, to right	Up, to right.
Electrical stimulation (−) zinc *on*	Down, to left (quick movement)	Up, to left (slow movement).
,, ,, ,, *off*	Slow, up, to right	Quick, down, to right.
,, ,, (+) carbon *on*	Down, to right	Down, to right.
,, ,, ,, *off*	Up, to left	Up, to normal.

Stimulation of both labyrinths simultaneously.		Left eye (deviation).	Right eye (deviation).
Left.	Right.		
Hot water	Hot water	Downward to left	Downward to right.
Ice	Ice	Upward	Upward.
− (zinc)	− (zinc)	No result	No result.
+ (carbon)	+ (carbon)	No result	No result.
− (zinc)	+ (carbon)	Down, to right	Down, to right.
+ (carbon)	− (zinc)	Down, to left	Down, to left.

Summary of Results.

(1) Under an anæsthetic a dog shows only a deviation of the eyes, varying with the labyrinth stimulated and with stimulus employed.

(2) (*a*) Hot water and the negative pole give the same deviation of the eyes.

(*b*) Cold water and the positive pole give the same deviation of the eyes.

(*c*) The deviation produced by the former (*a*) is in the opposite direction to that of the latter (*b*).

(3) In electrical stimulation of both labyrinths simultaneously, equal electrical stimulation of both sides gives no result. Any inequality of stimulation on the two sides is attended with eye movements *away from side on which the stronger stimulus is applied.* Zinc (−) pole is stronger stimulus than carbon (+) pole. Therefore, (1) when zinc pole is over left otic bone, as when left labyrinth only is stimulated with negative pole, *i.e.* both eyes move to right; (2) when zinc pole is over right otic bone, as when right labyrinth only is stimulated with zinc pole, *i.e.* both eyes move to left.

This is in line with the law of polar stimulation that stimulation occurs at the cathode on closing the current, and agrees with WALLER and DE WATTEVILLE'S* results on electrical stimulation of human nerves. The real cathode is where the current *leaves* the nerve and the real anode where the current *enters* it. The current density is therefore greatest at the real cathode when the zinc terminal is in the trephine hole, and we have the most favourable condition for stimulation on closing the current. The conditions are least favourable when the carbon terminal is in the trephine opening. If we assume that there are two sets of nerve fibres, and that the endings of one set are more easily stimulated but less numerous than those of the other set, the stronger stimulus will bring about excitation of the more numerous fibres, and will accordingly cause deviation of the eyes to the opposite side. Such an assumption agrees with the experimental results of LEE,† who found that mechanical stimulation might produce movements either in one direction or the other according to its intensity. Also with the histological findings of CAJAL,‡ who found two distinct types of nerve endings. The weaker stimulation—closing the current when the carbon pole is in the trephine hole—will stimulate the more easily excitable but less numerous set of fibres, and bring about deviation of the eyes to the stimulated side.

DESTRUCTION OF ONE AND OF BOTH LABYRINTHS.

The results of stimulation of one and of both labyrinths having been ascertained, it now was necessary to observe the nystagmus and the general attitude of the animal following extirpation of one or of both labyrinths. The series of observations has been divided into—

I. Unilateral destruction.
II. Bilateral destruction—on separate dates.
III. Bilateral destruction—at same time.

Only one experiment will be quoted under each of these divisions, having special regard to what we consider typical results. Other experiments will be referred to

* WALLER, 'Phil. Trans.,' 1882, vol. 173, pp. 961–991; 'Proc. Roy. Soc.,' 1882, vol. 34, pp. 366–370.

† LEE, 'Journ. Physiol,' 1894–5, vol. 17, p. 205.

‡ RAMON Y CAJAL, 'Histologie du Système Nerveux de l'Homme et des Vertébrés,' Paris, 1909, vol. 1, p. 758.

when it is necessary to illustrate certain phenomena, as, for example, when reference is made to swimming movements in the non-labyrinthine dog.

I. *Unilateral Labyrinthine Destruction.*

February 6, 1911.—Black dog. Left labyrinth destroyed under ether anæsthesia. Nystagmus appeared before operation was finished; in left eye vertical, slow movement down; in right eye horizontal, slow to left. Later there was a general direction of *slow to the left*, *quick to the right*, in both eyes. The occiput was approximated to left shoulder. The animal fell and rolled to left. There was facial paralysis on left side.

Two and a half hours after operation there was seen twitching of M. corrugator supercilii medialis on right side, not on left. The head was twisted distinctly to left, with occiput approximated to left shoulder. The hind leg on left side was thrust outwards from the body. When the dog walked, he turned towards side of lesion, and fell over towards the left side. If turned over on the back, he got up on left side. The nystagmus was very rapid; with the snout held upwards it was in the horizontal plane, but, as a rule, the nystagmus was so varied that little can be said about planes, though the general direction was always slow to left, quick to right.

February 7.—Nystagmus was not so rapid as yesterday; the slow movement was down and to left, the quick up and to right. The dog turned to left in walking, and rolled over to the left. Right limbs were extended, lay projecting when asleep, and seemed longer when walking. For the most part he lay on left side. The head was twisted so that the angle made with line drawn through the external canthi of the eyes made with the horizontal plane an angle of 24°.

February 8.—Nystagmus had almost disappeared, was slight and rotary, slow to left, quick to right. The staggering gait was less marked, but still to left, and was noted chiefly if dog tried to turn rapidly. Nystagmoid movements were observed in both corrugator muscles.

February 9.—Gait improved, but still tended to fall to left side. When walking forward lurched to left side. Nystagmus was very slight, and only observable if the upper eyelid were elevated and the blood-vessels watched. It was rotatory with the slow phase to left. Slight nystagmoid movements of corrugator muscles.

February 20.—Held head toward left side. No nystagmus. Facial paralysis on left side. Drop reflex shown in right hind leg, not in left.

General Summation of Results:

A. *Deviation of Eyes and Nystagmus.*—Immediately after unilateral destruction of the labyrinth the eye of the injured side is deviated down; later, down and slightly out; on the uninjured side the deviation is towards the side of the lesion, occasionally with a slight upward movement. The first result agrees with that of RISIEN RUSSELL,* the latter with those of VON BECHTEREW †; probably the difference between these two observers was due to the time at which the observations were recorded. Later, the deviation is down and to the injured side in both eyes. Speaking generally, it may be said that after labyrinthine destruction the eyes are deviated to the side of the lesion.

The nystagmus is composed of two distinct phases, a slow movement and a quick jerk back. The nystagmus is synchronous in both eyes, and is constantly present

* RUSSELL, RISIEN, 'Journ. Physiol.,' vol. 17, p. 13.

† BECHTEREW, quoted by R. RUSSELL, *loc. cit.*

for some days following the destruction. The irregularity of the direction of the movements of the two eyes within the first 24 hours is marked. When the animal comes out of the anæsthetic it is nearly vertical in the eye of the operated side and horizontal in the eye of the non-operated side. The variation appears to us to be due to the resultant (*a*) of the relative over-activity of the opposite labyrinth, and (*b*) the irritation of the vestibular nerve in the wound, and, it may be, the canal most affected. It reaches the maximum within 24 hours, and varies in intensity with the position of the head. Thus, if the head be turned 90° in the direction of the slow deviation it is diminished, if turned 90° to the opposite side it is increased. From that time on it becomes less marked, till finally it disappears on the fifth or sixth day. During the greater part of the time it is present it is more or less horizontal in both eyes. As the nystagmus begins to disappear the movements become distinctly rotary. But no matter how the nystagmus may vary, the general direction of the phases of movement is such that the slow phase is always directed to the injured side and the quick phase to the uninjured side. In other words, the slow phase corresponds to the direction associated with the ocular deviation following labyrinthine destruction.

B. *The General Attitude of the Animal* (figs. 2, 3, 4).—Immediately after the operation the attitude of the animal is very characteristic. After allowing the animal to come out from under the influence of the anæsthetic, if it be placed on the floor ventral side downward so that the hind feet are squarely on the floor, there is a torsion of the head to the injured side so that relative to the dorso-ventral axis of the body it is inclined about 30°–45° from the vertical at the shoulders. The injured side of the head lies towards the floor. The head is also twisted about 70° to the injured side. On attempting to move, the animal rolls over towards the injured side. The animal is unable to walk, and, if stood up on its feet, will fall over to the injured side.

On the following day the pronounced torsion of the head is decreased. The head is markedly inclined to the injured side, but the animal is able to stand alone, and even to walk a little. It falls over to the injured side on slight provocation, and goes continually in a circle, turning towards the injured side in walking. It may be able to cross a room by going in repeated circles.

On succeeding days the animal becomes more steady on its feet, until at the end of a week it seldom falls to one side, and walks in a straight line. At the end of the second week the animal has assumed its permanent attitude. It now stands erect with torsion of the head to one side, always with the occiput of the injured side twisted downward and forward, and the anterior part of the body inclined somewhat to the injured side.

The torsion of the head in the dog or cat persists (figs. 5, 6, 7, 8). It is diminished when the animal is at rest, but is markedly increased if the attention be directed to anything and especially if the hearing be stimulated, for example, by whistling or crying softly. This is in agreement with our conception that the torsion is due to over-activity of the uninjured labyrinth.

Walking or running in a straight line is now possible, and the animal becomes able to swim without much difficulty on the first trial. Its deportment when blindfolded does not differ essentially from that of a normal dog. The drop reflex is seen on the normal side only.

The results of intra-cranial section of the eighth cranial nerve, without injury to the fifth or ninth, are essentially the same as after destruction of one labyrinth. The nystagmus is similar though rotation of the eyes is more evident. There is the same torsion of the anterior part of the body and of the head to the injured side, and movement in a circle on attempting to walk.

II. *Bilateral Destruction on Separate Dates.*

February 20, 1911.—Destruction of right labyrinth of dog whose left labyrinth was destroyed on February 6, 1911.

Immediately after the operation, the eyes were deviated to right and slightly downward with nystagmus horizontal. After coming out of the anæsthetic (12.15 p.m.) the dog did not roll over and over as after extirpation of one labyrinth. Coarse tremors of the head were present. The animal was unable to stand, and fell to either right or left, mostly to left, but did not turn over. Lay with head and body erect, all four feet on floor and forelegs extended. Right legs appeared stiffer than left. Head still inclined to left as before second operation but less marked. Sometimes turned to right in effort to rise, but mostly to left. Apparently had less strength in left legs than in right. Panted from the exertion; head swayed widely from side to side. Rotary movement of whole head to the dog's right. Hind feet spread wide apart. Legs on right side stuck out at greater angle to vertical than on left. Nystagmus horizontal, quick movement toward left, slow toward right.

1.30 P.M.—Eyes still deviated to right. Nystagmoid movements especially marked in corrugator muscles of both eyes. Held head to left side. Inclined to roll toward the right. Deviated toward left in walking. Rotated whole body to right. Coarse tremors of head present, but not so marked. Left legs weaker than right. Left hind leg inclined to give way. Ran about incessantly, and panted from the exertion. Could not drink from basin.

February 21.—Nystagmus had disappeared. Eyes not deviated. Walked with limbs well apart. Staggered and tended to fall to right. Could not drink, fed water through stomach tube. Body rotated clockwise.

February 27.—When dog came out of cage it fell on right side. Tried to walk but was shaky and fell to left. Seventh nerve not cut on right side.

March 7.—Hood was placed over both eyes, then when sitting inclined to left; when dog walked revolved in circles to right; angle of head unaltered. Side to side movement of head similar to those of white pomeranian (p. 141). Curious stiffening of limbs. Without hood, head is turned at angle of 17° to the left—angle measured through canthus of eyes and horizontal.

March 22.—Beginning about two weeks back, had gone in small circles to right when eyes were bandaged. Could walk in a straight line when not blindfolded. When the bandage was first put on over eyes he would rotate rapidly in a small circle until fatigued. Held head slightly to the left side. Killed, lesions verified *post mortem.*

Summary of Results:

The effect of removal of the second labyrinth varies somewhat with the length of time after the first operation, but, in general, the effects are less severe the longer the interval between the operations. The head and anterior part of the body are not twisted to the recently injured side; on the contrary, the head comes nearly but not quite back to its normal position and remains there (fig. 9). The nystagmus is present for a few hours and has disappeared by the next day.

The direction of the nystagmus after removal of the second labyrinth is of particular interest in connection with the question whether the unilateral labyrinthine extirpation effects are due to stimulation of the vestibular nerve by irritative processes in the operation wound or are due to the relative over-activity or unbalanced action of the remaining intact labyrinth. In the event of unilateral extirpation, it is conceivable that both agencies are active and that the observed phenomena are simply the resultant of two forces. In the event of removal of the second labyrinth after an interval, stimulation is the only agency operative. If the effects of unilateral extirpation are due to stimulation in the operative wound, the intact labyrinth might be expected either to exert no influence on eye movements, or to exert an influence tending to diminish the effects of the stimulation. Under these conditions the nystagmus after removal of the second labyrinth should be just as marked as, or even more marked than, after removal of the first labyrinth, and the eyes should be deviated to the recently operated side as is invariably the case after unilateral removal. This, however, is not always the case; after destruction of the second labyrinth the eyes may be deviated to the opposite side. In a dog after the first operation (April, 1909), in which the right labyrinth was destroyed, the eyes deviated to right. At the second operation (March, 1911) the left labyrinth was destroyed and the eyes again deviated to the right. Moreover, in all the cases of bilateral operation the nystagmus was less marked after removal of the second labyrinth than after the first operation, and passed away in a shorter time. We have also found that hot water or the negative pole of the battery—the strongest stimulation for the intact labyrinth—when applied to the injured labyrinth will stop nystagmus following unilateral operation. The direction of deviation of the eyes after unilateral removal is opposite to the direction of deviation of the eyes on stimulation of that labyrinth with hot water or the negative pole of the battery, and in the same direction as the deviation on stimulation with cold water or the positive pole. Again, the head does not suffer torsion to the side of the second injury as it should if the first torsion was due to irritation in the wound. The conclusion is unavoidable that irritation plays very little part in the production of labyrinthine effects as the result of a clean operation without infection.

III. *Bilateral Extirpation of the Labyrinth—at Same Time.*

February 13, 1911.—Pomeranian dog. A cotton plug was left in trephine wound on left side. Right side done first.

One hour after operation there were coarse trembling movements of the head much like a turtle after loss of both labyrinths. No nystagmus on looking forward. On looking to left slight nystagmus appeared. No nystagmus on looking to right. The animal could not walk. When standing both forelegs were extended. No drop reflex. When held up on all four feet swayed from side to side, but settled down with a fall either to one side or the other; feet spread wide apart, and head swayed up and down about longitudinal axis, but not moved so much to the side.

After operation on the right side the nystagmus was very pronounced in both eyes on allowing the animal to come out of the ether slightly. After removal of the right labyrinth the canals of the left labyrinth were exposed and hot water in the left trephine wound caused nystagmus. The left labyrinth was now destroyed. The nystagmus was very slight on coming out of the ether. It was not at all noticeable when the animal was still. Rather slow nystagmus appeared after the head was moved about violently for some time. When lying on the left side some nystagmus from right to left. Right eye apparently not deviated; left eye showed considerable white on median side, that is, it was deviated to left. It is suggested that this deviation in the eye was due to the minimal stimulation of plug. On putting the animal down on the floor it turned first to the right side, hind feet squarely on the floor with torsion of body to the right, foreleg or right shoulder partly on floor, and head resting on right side on floor with the nose pointing to the left. Did not roll completely over. A little later it lay over on left side, but did not turn completely over. On carrying animal, head was moved about in the air very much as after unilateral extirpation.

February 16.—Attempted to sit up for the first time. There was oscillation of head when raised. No nystagmus. Lay flat on abdomen and head. If put on feet fell backwards. Afternoon—sat up and appeared better.

February 20.—Stood up and walked about room for the first time since operation. Could not eat or drink unaided till to-day. Did not turn to one side more than to the other. Walking slow and hesitating, with hind limbs far apart. Staggered, but to no particular side. Not so prone to sit or slide backwards, though this was still seen a little. Held head steady. No evidence of hearing. No nystagmus.

February 23.—Killed. No hæmorrhage in either fossa. Operation had opened superior semicircular canals and vestibule on each side.

January 19, 1912.—White-and-tan dog. Destruction of both labyrinths under morphia and ether. Considerable hæmorrhage on right side from deep artery in bone, and cotton plug left in wound on that side.

At close of operation, left eye was deviated down and to left, right eye up and to right; no nystagmus; some tendency to torsion of head to left, but not marked; no rolling to either side. One hour afterward, the nictitating membrane was drawn well over the eyeball of each side; the left eye was now turned somewhat upward and to the left; the right eye, slightly down and to the right.

