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DISCHARGES FROM VESTIBULAR RECEPTORS IN THE CAT

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The electrical activity of the vestibular nerve has been studied by Ross [1936], who recorded impulses in single fibres in the frog and was able to distinguish the discharges due to the various parts of the labyrinth. Sand [1938] and Löwenstein & Sand [1936, 1940] have made similar records from the dogfish and ray, but hitherto the Mammalia vestibular organs have not been investigated in this way. One reason for this is no doubt the great prominence of the cochlea activity in the 8th nerve of mammals and another the difficulty of reaching the vestibular fibres without interfering with the blood supply to the organ. In the present work this difficulty has been avoided by the use of a fine wire electrode thrust into the brain stem in the region of the vestibular nucleus so as to pick up impulses from the entering bundles of vestibular fibres. A disadvantage of the method is that the exact nature of the units which give rise to the electric charges must remain uncertain; but the records show the same general type of discharge as those found in the frog and seem to give a reasonable picture of most varieties of vestibular activity.

METHOD

All the experiments were made on cats anaesthetized with dial, nembutal or chloralose or else decerebrated under ether. In the decerebrate preparation the cerebellum was removed as well as the cerebrum; in the others partial removal of the occipital bone gave access to the cerebellum and most of it was removed to expose the floor of the 4th ventricle. A spiral of silver wire coated with silver chloride was sewn to the scalp to form an indifferent electrode and the other was a fine enamelled silver wire (no. 44 S.W.G.) fixed to a rod which could slide in a ball and socket mounting fastened rigidly to the skull. With this arrangement (described in detail by Adrian & Moruzzi, 1939) the wire could be thrust into any part of the brain stem and would not be disturbed by movements of the head.

In some of the earlier experiments and sometimes as a control the vestibular organs were stimulated by turning the head by hand, leaving the body all the time in the prone position. As soon as it was clear that vestibular impulses could be recorded in this way a swinging platform was arranged so that the whole animal could be turned laterally or tilted, without altering the position of the head in relation to the body (Fig. 1). The platform was hung at three points by parallel cords attached to spiral springs, the upper ends of which were fixed to the roof of the screening cage. The weight of the cat with the animal board, etc., was enough to extend the springs considerably, and they were flexible enough to allow the platform to be rotated horizontally through 45°, tilted laterally or in the long axis of the body or moved as a whole in the vertical or horizontal plane. This arrangement was fairly satisfactory though its range was limited and movements of constant velocity could not be studied. The nature of the suspension made it difficult to be sure of confining the movement of the platform strictly to one plane, but the amount of movement in a direction other than that intended was seldom enough to affect the record. The rate of movement was controlled by hand or by altering the moment of inertia of the system and allowing it to oscillate freely. A rough indication of the rate and extent of movement was given by a signal lever moved by a thread attached to one corner of the platform. In later experiments the reactions of the horizontal canals were analysed in more detail by mounting the animal on a turn-table which could be rotated at a constant speed, but the swinging platform was still used as the most convenient arrangement for the initial step of locating the vestibular discharges in the brain stem. With either arrangement the cat lay prone on the animal board with a mouth bar for the head and the body immobilized by sandbags.

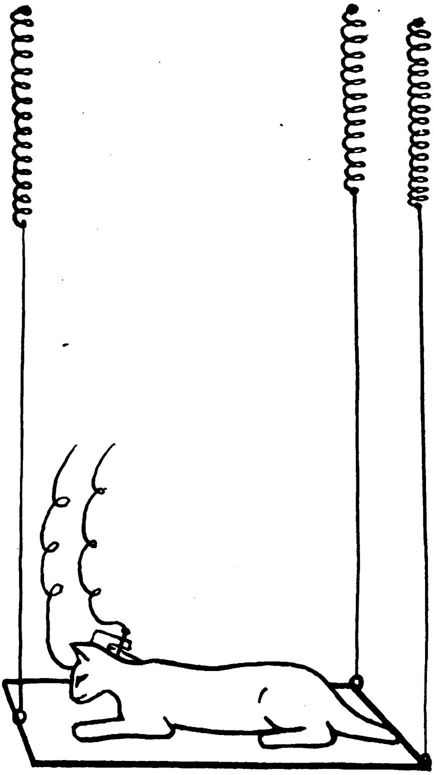

Fig. 1. Swinging platform for vestibular stimulation.

The usual procedure was to set up the animal on the platform and then to manipulate the electrode holder so that the wire was thrust about 1 mm. below the surface of the 4th ventricle in the region of the vestibular nucleus. As the wire penetrated the grey matter the platform was tilted and rotated to stimulate the vestibular organs. By listening to the potential changes reproduced by a loud speaker it was usually possible to detect vestibular activity at many points near the entry of the 8th nerve. The area giving vestibular discharges was about 4 mm. long and 3 mm. wide in the position shown in Fig. 2. With the tip of the electrode just below the surface the sound was usually that of many units and was often evoked by more than one type of movement, but with the aid of the loud speaker it was nearly always possible to adjust the electrode first to make one series of impulses appreciably louder than the rest and finally to make them appear alone without competitors in the background. Such a series would be found to depend predominantly on one kind of platform movement, and the relation of stimulus to discharge could then be studied in detail.

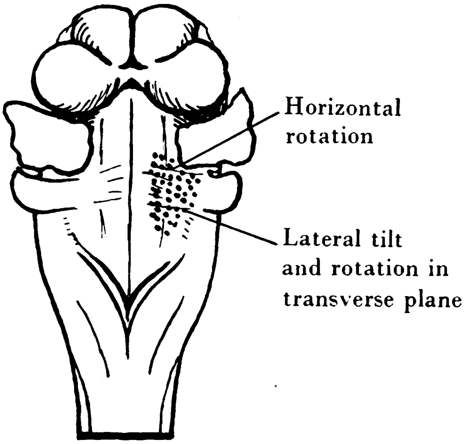

Fig. 2. Cat's brain stem after removal of cerebellum to show the region from which vestibular discharges can be picked up.

