ELECTRICAL STUDIES ON THE FROG'S LABYRINTH.

BY D. A. ROSS.[1]

(*From the Physiological Laboratory, Cambridge.*)

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THE investigation of the vestibular organs has hitherto been carried on largely by methods in which the experimenter observes changes in the character of the equilibrial reflexes resulting from operative interference with the internal ear. The present communication deals with an attempt to investigate the matter in greater detail by means of the somewhat more direct electrical method, in which the action potentials set up in the auditory nerve by the vestibular receptors are recorded and studied.

The choice of a suitable experimental animal was an unusually wide one, for the principal—and probably the only—equilibrial receptors found in the mammalian ear (*i.e.* the utricular macula and the cristæ of the three semicircular canals) occur almost entirely throughout the vertebrate phylum, and there seems to be no reason to suppose that their respective mechanisms differ fundamentally from one group to the next, especially in the case of the canals. For tilting and rotation experiments, however, the advantages of a small animal are self-evident, and the frog proved to be a satisfactory subject for a number of additional reasons. Its possibilities had been tried out by Dr W. J. McNally and the writer during the summer of 1934, and isolated preparations of the head had been found convenient to handle and to retain their activity for some 2 or 3 hours in the absence of the circulation. Moreover, the reflex equilibrial responses of the frog, both normal and after labyrinthine lesions, had been exhaustively studied [see McNally and Tait, 1933; and Tait and McNally, 1934], so that much was already known about the functions of its various balancing receptors. This, as will be seen below, was of fundamental importance.

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APPARATUS.

The recording apparatus consisted of the standard four-stage R.C.C. amplifier and pentode system driving a Matthews moving-iron oscillograph. The usual accessories—loud-speaker and viewing screen—were used, and records, when required, were taken on 35-mm. Ciné bromide paper. The sensitivity of the amplifier was varied widely from one experiment to another, as the size of the action potentials depended, among other things, upon the fineness and active length of the nerve filament being used; but the deflections in the original records commonly represent something of the order of 40 microvolts per centimetre. As no emphasis was to be laid on either the absolute size or shape of the action potentials, the time constant of the amplifier was kept small in order to minimize displacement of the base line resulting from contact and capacity effects incurred by the mass movement of the preparation and portions of the leads. Such behaviour of the base line where it appears in the records is, of course, not to be interpreted as having physiological significance.

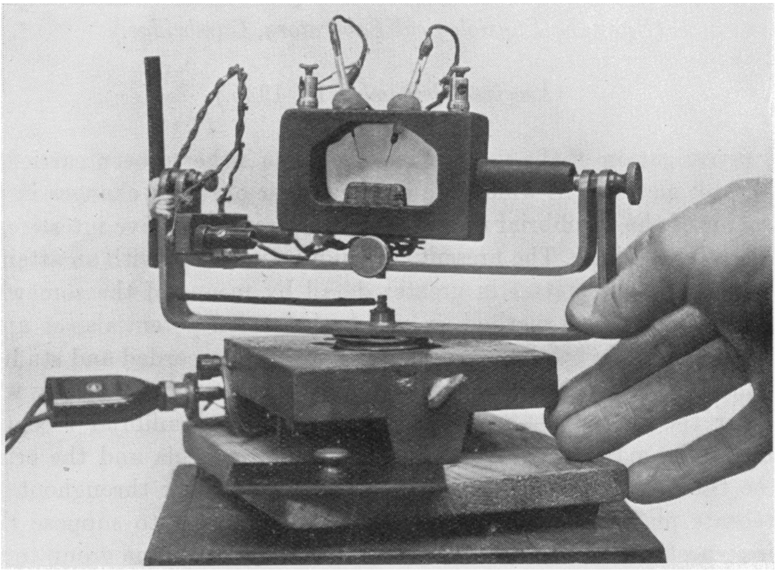

Fig. 1. The moist chamber, set up in position on the apparatus for tilting or rotatory stimulation.

The right-hand half of the frog's head was set up inside a moist chamber. The latter consists of a small block of hardwood ($8 \times 5 \times 2{\cdot}5$ cm.), excavated from one of its flat sides, as shown in Fig. 1. It may be supported by either of two metal rods—one in the bottom and the other (rubber-covered) in the side. To the floor of the chamber a small piece of cork is cemented, serving as a base to which the frog-head preparation may be pinned. In its roof are two holes to permit the entrance of the glass tubes which carry the electrodes. The holes are large enough to leave the tubes considerable freedom of movement. On top of the block are two terminals for the attachment of the lead wires. The whole box is thoroughly impregnated with paraffin wax. A light, hard-rubber cover (in the foreground of the photograph) is provided to close off the front face of the box when the preparation is ready. It is held in place by vaseline spread on the box. Aqueous saturation of the air inside the chamber is accelerated by the presence of three pieces of sodden sponge, one behind the preparation and one on either side. The photograph shows the preparation box without the sponges, and with a piece of white filter paper inserted at the back of the chamber.

The rest of the apparatus shown in Fig. 1 was designed to permit stimulation of the labyrinth either by tilting or by rotation in a horizontal plane. In order to avoid complications resulting from translatory motion and centrifugal force, provision was made to have the labyrinth placed approximately at the point of intersection of the horizontal and vertical axes of rotation. Arrangements were also made so that the head of the frog (which faces the left-hand wall of the chamber) could be made to face in any desired compass direction relative to the horizontal axis, so that by suitably orienting the box one could carry out a tilt in any vertical plane, whether antero-posterior, lateral or diagonal. Set-screws were provided for both the horizontal and vertical axes in order that movement about one could be prevented during investigation of the effects of rotation about the other.

It will be seen from the figure that by suitably fixing the horizontal axis and the pivot which attaches the preparation box, one may use horizontal rotation to stimulate either of the two vertical canals in its own plane. For example, if one wishes to bring the plane of the anterior canal into the horizontal position, one turns the preparation box through 45° to the left (from its position in the photograph) and then tilts it through 90° to the right about the horizontal axis. Counter-clockwise rotation of the apparatus at its basal joint will now cause the anterior canal to rotate, in its own plane, in such a direction that the ampullary end of the canal leads the longer and narrower portion. According to current opinion this should stimulate the nerve endings in the crista, whereas clockwise rotation should not stimulate the canal mechanism until the rotation is stopped—or, at least, sufficiently slowed. The device thus enables one to stimulate the vertical canals without changing, during the process, the position of the head relative to the earth's gravitational field, and in this way the stimulation of the otolithic organs of the labyrinth which normally accompanies tilting movements of the head is avoided. Moreover, it is possible by means of such horizontal rotation to subject the vertical canals to prolonged rotational stimulation without rolling the head over and over. The chances of dislodging the nerve filament from its electrode, or of otherwise disturbing it through excessive movement of surrounding tissues and fluid, are thus minimized.

During the progress of the work it became advisable to record the responses of the utricular macula to linear acceleration. For this purpose the preparation box is removed from the tilting-and-rotation apparatus and placed in a subsidiary holder which is arranged to slide horizontally on two metal tracks. In this case also, the compass direction of the head is adjustable at will, so that the motion can be made to take place along any desired horizontal line, whether antero-posterior, lateral or diagonal.

Electrical connection must, of course, be established between the nerve filament and the amplifier input. For tilting and acceleration stimuli this is accomplished simply by means of a suitable length of flexible wire arranged so that its free portion will not brush against any external structure throughout the course of the movement. For the horizontal rotation experiments, however, provision must be made so that the movement may, if necessary, continue for twenty or thirty revolutions. Investigation showed, somewhat to the writer's surprise, that sliding metallic contacts, if properly cleaned and lubricated, are sufficiently free from electrical artefact to suit the requirements. The central shaft of the vertical bearing is therefore drilled through its axis to permit the passage of an insulated conductor for the active or "grid" lead. This inner conductor is secured, at its upper end, to an insulated terminal for the attachment of one of the flexible leads; and, at its lower end, to a small, insulated, axially placed brass disc with which four small phosphor-bronze springs, also insulated and connected together, make firm contact. For the earth lead the contact in the bearing between the main post and the base would probably be sufficient, but for safety two auxiliary springs, connected to the base and bearing on the upright shaft, are provided. These two sets of springs are mounted on a wooden block under the cast-iron base of the apparatus. They remain stationary during a rotation experiment, and are connected to the input of the amplifier.

Tilting and small-arc rotational stimuli are registered on the record by means of a moving signal lever which, intercepting the beam of light from the oscillograph, casts its shadow vertically (or, in limiting positions, nearly so) on the camera slit. The lever is moved by a thread wound over a small drum moving with the preparation and centred on the axis of rotation. A gentle spring on the lever keeps the thread taut. The excursion of the shadow is, therefore, approximately proportional to the arc swept out by the rotary movement of the preparation. The two drums may be seen in the photograph, that for tilting being between the two brass uprights at the left of the machine, and that for horizontal rotation being on the end of the central pivot, under the insulated terminal for the active lead wire. They have equal diameters.