Three hours after operation: no constant nystagmus; may be quick either to right or to the left. Eyes deviated, each to the outside. Pupils rather wide, although the dog was still drowsy from the morphine. When put down on the floor would roll to left and then back to right. Head moved from side to side or up and down, but not rotated much. When put ventral side down on the floor with feet outstretched, dog would not allow hind feet to be abducted strongly, but would pull them back, so no loss of muscle sense on either side. No drop reflex.

January 20, 1912.—Had received no morphia since previous day. Lay quiet in the cage. No nystagmus. No drop reflex. No torsion of the head. No rolling over and over to one side. Unable to stand. Would not allow abduction of hind feet. The absence of eye movements indicated the minimal stimulation that arose from irritation in the wound. The muscular symptoms must be, then, deficiency phenomena. Photographed in two positions (figs. 10, 11).

January 22.—No nystagmus on looking straight ahead. No constant deviation of the eyes. Some nystagmus, small and very rapid, when the eyes were directed to either side. When dog looked to left it was quick to left, slightly rotatory in right eye. The looking to the left was a conscious effort, and the nystagmus seemed to be the resultant of a slow movement bringing the eyeball to the right and a quicker movement bringing it again to the left, in which direction the dog's attention was fixed. Walked about somewhat awkwardly, but without falling to either side. Turned in circles at times, sometimes repeatedly, going either to right or left. Could walk in a straight line. Hind feet usually held wide apart. When held closer together as in the case of a normal dog in walking, the hind part swayed to right or left, necessitating a step in one direction or another to keep from falling. Some tendency to settle back on haunches and to lie with feet outstretched. Head thrown backward at times. Scratched bandage about head with fore or hind feet.

Could drink from a basin on the floor. Considerable oscillation of the head. Rotatory motion of nose in getting it into a basin. Fluid thrown out on floor, mostly in front of nose, by tremors of head, when drinking. Lower lip gaped more on left side then on right. Tremors of head, about long axis, when standing still. When set down on the floor and suddenly let go, might stagger forward. Would not allow hind feet to be abducted, either when lying ventral side down or when standing. Could back out of a corner or from behind obstacles. Head sometimes swayed widely from side to side.

Summary:

When both labyrinths are removed at the same time the deportment of the animal shows several important departures from that seen after unilateral extirpation. Immediately following the operation the animal does not show the torsion of the head and anterior part of the body to one side, and does not roll over to either side. The animal refuses to stand, and if stood up, settles back upon its haunches and comes down upon the floor. The head sways from side to side with a coarse trembling movement. Nystagmus does not appear or is fleeting and inconstant for a few hours.

The picture is much the same on succeeding days. The animal refuses to stand or walk, and while there is no forcible rolling over and over as in the case of unilateral extirpation of the labyrinth, it may lie helplessly on its back with its feet in the air. The coarse tremors of the head persist, and extreme uncertainty of movement of the muscles of the neck and head is evident. The animal may be wholly unable to eat or drink unaided. It will swallow when liquid or solid food is placed in the mouth, but may be unable to grasp food set before it.

Some of these symptoms gradually become less and less prominent until they disappear. The animal may begin to stand and walk alone during the second week after the operation. The coarse tremors of the head persist, and uncertainty of movement is still manifest.

The drop reflex—the extensor thrust of the hind feet when the animal is held upright by the fore limbs or shoulders and suddenly lowered toward the floor—is absent in the hind leg of the side on which the labyrinth is destroyed, although the other leg reacts normally, after unilateral labyrinthine extirpation. This reflex is, apparently, homolateral with reference to the labyrinth. The drop reflex may disappear on both sides after bilateral labyrinthine destruction, but it is not abolished, though permanently reduced. We have seen it five months after removal of both labyrinths, the second labyrinth having been removed two weeks after the first. We do not know the minimal time required for its return.

Certain differences in the deportment of dogs with cerebrum intact as compared with decerebrated dogs are apparent after bilateral extirpation of the labyrinth. SHERRINGTON* states that the decerebrated dog will stand after destruction of both labyrinths or intracranial section of both acoustic nerves. In bilateral extirpation of labyrinth with brain intact the animal cannot stand. It is evident, therefore, that some cerebral influence enters into the deportment of the dog whose brain is intact. One gets a suggestion of what the cerebral influence is on observing the results of removal of both labyrinths in the white rat. Here the animal from the first fixes itself more or less firmly to the ground—within a few hours it has assumed a typical position with the whole body extended and resting with the ventral surface closely applied to the ground with limbs extended. The limbs, especially the fore limbs, firmly clutch the ground and any attempt to make him move results in a firmer grasp of the surface. It is a typical attitude suggesting vertigo (fig. 12).

In addition to the eye movements and general attitude of the animal, its deportment in swimming is of interest. We give abbreviated notes on swimming as observed in two dogs, one with unilateral destruction of the labyrinth, and one with bilateral destruction. The operations had been done about a year previous to the swimming trials.

May 21, 1910.—Dog, right labyrinth destroyed April 25, 1909. Taken out to swim. Had little or no difficulty in doing so. Sometimes turned over and over in the water before starting, but usually came to the surface when thrown in and started for the bank without rotation or turning in a circle.

May 21, 1910.—Female fox terrier, both labyrinths had been destroyed a year before. Taken out to swim. On being thrown into the water had difficulty in righting herself, sometimes kicked around in water, head down and belly up, or swam on side. When swimming on her side she would sometimes turn and go head downward into the water. When on her back with feet up she would sometimes turn head downward into the water. Sometimes moved in a circle without progression in any definite direction. Once or twice she righted herself and swam straight out to the bank, without turning over in the water. It would appear that in a certain number of trials she would be successful in swimming, but on the first attempt would apparently have drowned.

THE EFFECT OF LESIONS OF THE CEREBELLUM ON LABYRINTHINE REACTIONS.

Having defined the reactions which follow irritation and destruction of the labyrinth, it becomes necessary to ascertain what influence the cerebellum has on these results. In order to do so the cerebellum was removed partly or entirely, and

* SHERRINGTON, "Remarks on the Reflex Mechanism of the Step," 'Brain,' 1911, vol. 33, p. 1.

at a later date the labyrinth was stimulated and destroyed. The following are given as typical of a series of experiments :—

(1) Partial destruction.

(a) Dog, June 23, 1911—removal of left lateral lobe and the corresponding half of vermis.

(b) Dog, April 24, 1911—removal of posterior half of vermis, nearly whole of left lateral lobe, and anterior and medial part of right lateral lobe.

(2) Complete destruction of cerebellum ; dog, May 4, 1911.

Operation :—Under morphia and ether the muscles attached to the occipital bone were detached, together with the periosteum, and turned back. The skull of the dog was trephined near the middle line below the occipital ridge. The dura was opened, and the cerebellar tissue removed with a blunt curette. Hæmorrhage was stopped by pressure on the sinuses, and by the application of hot normal salt solution. The dura was then closed, the muscle replaced, and the external wound sutured.

(1) *Partial Destruction.*

(a) Removal of left half of cerebellum in dog.

June 23, 1911.—Immediately after the operation the left eye was nearly normal in position, but the nictitating membrane was more prominent than usual; the right eye was slightly deviated to the right, and down. Later the left eye was deviated to the right and up, the right eye to the right and a little down. Oscillation movements were present in both eyes; when first observed they occurred in a nearly vertical plane, either as one quick upward jerk, or two or three in succession. There was no labyrinthine nystagmus in either eye. There were slow rolling movements of the eyes when the head was turned. When the snout was turned 90° to the left and up, both eyes rolled slowly down and to the right; they came back to nearly normal position when dog lay quietly on the floor. When disturbed the head was turned to right; the animal might roll over to right and come to rest on right side.

June 24.—Dog twisted to left—left pleurosthotonos. There was extension and marked rigidity of left fore limb; the left hind limb was rigid, but to a less degree. At rest both eyes were deviated outwards and slightly up. When disturbed the eyes oscillated now in one plane, now in another. The dog preferred to lie on right (non-operated) side. (THOMAS* says on operated side.) When lying on right side, if head were turned 90° to the left, there was marked increase of oscillation of the eyes, which were now rolled slightly down. If dog were laid on the left side and head twisted 90° to the right the oscillations were diminished, or might even stop.

Post-mortem examination showed that the left lobe of the cerebellum had been completely destroyed, excepting a small part of the left lower border. The vermis was destroyed on the left side. The incision had gone through the left lobe down to the roof of the fourth ventricle (fig. 17).

(b) Removal of posterior half of vermis with anterior and medial part of right and most of left lateral lobe.

April 24, 1911.—Brown male dog. No oscillation of eyes on coming out of ether. Right eye looked straight ahead; left eye was strongly deviated in and down. Both pupils dilated, overcoming influence of morphia. Head drawn strongly backwards and somewhat to left. Some hours later some slight oscillations were observed. The head, which was turned to left, rotated counter-clockwise.

April 25.—No oscillation of eyes when animal was at rest. Strong extension of all limbs, fore and hind. Head drawn from the side while attitude of head was typical. Head rotated counter-clockwise.

* THOMAS, ANDRÉ, 'La Fonction Cérébelleuse,' Paris, 1911, p. 78.

Pupils widely dilated so that iris was almost completely obliterated; deviation of left eye still present, but not so marked as on previous day.

April 26.—Lying on right side in cage. When he tried to get up, snout went clockwise. Right limb extended and stiff; left fore limb drawn in strongly to side. Pupils dilated. No oscillation of eye. Right eye turned upwards so that white was seen below. Could not sit erect unless held; tended to fall back on haunches; when supported, fore limbs were firmly extended. Not able to drink water.

April 27.—Pupils dilated. No oscillation of eyes. Had still to be held on being fed. Unable to stand; when making an attempt to go forward, raised himself on haunches and worked his fore feet.

April 29.—No oscillation of eyes. Pupils not widely dilated ordinarily, but, on attempting to move, pupils become widely dilated. On attempting to move, dog would sit up and might rear over backwards. Head not held so far back as on first and second days. Still fed through stomach tube.

April 30.—Fed with pieces of meat; swallowed readily when meat was put in the mouth, but the muscular incoördination was so pronounced that he could not grasp the meat when it was held at a little distance from his nose. Head was thrust out in the attempt, but the snout struck to one side or above or below the meat, seldom touching it squarely. Held up its head in recognition and wagged tail when spoken to; tail movements were apparently normal.

(2) *Complete Destruction of Cerebellum.*

May 4, 1911.—Dog, light yellow, male. About one hour after operation the right eye was deviated strongly downward; the left eye looked straight ahead. No oscillation of eyes. Both fore legs in strong extension and both hind legs strongly flexed.

May 5.—Limbs rigid; fore limbs extended, hind limbs flexed. Taken out and fed with hot milk through stomach tube. Head drawn back. No attempt to stand (*cp.* non-labyrinthine dog, figs. 9, 10).

May 6.—No oscillation of eyes when at rest, but occasionally, when the animal moved, the eyes showed a slight oscillation, which was more a twitch than a nystagmus. Slight tremor, especially in lower limbs and lower part of body. Rigidity of muscles. Later in the day the head was held strongly bent toward right side, but not twisted to one side. The eyes were turned somewhat to right and upward. Slight, quick, oscillatory movements upward and to right.

May 7.—Twitchings of the eyes only occurred occasionally and in any direction to right or left or vertical, with quick movements. These were synchronous and in same direction in each eye. Hind limbs strongly extended and rigid. There was no relation between the twitching of body and the oscillations, *i.e.* the one occurred independent of the other. There was a little twitching of the facial muscles. The twitching was chiefly in lower part of body. Fore limbs more or less extended rigidly. Head showed slow tremulous movement when held up; if head were held forward the dog fell back. No drop reflex. If sole of foot were tickled, the foot was drawn up very slowly, sometimes not at all.

May 8.—Condition and appearance much the same as on previous day. Wagged tail when spoken to. Fore limbs stiffly extended when held up in one's arms. Feet were put down on the tip of the toes, and the toes were quite as apt to be doubled under, allowing the backs of the fore feet to touch the table, as to turn up and allow the soles of the feet to come down. Perhaps more marked tendency to rear over backwards than on previous day. General activity somewhat greater. Ate greedily of meat. At first meat had to be thrust into its mouth, but later it would take meat from the hand when its head was held. Water given through a stomach tube (fig. 13).

May 10.—Ate freely from floor, but could do so only with head turned back across body. Slight oscillations on forced movement of eye, none with eye at rest. Quivering of muscles all over body. Could not drink water, which had to be given through tube.

May 19.—Drank for first time to-day. Barked. Lay on stomach, hind feet extended. Head for most part resting on floor, but sometimes raised. When held up, head swayed constantly.

Post mortem.—Showed complete removal (fig. 18).

Summation of Results.

Deviation of Eyes.—When the left half of the cerebellum is destroyed, as soon as the animal comes out of the ether the left eye is normal and the right eye is deviated to the right and down; later, the left eye is deviated to the right and up, the right eye to the right and down. Later, when the dog lies quiet, both eyes may come to normal, and if the head be turned to the left the eyes will slowly draw to the right. On the next day when the animal is quiet there is an outward deviation of each eye. When destruction is not total but passes to both lobes of cerebellum, on coming out of ether the right eye is directed straight ahead, the left deviated strongly to the right and down; on the following day the left eye is still deviated to the right, but not so markedly as on first day; the position of the right eye is normal, but later is turned upwards.

So, while the deviations may be said to be irregular, the general character is toward the side opposite the lesion. This is in accord with the findings of LUCIANI that ablation of one lateral lobe caused both eyes to move to the opposite side; and of FERRIER that electrical excitation caused movement of both eyes to the same side. The deviation of one eye down and of the other up accords with HITZIG'S results on stimulation of the lateral lobe in the region of the flocculus.

Nystagmus.—When the left half of the cerebellum is destroyed, as soon as the animal comes out of the ether there are synchronous oscillations of both eyes nearly vertical in direction. When destruction is not total but passes to both lobes of cerebellum, on coming out of the ether there is no oscillation of the eyes, but some hours after the operation slight oscillatory movements are seen. On the next day in both cases oscillatory movements occur only when the animal is disturbed in any way. At first they are nearly vertical, next day they are well marked, now in one plane, now in another. If the head be turned 90° to the left the oscillations are increased, if turned 90° to the right the oscillations are diminished or may even stop. There never appears labyrinthine nystagmus, that is, oscillations showing the double phase of slow deviation followed by a quick return.

Attitude.—After the operation, when disturbed, the head is turned to the right and the animal may roll over to the right, coming to rest on the right side. Next day there is marked bending of the whole longitudinal axis of the body to the left (left pleurosthotonos). The left fore limb is markedly rigid; the left hind limb is rigid but to a less extent. The head is drawn somewhat to the back and to left, but there is no torsion of head about the long axis of body as after labyrinthine extirpation. The head rotates counter-clockwise. If the dog attempts to rise he gets into a state closely resembling convulsions.

The pupils, especially in (*b*), are dilated on coming out of the ether, showing overcoming of influence of morphia by some cerebellar effect. Next day the pupils are more widely dilated. There could have been no irritation of the pons, as this would tend to cause contraction of the pupil. The dilatation of the pupil gradually passes off, particularly when dog is quiet, but for some days the dilatation follows any violent attempts to move. For the first few days the animal is not able to take food and has to be fed through a stomach tube.

The main points in a comparison of destruction of the left labyrinth with destruction of left lobe of cerebellum are :—

	Left half of cerebellum.	Left labyrinth.
Deviation of eyes . . .	To right	To left.
Movement of eyes . . .	Quick oscillations in any plane, especially if disturbed	Slow movement to left with quick return to right (Labyrinthine nystagmus).
	If head is turned 90° to left oscillations are increased	If head is turned 90° to left, nystagmus is diminished.
	No twitching of M. corrugator supercilii medialis	Marked twitching of M. corrugator supercilii medialis.
Attitude	Left pleurosthotonus	Torsion of head so that occiput is approximated to left shoulder.
	Snout to left	Snout to right.
	Prefers to lie on right side	Prefers to lie on left side.
Part affected	Posterior chiefly	Anterior chiefly.

After complete destruction while still under morphia, the left eye is normal, the right eye is deviated down. Next day there is little or no deviation—nor is any observed later. While lying quiet there are no oscillatory movements, but when disturbed they may occur at any plane—synchronous and alike in both eyes. Nothing similar to labyrinthine nystagmus was ever observed.

Having produced and observed the lesions following removal of a part or the whole of the cerebellum it now appeared necessary to observe in the same dogs the effects of stimulation and destruction of the labyrinth.

May 1, 1911.—Destruction of left labyrinth under morphia and ether of dog of April 24, 1911 (Posterior half of vermis—left lateral lobe—anterior and medial part of right lateral lobe).