RESULTS

Various types of discharge

In Ross's analysis of the nerve discharges from the frog's labyrinth it was found that in some of the nerve fibres the discharge depended only on gross movement or on the position of the head in space, whilst in others it was produced by mechanical vibration. In the cat no vibration receptors have been detected. An electrode in the cochlea part of the nerve will of course pick up electrical activity due to sound vibrations, but no reactions either to sound or to mechanical vibration have ever been obtained from the region of the vestibular nucleus. Possibly a more thorough search would have revealed them, but it is more likely that in the cat the vestibular organs are not specially sensitive to vibration, the development of the cochlea having reduced the need for any other vibration receptors in the ear.

The responses to movement and position fall into two groups as in the frog. There is (*a*) the gravity-controlled type in which the discharge depends on the position of the head in space and is evoked by tilting into the stimulating position as well as by linear accelerations, and (*b*) the rotation-controlled type, where the response is not affected by the position of the head and is determined entirely by angular acceleration. As regards group (*a*) it has always been easy to find gravity-controlled discharges produced by tilting the head laterally, so that the side under examination is the lower; discharges controlled by the fore-and-aft position of the head have been less common but have been found in four out of six animals. As regards group (*b*), discharges in response to rotation in the horizontal and transverse planes have been easy to find. Those in response to rotation in the median plane have been more difficult, but like the response to fore-and-aft tilting they have usually been found in the end.

The gravity-controlled type of discharge will be dealt with first, since the relation between stimulus and response is more straightforward.

Gravity-controlled discharges

Lateral tilt. Typical records of a discharge controlled by the lateral tilt of the head are shown in Fig. 3. The tip of the electrode was 1·5 mm. below the surface of the brain stem in the middle of the striae acousticae on the right side. In this position it picked up a series of large potential spikes with a frequency of about 6 per sec. when the head was level. When the head was tilted to the left (i.e. with the left cheek down) the discharge ceased, and when it was tilted to the right the frequency increased, reaching 95 per sec. for a tilt of 20° from the level. The position of the head in each record is given by the signal line: the curves in Fig. 4 show the relation between the tilt and the frequency after the first second in this and in other preparations.

The records in Fig. 3 are from a decerebrate animal. In several cats under dial and nembutal discharges of this type have not reached higher frequencies than 40–50 per sec., and in some units the discharge has not started until the head has been tilted a few degrees down towards the side under examination, though it is more usual to find a discharge at a low frequency when the head is level (as in Fig. 3). In no case has there been an increase in frequency when the tilt has been in the opposite sense, i.e. raising the side under examination and lowering the other, and tilting in the median plane has rarely produced more than a slight effect on these units unless the snout has been turned up through a considerable angle.

Fig. 5 shows what happens when the head is tilted sideways through 15° and held in that position for 33 sec. The frequency declines slowly, for the receptor is of the slowly adapting type and the discharge depends principally on the position of the head and is not much affected by the time it has been in that position. It is also very little affected by the rotational movement as such, for rotation through a limited angle does not excite unless it brings the head into a position adequate to produce a steady discharge. Evidently we are

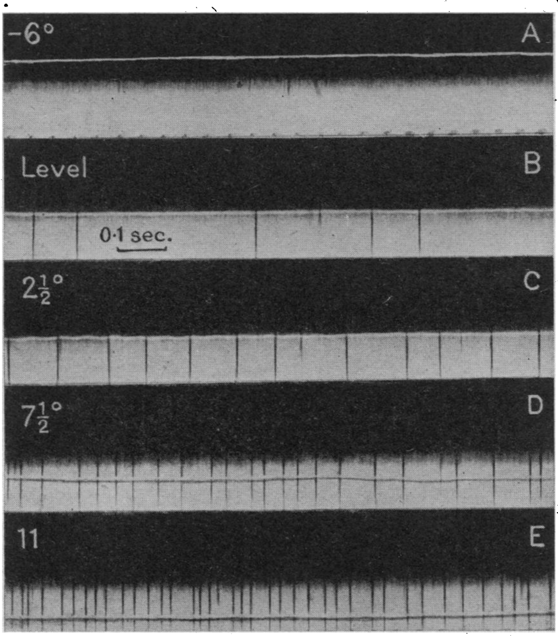

Fig. 3. Records of a gravity-controlled discharge from the right labyrinth signalling the lateral tilt of the head to the right. Decerebrate cat. The inclination of the transverse axis of the head is shown by the white signal line in each record. Time marker (black line in B) gives 0·1 sec.

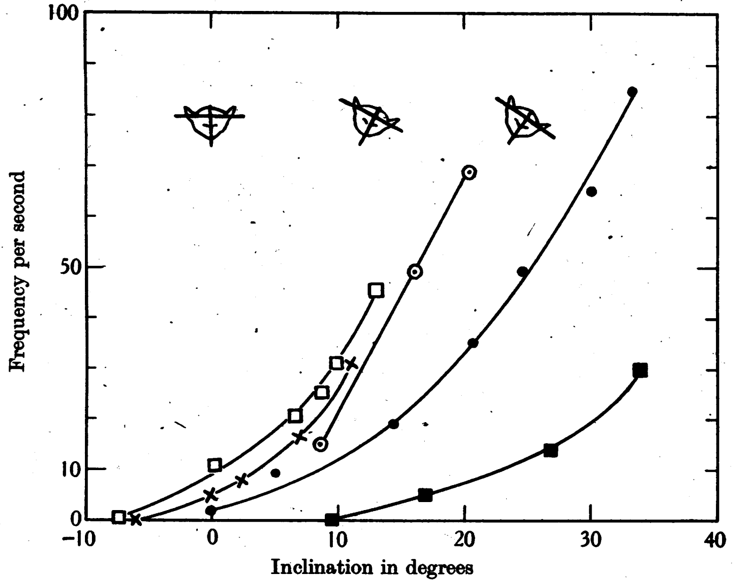

Fig. 4. Relation between lateral tilt and frequency of discharge in units from several animals: insets show position of head when tilted to the left.

dealing with a receptor which is stimulated when the gravitational pull acts on it in certain directions. The most likely receptor is the saccular otolith organ, and if so, it is stimulated when the otolith begins to pull away from the macular endings, as Magnus and his colleagues concluded from other lines of evidence [Magnus, 1924].