To facilitate the interpretation of the records, it was made standard practice, in tilting experiments, to arrange the signal so that its shadow fell about midway across the exposed (dark) part of the record when the preparation box was in the upright or "normal" position (cf. Fig. 5).

The same signal lever serves to record the movement during linear acceleration. A heavy thread is attached to the sliding portion of the apparatus and, at its other end, is fastened to, and wound around, a light wheel. The wheel is suitably geared to a shaft around which is wound the thread which moves the signal lever. The threads are kept taut during the course of the movement by springs. The excursion of the shadow here is also approximately proportional to the extent of the linear movement.

For prolonged horizontal rotation a different signal is used. It consists of a rotating disc, around the circumference of which eight narrow, radial slits, symmetrically distributed, are cut. A beam of light is arranged to fall on a sharply localized region at the top of the record, and the disc is placed so that the slits pass through an area where the beam is concentrated. During its rotation the disc therefore cuts off the beam except during brief intervals corresponding to the slits, and each of these intervals leaves a vertical (or nearly vertical) line at the top of the record. The disc is made to rotate by means of a pulley and a belt leading, in most cases, directly to the pulley shown in the photograph just under, and fixed to, the rotating part. The angular velocity of the signalling disc is thus proportional to that of the preparation, and the lines on the record may be regarded as "angular milestones" showing how the movement of the preparation is progressing. Fairly good estimates of the angular velocity, and even rough ones of the angular acceleration, may be obtained by measuring the distances between lines.

Such a signalling system possesses obvious drawbacks, but it is sufficiently accurate for the present purpose.

For all tilting, linear acceleration, and small-arc rotation tests the preparation was moved by hand. For very slow tilts a lever, fixed temporarily to the tilting portion of the apparatus, assisted in producing smooth motion. In cases where it was desired to observe the responses during constant velocity rotation, or at the cessation of rotation which had been steady for several revolutions, a governor-controlled clockwork motor (from a gramophone movement) was used. In the earlier experiments the signal disc and the turntable were both operated from the motor shaft, each from its own separate pulley; but in the later ones, the motor drove the signal by means of a multiple pulley, and the latter drove the turntable through a separate belt, thoroughly rubbed with beeswax to prevent slipping.

Sometimes a vibration receptor turned up instead of an equilibrial one, and the need arose for a source of vigorous, constant-frequency vibration. For this purpose a magnetic loud-speaker movement, an H.T. battery (tapped for 20 or 30 volts), a rotary contact-breaker, and a two-way switch were connected in series. The contact-breaker was fitted with two brushes, one making a single contact per revolution and the other making sixteen, and the switch was arranged to allow rapid change from one brush to the other. The commutator was driven by an electric motor, provided with a rheostat to adjust its speed. A small drop of sealing-wax was placed on the end of the loud-speaker arm, by way of insulation, and the preparation box and speaker movement were arranged so that the box, supported loosely by the rubber-covered rod in its right side, could have one of its sides placed in contact with the wax-covered tip of the speaker arm. Considerable shielding was found necessary in order to avoid electrical artefact from the motor and the contact-breaker brushes. Nevertheless, the device worked satisfactorily enough, and enabled one to make tests whenever vibration receptors were encountered. All vibration experiments were controlled with novocaine, as described below, in order to eliminate the possibility of either mechanical or electrical artefact.

PREPARATION.

The frog is pithed and decapitated, and the head is divided longitudinally by a section a little to the right of the mid-line. The right half of the head is used for all experiments. It is pinned securely to the top of the cork in the moist chamber, described above, with the snout pointing to the operator's left and the cut medial surface of the head toward him. The wet sponges are inserted, and the preparation is placed under a fairly high-power dissecting microscope. The remains of the brain are carefully removed, the auditory nerve being detached at its entrance to the medulla by gentle manipulation with a fine needle. The membranes covering, and in the immediate neighbourhood of, the nerve are then teased away with two pairs of very fine forceps.

The nerve is now lifted up and laid against the lateral wall of the cranium. This brings into view the two acoustic foramina, each containing a branch of the auditory nerve. The line of union of the two rami is distinguishable along the postero-inferior edge of the common nerve trunk, and with a pair of fine needles the two rami are separated along this line. The last possibility of interconnecting strands is eliminated by running one needle, with its point bearing against the bone, between the rami and well beyond them in both directions. One ramus is then teased down until a fine filament is obtainable, and this is mounted on the "grid" electrode.

Both this and the "earth" electrode are of fine silver wire, supported in glass tubes. The tubes are mounted in plasticine to allow of appropriate adjustment, and the two lead wires from the upper ends of the tubes are clamped into separate terminals on the top of the preparation box, each along with the corresponding flexible lead wire. The earth electrode is bent at its tip in such a way that it can be made to lie along the wall of the cranial cavity in the olfactory region. Good contact is assured by covering the bent tip with a small triangle of well-soaked filter paper. To the tip of the active electrode wire a short length (2 or 3 mm.) of silk thread is tied. A drop of Ringer's fluid is placed so as to cover the knot on the wire and keep the thread moist by capillary action. The nerve filament, when lifted into the air and brought into contact with the tip of the thread, adheres in position, and is kept moist by the reserve fluid on the thread.

When the filament has been mounted, the preparation is roughly tested to see how many receptors are still in functional connection, through the nerve, with the oscillograph. If there are too many the filament must be removed and dissected down still further.

It will be seen from the foregoing description that there is no way of telling, in advance, with what type of receptor one will finally end up. One can choose to work on either the anterior or the posterior ramus of the nerve, but it is impossible to select particular nerve fibres for isolation. It will be shown below, however, that if one succeeds in isolating the responses of a single receptor (or of a group of receptors all behaving similarly) one can frequently, by considering the type of stimulus to which the preparation responds, deduce the source of the observed impulses with a high probability of correctness. This statement applies especially to those cases in which the filament is taken from the anterior ramus, for the end organs supplied by this branch all have known functions.

CONTROLS.

The general characteristics of the discharges leave little doubt that they represent true action potentials in the nerve filament, but as a precautionary measure the matter was frequently tested by novocaine controls. For this purpose one or two minute crystals of the drug are placed on the mush of tissues and fluid from which the nerve filament emerges. One can do this quickly and without taking the filament off the electrode or greatly disturbing the electrical conditions in its neighbourhood. The invariable result of this procedure was to abolish the response to any of the tilting or vibrational stimuli used. As mentioned above, all vibration experiments were controlled in this way, but the negative result of the control appeared so consistently that in the equilibrial experiments controls were performed only here and there throughout the series.

THE IDENTIFICATION OF THE RECEPTOR ORGAN.

The manner of distribution of the auditory nerve in the frog is well known, and is represented diagrammatically in Fig. 2 [after de Burlet, 1929]. It will be seen that the nerve has two principal branches. Of these the anterior supplies the saccular and utricular maculæ and the two cristæ of the horizontal and anterior semicircular canals; while the posterior ramus is distributed to the lagena, the pars basilaris, the pars neglecta (the "pars amphibiorum" of de Burlet [1928]), and the crista of the posterior canal. Since it is possible to separate completely the two rami inside the cranial cavity, the maximum number of end organs which might be connected to any given filament under investigation can conveniently be reduced to four. In the case of the anterior ramus all four receptor organs have known functions, but with the posterior ramus the functions of three of the receptors have not yet, as far as I am aware, been established. The one whose function is known is, of course, the posterior canal.

The evidence which enables one to infer the source of the impulses obtained in a given nerve filament is based upon the remarkably close correspondence between the type of stimulus which is found by trial to elicit a response from the preparation and one or other of the various stimuli which, on the basis of previous work involving differential ablations, are known to cause activity in at least some of the several sensory organs of the frog's labyrinth. As the validity of this evidence is of considerable importance in the interpretation of the records, it may well be considered at once in detail.

It has been found that the response of a single end organ (or of a group of organs all behaving similarly) has always been capable of classification into one or other of several readily distinguishable categories, according to the kind of stimulus which elicits it. The characteristics of these categories may be summarized briefly as follows.

Group I. Responds to crude mechanical vibration of the head, and fails to react to tilting movements unless these are accompanied by jarring or other forms of vibration.