Immediately after the operation the left eye was turned strongly down and to the right. Nystagmus first appeared in right eye* about one hour after the labyrinth was destroyed, slow to left, quick to right. There was no nystagmus in the left eye, but it appeared soon after, although it was still turned down and to the right. The head was held to the left side with corkscrew rotation. The animal was still drowsy and stupid under the effects of morphia.

May 2.—There was marked nystagmus, horizontal, slow to left, quick to right. Held head to left and back. Tended to fall to left side and back, with twisting movement of body.

Killed. *Post mortem.*—Very little hæmorrhage about operation wound. The posterior part of the vermis had been completely removed. Nearly the whole of the left lateral lobe had been taken away, and the interior of the right lateral lobe. The curette had removed so much of the cerebellum that the fourth ventricle was exposed, but uninjured. There was no injury to the vestibular nerves on either side.

* It is frequently the case that after destruction of the left labyrinth and section of left VIII nerve that the nystagmus appears first and most marked in the right eye, but it is not invariably so.

May 20, 1911.—Destruction of the left labyrinth of dog of May 4, in which there was complete destruction of cerebellum.

After removing the bone, but before opening the canals, the left labyrinth was stimulated with hot water. The eyes moved down and to the right, and slowly returned to normal on removal of stimulus. Observation repeated. The chisel struck into canal had the opposite effect to hot water. At the end of the operation the hot water produced no movement in eyes, but, when a probe was passed forcibly into the opening of a canal, the eyes turned up and to the left. On continued irritation with probe, the eyes moved slowly down and to the left. On coming out of ether there was continuous oscillation to the dog's left. This slowly disappeared, so that, 30 minutes after the operation, both eyes were deviated down and to the left, with occasional nystagmus, quick to the right and up; now and again there was a deviation of both eyes to the right.

May 21.—When the dog was first observed he was curled up to right, with nose resting on hind legs. There was horizontal nystagmus, slow to left, quick to right. When disturbed the nystagmus varied, and might be opposite in direction. When the head was brought slowly round in line with the body there was nystagmus of the eyes, slow to left, quick to right, at times showing reversal of direction. There was torsion of the head, with snout turned to right. When head held forward in line of body, getting rid of torsion, there was marked deviation of both eyes to dog's right, followed by several successive quick twitches to left. Then the left eye moved somewhat upwards, but slow up and quick down. If the snout were held up both eyes deviated down and to right, but when he came to rest the nystagmus appeared; the left eye moved slowly up to left, quick down and to right; the right eye moved slowly down and to left, quick up and to right. When the head was again held in horizontal plane in line of body, the nystagmus was horizontal—slow to right, quick to left, but at times it was slow up and to left. With head held upwards, left eye moved slowly up and to left, quick down and to right; right eye—slow down and to left, quick up and to right. Eyes might roll up and to right, with quick movement to left. Paralysis of left facial; twitching of M. corrugator supercilii medialis on left side. When head was turned to left side of body, there was quick movement of nystagmus to left and slow to right. When head was in line of body and dog's eyes directed to right, the slow movement of eyes was to right and down, quick to left and up; if the attention were directed to the left, the quick movement was to left. When the dog held his head up from the table, and turned it to the right, there was a slow oscillation to the right, the left eye frequently strongly deviated upward and to the right.

May 22.—Snout turned to the right (sound) side, so that line through external canthi of eye made an angle of 30°–35° to horizontal plane. When head was to front, eyes were deviated to right (sound) side, quick movement in nystagmus to left (uninjured) side, slow movement to sound side; both eyes moved synchronously. Marked tremors of limbs, particularly of the lower, but these had no relation to the nystagmus. When dog was allowed to lie quiet, with right side of head around on right hip, the head was inclined to right at an angle of 35°–45° to the horizontal; with right ear resting on right hind limb, head slipped down and came to rest on hind leg; eye movements were not regular, but showed quick jerking movements to various sides, but no regular nystagmus. When head was again held with snout upward, right eye—slow movement down and to right; left eye—slow movement up and to left, with slight counter-clockwise rotatory action. Rotation not so marked in right eye. When dog was allowed to lie quietly for a time on left side, with head fully extended in line of body, nystagmus in both eyes was slow to left and down, quick to right and up. These observations make it clear that the nystagmus observed to-day differs from nystagmus following unilateral labyrinthine destruction in the following particulars: (1) it shows great variations, but, if the dog is at rest, or the head is held, it is of labyrinthine type; (2) there is less distinction between quick and slow than occurs in ordinary labyrinthine nystagmus.

When dog ate, his head was held to right so that the eyes were inclined 80° to horizontal plane.

To observe more closely the difference between the effects of labyrinthine and cerebellar lesions, both on the same side, two cats were operated on the same day. The cerebellum is easily accessible in the cat, being reached through an opening in the skull extending just anterior and parallel to the linea nuchæ superior and behind the tentorium which lies nearly a centimetre anterior to it. There is no troublesome hæmorrhage, and the bone may be removed from a point immediately above the petrous portion of the temporal bone to the median line, affording a good view of the cerebellum. It is necessary to free the bone from the posterior part of the temporal muscle only, as the muscles of the neck lie outside the field of operation.

March 17, 1911.—Cat, three-fourths grown. Destruction of left half of cerebellum. Cat lay quiet afterwards, not moving unless disturbed. Some extensor rigidity in fore and hind limbs of left side; limbs of right side flexed, particularly the fore limb. Toes strongly flexed on sole of foot, not spread and claws not protruding. Preferred to lie on right side. When placed on left side, turned over at once, or lay on its left side and back with feet in the air making efforts to turn over. Nictitating membrane drawn well over eyes, particularly the left. Pinna reflex present on both sides. When held up by skin of the back, left limbs were rigidly extended; right flexed. Eye movements were not nearly so marked as in cat with labyrinthine lesion; slow wide movement of eyeballs to left, with slow return; some small trembling movements of eyes, not nearly so marked as in labyrinthine cat. No true nystagmus.

When placed with all four feet on the table, head was drawn upward, backward and to the left. Might also twist the head with nose to the right and occiput to the left, as labyrinthine cat does. Some tendency to rear backward, but such tendency was not marked ordinarily. When disturbed it turned a peculiar back-somersault, going back first on its haunches, then on pelvis, then on base of tail, and so on over, immediately turning over on right side when head struck the table.

Rather marked eye movements to left on anæsthetising preparatory to killing and removing the brain.

Cat, same date, adult. Destruction of left labyrinth in the morning. Nystagmus on coming out of ether; slow at first, quick movement to right, slow to left. Little permanent deviation of eyes; left was turned slightly outward. Lay outstretched on table, forelegs widespread to each side, head turned with left side down to table, hind feet turned to right. Nystagmus in various planes; sometimes rotatory. Left eyelid paralysed; nictitating membrane drawn over eye when eyeball was touched. Muscles on both sides of body rather rigid. Unable to stand. When placed with all four feet touching the table, head was twisted to left. When lifted and let down on table, all four legs were extended. Sole of right fore foot placed flat on table on lowering the cat, but left fore foot was turned under so that upper surface touched the table. Both hind feet touched in about the same way, but left one usually appeared to touch first.

When lying on left side, right legs might be extended and left legs flexed, both fore and hind. Not observed to roll over and over very much. Reflexes generally were apparently hyperexcitable. Would not lie on right side, but always turned over on left side when so placed. Lay quietly on left side for considerable periods.

Head turned toward body so that chin approximated ventral side—the opposite of opisthotonus observed in cerebellar cat of this date. Lay on opposite side of body from that assumed by cat with cerebellar lesion, although both lesions were on left side.

Jerked convulsively when table was struck or jarred, extending hind legs with feet widespread and claws protruding; left fore paw strongly flexed; right extended, with toes spread and claws protruding.

Summary.

The absence of the cerebellum does not in any way interfere with the normal reaction of the eyes to stimulation of the labyrinth by hot water. The nystagmus on the first day was of the usual labyrinthine character. The eyes were deviated toward the injured side as usual. Occasionally, however, both eyes were deviated to the uninjured side. The nystagmus when first seen on the second day was of the usual labyrinthine type. Variation and reversal of direction of the nystagmus became apparent on this day, and the quick twitches seen after removal of the cerebellum alone were in evidence. The nystagmus, varied and confused as it was, was a composite of labyrinthine and cerebellar influences, the former being evident in the slow wide deviation of the eyes and the latter in the quick irregular twitchings in every possible plane. When the dog was quiet the labyrinthine type was in evidence, when the dog was disturbed the cerebellar type became prominent. In time the labyrinthine effect wore off completely and only the cerebellar effects persisted. It is evident that if labyrinthine nystagmus ceases because of inhibition or compensation the inhibitory or compensatory mechanism, wherever it may be located, does not lie in the cerebellum. If the inhibitory mechanism lay in the cerebellum, removal of the cerebellum should increase labyrinthine nystagmus. This, however, was not the case nor did it last longer than usual. Whether or not there is a real inhibitory mechanism for labyrinthine nystagmus, there is apparently no such inhibitory mechanism, or at least none that is effective in the same length of time, for the ocular movements, arising from cerebellar ablation.

Another point of difference between the labyrinthine and cerebellar ablations lies in the general part of the body affected. LEE noticed that in the dog fish the anterior portion of the body was much more affected by labyrinthine removal than the posterior. The same conditions are seen in dogs and cats. Cerebellar lesions, on the other hand, are generally known to affect the posterior part of the body as well as the anterior, and the effect may be even more severe in the hind limbs than in the fore limbs.

THE EFFECT OF LESIONS OF CEREBRUM ON LABYRINTHINE REACTIONS.

Removal of a part or of the whole of the cerebellum made it obvious that the deviation of the eyes and the nystagmus resulting from labyrinthine stimulation or destruction was little if at all influenced directly from the cerebellum, and further that the pathway to the eye nuclei lay outside the cerebellum. It therefore became necessary to ascertain

(1) Whether the path from the labyrinth to the eye nuclei is direct by the fasciculus longitudinalis medialis (posterior longitudinal bundle) or whether other higher centres are involved.

(2) Whether removal of various parts of the cortex of the cerebrum changes the

labyrinthine effects. Since the quick component in the labyrinthine nystagmus could occur and could be produced only in the conscious state, suggesting a cerebral origin, it was determined to ascertain—

(3) From what portion of the cerebrum the quick component comes.

To accomplish this it was necessary to remove various parts of the cerebrum, and either immediately after or at a later date to observe the effects of labyrinthine stimulation or destruction. Our results are given in the following experiments:—

(i) Destruction of both occipital lobes of the cerebrum.

(ii) Destruction of approximately half of the cerebral cortex.

(iii) Removal of entire cerebral cortex.

(iv) Complete removal of whole cerebrum with severance of corpora quadrigemina and splitting of cerebellum in the median line.

(v) Effect of labyrinthine stimulation and destruction on decerebrated animal.

(i) *Destruction of Occipital Lobe of Cerebrum.*

Dog, June 12.—Left labyrinth had its bony covering partially removed, but still was intact. Then stimulation by hot and cold water and by the constant current gave the usual normal results, namely, the hot water and zinc pole deviation to right; cold water and carbon pole deviation to left.

(*a*) The left occipital lobe of cerebrum was now destroyed, and electrical stimulation of the left labyrinth gave usual normal results. The dog was allowed to come out of ether and nystagmus was observed slow to right in both eyes. The nystagmus could be arrested by the carbon pole in the trephine opening over the left labyrinth. On removing the carbon pole the nystagmus recurred. Slight ether anæsthesia arrested the nystagmus, then the eyes deviated to right, indicating an over-activity of the left labyrinth.

(*b*) The right occipital lobe of cerebrum was now destroyed. Stimulation of the left labyrinth with hot and cold water and with the constant current gave normal results. Later when the dog was less deeply under the anæsthesia, hot water in labyrinth produced a distinct horizontal nystagmus—labyrinthine in type, slow to right, quick to left. *Post mortem* showed both occipital lobes of the cerebrum removed (fig. 19).

Summary of Results:

(1) Removal of the occipital cerebral cortex has no effect on labyrinthine stimulation, nor on the resulting nystagmus.

(2) The normal labyrinthine stimulation can be checked by the carbon pole in the trephine opening.

(ii) *Removal of the Cortex of the Right Cerebral Hemisphere.*

Dog, October 25, 1911.—A large part of the right parietal bone was removed. The dura was opened and the right half of the cerebrum removed. There was little hæmorrhage.

Immediately after the operation the left eye was deviated markedly down and to the left, the right eye very slightly down and out, but so slightly that it might be regarded as normal. No nystagmus. Corneal reflex normal.

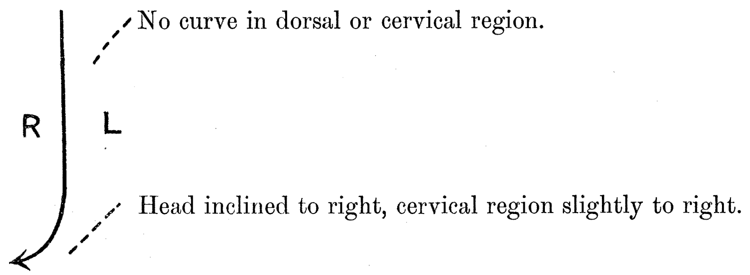
Two hours later: animal recovering from the effects of the anæsthetic, left eye deviated to left and head turned to left; could not stand; when held up left legs were extended, right more flexed. No nystagmus.

October 26.—Left eye was deviated to left and downward; right eye normal. No nystagmus. When finger was approached to right eye dog winked; when approached to left eye he took no notice. There was an occasional nystagmoid jerk in left eye, with slightly quicker movement to the right. Moved eyes in all directions. If dog observed an object both eyes could look straight ahead; if then the right eye were closed, the left eye deviated to left.

October 28.—The dog was found standing up leaning against the side of the cage. The right eye was now deviated to the right and the left eye normal. When eyes were turned very much to the right and attention was attracted, very slight oscillatory jerks were seen just for a moment; but these occurred only in the left eye. The dog was very somnolent. Attempted to walk about on the floor but tended to slide down. If placed on his feet could stand fairly well.

October 29.—Dog could now walk for a yard or two on the floor; in doing so there was a curious up-lift of right hind limb. This limb was raised higher than left, and thrust backwards. Only saw food placed directly to his right side; left eye appeared to be nearly if not entirely blind. The right eye was less markedly deviated to the right and down; the left eye is turned very slightly in.

Attitude of dog



November 1, 1911.—Stimulation and destruction of the left labyrinth of dog whose right cerebral cortex was removed October 25, 1911.

Before administering the ether it was noted that both eyes were normal; the former deviation of right eye down and to right had almost disappeared. When walking he turned more frequently to right than to left. When going under the ether, there was seen a maximum deviation of the right eye down and to right, but none in the left, an apparent return of the paralytic deviation.

The left labyrinth was now exposed but not opened. Repeated observations on the results of stimulating the left labyrinth with hot and cold water and with the constant current gave the usual normal results.

The left labyrinth was now destroyed. When coming out from the ether the left eye was deviated to the left and down, the right eye was deviated to the left.

November 2.—The dog lay with left ear twisted toward the shoulder. There was marked nystagmus in both eyes, slow to left, quick to right. When quiet there was a marked deviation of both eyes to the right, more marked than on previous days; superadded to this was the nystagmus alternately slow and quick in character, characteristic of left labyrinthine destruction. The marked deviation of eyes was cerebral.

November 3.—The dog was lying on the right side with head twisted so that snout and left ear were on ground. The deviation of eyes was to the right, but not so marked as yesterday. Nystagmus still present, slow to left, quick to right. When walking, tended to turn to the right. When sitting up, there was torsion of the head with snout to right.

It was noted that (1) if the snout were turned 90° to the right the nystagmus was very slightly increased, sometimes apparently not at all; (2) if the snout were turned 90° to the left the nystagmus was very slightly decreased, sometimes not at all, and (3) if the snout were turned 90° up there was no effect on the nystagmus.

Therefore, turning the head 90° to the right or left had little or no effect on nystagmus following left labyrinthine destruction subsequent to removal of right cerebral cortex, suggesting a cortical mechanism affecting the nystagmus.

November 4.—Dog rested his head on right foreleg with torsion of his head so that left ear was approximated to ground. Eyes were deviated to right, but not so marked as yesterday. The nystagmus, horizontal, with slow movement to left, quick to right, though still marked, was not so violent as yesterday. Sight wanting in left eye and nasal side of right eye.

November 5.—Torsion of head obvious. Deviation of both eyes to right, especially of right eye, but not so marked. On walking, turns to right. If head be turned 90° to right, nystagmus is not increased; if head be turned 90° to left, nystagmus not affected. Dog resisted very forcibly the turning of head to left.