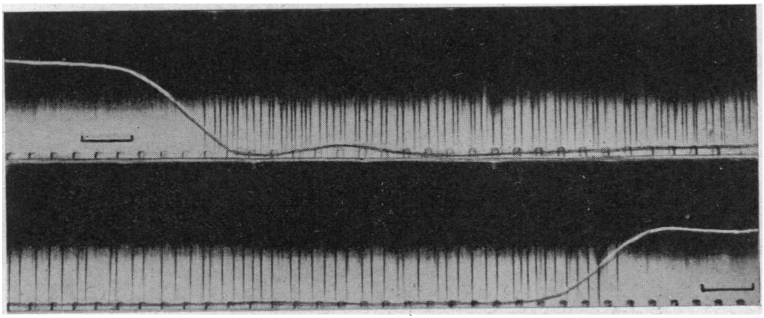

Fig. 5. Beginning and end of a discharge produced by a lateral tilt of 15° (same unit as in Fig. 3). The position was maintained for 33 sec. Initial frequency 68 per sec., final 40 per sec. Time marker (black line) gives 0·1 sec. in these and all other records.

Since these discharges are due to the gravitational pull on a receptor mechanism they ought to be produced by linear acceleration in certain directions as well as by particular positions of the head. In every case it was found that movement sideways in the horizontal plane could be made to evoke or increase the discharge. The stimulating effect occurs only when there is an acceleration away from the side examined, so that if the electrode is in the

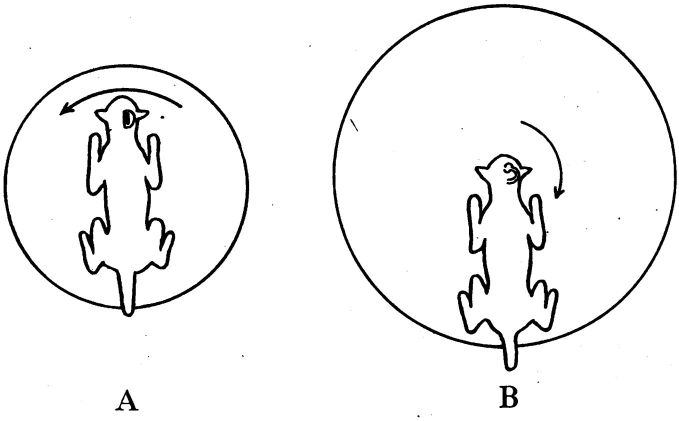

Fig. 6. Illustrating (A) stimulation of right lateral gravity receptor by acceleration of head to left when the axis of rotation is in the centre of the trunk. When the axis passes through the head (B) the gravity receptors are not stimulated. The horizontal canal is stimulated by rotation to the right.

right vestibular nucleus a discharge will occur when the head is accelerated to the left and vice versa. This can be seen by allowing the platform to swing from side to side without tilting or rotating, but it is shown very clearly when the animal is on the turn-table and is rotated in the horizontal plane: rotation about an axis passing through the head (Fig. 6 B) has no effect on a gravity-controlled discharge, but if the axis passes through the trunk a discharge occurs whenever the head is accelerated to the left (Fig. 6 A). Evidently an acceleration to the left would have the same effect as a gravitational pull to the right whatever the precise mechanism of the gravity receptor may be.

Two of the discharges controlled by lateral tilt and lateral acceleration have responded also to rapid fore-and-aft and vertical up-and-down acceleration. Both were modified by the fore-and-aft tilt of the head though not so much as by the lateral tilt. As both were single unit discharges we must suppose that the saccular endings (if these are responsible) can sometimes be stimulated by a pull of the otolith in the same plane as the macula, though a pull away from the macula is always more effective.

Controls. Before we can be sure that these discharges really represent the activity of a vestibular organ we must rule out the possibility that they are due to a movement of the electrode in the brain stem. When the wire is thrust into the floor of the 4th ventricle it must cause some injury, and the penetration often evokes trains of potential spikes which last for a few seconds and are presumably caused by damage to nerve cells or fibres. Such injury discharges, like those in the cerebrum, can often be modified by slight movement of the nervous tissue relative to the electrode, and though the modification is usually no more than a change in the size of the recorded potentials there is sometimes a rise and fall of frequency as well. Thus a sideways tilt might cause an increased frequency of discharge, not because the electrode was recording the signals of a gravity receptor, but because it was altering the deformation of injured nervous tissue.

There are two reasons for rejecting such a view, first that the responses usually persist unaltered for an hour or more, and second that they are only evoked by the one kind of movement, a gravity-type discharge from the right vestibular region being increased only by tilting down to the right or by linear acceleration to the left. No such permanence or specificity would be likely to occur in an injury discharge, and it can scarcely be a coincidence that the movements which stimulate are precisely those assigned by Magnus and de Burlet to the lateral gravity receptors. On several occasions, also, a discharge evoked by tilting the whole platform has been evoked just as clearly by tilting the head alone, though the shift of the brain stem would probably differ considerably. It does seem possible, however, that injury may be responsible for one feature of the records, namely, the occasional appearance of brief high-frequency groups of impulses instead of single spikes. These have not been examined in detail, but they suggest some interference with the normal mechanism of the nerve fibres.