Group II. Responds to specific gross movements of the head, but not to vibration. This group may be further subdivided into:

(*a*) The "gravity" group, which responds, in the simplest case, to tilting movements. Its receptors can also be stimulated by linear accelerations in a horizontal plane, and they would presumably react to centrifugal force, although this has not been tried. Their action is intimately dependent upon the lie of the head in the earth's gravitational field. There are two kinds of gravity receptors: (i) a type which gives its best response when the head is tilted *out of* the level position; (ii) a type which, as far as information is at present available, responds only when the head is tilted from some inclined position back *into* level.

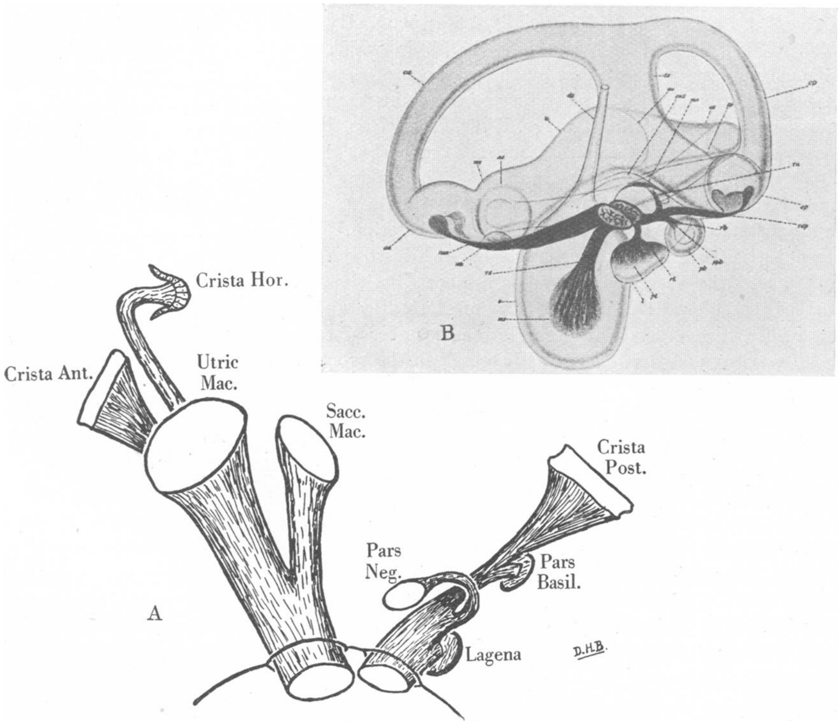

Fig. 2. A, diagrammatic representation of the course of distribution of the auditory nerve in the frog. Redrawn from de Burlet [1929]; B, diagrammatic representation of the vestibular organs in the frog. From Retzius [1881].

(*b*) The "rotation" group proper, the members of which are stimulated by rotatory acceleration, whether the movement involves a tilt or not. The inclination of the axis of the rotation with respect to the earth seems to make little or no difference, so long as it cuts the head in the proper manner.

It should, perhaps, be mentioned in passing that the receptors of Group II do not respond to *any* tilt, or to *any* direction of rotation. Both the plane in which the tilt or rotation occurs, and the direction of motion in that plane, are decisive factors in determining the vigour of the response.

Now the results of previous investigations on the frog's labyrinth [see Tait and McNally, 1925, 1929, and especially 1934; McNally, 1932; and McNally and Tait, 1925, 1934 *a*, 1934 *b*, and especially 1933], in which the functions of the individual balancing organs were studied by the methods of isolated ablation and sole persistence, enable one immediately to place four of the eight receptors into either the gravity or the rotation groups, as defined above. Thus, it is clear that the utricular macula with its accessories is a gravity organ (Group II *a*), and that the cristæ of the three semicircular canals are rotation receptors (Group II *b*). The placing of the canals in the rotation group is also strongly supported by the work of Steinhausen [1931, 1933, 1934], in the pike, on the intimate mechanism of canalicular stimulation. With regard to the saccular macula, the negative equilibrial experiments of Laudenbach [1899] and McNally and Tait [1925], and the electrical observations, both positive and negative, of Ashcroft and Hallpike [1934 *a*, 1934 *b*], and also of McNally and the writer (unpublished), have established the fact that this organ is a receptor for vibration, and that it does not respond to tilting provided that it is not "joggled" in the process. The saccular macula therefore belongs to Group I.

The above information enables one immediately to deduce the source of impulses derived from any part of the anterior ramus, particularly when the subdivision of the nerve has been carried down to a point at which the response obtained is pure. Thus, a response to vibration, but not to gross movement, indicates the saccular macula; a gravity response must arise in the utricular macula; and while a rotation receptor may lie in either of the two cristæ supplied by the anterior ramus, the one concerned may readily be determined by ascertaining in which plane of rotation the discharge is most easily elicited. In experiments where the filament has been taken from the posterior ramus the matter is less definite, for whereas a rotation receptor is almost certain to lie in the posterior crista, a gravity or a vibration receptor may lie in any of the other three organs supplied by the posterior ramus.

The considerations mentioned above should suffice to establish, beyond reasonable doubt, the identity of a sense organ which in an experiment gives rise to (*a*) any pure response in a filament of the anterior ramus, or to (*b*) any rotation response in the posterior ramus; but the parallel between the known properties of the various labyrinthine organs and those experimentally determined by the procedure herein described extends considerably further than has already been indicated. It is best illustrated by the rotation receptors, which, as stated above, are taken to be the semicircular canals. If this assumption is to be proved incorrect, the following formidable set of coincidences will have to be explained away:

(*a*) Three, and only three, different kinds of rotation receptors have been encountered.

(*b*) Of these three kinds, two occur on the anterior ramus, and one on the posterior.

(*c*) It is known that each canal responds best to rotation in its own plane. Of the two rotation receptors on the anterior ramus, one responds most readily to rotation in the plane of the horizontal canal, and the other to rotation in the plane of the anterior canal; while the single posterior rotation receptor invariably responds best to rotation in the plane of the posterior canal.

(*d*) Any preparation can be brought from a state of rest into one of constant angular velocity, in a given plane, by rotating it in either one of two opposing directions. In the case of a canal being rotated in its own plane in this manner, it is almost certain that only one of the two directions causes stimulation. The same is found to be true for each rotation receptor, and the direction which stimulates any rotation receptor in the above manner has in every case been the same as that which stimulates the corresponding canal. This is true in spite of the fact that the horizontal canal is stimulated by rotation in a sense opposite to that which stimulates either of the two vertical canals.

(*e*) It has been shown that when a canal has been rotating in its own plane for several seconds in a direction which did *not* cause stimulation at the onset of the rotation, cessation of the movement will stimulate the end organs of the crista. The same is true for each of the three rotation receptors.

(*f*) Sufficiently vigorous horizontal rotation can stimulate a vertical canal in the frog if the head is turned so that the motion possesses at least some rotatory component (in the correct direction) in the plane of the canal concerned. This is also true for the rotation receptors corresponding to the vertical canals.

These considerations show that although it would, strictly speaking, be unfair to state that the response of any canal can be recognized with complete certainty, one can legitimately claim a canalicular origin for a rotation receptor response with a very considerable degree of confidence.

A utricular receptor is identified with equal ease, for any anterior-ramus organ which remains unresponsive to tapping or other vibratory stimuli must lie in either the utricular macula or a canal ampulla; and the canal responses are so highly specialized that it is quite easy to distinguish a gravity response from them.

Thus it is clear that whereas one cannot, when using the technique described above, plan an experiment on any particular labyrinthine organ, one can study the properties of the saccular macula, of the utricular macula, or of any of the three semicircular canals whenever they turn up in the nerve filament which has been dissected out. It is also possible to study responses in the posterior ramus even if they are quite obviously not derived from the posterior canal, and in this way to obtain information regarding the functions of the lagena-basilaris-neglecta group, as a group if not as individuals. These have been the main objects of the investigation.

TERMINOLOGY.

Before describing the experimental findings, it will be well to adopt some system by means of which a tilting or other rotatory movement may be clearly described. The following plan has proved useful in making notes during the course of the experiments, and will be used throughout.

By tilting is meant any movement of rotation about the horizontal axis of the apparatus (Fig. 1). By tilting to the right is meant that direction of rotation which would tend to make a normal frog, squatting upright on a previously level plane, slide to his right. A tilt to the rear would similarly tend to make him slide backwards, and so forth. As the preparation is invariably taken from the right-hand side of the frog's head, diagonal tilting is conveniently described by naming the vertical canal in whose plane the tilt occurs. The direction of a diagonal tilt, or of any other form of rotation in the plane of a vertical canal, is designated by reference to the canal itself. The axis of the rotation is regarded as passing through the loop of the canal, and if the movement is in such a direction that the ampulla precedes the adjacent, narrower portion of the canal, it is referred to as being in the "ampulla-leading" direction. The opposite direction of rotation is referred to as "ampulla-trailing". Normal horizontal rotation with the head level is best designated simply by calling it rotation to the right (clockwise) or to the left (counter-clockwise); but, for the sake of comparison, such right-hand rotation could be called "ampulla-trailing" in the plane of the horizontal canal.