November 6.—There was no nystagmus when dog looked forward, and none when looking to right or left. When head turned 90° to right there was a slight slow nystagmus, very slight, but labyrinthine in character. Dog resisted turning 90° to left; but when this forced movement of the head was done he showed slight nystagmus, labyrinthine in character. When standing, head had a twist so that snout was to right, left ear approximated to ground.

November 6, 6 P.M.—Dog killed. *Post-mortem* examination showed that the opening into the dura was absolutely closed. The whole upper and lateral surfaces of the right cerebral cortex had been removed including the occipital, parietal and frontal lobes, excepting the most anterior part of the frontal lobe, the orbital and olfactory lobes.* The lateral ventricle was opened into on the right side. There was no meningitis on the floor of the middle or posterior fossa of either side. The left labyrinth had been opened into, and the superior and lateral canals were lying loose. The base of the brain showed no inflammation, except that the temporal lobe on right side was a little more injected.

Summary of Results after Removal of Cortex of Right Cerebral Hemisphere:

(1) Stimulation of labyrinth gives normal reactions of deviation.

(2) Destruction of labyrinth gives usual torsion of head and signs of normal nystagmus.

(3) The normal nystagmus differs from ordinary labyrinthine nystagmus in that it is not affected, or very slightly, by turning head 90° to right or left.

(iii) *Destruction of Left Labyrinth, followed by Removal of Cortex.*

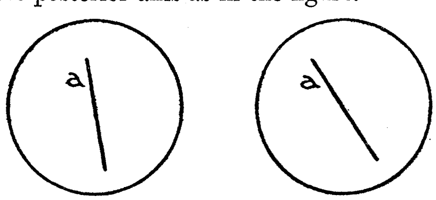
Cat, December 27, 1911.—Before labyrinth was opened the caloric tests gave normal reactions. Eye slits were perpendicular.

11.30 A.M.—Left labyrinth destroyed.

1.0 P.M.—Torsion of head to left; eyes deviated to left. Nystagmus slow to left, quick to right. The two phases of the nystagmus were not so markedly differentiated as in the dog; the quick nystagmus was not so rapid as in the dog. Slits perpendicular.

The cortex was removed. The cat's eyes were now deviated to left side. Corneal reflex present, but no nystagmus. Oscillations were seen in both eyes if animal were disturbed in any way; these ceased when animal lay quiet. These oscillations had a tendency to be slow to the left and quick to the right. The eyes were rotated about antero-posterior axis as in the figure.

Right eye.



Left eye.

a = corneal slits.

* 'Anatomie des Hundes,' Ellenberger and Baum, 1891, p. 493.

Especially was this marked in the eye homolateral to the destroyed labyrinth. The rotation of the eyeballs about an antero-posterior axis is a deviation appearing most markedly after removal of the higher motor levels in the cat.

If cat's head were turned so that eyes were strongly deviated to side of lesion there was no nystagmus. But immediately the head was turned to right side the nystagmus appeared. But even when the head was turned to right side, if it lay perfectly quiet, the eye movements ceased. The cat lay as easily on right side as on left.

N.B.—Cat with left labyrinth removed will not lie on right side if cerebrum be intact.

3 P.M.—Climbed up side of cage and then fell back, moved about apparently voluntarily, putting its claws in the meshes of the cage and dragging itself along. Some nystagmus when moving, or immediately after; none when lying quiet. Animal cried at times.

4.15 P.M.—Lying quiet on left side. Eyes deviated to left. Nystagmus now constant, slow to left, quick to right, but the movements were less in amplitude than when cerebrum was intact.

Killed. On *post-mortem* examination, looking into skull cavity, tentorium was plainly seen. The whole cerebral cortex had been removed on both sides. The olfactory nerve and a part of the olfactory lobes were found intact. The temporal, parietal, frontal, and occipital lobes had been removed. On *both* sides the corpora quadrigemina and thalamus were intact.

Summary after Destruction of Left Labyrinth, followed by Removal of Cortex:

1. Removal of cerebral cortex in cat does not affect deviation of eyes nor torsion of head following left labyrinthine destruction.

2. After removal of left labyrinth and cerebral cortex, deviation appears at the same time as the corneal reflex.

3. Nystagmus, labyrinthine in character, at first only appears when animal is disturbed. It is produced or increased by the moving of the head in the direction of the quick phase (compare dog, October 25, 1911).

4. Nystagmus, constant and spontaneous, labyrinthine in character, appears four hours later, although movements of locomotion had been present about one and a half hours before, when the effects of the ether had passed off.

5. The animal can lie on either side, notwithstanding removal of left labyrinth. The rotation of the eyes about the antero-posterior axis is the result of cortical ablation (compare cat, November 23, where eyes rotated to equal degree, p. 156).

(iv) *Complete Removal of Cerebrum with Severance of Corpora quadrigemina and Splitting of Cerebellum in Median Line.*

June 23, 1911, A.M.—Dog had left labyrinth exposed but canals not opened.

Zinc in left labyrinth caused deviation to right and down on closing current, to left on opening. Carbon in labyrinth—deviation to left on closing current, to right on opening.

The cerebrum was now removed. The left labyrinth was stimulated immediately afterward. The zinc pole gave deviation up and to right; off, down and to left. The carbon pole gave deviation down and to left; off, up and to right. Hot water applied to labyrinth gave deviation to right, going very slowly at first and then rapidly. Head turned strongly to right. Observations repeated.

The connection of corpora quadrigemina with thalamus was now severed. The electrical poles when now applied to left labyrinth showed more marked normal effects when current was removed than when applied. When further out from ether there were perfectly normal reactions, eyes to right with the zinc, to left with the carbon immediately upon application of the current. The opposite effect followed the removal of current.

The brain stem behind anterior corpora quadrigemina was now severed. Then the zinc pole gave deviation of eyes to right, carbon to left. The opposite effect was seen upon removal of the current. Observation repeated. The movements were prompt. Corneal reflex persisted.

Cerebellum split in median longitudinal plane and labyrinth stimulated. Carbon pole gave normal eye movements to right on opening circuit, no effect on closing. Zinc pole gave eye movements to left on opening and to right on closing circuit. Repeated: Carbon now gave effects both on opening and closing circuit. There were marked effects with the zinc. No rigidity.

Post mortem.—The cerebrum had been completely removed. The whole frontal region had been removed, including the optic thalamus. All that was left were the olfactory lobes and the base of the brain. The nerves to the eye muscles were intact as was also the optic nerve. The pons and medulla were united at base to the mesencephalon anteriorly. All of the nerves coming out from the base of the brain were intact. The section through the posterior part of the corpora quadrigemina passed right through to the anterior part of the pons, but the anterior part of the pons was not separated from the mesencephalon. The anterior part of the pons was uninjured. The line of division had gone between the pons and the crura cerebri.

Summary:

Normal results from stimulation of the labyrinth can be obtained when the whole cerebrum and thalami are removed, leaving nothing but pons, medulla and their connections with the cranial nerves. The ocular movements in labyrinthine stimulation and after labyrinthine destruction are not merely the spasmodic flickerings of a muscle, or an inaccurate and impotent movement as of a foot that never hits anything, such as pass for reflex responses in a dog with transected spinal cord, but full exact movements of normal magnitude.

(v) *Labyrinthine Stimulation and Destruction on Decerebrated Animal.*

June 22, 1911.—Dog. After destruction of cerebrum the nictitating membrane was pushed toward the middle line on both sides. The left eye was very slightly deviated outward, the right eye looked straight forward. There was a very slight, slow movement of the eyes backward and forward, not amounting to an oscillation.

Some of the bone was now taken away over the left labyrinth. The eyes were now deviated to the left and somewhat down. Hot water applied: eyes were turned first to the left for a second, then strongly to the right and down. Cold water applied: deviation to the left. Hot water again applied: deviation to the right and down, first discernible in the left eye. When the stimulation was withdrawn the eyes deviated down and to the left. The carbon pole was now applied to labyrinth and the eyes moved farther to the left and down. The zinc pole was now applied to the labyrinth, and the eyes moved down and to the right. The effects of stimulation were repeatedly observed. It was especially noted that the zinc pole gave movement of the eyes both on opening and closing the current, respectively to left and right, but no nystagmus was seen.

The left labyrinth was now destroyed. One hour later there was marked deviation of the head to left, and the animal rolled over to the injured side. The eyes were deviated to the injured side. There was a slight oscillation of the eyes, more marked in the right eye, with nystagmoid movements of the internal part of the M. corrugator supercilii medialis, but nothing approaching to a nystagmus.

The zinc pole was now applied to the left labyrinth and the eyes turned to right. The carbon pole was applied to the left labyrinth and the eyes deviated to left. When the eyes were very much deviated to the injured side, hot water was applied and the eyes turned very slowly to the right.

The right labyrinth was now exposed and the eyes deviated to the left. The zinc pole in the right trephine opening caused the eye to rotate downward and to the left. The carbon pole gave eye movements to the left but much slighter than those produced by the zinc pole. Hot water gave deviation to the left and down but very slow in coming on. Observations repeated. No reaction now from left labyrinth with hot water or current.

Right labyrinth when stimulated with zinc pole frequently gave a twitch of eyes, a quick movement to right followed immediately by a deviation to the left.

Post-mortem Examination.—Cerebellum and cord intact. The base of the brain was intact, the optic nerves and all other nerves were uninjured. The cortex cerebri had been completely removed, except a small piece of left inferior posterior cerebral lobe. The occipital lobe had been completely destroyed and also the frontal lobe. The lateral ventricles were exposed, showing on the surface both optic thalami. The optic thalamus was intact on the left side, the right had its interior scooped out. The thalami were torn apart from each other. The colliculi, anterior and posterior, were uninjured. The temporal lobe was destroyed. The olfactory lobes were destroyed. The lobus piriformis was intact on both sides with its anterior prolongation on the left side.

Summary after Removal of Cerebral Cortex and Injury to Thalamus:

1. Stimulation of labyrinth gives normal reactions.

2. Destruction of labyrinth gives (*a*) normal deviation; (*b*) normal torsion of head; (*c*) no nystagmus.

N.B.—Two apparently aberrant results of stimulation of the labyrinth have been observed after decerebration; (*a*) hot water applied to left labyrinth gave quick deviation to the left for a second, then strongly to the right; (*b*) the carbon pole in the right labyrinth after the left has been destroyed gave deviation to the left.

November 23, 1911.—Cat. Decerebrated under ether behind the thalamus and left labyrinth destroyed. Animal was deeply under anæsthetic and did not show any movements of the eyes. As the anæsthetic passed off eyes deviated to the left.

In about 40 minutes after decerebration, the left hind foot was drawn up on pinching. The head, at this time, was turned strongly toward the left, amounting almost to pleurosthotonus, with torsion to the left. Pupils, which were wide at beginning of experiment, now narrowed to moderate slits, scarcely wider than those of normal cat in the same light. Eyes rotated so that pupil was no longer vertical, but the top turned 30° or 40° to the animal's left, with the bottom of the slit to the right. No nystagmus. Nictitating membrane drawn well over eyes, so that it had to be drawn back to afford a view of the pupil. One or two slight twitches of left eye observed about 90 minutes after decerebration, on drawing back the nictitating membrane, but these twitches were extremely slight, and were not observed afterward. As all the ocular reflexes of the animal were fairly active at this time, the ocular twitches may have been a reflex response to irritation of the eyeball.

Post-mortem examination showed that the section passed through brain stem just anterior to anterior corpora quadrigemina.

Summary:

All the essential phenomena of elimination of the labyrinth, with the exception of nystagmus, were observed in this cat.

Discussion of Results.

Destruction of the semicircular canals in whatever form of vertebrate so far studied is attended by a definite and uniform group of motor disturbances not seen in experiments on any other part of the central nervous system. Transection of the spinal cord in the lower vertebrates produces trifling disturbances in the reflexes, while transection of the spinal cord of a monkey produces more severe disturbances of the reflexes, which end only with the death of the animal after months or years. Loss of the cerebral cortex in the frog gives a different picture from that attending removal of the motor area of the cerebral cortex in the dog. Removal of the cerebellum in the land turtle is not attended in any noticeable degree by the motor disturbances attending such a procedure in mammals (unpublished results). But in all these forms, lesions of the membranous labyrinth of the ear are, without exception, attended by torsion of the anterior part of the body, and displacement of the eyes. The torsion of the head is permanent in all these forms. The eye movements alone differ, and these differences are intimately associated with the increasing magnitude and complexity of development of the cerebrum in the vertebrate phylum. The typical results of lesions of the membranous labyrinth, excepting nystagmus, are very largely unaffected by the presence or absence of the phylogenetically newer pathways.

The inference from these facts appears to be that in the vestibular system and its central connections we have a phylogenetically primitive nervous mechanism which has persisted throughout the vertebrate phylum—or, at least, in all orders above and including the fishes—relatively unaffected, either morphologically or functionally, by the profound and even revolutionary changes occurring in the general somatic motor system. It seems probable, also, that the lateral lobes of the cerebellum are associated far more closely with the phylogenetically newer somatic motor system than with the primitive motor system. We believe that while this phylogenetic primitive vestibular mechanism persists, it has acquired in the higher vertebrates an ever increasing association with newer pathways.

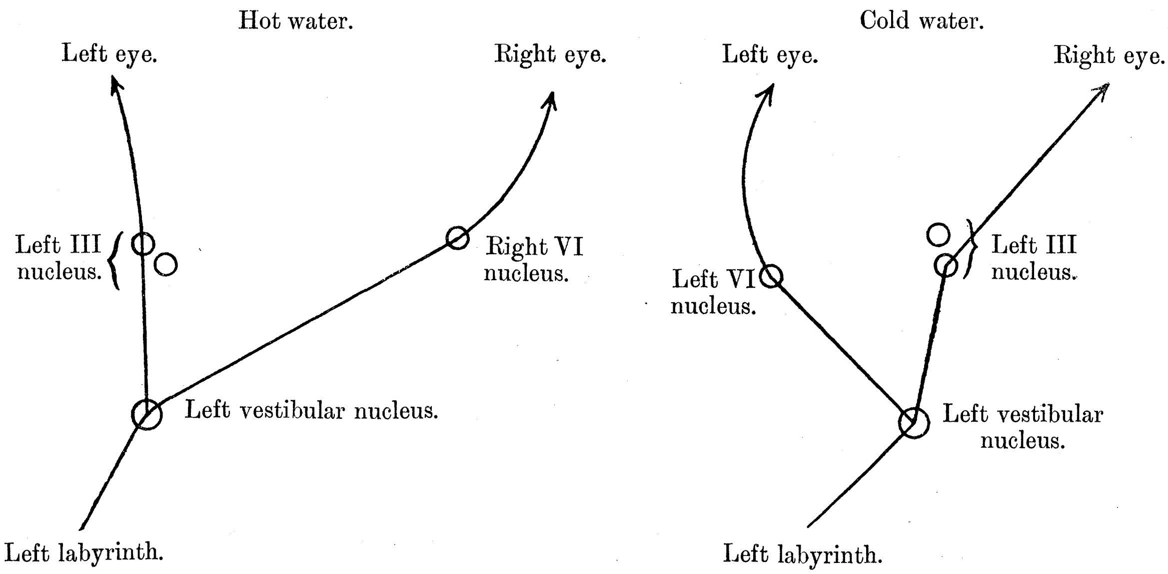
The greater capacity for adjustment following certain lesions or removals of nervous substance, inherent in the enormous development of association tracts in the central nervous system of the higher vertebrates, may tend to obscure or mask, because of the completeness of recovery following labyrinthine extirpation, some of the essential features of such a lesion in the higher forms. But the certainty and the severity of the motor disturbances immediately attending labyrinthine extirpation in the higher mammals is evidence of the persistence of the function of the vestibular mechanism. The more complete recovery in man is not necessarily to be interpreted, as Bárány* believes, as evidence of the retrogression of the vestibular system in man, but may be regarded as evidence of the much greater degree of adaptability on the part of the

* Bárány, R., "Zur Theorie des Bogengangapparates," 'Zeitschrift für Sinnesphysiologie,' 1911, vol. 45, p. 63.

highly complex somatic motor system, a point of view widely at variance with BÁRÁNY's. We shall return to this in a later paper.

Nystagmus occurring in the dog and cat, as a result of labyrinthine stimulation or destruction, consists of two phases—a slow deviation followed by a quick return—varying definitely in direction with the labyrinth which is stimulated or destroyed. As we have shown, these phases are distinct. Thus the slow deviation is not affected by removal of the cerebellum, nor is it affected by complete removal of the cerebrum, optic thalamus, partial removal of the anterior corpora quadrigemina, and longitudinal splitting of cerebellum. In short, if the anatomical path from the labyrinth through the vestibular nuclei to the eye nuclei (posterior longitudinal bundle) be intact, the deviation can be produced by stimulation, and appears after destruction, so soon as the animal begins to pass out from under the influence of the narcotic. Deviation appears at a time when the reflex responses of the leg muscles are completely in abeyance, and *pari passu* with the corneal reflex.