Controls have also been made from time to time to ensure that the discharges ascribed to the vestibular apparatus are not due to receptors belonging to the 5th nerve stimulated by air currents on the ears or vibrissae when the head is turned. Discharges from the face, jaws and vibrissae are easily picked up in the brain stem, but the electrode must be deeper and further from the midline, and the response is clearly related to stimulation of the receptors of the face and not to those of the vestibular organs.

Fore-and-aft tilt. Persistent discharges controlled by turning the snout of the animal upwards have been found in four animals but only after considerable search. This may be due merely to the arrangement of the platform which made it difficult to produce an upward tilt in which the line of the jaw made an angle of more than 10° with the horizontal; such a tilt may well have been inadequate to stimulate the majority of the receptors. The four examples were probably from gravity and not rotation receptors, for angular acceleration did not stimulate unless it brought the head into the upturned position; linear acceleration sideways or forwards was moderately effective in one animal, but linear acceleration downwards was effective in all. This would agree with Magnus's view that the utricular otolith organ is stimulated by a movement or position which pulls the otolith away from the macula on which it rests.

In several preparations discharges have been found in response to vertical upward or downward acceleration and to nothing else. These may well have come from gravity receptors which would have responded to a tilt of sufficient extent but were not stimulated by the positions available with the platform. It is doubtful whether the utricular otolith organ should be held responsible for the discharges due to upward acceleration as well as for those to downward; the former may possibly come from the dorsal lobe of the saccular organ, since it faces downwards instead of upwards and its nerve fibres run with those from the utricle [Oost, 1918; de Burlet & de Haas, 1923].

Rotation-controlled discharges

These are the discharges which are produced by angular acceleration of the head in various planes and are not affected by its initial or final position with respect to the earth. They are presumably derived from the semicircular canals, for it is found that for each single-unit discharge the most effective stimulus is a rotation in a particular plane, rotation in planes at right angles having little or no effect. The difference between the gravity type and the rotation type can be seen by comparing Fig. 3 and Fig. 7, which shows a unit responding to rotation in the transverse plane (lateral tilting). As in Fig. 3 the vertical position of the signal line shows the tilt of the head, and it will be seen that in this case the amount of tilt is immaterial and the movement all important.

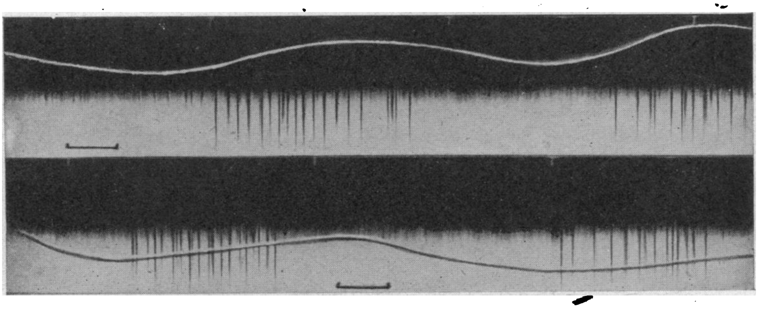

Fig. 7. Effect of lateral tilting on a rotation-controlled discharge (unit responding to rotation in transverse plane). Decerebrate cat. The initial position of the head does not affect the response.

Rotation in different planes. With the simple tilting platform arrangement it was difficult to test the effect of rotations in very many planes, but there is no doubt that for some units horizontal rotation is a far more effective stimulus than rotation in any other plane. For other units, rotations in the transverse or in the median plane of the body were the most effective, but with these two planes the best position was less sharply defined. In every case the cat lay prone with the head in the normal position, i.e. with its long axis inclined about 45° from the horizontal. Minor variations in head posture made little difference, but a sideways tilt would sometimes complicate the result.

In all the units which have been controlled by horizontal rotation the discharge has been stimulated by rotating the head towards the side from which the unit comes and suppressed by rotating it towards the opposite side (Fig. 8 A). Thus for the horizontal canal the stimulating direction is with the ampulla trailing. In the units controlled by rotation in the transverse plane the discharge is increased by rotating the top of the head towards the side from which the unit comes, so that if we are dealing with the posterior canal this is stimulated by ampulla leading rotation (Fig. 8 B). These results support the accepted view of the canal mechanism. With rotation in the median plane (anterior canal) the results are less clear. In the frog, Ross found that the anterior canal was stimulated by ampulla leading (snout down) rotation and Löwenstein & Sand found the same with the ray, but in the present experiments there have been several clear examples of units apparently of the rotation-controlled type stimulated by tilting the snout up as well as units responding to tilting it down (Fig. 8 C). The imperfections of the apparatus have made it difficult to decide whether these were really of the rotation- or the gravity-controlled type. It has already been noted that the gravity receptors for lateral tilt will also react to horizontal rotation if it produces some lateral translation of the head. In the same way therefore a rotation in the median plane involving an upward or downward translation of the head might stimulate the utricular otolith organs and these may have caused the discharges mentioned above. In any case it is presumably useful for the vestibular apparatus to signal rotation in either direction.

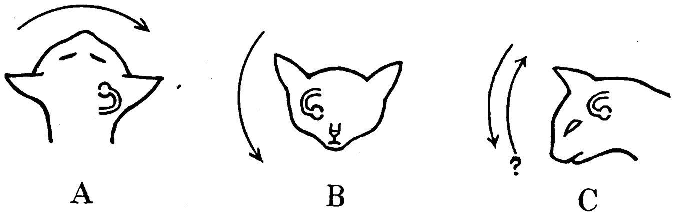

Fig. 8. Direction of rotation which stimulates the three canals. See next.