For the recording of responses to tilting and small-arc horizontal rotation the continuous-line signal was used, and the relation between the direction of the tilt and the movement of the signal is given in the legend under the figure by some such statement as "signal up = ampulla-leading"—"signal up" simply meaning movement of the signal line toward the top of the printed page. The number of degress of rotation of the preparation corresponding to the movement of the signal line in the reproduction is also given where necessary in the legend (*e.g.* 1 cm. = 123°).

It should be emphasized here that the placing of the head preparatory to stimulation by tilt or other rotation in some special plane was by no means mathematically precise. The various axes in the apparatus (Fig. 1) were set purely by inspection, the setting being based on the assumption that the three axes of the frog's head were respectively parallel to those of the preparation box. Inasmuch as the cork to which the head was fastened was roughly shaped to fit the head, the above assumption was approximately correct, but individual differences in the size of the head and the exact manner of dividing it in two could certainly have caused variations in its alignment. Consequently the planes in which the preparations were tilted or rotated corresponded only approximately with the equivalent ideal planes defined with reference to the frog's head, but the discrepancy between the two for any given test was probably not more than 10 or 15°.

The time marker has a period of (nearly) 0·54 sec. in all the records.

RESULTS.

One of the early findings was that in the frog the receptor mechanisms for gravity and for vibration are both at least twofold (Fig. 3). Hitherto the main emphasis has been laid on the utricular macula as the principal gravity organ (in the sense used here), but there is another strikingly similar gravity organ somewhere on the posterior ramus. Of how much importance this latter is in the reflex balancing mechanism it is at present impossible to say, but there are certainly two, and perhaps three, distinct receptor organs in the frog which fall into the gravity class. There is likewise another vibration receptor besides the saccular macula. The actual identities of these "new" organs are, as far as I am aware, unknown. Various conjectures may be made on morphological grounds, but all that one can definitely state at present is that they are to be found somewhere in the lagena-basilaris-neglecta group.

General characteristics of the discharge.

A peculiar feature of nerve filaments which still contain a fair number of active fibres is the marked tendency for impulses to keep appearing in the filament for no very good or obvious reason. Any movement of the preparation sets up a barrage of impulses which may take an uncommonly long time to die away, and often gives the impression of subsiding to a resting level of random activity and remaining there more or less indefinitely. Whether or not this type of activity is characteristic of the normal labyrinth is uncertain. It must be borne in mind that the ear has been deprived of its blood supply, and that the nerve, although still capable of conducting impulses, has on account of its small size been subjected to a certain unavoidable amount of maltreatment during its dissection. It is certain, at any rate, that when single-fibre preparations are obtained, the occurrence of a resting discharge is rather rare. When it does occur it usually possesses no regular frequency, and it can, as a rule, be momentarily suspended by a movement in the direction opposite to that which stimulates the end organ.

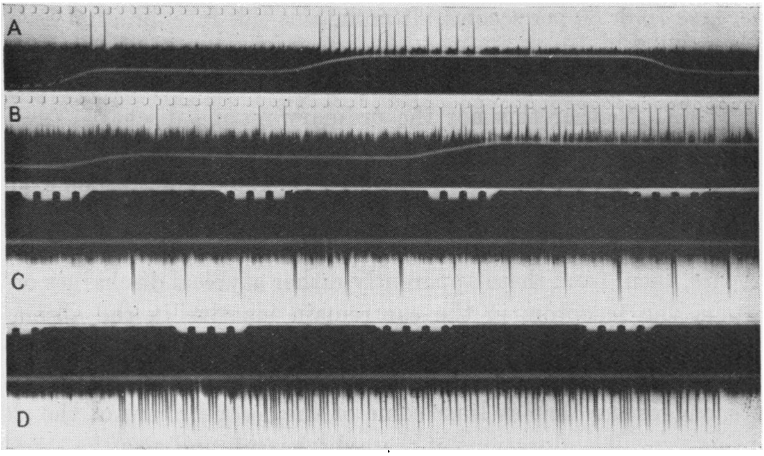

Fig. 3. A and B. A comparison of the anterior and posterior type (i) gravity receptors. A, anterior ramus; tilt in the plane of the posterior canal; signal up = ampulla-leading; 1 cm. = 220°. B, posterior ramus; antero-posterior tilt; signal up = tail down; 1 cm. = 210°. C and D, records from a preparation of the (unidentified) posterior vibration receptor. C, single contact per revolution of circuit-breaking commutator. D, the same preparation, same commutator speed, 16 contacts per revolution.[1]

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[1] In this and in some other early records the impulses appear with their spikes pointing downwards, while in the majority of the records they stand upright on the base line. This does not mean that the polarity of the discharges varied from one experiment to another; it was entirely consistent throughout the whole of the investigation. The reversal is due to the rearrangement of the oscillograph, which was made to deflect the other way in order to leave room at the top of the record for the rotation signal, which for technical reasons could not easily be arranged to record at the bottom.

Another type of spontaneous single-fibre discharge has been met with occasionally, this variety being presumably of pathological origin. It immediately precedes the failure of excitability of the sensory unit, and its frequency is sufficiently regular to make it heard, in the loud-speaker, as a wailing note. Its occurrence, though rare, usually follows some rather rough handling of the preparation, such as the turning of a gravity organ upside down, or flat on its side or end. The discharge then starts at a frequency which is low at first, but which gradually increases up to perhaps 70 or 80 per second. It maintains this rate for a few seconds; then rapidly becomes irregular and ceases altogether, after which the preparation responds only to very strong stimuli, or, more likely, to none at all. Neither this nor the ordinary resting discharge (nor any other discharge, for that matter) has ever been observed with the action potentials reversed in sign (see footnote on p. 129); a fact which excludes the possibility of an origin at or near the cut end of the fibre rather than within the labyrinth.

Apart, then, from these apparently rather atypical discharges of long duration, the receptors in the ear remain inactive in the absence of movement or vibration. Fairly prolonged discharges—*i.e.* several seconds—may, however, be obtained by appropriate stimulating movements, suggesting that at least some of the receptors are of the slowly adapting type. The durations of these discharges, and also the threshold intensities for their various stimuli, are subject to a good deal of fluctuation between one experiment and another. This may mean that in the intact frog the different receptors in any one labyrinthine organ are graded as regards threshold and rate of adaptation, but it is more likely that the variation is largely due to the artificial conditions of the experiment. For this reason, the present communication deals mainly with the purely qualitative, rather than the quantitative, aspects of the stimuli used.

The vibration group.

The main interest in the investigation centred around the equilibrial receptors, for all the balancing organs found in the ears of the higher vertebrates also occur, and presumably function somewhat similarly, in the frog. Vibration receptors turned up in the preparations from time to time, however (they appeared quite frequently in the initial rough tests of the nerve filaments), and occasionally a single-organ preparation would be obtained. Fig. 3 C and D show sample records of the responses of the so far unidentified posterior vibration receptor. They were both taken from the same preparation, and within a second or so of each other. In C the contact-breaker circuit of the stimulating device was thrown onto the commutator brush which gave a single contact per revolution, while in D the other brush was used, giving sixteen similar contacts per revolution—which at this motor speed represents a frequency in the neighbourhood of 100 per second. No attempt has been made to explore the frequency range of these vibration receptors with the present crude stimulating apparatus.

This and similar experiments show only that the receptor concerned is capable of responding to crude vibration of the head, and should not be interpreted as either for or against the idea that the frog possesses a receptor mechanism for air-borne sound. It is true that no responses to air-borne sound have during this investigation been obtained from single vibration receptors, even if the lid of the preparation box was temporarily removed, but it would probably be safer for the moment to suspend judgment on this question.

None of the receptors in the vibration group responded to tilting movements in any consistent way. A few erratic impulses might be discharged during the course of a tilt, but such responses are best interpreted as being due to jarring or other vibration occurring accidentally in the course of the movement. Some of the preparations were certainly remarkably sensitive to vibration. Responses were occasionally obtained merely to the slight jarring caused by the writing of notes in pencil on a small note pad while it lay on the top of the table a foot or two from the stand or rotation apparatus on which the preparation box was supported.

The gravity group.