Diagram of Action of Hot and Cold Water.*



On the other hand, the quick phase of nystagmus, though not affected by removal of the cerebellum or of the occipital cortex, is affected by removal of the whole cerebral cortex. It does not occur in animals completely decerebrated, including optic thalamus, even though the oculo-vestibular tract be unimpaired. Further, it appears later than the deviation, and can only be produced, or will only occur, when the animal emerges from the effect of the anæsthetic.

The explanation usually given, that the deportment of the animal in the early post-operative period following unilateral labyrinthine removal is due to loss of

* TOLDT, CARL, 'Anatomisch. Atlas,' Wien, 1903, p. 799; WINKLER, C., 'The Central Course of the Nervus Octavus,' Amsterdam, 1907, pp. 125, 120, 126.

tonus of the muscles on the side of the body opposite to the lesion,* does not seem to us adequate. The dog turns in a circle, not towards the side of decreased muscle tonus, but towards the side on which the muscles are supposedly normal. He turns and falls in the direction of the slow component of nystagmus—the significance of which we will discuss in a later paper. Thus, after left labyrinthine destruction, he falls to the left, and turns in a circle to the left.

In contrast to this, when we turn our attention to the motor cortex, we note that, after ablation of the motor cortex of the left cerebral hemisphere, the dog turns in a circle towards the right. In this case there is loss of muscle sense on the right side of the body and a decreased muscular tone. The animal falls toward the right in the early post-operative period, and the control of the muscles on the right side never becomes as exact and precise as it was before, although the animal becomes able to walk or run in a straight line, and shows none but extremely slight motor disturbances or inaccuracies. The muscular sense is never fully recovered. It is to be noted that there is no loss of muscle sense following either unilateral or bilateral labyrinthine removal.

It is inconceivable, if turning in a circle and falling toward the injured side after the labyrinthine extirpation is a mere matter of differences in tonus, that the deportment of a non-labyrinthine dog should be the exact opposite of that following unilateral ablation of the cerebral motor cortex. On the other hand, both the attitude and motor disturbances are intelligible in the dog if we regard them as the forced motor resultant of the remaining intact labyrinth.

EXPLANATION OF PLATES.

Plate 13.

Fig. 1.—(*a*) Normal skull. (*b*) Skull with trephine opening.

Fig. 2.—Destruction of right labyrinth. Dog, April 25, 1909. Photographed May, 1909.

Fig. 3.—White rat, left labyrinth destroyed.

Fig. 4.—White rat, left labyrinth destroyed.

Fig. 5.—Right labyrinth destroyed. Dog, April 25, 1909. Photographed March 5, 1911.

* Ewald, J. R., 'Physiol. Untersuchungen über das Endorgan des Nervus Octavus,' Wiesbaden, 1892 p. 296.

Plate 14.

Fig. 6.—Cat. Removal of right labyrinth. Photographed while sitting quietly on the table with eyes closed. The eyes were opened at the first click of the shutter and remained open during the exposure. Exposure, $\frac{1}{4}$ second.

Fig. 7.—Cat. Removal of right labyrinth. Exposure, $\frac{1}{10}$ second.

Fig. 8.—Cat. Removal of right labyrinth. At the first click of the shutter the cat turned its head to the right (the auditory reinforcement). The slight blurring of the photograph seen about the eyes, and particularly about the left eye, shows the character and extent of this movement. The blurred streak under the left eye shows the upward movement of this eye. Exposure, $\frac{1}{4}$ second.

Plate 15.

Fig. 9.—Right labyrinth destroyed; dog, April 25, 1909 (figs. 2, 5). Left labyrinth destroyed; dog, March 20, 1911. Photographed May, 1911.

Fig. 10.—Destruction of both labyrinths at same time. Dog, January 19, 1912. Photographed January 20, 1912.

Fig. 11.—Another photograph of dog of fig. 10.

Fig. 12.—White rat, both labyrinths destroyed. Photographed same day.

Fig. 13.—Complete cerebellar removal. Dog, May 4, 1911.

Plate 16.

Fig. 14.—White rat, left lateral lobe of cerebellum removed. Photographed same day.

Fig. 15.—White rat, cerebral cortex removed on right side. Photographed same day.

Fig. 16.—Normal brain of dog.

Fig. 17.—Removal of left half of cerebellum. Dog, June 23, 1911.

Fig. 18. Removal of whole of cerebellum. Dog, May 4, 1911.

Fig. 19.—Removal of both occipital lobes of cerebrum. Dog, June 12, 1911.

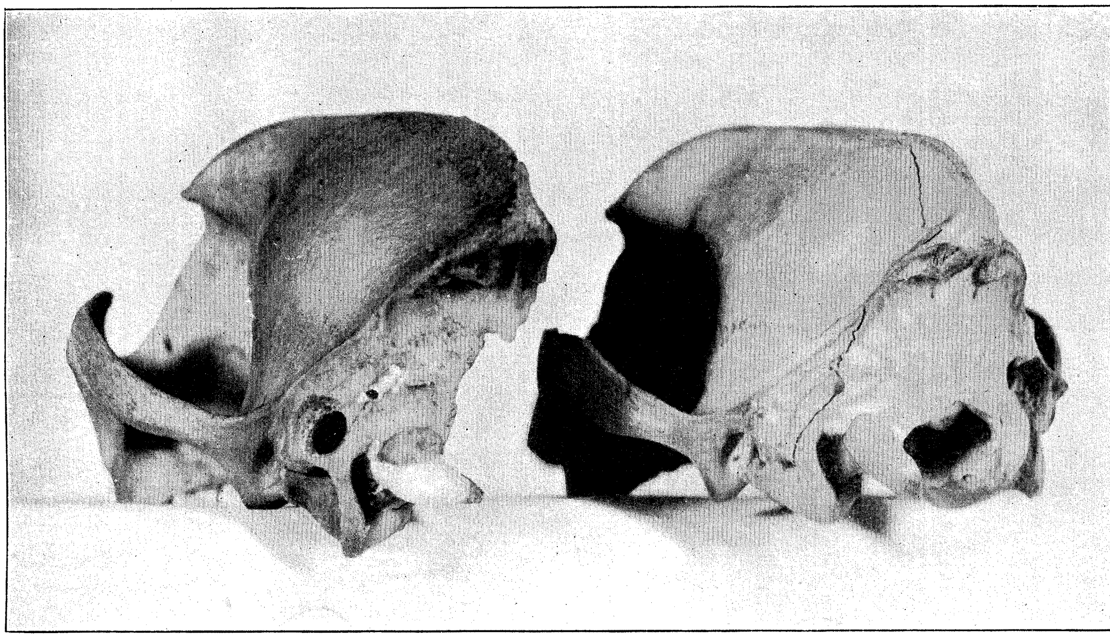


FIG. 1 (*b*). FIG. 1 (*a*).

FIG. 2.

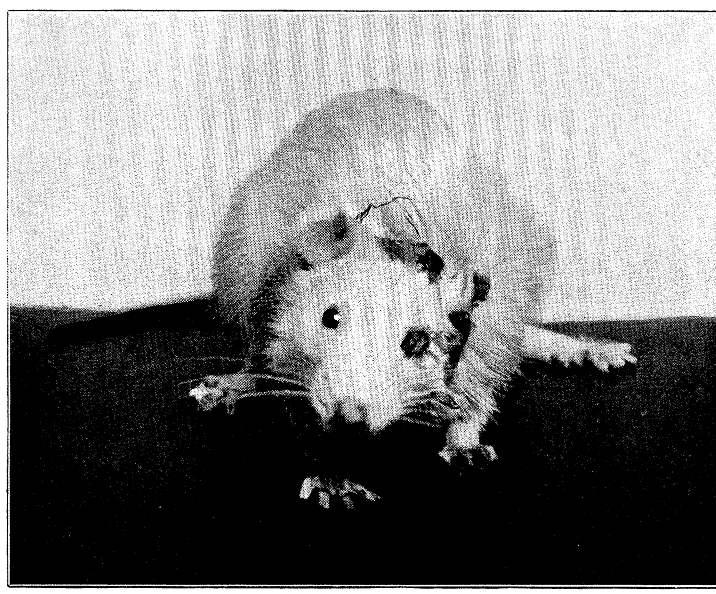


FIG. 3.

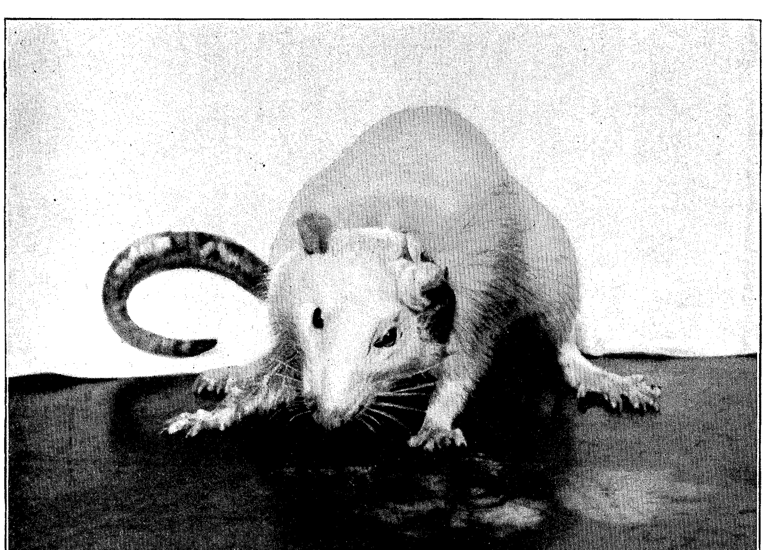


FIG. 4.

FIG. 5.

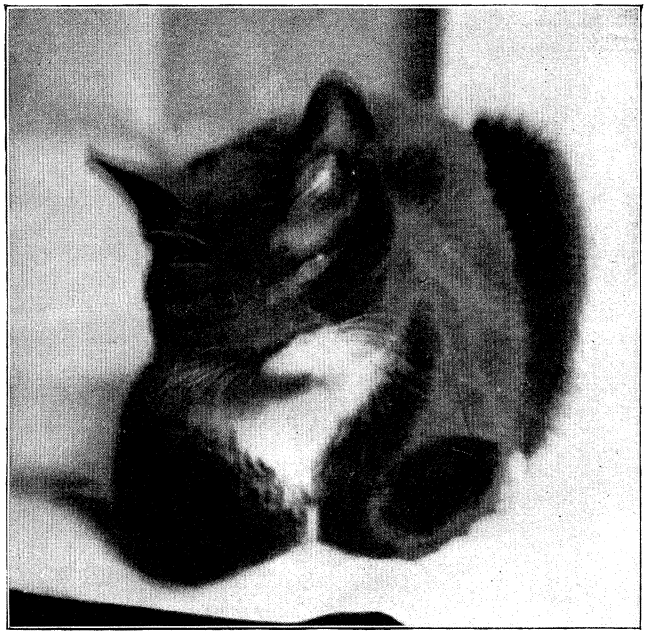


Fig. 6.

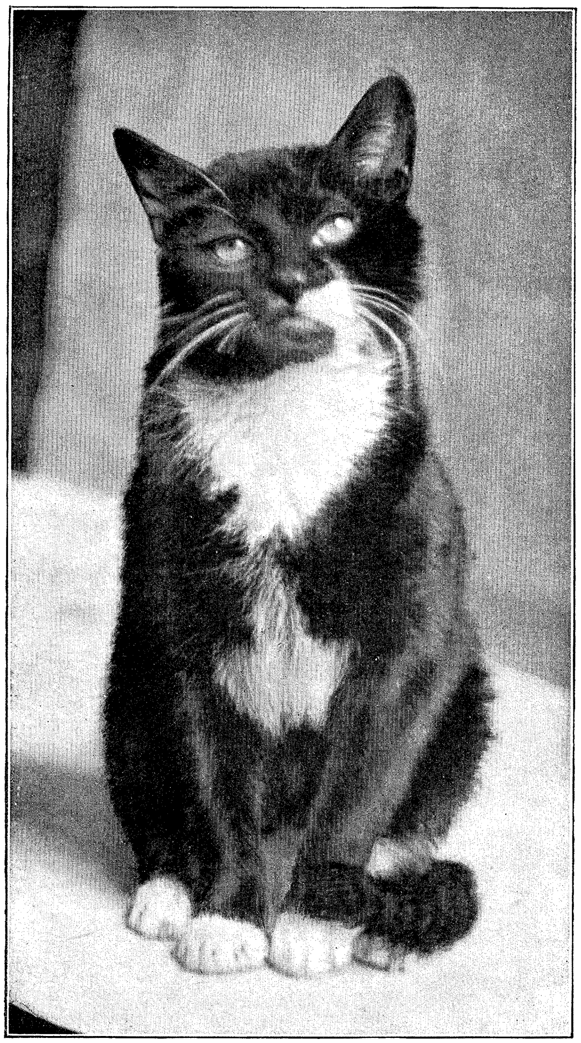


Fig. 7.

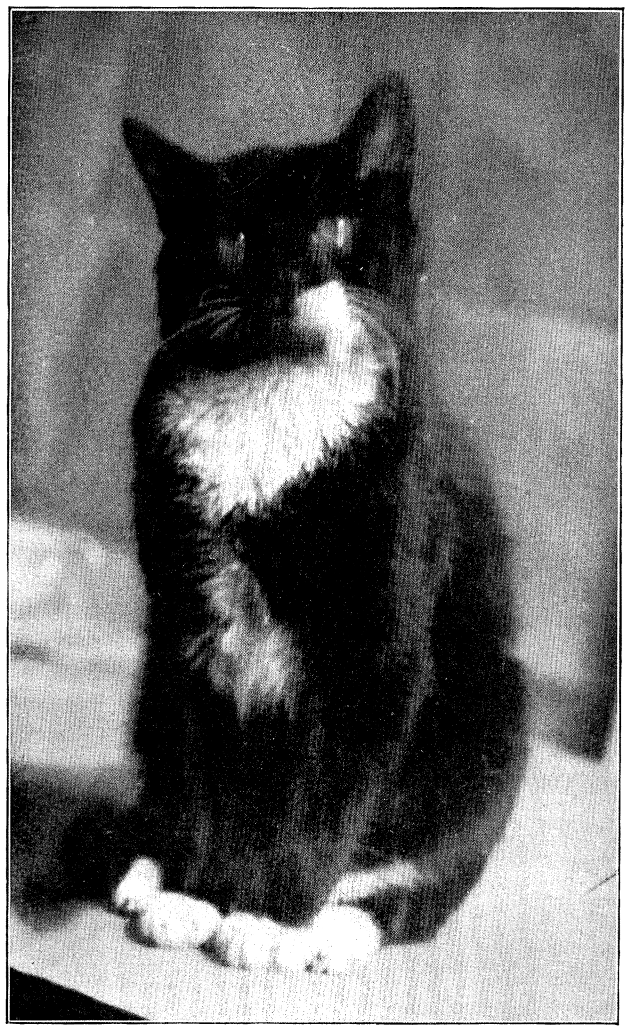


Fig. 8.

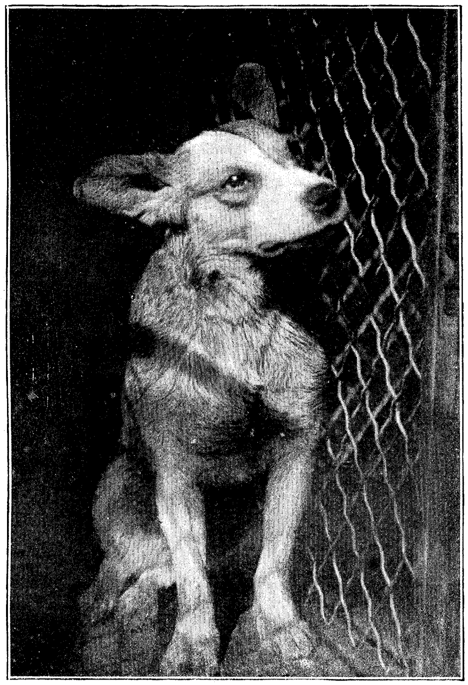


FIG. 9.

FIG. 10.

FIG. 11.