The discharges controlled by horizontal rotation and fore-and-aft tilt have usually been found further forward in the brain stem than those controlled by lateral tilt (gravity or rotation type), the former being near the oral and the latter near the aboral margin of the striae acusticae (cf. Fig. 2). As regards the specificity of the stimulus: the discharge to horizontal rotation is usually quite unaffected by rotation in the transverse or median plane, but rotation in one of these two will often produce some effect on a discharge which is mainly controlled by rotation in the other. Löwenstein & Sand found that the anterior and posterior canals in the ray would respond to rotation about any of the three primary axes, but in the cat horizontal rotation has had very little effect on the units stimulated by transverse or median plane rotation.

Magnus suggested that linear acceleration forwards might be expected to stimulate the horizontal canal. In the present experiments it has never produced more than an occasional impulse in a unit reacting to horizontal rotation, and linear acceleration sideways has been equally ineffective.

The resting discharge. Rotation-controlled discharges have been described for the frog by Ross and for the dogfish and ray by Löwenstein & Sand, and there is one point on which their findings are not in complete agreement. Ross says that in the frog a small proportion of his single-fibre preparations showed a persistent resting discharge which 'could be momentarily suspended by a movement in a direction opposite to that which stimulates the end organ'. But Löwenstein & Sand find such a discharge in all their preparations of nerve fibres from the horizontal canal of the dogfish. Since it is suppressed by rotation in the non-stimulating sense they regard it as an important feature of the receptor mechanism, for as they point out it provides a means by which a single receptor can signal rotation in either direction instead of in one direction only.

In the cat's brain stem under the conditions of these experiments the rotation-controlled discharges are very often of the persistent type, continuing at a low frequency when the head is at rest and ceasing only with rotation in the non-stimulating sense; but in some units there has been no resting effect, although rotation through a very small angle has been enough to evoke a discharge. Examples of the two kinds of response are shown in Fig. 9. In Fig. 9 A the discharge is from the right posterior canal; it continues at 9 per sec. during rest, is suppressed by tilting the head to the left, and is increased by tilting it to the right. In Fig. 9 B the discharge (also from the posterior canal) is absent at rest and appears only with rotation in the one sense. In Fig. 9 C the discharge varies in frequency, but is never completely suppressed.

What proportion of the receptors give resting discharges is hard to say. About two-thirds of the present series have done so, though it is naturally easier to locate a unit which is always in action than one which is quiet until the head is turned. There is evidently a wide variation in the excitability of the different units: the frequency of the resting discharge has varied from about 2 to 30 per sec., and there is probably a continuous gradation from the receptors which need a movement to make them discharge at all (cf. Fig. 9 B) to those which continue at a fairly high frequency all the time (cf. Fig. 9 C). The nature and depth of the anaesthetic has no obvious effect on the prevalence of resting discharges, decerebrate cats with a high blood pressure showing no greater proportion than cats under deep dial; and a mild degree of hyperventilation, an injection of adrenalin or of intravenous saline has produced no definite modifications of the response.

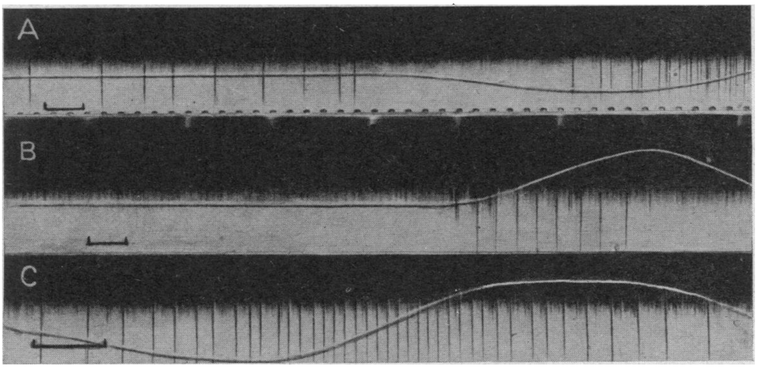

Fig. 9. Units with and without a resting discharge. A and B are units controlled by rotation in transverse plane (posterior canal). In A there is a resting discharge at 9 per sec. suppressed by tilt to the left and increased by tilt to the right. In B there is only a discharge on tilting to the right. Both decerebrate cats. C is a unit controlled by rotation in median plane with a discharge which is never completely suppressed. Cat under nembutal.

The relation of stimulus to response: after-discharges, etc.

With the swinging platform a rotation through a small angle involves an acceleration followed immediately by a deceleration, and this is usually followed by a similar movement back again to the initial position. Though this rapid sequence of changes complicates the picture it is not unlike the sequence to which the canals are subjected in life, for the turning of the head must always involve an acceleration and deceleration with little or no interval between. The records in Figs. 10, 11 and 13 show what kind of discharge comes from a canal in these circumstances. The frequency increases during the acceleration; during the deceleration and the movement back it falls to zero or to a value lower than that of the resting discharge. The maximum frequency is evidently related to the acceleration, but owing to the deceleration which follows it is impossible to say how rapidly the receptors would become adapted to the stimulus or indeed to decide what it is that stimulates them.

To investigate this a turn-table was substituted for the swinging platform. It could be rotated at a fairly uniform rate which was recorded by an interrupted light signal. The electrical changes from the brain stem were led off by connecting the electrodes to a length of light flex hung from the ceiling over the centre of the turn-table. This allowed the platform to make up to 20 revolutions without undue twisting or untwisting of the wires. Only the horizontal canal discharges were investigated in this way, since it was difficult to arrange the cat in anything but the prone position.