This is the group which responds to tilting or to linear acceleration, but not to vibration nor, if precautions are taken to avoid the interference of centrifugal force, to rotation in a horizontal plane. These receptors are readily distinguished from those of the rotation group by their dependence upon the way in which the head lies in the earth's gravitational field during the progress of the movement. Thus, if one uses two tilting stimuli which are both in the same plane and also in the same direction in that plane, it makes considerable difference to a gravity organ whether one tilts the head up into the level position or down from the level position (Fig. 3 A and B), whereas these two stimuli have virtually the same effect on a rotation receptor. In addition, the duration of the response differs markedly between the two groups. The discharge of a rotation receptor to a tilt (in which the arc swept out will be at most 180°) is invariably brief, while under favourable conditions the discharge from a gravity organ may last several seconds.

The differences between the two groups are strikingly illustrated in Fig. 4. In all three records the impulses were obtained from the posterior ramus, and in B and C the stimuli were (as nearly as possible) the same. They consist of, first, a series of tilts back and forth on one side of the normal (level or nearly level) position, and, secondly, a similar series of tilts on the other side of the normal. It is obvious that the two varieties of tilt have quite different effects in C (gravity receptor), but in B the end organ responds equally well to both (rotation group).

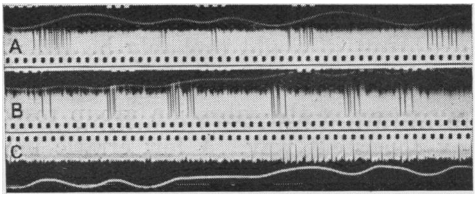

Fig. 4. Illustrating the differences in character between typical discharges from the posterior canal (A and B) and from a type (i) posterior gravity receptor (C) which responds to a tilt both in the same plane as the canal and to the same direction of tilt in that plane. A and B are from a posterior ramus preparation. A, small-arc horizontal rotation in the plane of the posterior canal. B, tilt in the plane of the posterior canal. C is from another posterior ramus preparation, tilted in the plane of the posterior canal. In all three records signal up = ampulla-leading, and 1 cm. = 310°.

The most conclusive test for a rotation receptor is to establish its response to horizontal rotation in an appropriate plane. This has been done in record A. The head has been turned so that the posterior canal lies in the horizontal plane, and the receptor which gave the responses in B is being stimulated by small-arc horizontal rotation. The discharge is elicited just as readily as before.

Gravity Group, Type (*i*). The gravity responses illustrated so far (Fig. 3 A and B, and Fig. 4 C) belong to the first type of gravity organ, for their discharge is most vigorous when the preparation is tilted out of the level position. Whether or not they react to a tilt into level (in the same direction) is debatable. Some apparently do (Fig. 3), and others apparently do not (Fig. 4). The difficulty is that one cannot tell from the position of the apparatus just when the head is in what would be, in the intact animal, the normal and symmetrical position. Responses to an into-level tilt (as judged by the apparatus) are obtained quite frequently, and they are almost always, if not invariably, weaker than the corresponding out-of-level tilt. But in these cases one is never sure that the *head* may not have been tilted just a little past the level position, and down on the stimulating side. In the absence of more accurate information, the question of this into-level response must remain open for the present.

It is of interest to note in passing that, whatever the cause of the apparent into-level responses from type (i) gravity organs, they can nearly always be considerably strengthened by leaving the head in the down position (non-stimulating direction) for half a minute or so before tilting it back into "level" again for the response. This property is illustrated in Fig. 5. The receptor is the same as that of Fig. 3 B, and the sensitized "into-level" response, A, now compares very favourably with the normal "out-of-level" discharge, B, which was obtained from the same preparation a minute or so later. Both discharges lasted several seconds.

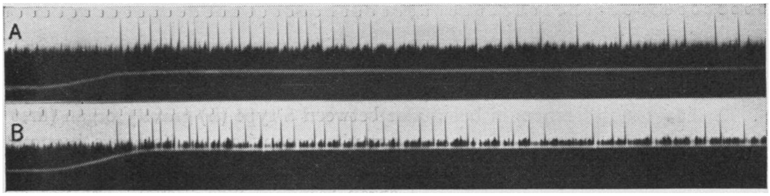

Fig. 5. A shows the sensitized "into-level" response of a type (i) gravity organ, for comparison with, B, the normal "out-of-level" response, taken a little later. The preparation is the same as that in Fig. 3 B, and it was tilted into the nose-down position about half a minute before the "return-to-level" tilt shown in A. Compare this discharge with the first one in Fig. 3 B. The tilt in B is tail-down. Signal equivalents: A, 200° per cm.; B, 210° per cm.

Type (i) gravity organs respond only to one direction of tilt in any plane. The stimulating direction is the same whether the tilt is rapid or slow (see Fig. 7, and also later in text). The plane of the stimulating tilt is, however, not at all sharply defined. One can usually find, by trial, some plane in which the receptor responds best, but in other planes on either side of this maximal one the response falls off not at all steeply. It seems probable that an out-of-level tilt in order to stimulate must possess at least some component in the direction of the most effective tilt, but that within these limits almost any tilt is likely to have some effect if the receptor is at all sensitive.

Receptors designed to respond to a lateral tilt to the left are by no means confined to the left labyrinth, for they have turned up in the course of this work on the right ear. This finding is in agreement with the reflex work of Tait and McNally [1934, p. 253], who find that the tilting of a single utriculus to its mesial side does elicit some compensatory response, if only a rather weak one.

Gravity Group, Type (*ii*). Information regarding this peculiar and interesting type of gravity organ is rather scarce, for these receptors have been encountered only a few times. It seems to be indisputable, however, that there are certain gravity organs which respond only when tilted up towards the level position, and which cease to discharge even if the tilt is continued out of level in the same direction. If one tilts a multi-receptor preparation, containing both gravity types, right through level from one side (or end, or corner) to the other, one hears a definite double discharge in the loud-speaker—an initial burst from the type (ii) receptors while coming into level and a subsequent discharge from the ordinary type (i) receptors. Only one reasonably good record illustrating the action of a type (ii) receptor has been obtained; it is shown in Fig. 6. This experiment was particularly fortunate, for the preparation supplied a type (i) gravity organ in the same nerve filament for purposes of comparison; moreover the two sets of impulses were readily distinguishable (in the original record at any rate) since the type (ii) impulses were diphasic and the others monophasic. It is seen that the tilt into level is signalled by a receptor which refuses to respond to a further tilt out of level, and that the second receptor, which does react to the out-of-level

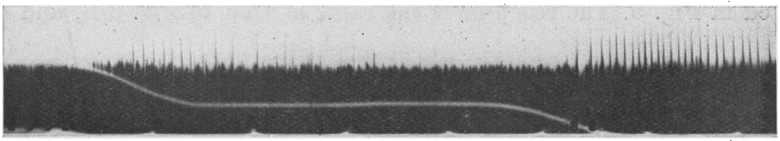

Fig. 6. To show the differences in behaviour between a type (ii) gravity organ (first discharge, diphasic impulses) and a type (i) gravity organ (second discharge, monophasic impulses). Posterior ramus preparation; rather extensive lateral tilting; signal up = to the right; 1 cm. = 150°. The type (ii) organ responds into "level" but not out of "level"; whereas the type (i) organ responds well out of "level" but not, in this case, into "level". A moment after the end of the portion of record shown, a signal-up tilt into "level" was also found to give diphasic impulses indistinguishable from those in the first tilt, suggesting a bidirectional action for the type (ii) organ. The presence (unmistakable in the original) of another, smaller, diphasic impulse, which also appears (only) in response to both into-"level" tilts, confirms this suggestion.

tilt, failed to respond previously. The original record also reveals (immediately after the portion shown) the rather startling fact that the type (ii) organ reacts, in its own peculiar manner, to both directions of the tilt into level. Whether this behaviour is typical of these organs it is at present impossible to say, but other records suggest that the response can at least sometimes be unidirectional in character.

Type (ii) receptors have been encountered on several occasions in mixed preparations, but have not so far been found in preparations of the anterior ramus. The rather fundamental difference in behaviour between these receptors and those of type (i) tempt one to imagine that they lie in a special organ—the third of the three unknown organs of the posterior ramus.

The utricular macula. On the assumption, discussed above, that the gravity organ of the anterior ramus is the utricular macula, this sense organ received particular attention; for it has been suggested [McNally and Tait, 1933, 1934 *a*, 1934 *b*; and Tait and McNally, 1934] that in the frog the utricular macula may possess, to some extent at least, properties more typical of a rotation receptor, and may respond to tilting rotation as such. Tait and McNally found that if a "bisoliutricular" frog (*i.e.* one in which both labyrinths have been completely denervated except for the two utricular maculæ) were subjected to a slow tilt in any given direction, the animal's reaction was truly compensatory in nature; whereas if the same tilt were performed rapidly the initial reaction was decidedly anti-compensatory, and consisted of a violent bodily heave or plunge in exactly the wrong direction. In other words, the response of the animal to slow tilting is such that its balance tends to be maintained; but if the tilt is rapid the reaction elicited is the one which would have been admirably suited to maintain the animal's balance if the tilt had only been in the other direction. In order to explain this peculiar finding, these investigators were led to postulate that a slow tilt in one direction would excite the same utricular receptors as would be stimulated by a rapid tilt in the opposite direction; and they devised a scheme of utricular structure which would be expected to produce this effect. Because their hypothetical scheme has at best rather scanty histological support, it seemed advisable to subject the matter to experimental test using the electrical technique described, which could presumably settle the question one way or the other.