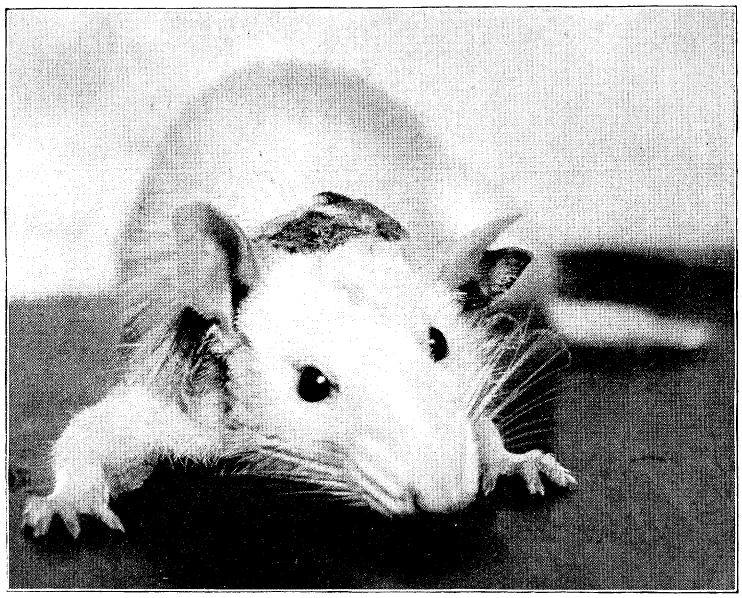


FIG. 12.

FIG. 13.

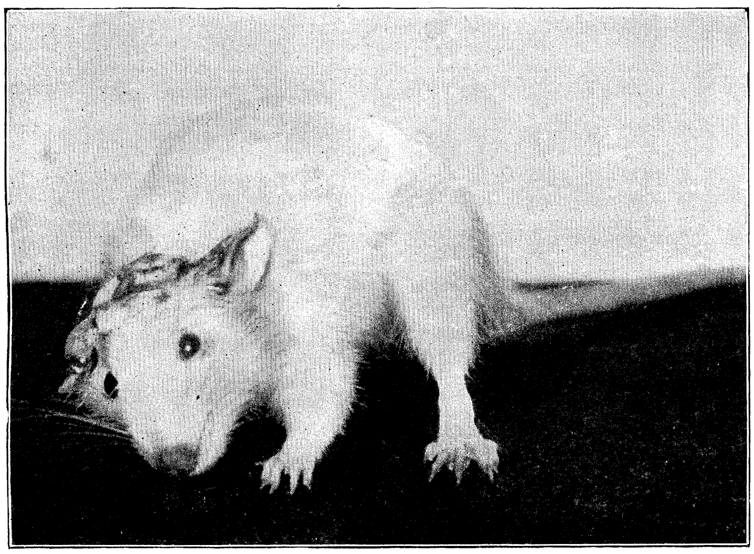


FIG. 14.

FIG. 15.

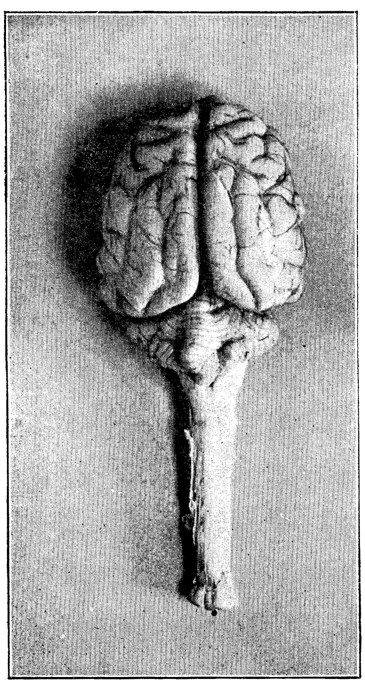


FIG. 16.

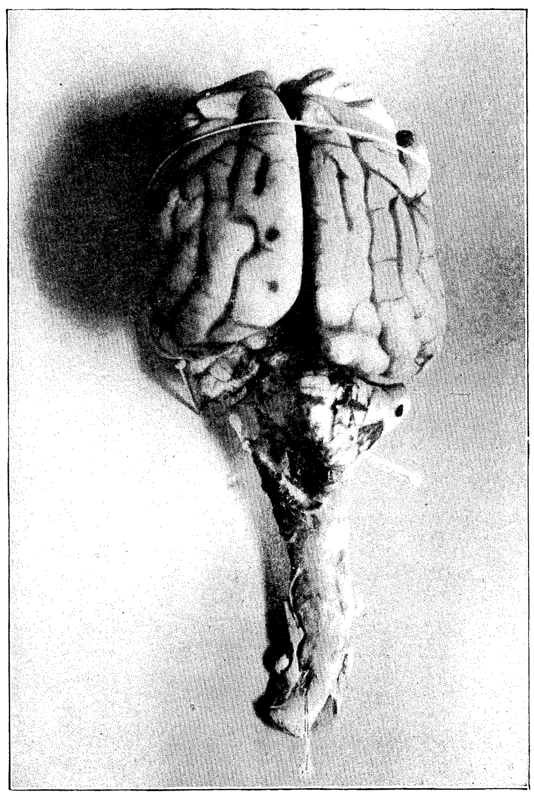


FIG. 17.

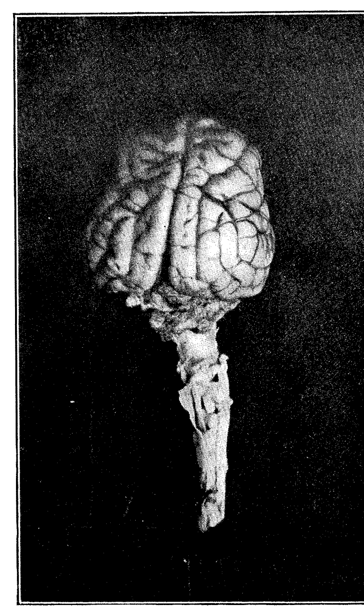
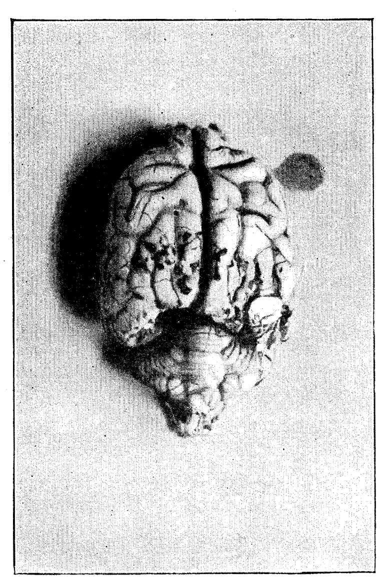


FIG. 18.



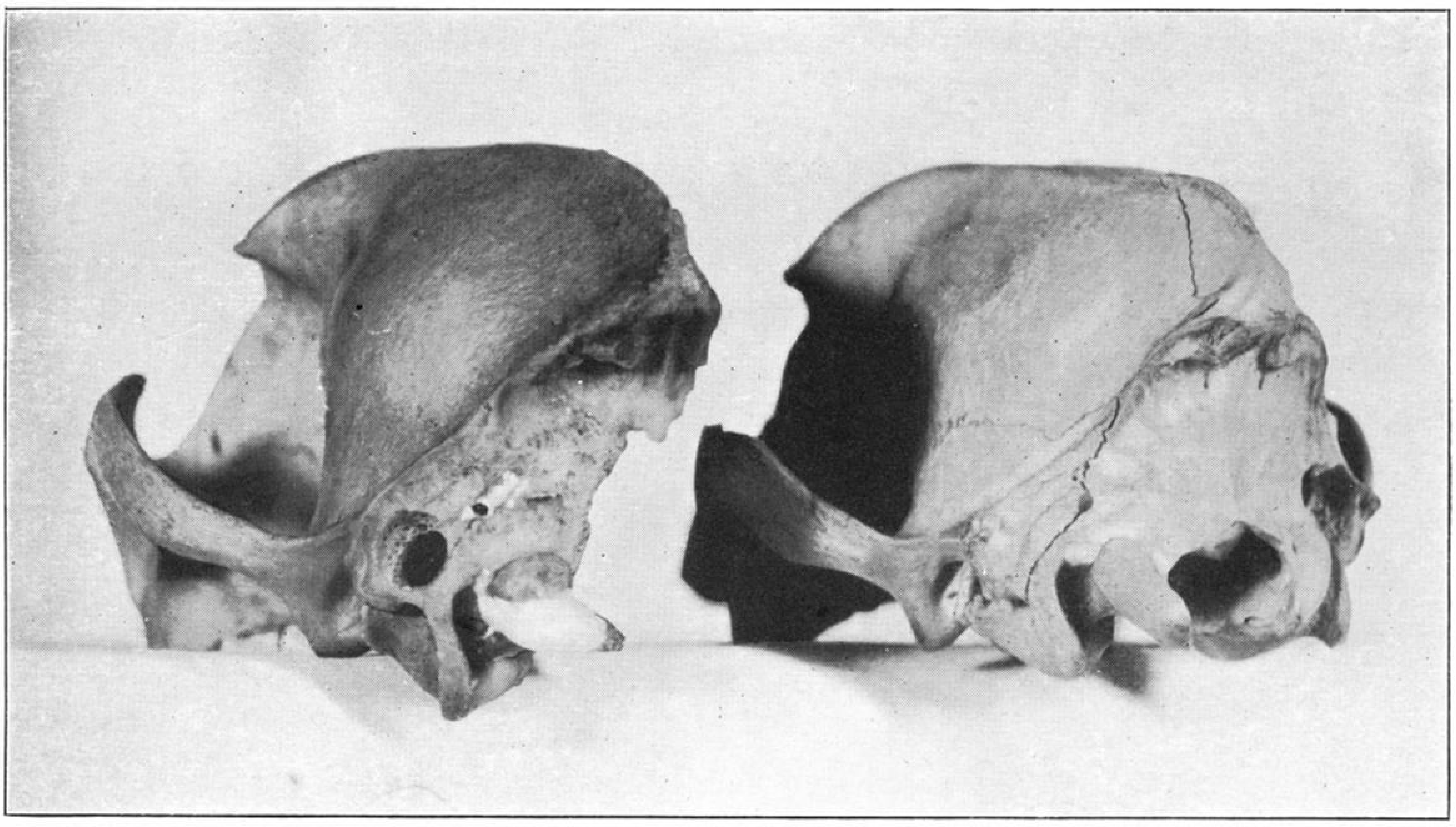


Fig. 1 (*b*). Fig. 1 (*a*).

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Plate 13.

Fig. 1.—(*a*) Normal skull. (*b*) Skull with trephine opening.

Fig. 2.—Destruction of right labyrinth. Dog, April 25, 1909. Photographed May, 1909.

Fig. 3.—White rat, left labyrinth destroyed.

Fig. 4.—White rat, left labyrinth destroyed.

Fig. 5.—Right labyrinth destroyed. Dog, April 25, 1909. Photographed March 5, 1911.

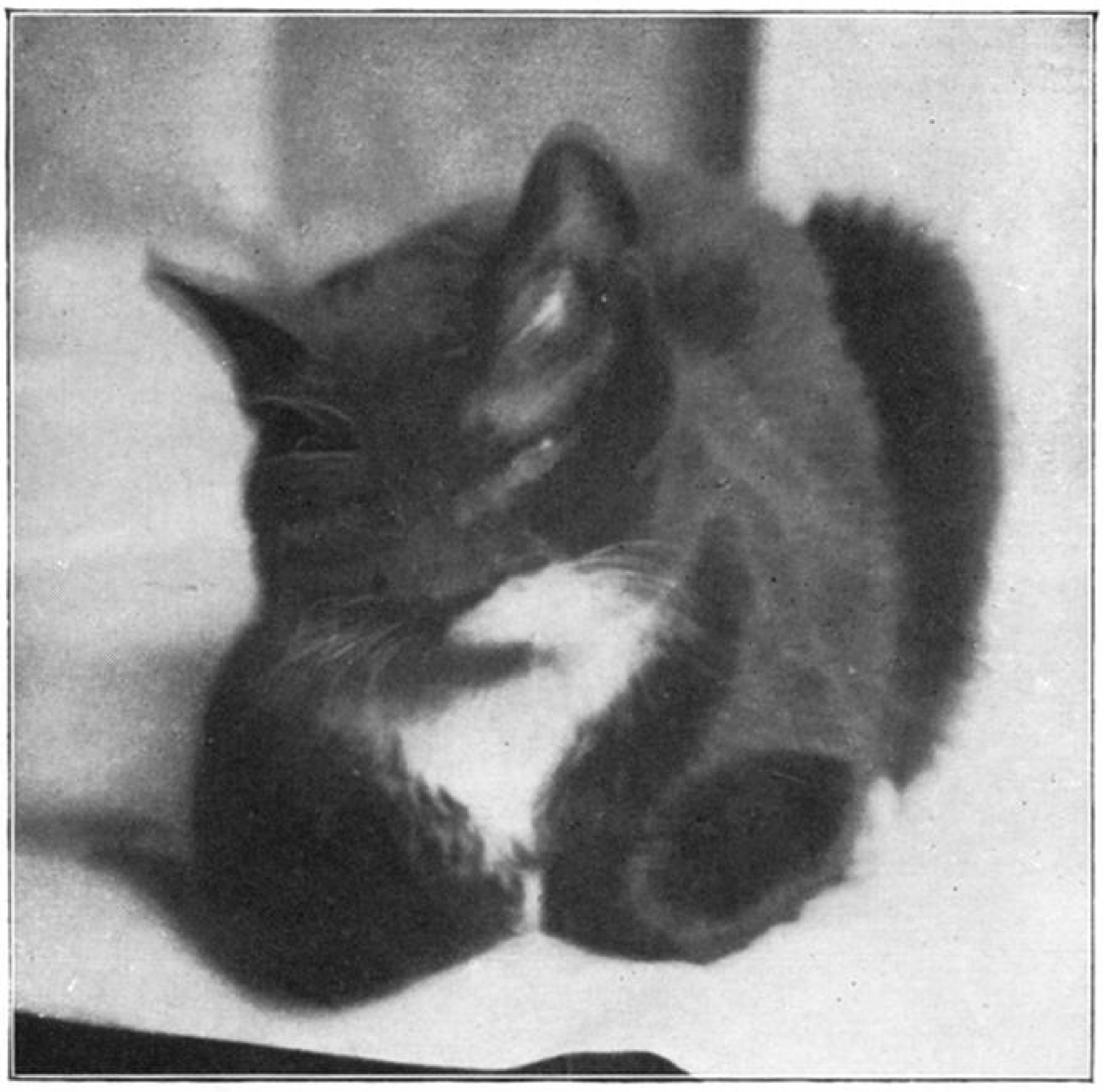


Fig. 6.

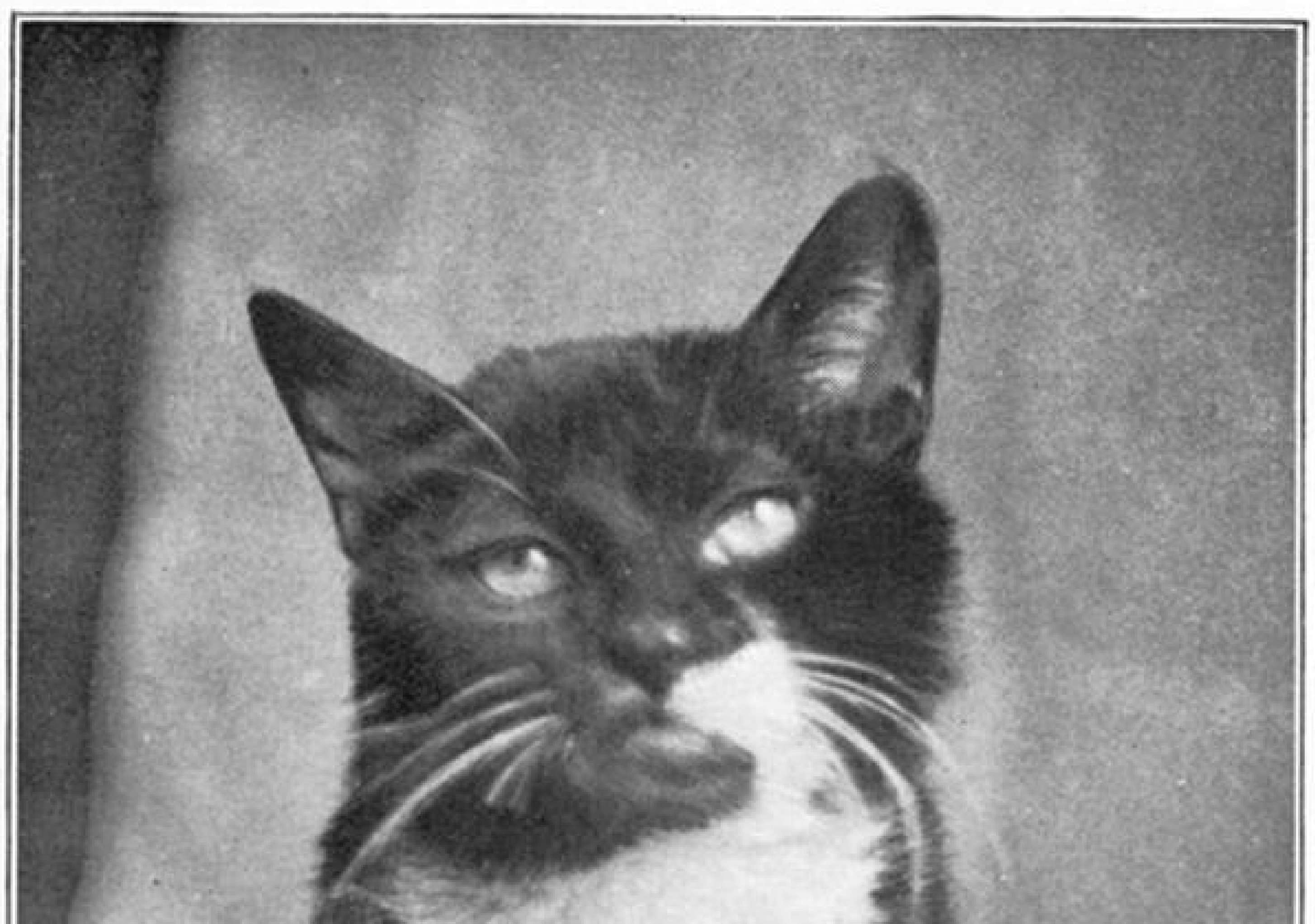


Fig. 7.