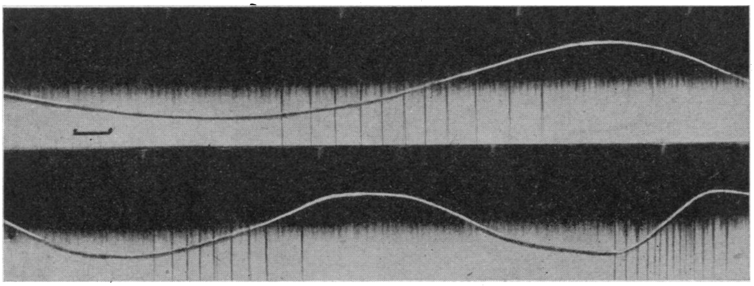

Fig. 10. Discharges from the posterior canal (rotation in transverse plane) showing effect of different rates of swing. Decerebrate cat (same as Fig. 9 B).

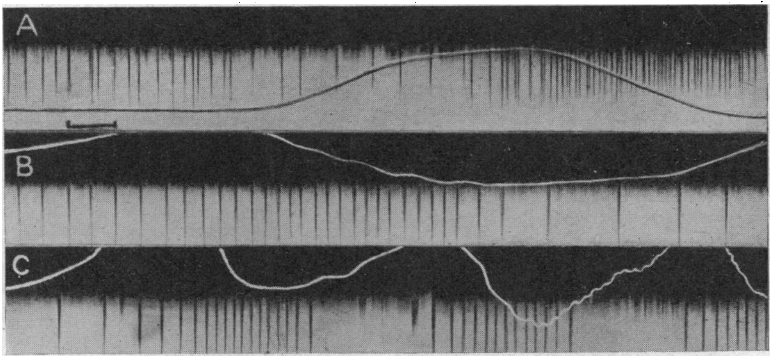

Fig. 11. Discharges from horizontal canal. A, unit from left side with resting discharge. Signal shows swing to the right and back.. Cat under nembutal. B and C, unit from left side with resting discharge, showing effect of horizontal swings at different rates. Cat under dial.

The results obtained with the turn-table agree with Ross's for the frog and support his view of the receptor mechanism, which is that the receptors adapt slowly, the excitation varying with the deflexion of the cupola. It is found, as in the frog, that the frequency rises to a maximum as the turn-table accelerates and then declines slowly as the rotation is continued at constant speed. With a speed of rotation of 1 rev. in 2 sec. attained in the first $\frac{1}{2}$ sec. the discharge does not revert to its resting level for 10–15 sec. With slower acceleration and rotation the maximum frequency is lower and the discharge briefer: but with any turning movement in which the acceleration is not immediately followed by a deceleration the increased activity outlasts the period of acceleration by several seconds.

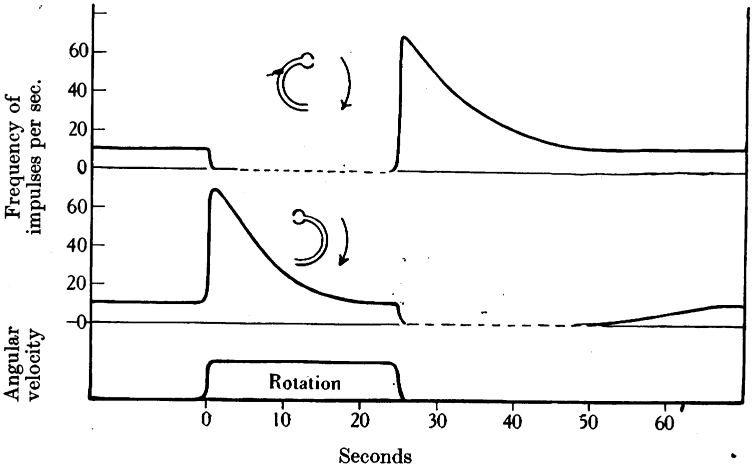

Fig. 12. Average time course of after-discharges and silent periods when acceleration and deceleration are separated by an interval of steady rotation. Both of the units are shown as having a resting discharge and as giving effects of maximum duration (such as would follow 25 sec. rotation at 0·5 rev./sec.). The vestibular discharge gives a misleading picture of the head movement (cf. Fig. 13).

TABLE 1

Preparation	Unit	Resting discharge per sec.	Longest after-discharge sec.	Longest suppression of resting discharge (until complete return) sec.
Cat A (dial)	1	25	20	25–35
	2	0	12	—
	3	1	9	30
	4	7	8	15
Cat B (dial)	1	0	10	—
Cat C (nembutal)	1	10	15–25	25–30
	2	6	20	20–30
	3	4–5	15–20	15–20
	4	0	15	—
	5	9	8	12
Cat D (decerebrate)	1	14	16	25–30
	2	3–6	12	15
	3	0	10–15	—

When two figures are given these are the values obtained in different trials.

If the rotation is stopped during the discharge there is an immediate fall in frequency to zero or to a value lower than that of any resting discharge which was present initially. Again, the effect varies with the speed of deceleration, but with a sudden stop there is usually a complete suppression of all activity and the resting discharge does not return for 10–30 sec. Thus the angular acceleration causes an excitation which takes some time to die down, and the deceleration has the reverse effect, suppressing all activity for an even longer period.

Similar effects are shown by rotating the head in the reverse, or non-stimulating sense. If the units are from the right side so that angular acceleration to the right stimulates the receptors, then angular acceleration to the left suppresses any resting discharge there may be. When rotation to the left has settled down to a constant speed the discharge builds up again to the resting frequency within 10–30 sec. And if at any time the reversed rotation is stopped the discharge immediately rises to a high frequency which declines gradually for the next 10–15 sec. Thus in its action on the rotation receptors angular acceleration to the right has the same effect as angular deceleration to the left, and deceleration to the right the same as acceleration to the left.