On the basis of their postulate, one would expect that any given utricular receptor would respond to a slow tilt in one direction, but that if the movement were rapid, the receptor would respond only when tilted in the opposite direction.[1] This does not seem to be the case. The record in Fig. 7 A was taken very shortly after that of Fig. 3 A, from the same preparation. It shows this receptor (a type (i) gravity organ, on the anterior ramus) responding to rapid tilting. It discharges in each case to the signal-up tilt as before, and refuses to react when tilted in the other direction, no matter how abrupt the motion may be. This experiment, of comparing slow and rapid tilts in type (i) gravity organs, has been tried on ten separate preparations (eight on the anterior ramus, one on the posterior ramus, and in one early experiment in which the rami had not been separated). In nine of these cases, of which Fig. 7 A is a functionally representative one, the preparation gave no sign of a reversed response with quick tilting. The tenth case is not entirely above suspicion, and is shown in Fig. 7 B and C. This exceptional case may be important, and deserves a little consideration. The writer is, however, of the opinion that the first and last discharges in record C do not represent *bona fide* reversed responses, for the following reasons.

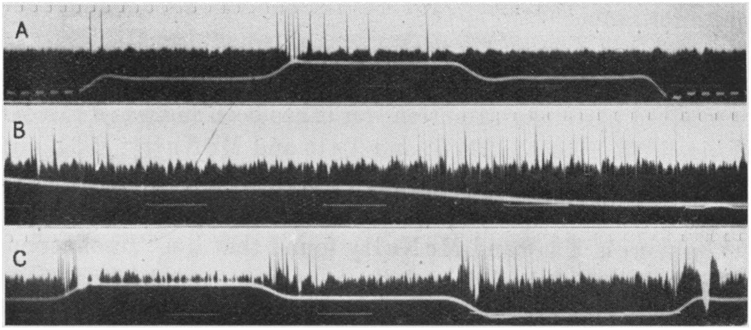

Fig. 7. To illustrate the inability of a quick tilt to reverse the stimulating direction (of tilting) for anterior gravity receptors. A shows the same receptor as in Fig. 3 A, the records having been taken within a few seconds of each other. The tilt is in the plane of the posterior canal; signal up = ampulla-leading; 1 cm. = 190°. B shows another anterior gravity receptor. Slow tilting in the plane of the anterior canal; signal up = ampulla-leading; 1 cm. = 160°. C, same preparation as B, rapid tilting. Signal as in B, but 1 cm. = 190°. For discussion see text.

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[1] This is stating the matter rather more simply than accurately, for the response of a bisoliutricular frog to a rapid tilt occurs in two phases; viz. a prompt anti-compensatory reaction during the tilt, followed quickly by a secondary, compensatory movement which adapts the animal's posture to the new inclination of the substratum. For the moment, however, we are concerned only with the anti-compensatory primary reaction and with the utricular events which produce it, and can leave out of consideration the secondary reaction, which exhibits no unexpected features.

Record B shows that at least two receptors are present, the more sensitive one giving a diphasic impulse. Both (or all) these receptors respond unidirectionally to the slow tilt, except for one stray diphasic impulse near the start of the slow up-signal tilt (not on the portion of record shown). Both (or all) respond to the same direction of quick tilt (second and third responses, record C), so that in this respect at least the response has not been reversed. The suspicious parts of the record are the first and fourth responses in record C, which might conceivably be the monophasic receptor. If this is so, it is difficult to understand why the more sensitive diphasic receptor did not discharge vigorously here; and why, in addition, monophasic impulses still appear in response to the second and third tilts. It therefore seems probable that the responses to the first and fourth tilts arose in some other receptor giving monophasic impulses, but whose threshold was too high to enable it to react to the slow tilt. In appearance these two discharges are typically canal-like, and as the plane and direction of the tilt were suitable for anterior canal stimulation it seemed likely that the aberrant impulses originated in the anterior crista. A test was accordingly performed in order to decide this point. It happened that the gravity receptors in question—both monophasic and diphasic—responded well (probably best) to a rearward tilt; but they also responded easily to tilts in the two diagonal planes, ampulla-trailing in the plane of the anterior canal (as shown) and ampulla-leading in that of the posterior canal. The slow and fast tilting was therefore tried in this last plane, a procedure by which any stimulation of the anterior canal would almost certainly be avoided. In this experiment the responses fell into line very well with the other nine cases, impulses appearing in all ampulla-leading tilts, whether fast or slow, and failing to appear for ampulla-trailing motion. It is therefore highly probable that the questionable monophasic discharges in response to the first and fourth tilts had a canalicular, and not utricular, origin.

One has still to explain the single diphasic impulse which occurred towards the end of the last discharge in record C, and this is puzzling. It is probably due to some inertia effect consequent upon the very abrupt movement of the head, for the whole into-level tilt was completed in something like one-eighth of a second. But whatever its cause, one such impulse cannot explain the vigorous reversed reactions observed by Tait and McNally, even if it occurred regularly, and this is the only instance in which even one impulse is observed in this position.

It is therefore fairly safe to conclude that no straightforward case of a reversed response to quick tilting has yet been encountered.

In view of this negative finding, it seemed advisable to check up the responses of the utricular macula to simple linear acceleration in a horizontal plane, for in such experiments there can be no question as to whether or not rotation plays a part *per se* in the stimulating process. Anterior gravity preparations were accordingly set up in the sliding device previously described and were moved to and fro in the plane of the most vigorous tilting response. Such experiments showed that if a gravity receptor type (i) responds to tilting in one direction, it responds to positive linear acceleration in the other direction, or to negative acceleration (slowing down) when moving linearly in a direction the same as that of the stimulating tilt. Thus, a receptor responding to a rearward tilt will discharge (*a*) when accelerated linearly forward, or (*b*) when rearward motion is slowed; and correspondingly for other receptors responding to other directions of tilt and translation. This rule held in all cases, whether the acceleration was high or low. Fig. 8 shows records taken from one such experiment. In A the preparation was being tilted antero-posteriorly. The response was similar a moment later to rapid tilting. B shows the same preparation being moved horizontally forward and backward. The record is somewhat obscured by the presence of a vibration receptor which (as was demonstrated by tapping on the horizontal arm of the preparation box immediately after the acceleration record was taken) is responsible for the heavy, monophasic impulse.

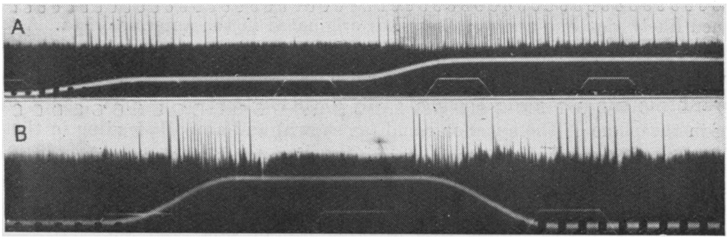

Fig. 8. Showing the behaviour of a gravity receptor, type (i), to both tilting and linear acceleration. Anterior ramus. A, antero-posterior tilt; signal up = tail down; 1 cm. = 190°. B, front-and-rear linear horizontal translation; signal up = to the rear; 1 cm. (signal) = 33 cm. (preparation). The gravity receptor shown in A gives only the thin, partially diphasic impulse in B. The fat, monophasic ones arise in a vibration receptor—see text.

The thin, partially diphasic impulse is the gravity one. It is seen that it occurs only when the preparation is accelerated forward (signal down) or when rearward motion begins to slow down.

The behaviour of the vibration receptor in this experiment is peculiar and interesting, and somewhat similar responses have also been obtained from other anterior vibration receptor preparations. The main discharge occurs after the motion has stopped, suggesting that the saccular otolith was thrown over in one direction by the arrest of the movement, and that it was stimulated as it sagged back into its normal position. Three utricular impulses are mixed in with this post-arrest discharge, suggesting that the same thing happened to the utricular otolith, but it is much easier to understand a utricular discharge under these conditions than a saccular one. The latter may have been caused by the peculiar suspension of the saccular otolith [see McNally and Tait, 1925], but the direct cause of these somewhat unorthodox saccular discharges is still unknown.