Fig. 8.

Plate 14.

Fig. 6.—Cat. Removal of right labyrinth. Photographed while sitting quietly on the table with eyes closed. The eyes were opened at the first click of the shutter and remained open during the exposure. Exposure, $\frac{1}{4}$ second.

Fig. 7.—Cat. Removal of right labyrinth. Exposure, $\frac{1}{10}$ second.

Fig. 8.—Cat. Removal of right labyrinth. At the first click of the shutter the cat turned its head to the right (the auditory reinforcement). The slight blurring of the photograph seen about the eyes, and particularly about the left eye, shows the character and extent of this movement. The blurred streak under the left eye shows the upward movement of this eye. Exposure, $\frac{1}{4}$ second.

Fig. 9.

Fig. 10.

Fig. 11.

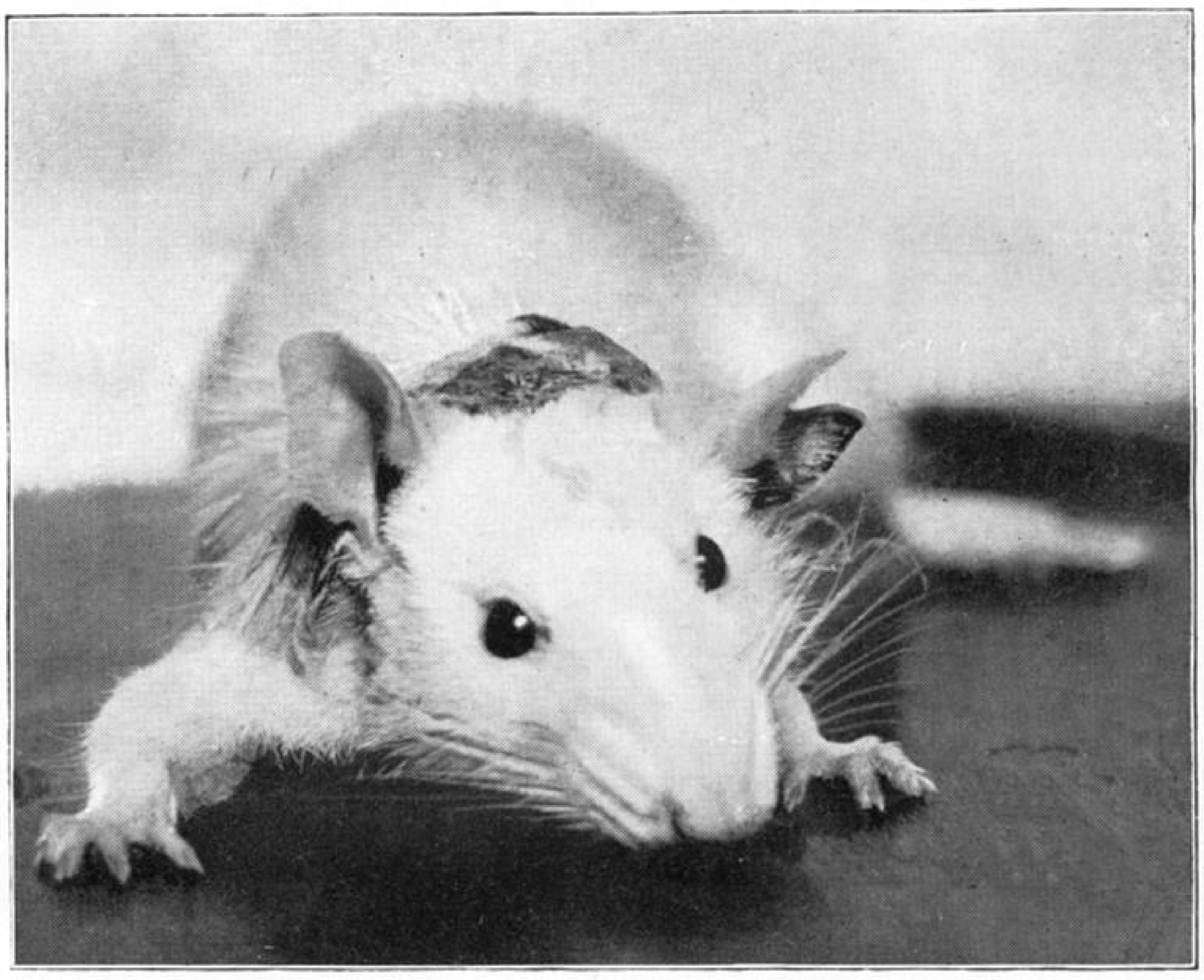


Fig. 12.

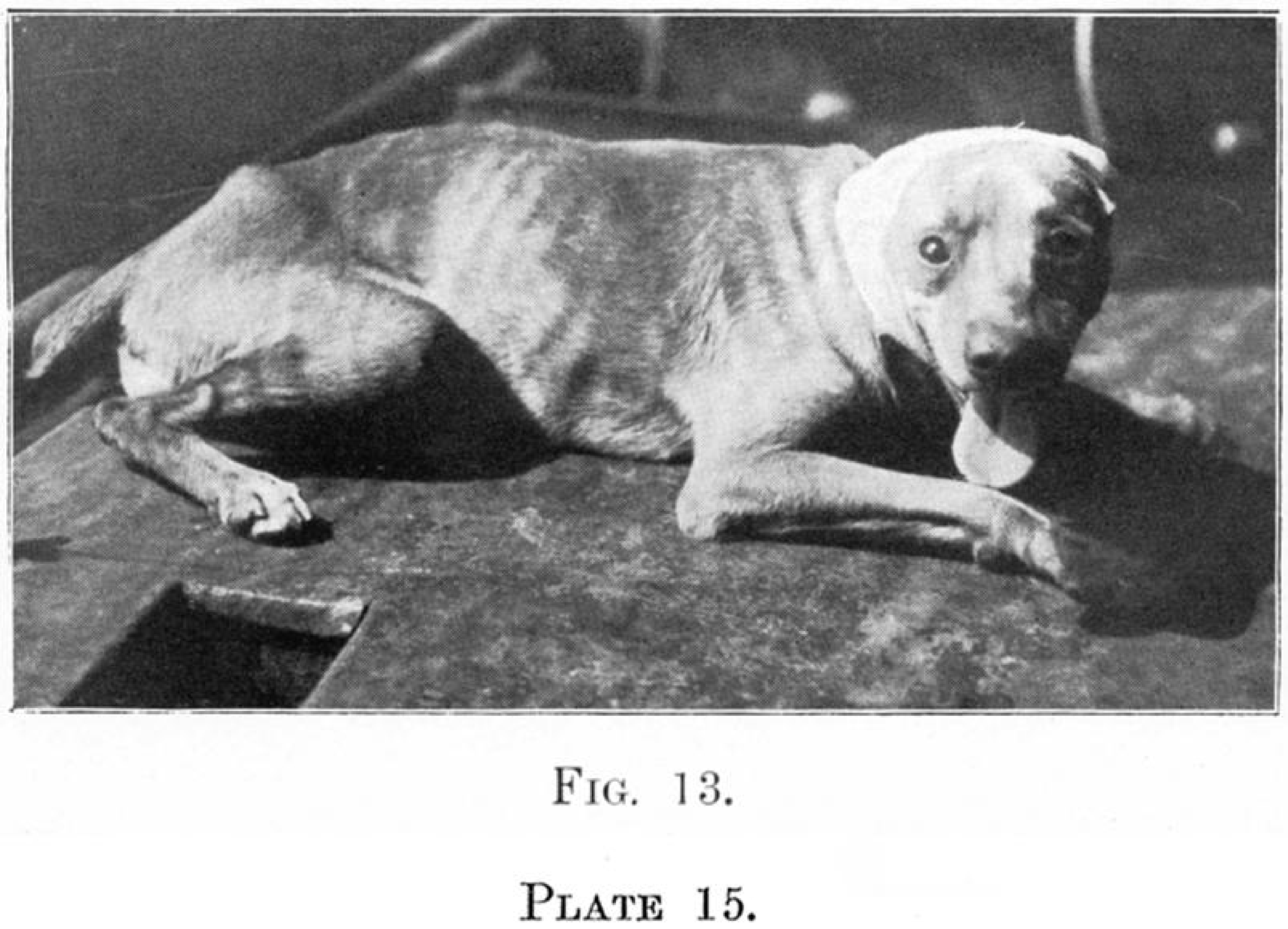


Fig. 13.

Plate 15.

Fig. 9.—Right labyrinth destroyed; dog, April 25, 1909 (figs. 2, 5). Left labyrinth destroyed; dog, March 20, 1911. Photographed May, 1911.

Fig. 10.—Destruction of both labyrinths at same time. Dog, January 19, 1912. Photographed January 20, 1912.

Fig. 11.—Another photograph of dog of fig. 10.

Fig. 12.—White rat, both labyrinths destroyed. Photographed same day.

Fig. 13.—Complete cerebellar removal. Dog, May 4, 1911.

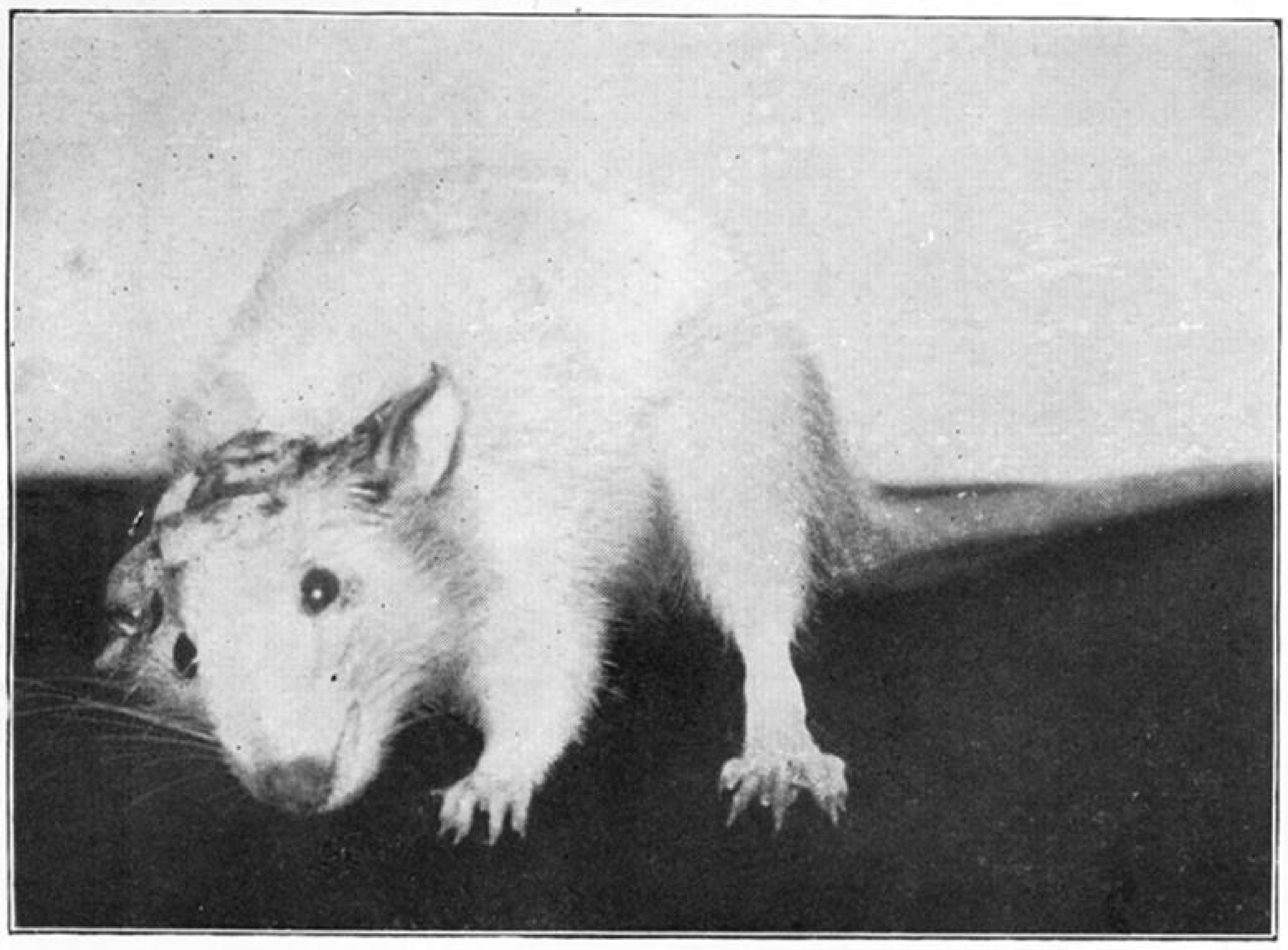


Fig. 14.

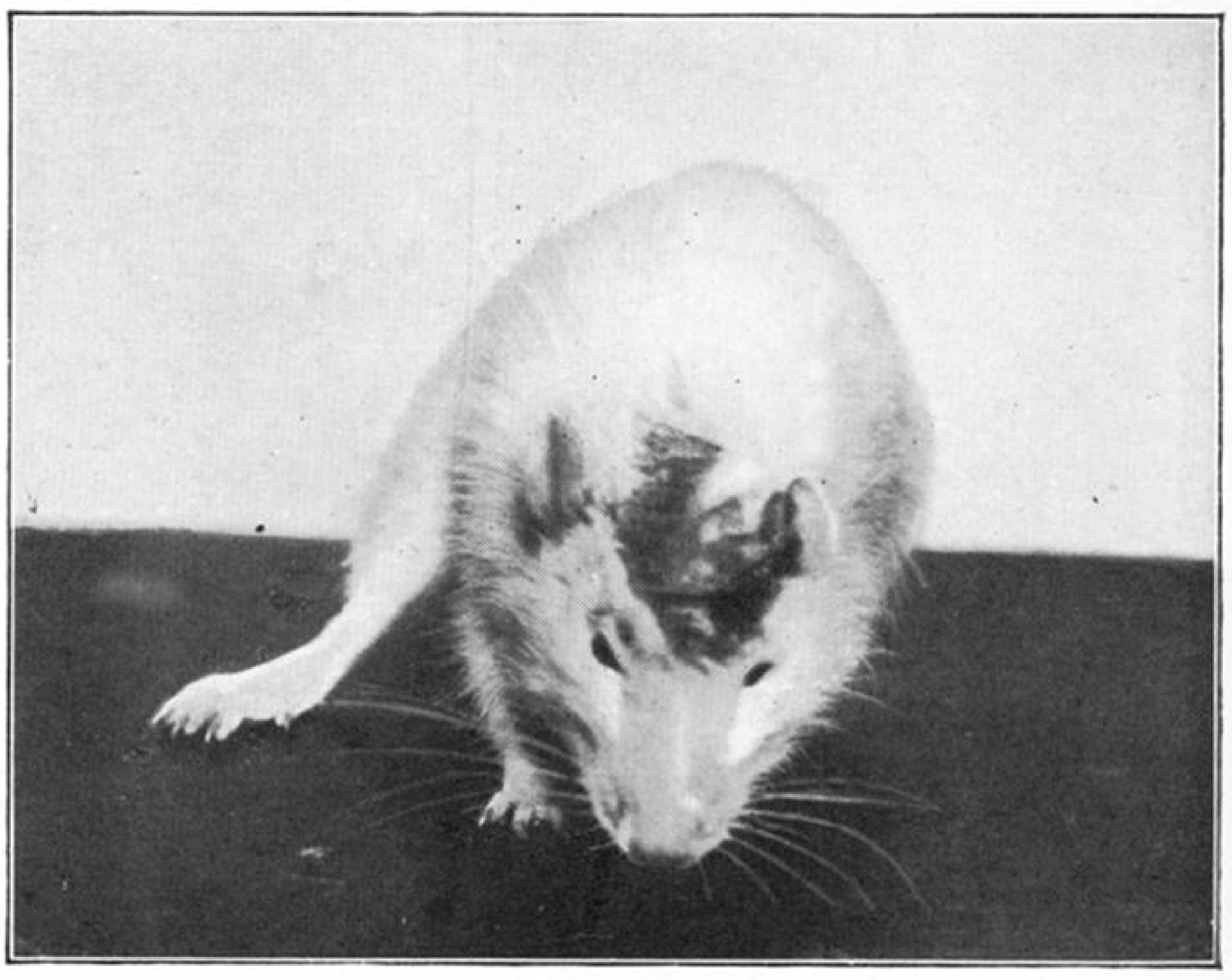


Fig. 15.