The results are summarized in Fig. 12, and the data for several experiments are given in Table 1. The after-effects of rapid accelerations and decelerations persist for 10–30 sec. and there is not much variation from one unit to another. Briefer effects could be obtained by smaller changes in velocity, but it did not seem likely that the after-effects would last much more than 30 sec. whatever the intensity of the stimulus. It may be significant that a resting discharge was present in the two units which gave some of the longest after-effects, but those with no resting discharge or with a very low frequency do not differ much from the others on the list. The uniform duration of all these responses suggests that they are determined by some relatively stable property of the semicircular canal mechanism such as the rate of subsidence of endolymph currents or the rate of return of the deflected cupola. They will evidently account for many of the reactions of the intact animal to rotation and theories of the canal mechanism based on these reactions ought equally to account for the main features of the receptor discharge.

The receptor mechanism of the canals

It is generally held that the excitation of a canal depends on a deflexion of the cupola by the flow of endolymph past it. This is enough to explain the excitation which accompanies acceleration or deceleration, since both will certainly produce a flow of endolymph, but something more is needed to explain the after-effects. It might be (*a*) that the movement of fluid outlasts the period of acceleration and of deceleration, or (*b*) that owing to its structure, etc. the deflected cupola takes some time to return to the mid-position when the deflecting force (i.e. the endolymph current) ceases, or a combination of (*a*) and (*b*). It is unlikely that (*a*) is the sole cause, for the flow of endolymph can scarcely continue for 10 sec. or more after rotation is stopped. Thus (*b*) is the most likely cause of the after-effects. In any case we may reasonably assume an immediate deflexion of the cupola during accelerations and decelerations and a slow return to the mid-position when these have ceased.

If we suppose in addition that the canal receptors are slowly adapting like those of the saccule and utricle the main features of the nervous discharge are easily understood. Angular acceleration followed immediately by deceleration would give no more than a brief deflexion of the cupola and a brief discharge, and angular acceleration followed by rotation at a constant speed would give a longer discharge declining slowly as the cupola returned to its undeflected position. If the rotation was stopped abruptly the endolymph would flow in the opposite direction, the cupola would be deflected by it in the non-stimulating sense and would again return slowly to the mid-position. The opposite deflexion and gradual return will explain the silent period and the gradual return of the resting discharge, for where a resting discharge is present the mid-position must be one of slight excitation.

This view of the receptor mechanism has been dealt with already by Ross. It implies that the suppression of the discharge by deceleration, etc., is not due to any special inhibitory process acting on the receptors but is merely due to the removal of the stimulus. The physical properties of the system favour such an idea, for angular deceleration would be likely to cut short the stimulating effect of angular acceleration and acceleration in the opposite sense would deflect the cupola away from the positions which stimulate. But although the movements of the cupola seem enough in themselves to explain the main features of the discharge, it may be that there are also minor effects due to changes in the receptors. Many other kinds of receptor show a silent period following activity—for instance, when a stretched muscle spindle is released the impulse frequency falls to zero and the resting discharge, if present initially, does not return for several seconds. Here the removal of the load will restore the initial conditions, but there is no reason to believe that it will go beyond this and produce a state in which the receptor is exposed to a smaller stimulus than that afforded by the initial conditions. In fact there are cases in which a silent period following increased activity seems to depend on a fall of excitability in the receptors as well as cases in which it depends on the diminution of the stimulus which causes the resting discharge. Sometimes both kinds of effect may be found within a group of similar receptors, e.g. those of the cat's vibrissae [Fitzgerald, 1940].

With the canals there is reason to think that the suppression of a resting discharge sometimes depends on a fall of excitability as well as on a failure of the stimulus. For instance, it has been pointed out that the periods of diminished activity after deceleration are on the whole longer than those of increased activity after acceleration. This suggests a fatigue effect, a fall of excitability following activity added to the effect produced by the deflexion of the cupola away from the stimulating position. It has also been found that in the earliest stages of the silent period following abrupt deceleration a rapid to-and-fro movement will produce no discharge although the turn-table is rotated through 45° or more. A few seconds later rotation through a smaller angle will give a brief discharge and the threshold stimulus becomes less and less as the resting discharge builds up again. This gradual increase in sensitivity may be due principally to the gradual return of the cupola after its deflexion away from the mid-position; this would certainly account for the smaller and smaller angle of movement which will stimulate. But unless there is also a fall of excitability in the receptors themselves it is difficult to account for the complete failure to arouse a discharge in the early stages. But such evidence is scarcely conclusive and the point was not investigated in detail, as there is no reason to doubt that the deflexion of the cupola is the main factor in determining the production or suppression of a discharge from the receptors.

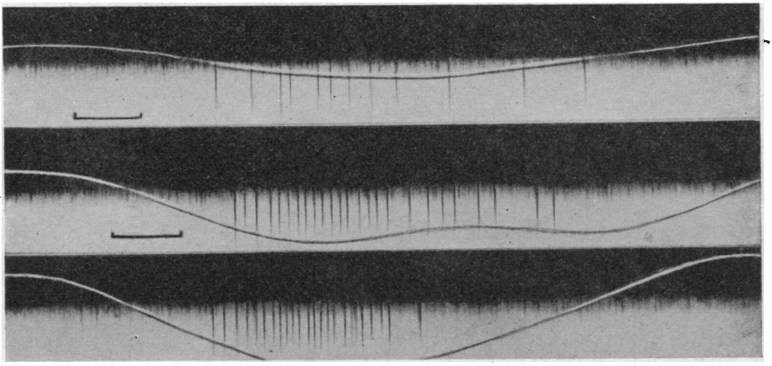

Fig. 13. Discharge from the anterior canal (rotation in median plane), showing effect of brief downward tilting of the head. The vestibular discharge gives an accurate picture of the head movement (cf. Fig. 12).