These observations on the effect of horizontal linear acceleration fully confirm the experiments of Tait and McNally [1934], in which bisoli-utricular frogs were subjected to linear acceleration in various directions without changing the direction of the reflex response when a transition was made from low to high acceleration, or *vice versa*. The findings can be explained by any theory of utricular mechanism which hinges upon a difference in density between the otoconium and the surrounding fluid, whether the otoconium acts as a weight, a float, or a semi-buoyant structure of the kind postulated by Tait and McNally. The results of the slow and quick tilting experiments, however, do not seem compatible with the hypothetical scheme proposed by these authors.

The failure to confirm their postulate unfortunately leads nowhere. Attempts to find an alternative explanation for the reversal phenomena observed by them have met with little success. It was thought for a time that vigorous stimulation of the utricular macula might, through some peculiar central effect, bring about a reflex response opposite in nature to that elicited by gentle stimulation of the same kind; but this possibility had to be discarded. It is refuted by the linear acceleration experiments of Tait and McNally [1934]; and also by the observation that in the present rapid-tilt experiments the number of impulses discharged in response to a quick tilt has in no case been appreciably greater than that elicited by the same slow tilt, and has, in fact, almost always been considerably smaller (see Fig. 7). On the other hand, if one postulates for the utricular macula a system of high-threshold receptors (rather sparse, to account for their having been missed in the present work) which would be responsible for the vigorous reflexes (such as, for example, the "irrelate reaction") elicited by rapid linear acceleration, one has still to explain why only these, and not the ordinary gravity receptors, are stimulated by the "wrong" direction of quick tilting. It would therefore seem advisable to suspend judgment on the subject of the bisoliutricular rapid-tilt phenomena until further experimental evidence is available.

One other finding is worthy of note in connection with the peripheral mechanism of the utricular macula. Tait and McNally [1934] have shown that the reactions of a normal frog to continuous, very slow tilt are intermittent in nature, consisting of a series of abrupt movements rather than a gradual compensatory adjustment corresponding with the progress of the tilt. The most obvious hypothetical explanation of this discontinuity in the response is that the utricular otolith remains in position in virtue of its friction against the underlying structures until the tilt arrives at a critical point. Here one imagines that the otolith slips a little, and in doing so gives rise to a brief sensory discharge which causes the abrupt compensatory reaction. One assumes that after this the tilt continues with no further discharge from the utricle, or reaction on the animal's part, until the otolith slips again, and so on. On several occasions, however, I have subjected anterior gravity preparations to very slow tilt, and have been able to detect no sign of discontinuity in the discharge. The frequency of the impulses, to be sure, is not regular, but their distribution seems to be entirely random, with no tendency to collect in bunches, as the above hypothesis would require. It therefore appears that the discontinuity in the normal response to slow tilting must be due to some property of the central nervous system, for the peripheral mechanism seems continuous in its action. As a matter of fact, the wide individual and diurnal fluctuations in the "angle of adequate stimulation" reported by Tait and McNally [1934] (as well as those fluctuations consequent upon changes in temperature) rather strongly favour the idea of a central origin of the discontinuity, for one would expect the peripheral mechanism to be a little less capricious in its action.

The rotation group.

These receptors are substantially independent of the action of gravity, and respond with the same readiness to rotation in either a horizontal or a vertical plane, so long as the position of the head is properly adjusted first. The existence of three kinds of rotation organs has been mentioned, each responding best to rotation in the plane of one of the three semicircular canals. Their distribution along the course of the auditory nerve has been indicated, and the remarkable correspondence between the properties of each rotation receptor and those of the canal in whose plane the receptor responds most readily has been discussed. On the basis of this evidence it is concluded that the canals and the rotation organs are one and the same.

The characteristics of the discharges from the three canals are remarkably similar—so much so that it would at present be impossible to tell which canal produced a given record if one did not know the plane of the stimulating rotation. The three canals differ one from another in that (*a*) the plane of rotation for maximal stimulation is different in each case, and (*b*) the two vertical canals respond to the onset of ampulla-leading rotation, whereas for the horizontal canal the stimulating direction is ampulla-trailing. Apart from these differences, the fundamental behaviour of the canals is the same throughout, and, as far as is known at present, what applies to one holds for all three.

If a given canal responds to the onset of rotation in one direction, it can be made to respond equally well to cessation of rotation in the opposite direction, provided that provision has been made so that such non-stimulating rotation can if necessary be carried on through a few revolutions before being stopped. Some sensitive preparations will, however, show this after discharge even if the arc through which the preparation has travelled is surprisingly small; *e.g.* in Fig. 9 A, in which the rotation has progressed through less than 40°.

If a canal is brought from rest to a state of constant velocity in the stimulating direction, its discharge begins very soon after the motion starts (as in Fig. 9 A) and rises to a maximum, after which it dies away more or less rapidly according to the sensitivity of the receptor. The discharge obtained at the cessation of rotation in the non-stimulating direction is exactly analogous; it begins a little after the onset of negative acceleration, rises to a maximum, and then subsides. With sensitive preparations, the duration of the discharges and after discharges may be surprisingly long—one was still firing after 17 seconds [cf. Mowrer, 1935]. Fig. 9 B shows an anterior canal preparation responding to cessation of ampulla-trailing horizontal rotation, and Fig. 9 C illustrates an analogous response from the horizontal canal, the head in this case being upright and the direction of the rotation counter-clockwise.

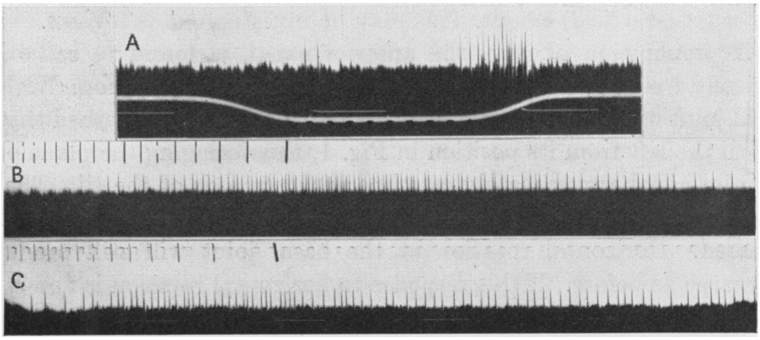

Fig. 9. **Responses from rotation receptors. All were obtained from the anterior ramus. A shows reaction and after reaction to small-arc horizontal rotation with the head "level". Signal up = to the right; 1 cm. = 140°. B and C show responses to the cessation of more prolonged horizontal rotation; B with ampulla-trailing rotation in the plane of the anterior canal; C with left-hand rotation in the normal upright position. In both B and C each stroke of the signal registers movement of the preparation through 20°.**

As is the case with the gravity receptors, the vertical canals can be made to respond to tilts in planes other than their own. The threshold is raised for planes on either side of that of the canal, and usually becomes impossibly high when the plane of the canal is lying in the axis of the tilt. If the preparation box is turned beyond this null point, the direction of the stimulating movement of the apparatus is found to be reversed, as would be expected.

Sensitive vertical canal preparations may respond to horizontal rotation with the head (or, rather, the preparation box) in the normal upright position. This would be expected in view of the results of the horizontal rotation experiments of Tait and McNally [1934] on "biconjoint" and other allied operated frogs. Experiments with the present technique suggest that any response of the vertical canals to rotation of the head about a dorsoventral axis is due only to the possession, by the rotary movement, of a component in the plane of the canal—in other words, to poor alignment of the vertical (or, better, not-quite-vertical) canals. This may be investigated as follows.

A preparation of, say, the anterior canal, is found to respond to horizontal rotation when the box is in the upright position. With the basal joint of the apparatus fixed, the preparation box is turned through 45° to the left from its position in Fig. 1, thus bringing the plane of the anterior canal appoximately into line with the axis of the tilt. The box is clamped in this position, and the basal joint of the apparatus is released. Horizontal rotation at the basal joint will still produce a discharge as before. If this response to horizontal rotation is now tested with the preparation box tilted at various small angles to its upright position (these positions are attained by appropriate adjustment of the horizontal axis), a setting can be found with which the response to horizontal spin cannot be elicited, and on either side of which setting the stimulating direction is reversed. This must mean that the plane of the canal was originally not quite vertical, and that if it is made so the response disappears. This conclusion is in agreement with the work of Steinhausen [1934], who concludes that the stimulation of the canals involves movement of the cupula; for although horizontal rotation of the type described above should produce momentarily a minute vortex in the ampulla, it is unlikely that such a vortex would in itself be capable of moving the cupula and so causing stimulation.