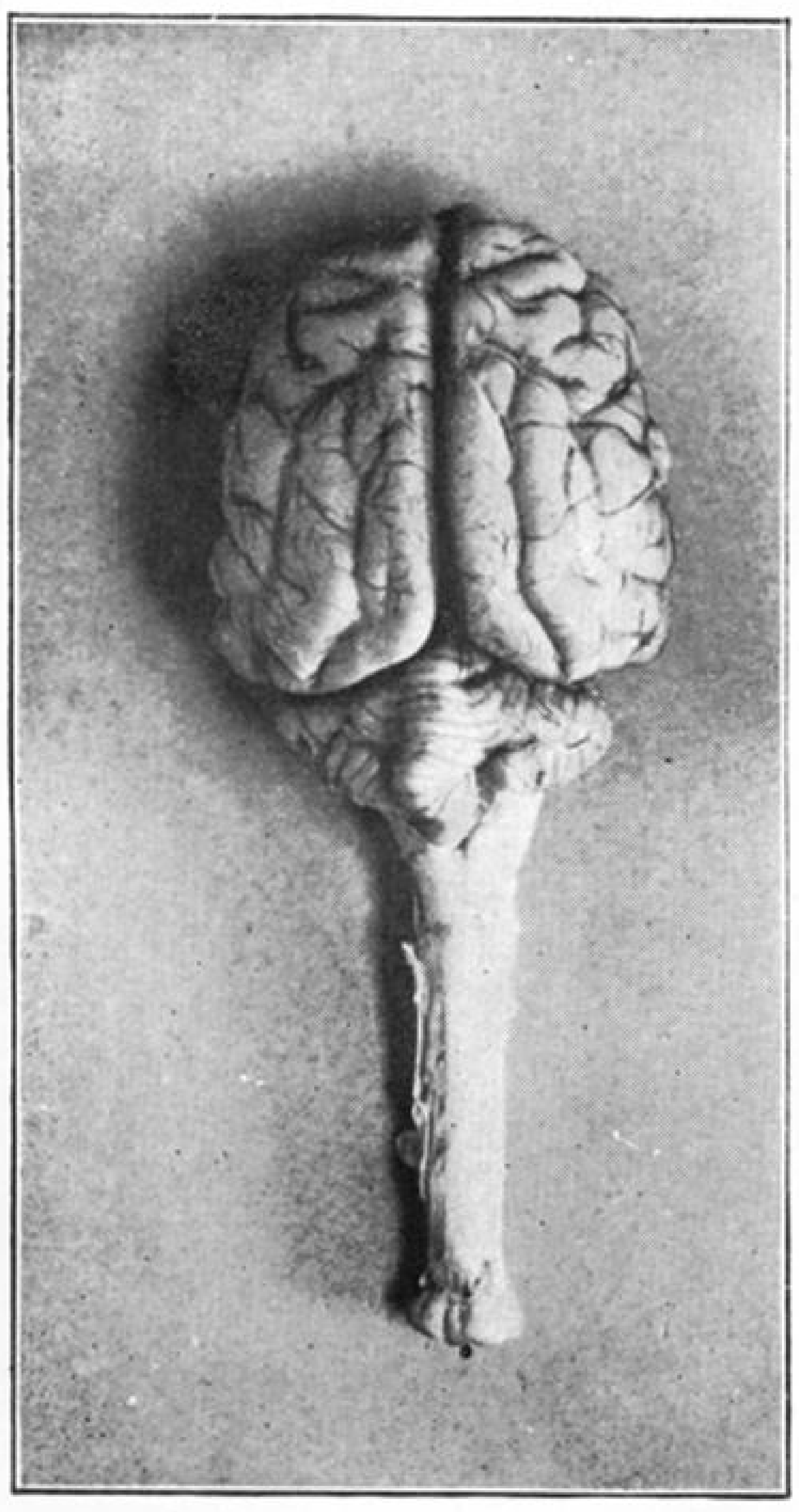


Fig. 16.

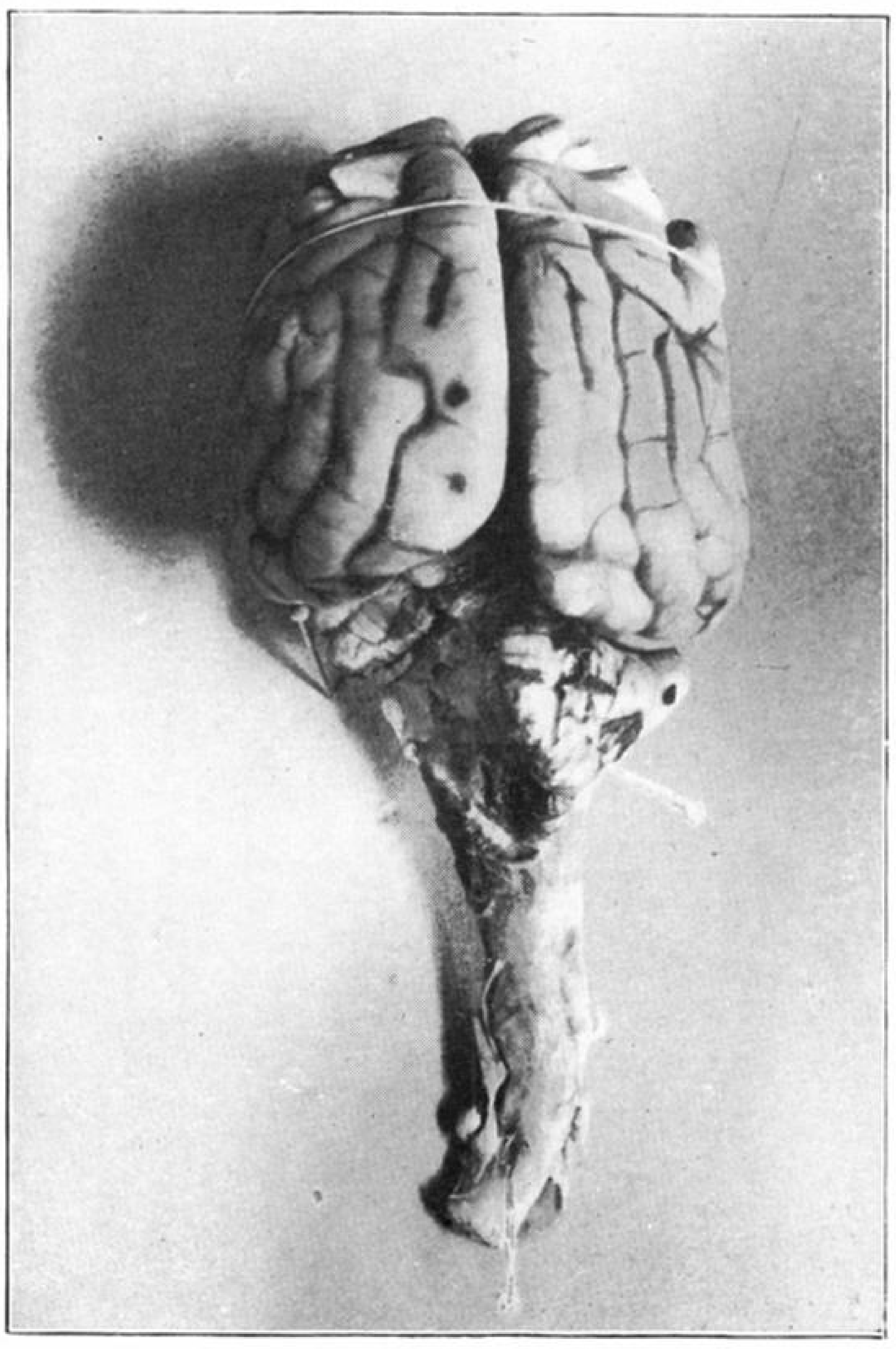


Fig. 17.

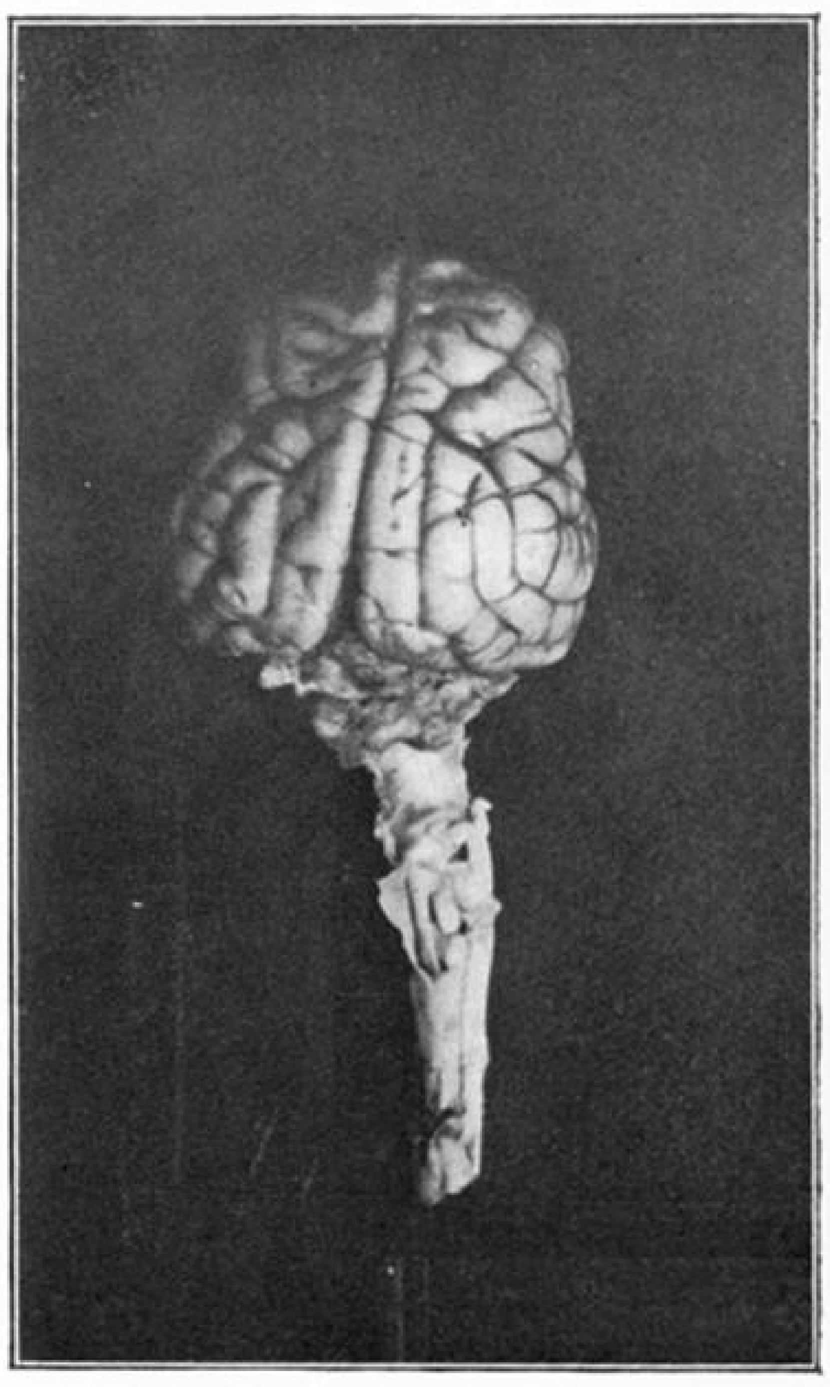


Fig. 18.

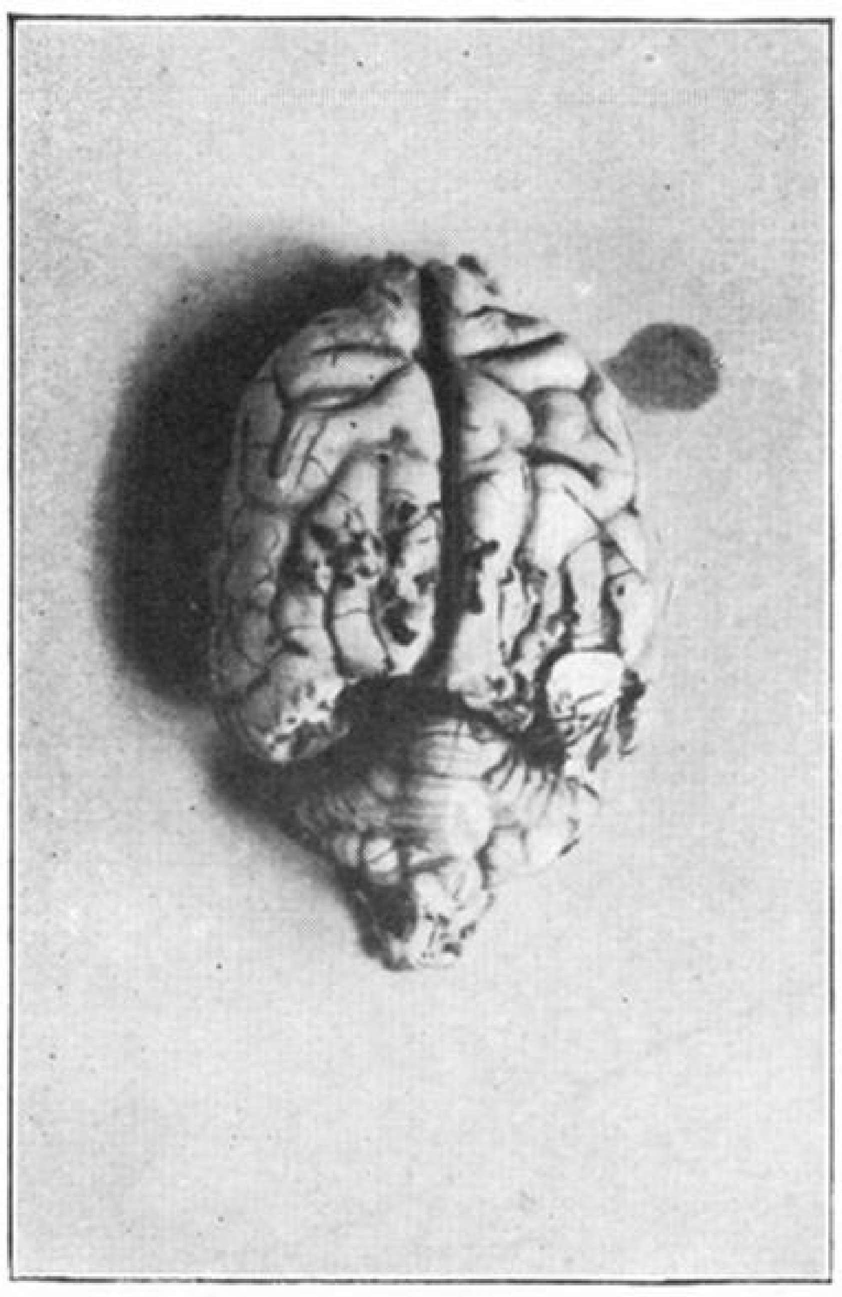


Plate 16.

Fig. 14.—White rat, left lateral lobe of cerebellum removed. Photographed same day.

Fig. 15.—White rat, cerebral cortex removed on right side. Photographed same day.

Fig. 16.—Normal brain of dog.

Fig. 17.—Removal of left half of cerebellum. Dog, June 23, 1911.

Fig. 18. Removal of whole of cerebellum. Dog, May 4, 1911.

Fig. 19.—Removal of both occipital lobes of cerebrum. Dog, June 12, 1911.