DISCUSSION

The foregoing results have not shown any marked difference between the cat's vestibular apparatus and that of the frog or fish. There are the gravity receptors to signal the posture and linear acceleration of the head and the rotation receptors to signal turning movements, and all of them react in a manner which is consistent with the structure of the sense organs and with the reactions which it produces in the intact animal. Thus the duration of the after-effects when rotation is stopped is of the same order as that of the post-rotatory nystagmus in man; the planes of rotation which are most effective for the different units correspond more or less with those of the three canals, etc.

No attempt could be made with the present method to trace an anatomical connexion between a particular unit in the brain stem and a particular receptor organ. However, the work of Löwenstein & Sand removes any doubt that the unit discharges controlled by horizontal rotation are in fact derived from the horizontal semicircular canal. The origin of the discharges controlled by rotation in the transverse and median plane is almost as certain, but that of the gravity-controlled discharges less so. Those controlled by lateral tilt behave as might be expected from Magnus's account of the saccular otolith organ, but his evidence was indirect and the work of Versteegh [1927] has thrown some doubt on the functions of this organ. For the present, therefore, it is enough to say that there are units of two kinds, one reacting to lateral and the other to fore-and-aft tilt.

The method leads to another anatomical uncertainty. It has been tacitly assumed that the discharges come from the fibres of the vestibular nerve as they enter the nuclear region, but some of them might have come from the axons of cells in the nucleus. Against this is the fact that the discharges have the same character in preparations deeply anaesthetized with dial or nembutal as in the decerebrate preparation without an anaesthetic. In any case the discharges sought for and examined have been so closely related to the stimulus that if they have been in secondary neurones they must have been a fairly close copy of those in the primary receptor fibres.

Finally, the present results emphasize the points discussed by Ross in regard to the function of the semicircular canals. As may be seen from records like those in Fig. 13 the mechanism is excellently adapted to signal a rapid turn of the head, for the nervous message agrees very closely with the tracing of the lever which records the head movement and ceases as soon as the movement is over. But the mechanism is not well adapted for signalling continued rotation or the change between the resting and the rotating state. There is little reason why the body should have receptor organs for such unlikely occurrences and the semicircular canals can only give a misleading account of what is happening. It is misleading because of the gradual return of the deflected cupola when the flow of endolymph ceases. This brings the cupola back to the mid-point after the speed of rotation has become constant and accounts for the long suppression of activity in the one canal and the long after-discharge in the other when the rotation is stopped and the cupola is deflected in the opposite direction. These after-effects give the confusing impression of reversed rotation and the reactions which accompany it; at any rate they last long enough to do so. If they are to be avoided, continued rotation must be carried out by a series of accelerations and decelerations as in the dancer's pirouette. The cupola is then pushed to and fro repeatedly by the current of endolymph and there is no time for the slow drift back to the mid-position. In fact the canal mechanism suffers from the same defect as an amplifier with condenser coupling, the tendency for the output to revert to the initial state whenever the input conditions have become constant.

SUMMARY

1. The impulses from vestibular receptors can be studied in the cat by a fine wire electrode thrust into the brain stem in the region of the vestibular nucleus. The results are in general agreement with those from cold-blooded vertebrates.

2. Discharges in single units belong to one of two main types, gravity-controlled and rotation-controlled. The former depend on the position of the head in space, the latter only on angular accelerations or decelerations. Discharges controlled by horizontal rotation and by the tilt of the head in the median plane are found near the oral border of the striae acusticae, those controlled by lateral tilt and by rotation in the transverse plane are nearer the aboral border. Responses to vibration have not been found.

3. The gravity receptors are increasingly stimulated as the head is tilted out of its normal position and become very slowly adapted to the stimulus. They react to linear accelerations as well as to the pull of gravity.

4. The rotation receptors are stimulated by angular acceleration in the horizontal, median or transverse plane or by deceleration of steady rotation in the opposite sense. For the horizontal canal the stimulating sense is with the ampulla trailing, for the posterior with the ampulla leading. With rotation in the median plane some units have reacted to snout up and some to snout down movement, but some of these may have been gravity receptors reacting to linear acceleration.

5. Quick turns of the head are signalled by brief discharges which coincide with the movement, but an acceleration not followed at once by deceleration gives a discharge lasting up to 25 sec. Equally long after-discharges follow deceleration from steady rotation in the non-stimulating sense.

6. The majority of the rotation receptors, though not all, give persistent low-frequency discharges when the head is at rest. These are suppressed by acceleration in the non-stimulating sense and by deceleration of steady rotation in the stimulating sense, and it may be as long as 30 sec. before the resting discharge is fully restored.

7. These results support Ross's view that the canal receptors adapt slowly, the stimulus being proportional to the deflexion of the cupola. With a brief turn the reversal of the endolymph flow brings the cupola back at once to the mid-position; with continued rotation the deflected cupola is brought back slowly by elastic forces and is then deflected the other way when rotation is stopped. The resultant suppression of activity may be reinforced by fatigue.

REFERENCES

Adrian, E. D. & Moruzzi, G. [1939]. *J. Physiol.* **97**, 153.
de Burlet, H. M. & de Haas [1923]. *Z. ges. Anat.* 1. *Z. Anat. EntwGesch.* **68**, 177.
Fitzgerald, O. [1940]. *J. Physiol.* **98**, 163.
Löwenstein, O. & Sand, A. [1936]. *J. exp. Biol.* **13**, 416.
Löwenstein, O. & Sand, A. [1940]. *J. Physiol.* **99**, 89.
Magnus, R. [1924]. *Körperstellung.* Berlin: Springer.
Oost, H. [1918]. *Anat. Anz.* **51**, 272.
Ross, D. A. [1936]. *J. Physiol.* **86**, 117.
Sand, A. [1938]. *Proc. Roy. Soc.* B, **125**, 524.
Versteegh, C. [1927]. *Acta oto-laryng., Stockh.*, **11**, 393.