It is now generally accepted that the physical process which is responsible for the stimulation of the canals is not rotatory movement *per se*, but rather angular acceleration. It should be pointed out, however, that the results of the present investigation show clearly that, while the canals may be (and almost certainly are) stimulated by processes consequent upon angular acceleration, it is not angular acceleration that they signal to the brain. A glance at Fig. 9 B and C is sufficient to convince one that given certain conditions the canal receptors can, and do, discharge for a time in the complete absence of either rotatory movement or angular acceleration. The same is true of the discharge which occurs at the onset of rotation, which may similarly continue for several seconds after constant velocity has been attained (although here it might be urged that the angular velocity cannot have been absolutely constant). It is apparent, however, from the records shown of the canal responses to small-arc tilting and rotation, that for all purposes of usefulness to the animal the canals mainly signal rotatory movement; for in the state of nature they contribute to the adjustment of the frog's posture if the head is tilted or turned accidentally this way or that, and to keeping him straight and level during crawling, swimming, jumping, or other types of progression. It is hard to conceive of any frequently occurring natural contingency which might subject a frog to several complete revolutions in any one direction. The biological usefulness of the canals therefore lies in their efficiency in signalling short, quick twists and turns of the head, under which conditions the possibility either of rotation in the absence of supra-liminal acceleration, or of discharge in the absence of rotation, is only trivial.

While it is widely agreed that angular acceleration is the basal condition which sets up stimulating processes in the crista, there is considerable dispute as to just what the stimulating process consists of. It is obvious that if a canal is subjected to accelerated rotation in its own plane a flow of endolymph will tend to be set up within the canal; but whether, in the intact animal, such a flow actually takes place, or whether stimulation occurs merely in virtue of the pressure brought to bear against the cupula by the fluid's tendency to flow, is a question that has been rather warmly debated. In a series of ingenious experiments on the pike, Steinhausen [1931, 1932, 1933, 1934] has succeeded in observing the exposed ampulla of the horizontal canal through the microscope and in watching the cupula deflect in response to conditions (such as rotatory accelerations) calculated to cause flowing movements of the fluid inside the canal. Nevertheless, his conclusions—viz. that adequate stimulation in the intact animal involves a deflection of the cupula—have been condemned by Wittmaack [1932 *a*, 1932 *b*, 1933, 1935], mainly on the ground that a labyrinth in which the ampulla has been exposed is not in a physiologically normal condition, and that any observations made under such circumstances are likely to be misleading. Wittmaack believes that the cupula is essentially a pressure receptor, and that stimulation does not involve its displacement.

It will be realized at once that the prolonged discharges obtained by me (in preparations exhibiting no resting discharge), both as primary reactions and after reactions, have a very definite bearing on this point; for it is extremely unlikely that a difference between the endolymphatic pressures on either side of the cupula could exist in a stationary labyrinth for more than a fraction of a second. It seems practically certain that the end organs in the cupula are of the slowly adapting type; that they are stimulated by deflection of the cupula in one direction but not in the other; that when non-stimulating rotation ceases the cupula is deflected in the stimulating direction by the inertial forces of the endolymph; and that the receptors continue their discharge, with declining frequency, while the cupula by virtue of its weakly elastic properties is gradually returning to its position of rest. Needless to say, Wittmaack's objection to the opening of the bony labyrinth does not apply here.

DISCUSSION.

It should be remembered that many of the findings of the present investigation are subject to the possible interference of coincidence or chance. For example, when a statement is made to the effect that the horizontal canal does not respond to the onset of counter-clockwise rotation, it obviously means that nerve filaments containing fibres from the horizontal rotation receptor, and giving discharges to the onset of left-hand rotation have not been found. Strictly speaking, one ought not to assume their non-existence until one had tried every fibre from one particular horizontal canal and found that they all gave responses only to right-hand rotatory acceleration; but with the present technique this procedure is out of the question. On the other hand, the large number of cases in which a response only to right-hand acceleration has been observed makes it very unlikely that receptors for the other direction exist; but one must, in all fairness, admit the possibility. Similar criticisms might be urged against some of the other conclusions, and for the present these can be answered only by the claim of high improbability.

Other points arising in connection with the findings have already been discussed.

SUMMARY.

A method is described whereby the functions and mechanism of the frog's labyrinth may be studied, especially as regards the relations between stimulus (gross or vibratory movement) and response (action potentials in the auditory nerve).

The types of response obtained are classified into several groups and sub-groups according to the characteristics of the stimuli which elicit

them, and the distinguishing properties of the various groups are enumerated.

Evidence is adduced in support of the belief that the source of a sensory discharge originating in the utricular macula, the saccular macula, or any of the three canal cristæ can be inferred with almost complete, if not complete, certainty.

It is found that a vibration receptor, and at least one (and probably two) gravity receptors, are supplied by the posterior ramus of the auditory nerve. The labyrinthine receptor mechanisms for both gravity and vibration are thus at least twofold.

Gravity receptors fall into two classes: type (i) responding best when the head is tilted out of the level position, and type (ii) signalling only the return of the previously tilted head to level. Type (ii) receptors have not been encountered often, but so far they have always been found on the posterior ramus. It is tentatively suggested that of the three organs of unknown function found on the course of distribution of the posterior ramus (*i.e.* the lagena, the pars basilaris, and the pars neglecta) one is a vibration receptor, one a gravity organ type (i), and the remaining one a gravity organ type (ii). No experimental evidence is yet available on the subject of which is which.

It is concluded that the reactions of the utricular macula to slow tilt are not discontinuous; that the majority of its receptors react to only one of the two directions of tilting in the maximally-stimulating plane; and that the stimulating direction is the same whether the rate of tilting is rapid or slow. Attempts to reconcile these findings with the results of reflex studies on operated frogs have so far met with failure.

The findings in connection with the semicircular canals are in complete agreement with the current theory that the cristæ are stimulated as a result of positive angular acceleration in one direction, or (what amounts to the same thing) negative angular acceleration in the other. The direction of the exciting positive acceleration has in every case been the same for any given canal; viz. it has always been ampulla-leading for the two vertical canals, and ampulla-trailing for the horizontal canal. It is shown, however, that the canals do not signal angular acceleration to the brain. Their action is found to be entirely consistent with Steinhausen's concept of a deflecting cupula.

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REFERENCES.

Ashcroft, D. W. and Hallpike, C. S. (1934 *a*). *J. Physiol.* **81**, 23 *P*.

Ashcroft, D. W. and Hallpike, C. S. (1934 *b*). *J. Laryng.* **49**, 450.

de Burlet, H. M. (1928). *Anat. Anz.* **66**, 199.

de Burlet, H. M. (1929). *J. comp. Neurol.* **47**, 155.

Laudenbach, J. (1899). *Pflügers Arch.* **77**, 311.

McNally, W. J. (1932). *Trans. Amer. laryng. rhin. otol. Soc.* (38th Annual Meeting; May, 1932) pp. 8–12.

McNally, W. J. and Tait, J. (1925). *Amer. J. Physiol.* **75**, 155.

McNally, W. J. and Tait, J. (1933). *Quart. J. exp. Physiol.* **23**, 147.

McNally, W. J. and Tait, J. (1934 *a*). *Acta oto-laryng.*, Stockh., **20**, 73.

McNally, W. J. and Tait, J. (1934 *b*). *Trans. Amer. otol. Soc.* **24**, 152.

Mowrer, O. H. (1935). *Science*, N.S. **81**, 180.

Retzius, G. (1881). *Das Gehörorgan der Wirbelthiere*, Stockholm, **1**.

Steinhausen, W. (1931). *Pflügers Arch.* **228**, 322.

Steinhausen, W. (1932). *Arch. Ohr.-, Nas.-, u. KehlkHeilk.* **132**, 134.

Steinhausen, W. (1933). *Pflügers Arch.* **232**, 500.

Steinhausen, W. (1934). *Zool. Anz.* Suppl.-Bd. **7**, 85 (= *Verh. dtsch. zool. Ges.* **36**)

Tait, J. and McNally, W. J. (1925). *Amer. J. Physiol.* **75**, 140.

Tait, J. and McNally, W. J. (1929). *Ann. Otol., etc.*, St Louis, **38**, 1121.

Tait, J. and McNally, W. J. (1934). *Philos. Trans.* B 513, **224**, 241.

Wittmaack, K. (1932 *a*). *Arch. Ohr.-, Nas.-, u. KehlkHeilk.* **130**, 254.

Wittmaack, K. (1932 *b*). *Ibid.* **132**, 167.

Wittmaack, K. (1933). *Ibid.* **135**, 41.

Wittmaack, K. (1935). *Ibid.* **139**, 1.