THE ACTIVITY OF THE HORIZONTAL SEMI-CIRCULAR CANAL OF THE DOGFISH, *SCYLLIUM CANICULA*

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(With Six Text-figures)

I. INTRODUCTION

THE functional differentiation of the superior and inferior parts of the labyrinth of fishes has been established by the work of von Frisch and Stetter (1932) and of Löwenstein (1932). The pars superior, consisting of the utriculus and the semi-circular canals, is concerned exclusively with the maintenance of static and dynamic equilibrium, while the pars inferior comprises the sacculus and lagena and is the organ of auditory reception.

The extensive literature on the equilibrium function of the labyrinth has been recently reviewed by one of us (Löwenstein, 1936). Investigations in this field have, for the most part, dealt with the effects of surgical injury to the labyrinth, or some part of it, upon the reflex responses of the body limbs and eyes to rotation and tilting. Such observations are necessarily indirect, and furnish a picture which, although of great value in interpreting the reflex behaviour of the animal, does not justify a precise description of the activity of the individual sense organ. When, for example, the extirpation of a part of so complex a structure as the labyrinth results in the appearance of a deficiency phenomenon, it is frequently doubtful whether the effect was not due to general damage to the whole, rather than to the exclusion of the particular part. Moreover, reflex observations have in some cases revealed a complexity of response from a single semicircular canal which could only be interpreted by postulating a double and functionally specialised innervation to its ampulla. This was the view held by Lee (1894–5), who said, "the doctrine of specific nerve energies impels us to believe that two functionally different groups of nerve endings are present in each crista; one of which is predominant over the other". Such is the case, for instance, with the problem of the response of a single semicircular canal to rotation in opposite directions.

Observations on fishes by Lee (1894–5), Maxwell (1920, 1923), Löwenstein (1932) and Steinhausen (1933) are not in agreement on this point. Lee worked on *Galeus canis*, and found that mechanical stimulation of individual ampullae evoked

two kinds of reflex response of the eyes, depending on the intensity of the stimulus. The two reflexes corresponded to responses to rotations in opposite directions in the plane of the semicircular canal concerned. Maxwell observed only one kind of reflex response from each semicircular canal in selachians when the ampulla was directly stimulated, or when, after unilateral extirpation of an ampulla, the fish was rotated in opposite directions in the appropriate plane. After unilateral extirpation of the pars superior in *Phoxinus laevis*, Löwenstein found that a reflex eye response was at first evoked by horizontal rotation in one direction only, but after a period of recovery the reflex in response to rotation in the opposite sense reappeared. Steinhausen made direct observations of the displacement of the cupula when the horizontal canal in the pike was mechanically stimulated, and concluded that only a unidirectional response can occur. In Amphibia, McNally and Tait (1925, 1933) and Main (1931) maintain that the individual semicircular canal responds in one direction only, and Trendelenburg and Kühn (1908) hold the same opinion with reference to reptiles. In birds and mammals the individual semicircular canal has been found to respond to rotation in both senses by a number of workers (Ewald, 1892; Benjamins and Huizinga, 1928; Magnus and de Kleijn, 1926; Lorente de Nó, 1931).

In the dogfish, *Scyllium canicula*, we have found it possible to expose the branch from the horizontal ampulla in such a way that it could be placed on an electrode, and oscillographic records could be obtained of the sensory discharge from the ampullary organ in response to rotatory stimulation. Electrical recording from a single ampulla is, so far as we are aware, technically impossible in teleostean fishes, Amphibia, reptiles, birds and mammals, and even in the closely related nurse-hound, *Scyllium catulus*, the anatomical relations are different, and we were unable to obtain a suitable preparation.

We are acquainted with only two attempts to record electrically the responses of the labyrinth to rotatory stimuli. Ashcroft and Hallpike (1934) found that rotation and tilting did not produce a response in the saccular nerve of the frog. Ross (1935) obtained oscillographic records of the action potentials occurring in the eighth cranial nerve of the frog, after splitting up its intercranial portion into very slender filaments. A discharge of impulses occurred in response to ipsilateral[1] rotation in the horizontal plane, but not to contralateral rotation. It was concluded that the receptor concerned was almost certainly the horizontal canal.

II. TECHNIQUE

The dogfish was anaesthetised in 1 per cent. urethane solution in sea water, and a spinal transection was made behind the medulla. This served to immobilise the fish sufficiently for the purposes of the experiment. The fish was securely fixed to a brass plate, which could be mounted on a stand in a sloping position, so that

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[1] We shall employ the term ipsilateral rotation to designate horizontal rotation to the side of the canal in question, and contralateral rotation for turning in the opposite direction, *i.e.* for the left horizontal ampulla anticlockwise rotation is ipsilateral, and clockwise is contralateral.

the left orbit was easily accessible to operative manipulation under a low-power Leitz dissecting microscope fitted with a pair of Minot lamps giving a practically shadowless field of illumination. The nerve of the left horizontal ampulla was approached not in the orthodox way through the roof of the skull, but through the orbit, after enucleation of the eyeball. The nerve is exposed by removing a layer of cartilage 1 or 2 mm. thick from the posterior wall of the orbit.

The nerve arises at the anterior wall of the horizontal ampulla and runs dia-gonally downwards to join the main bundle of the superior branch of the eighth nerve at the bottom of the utriculus. Considerable variability in the structure of the nerve was encountered in different individuals. In some cases it was composed of several independent strands, in others most of the strands were assembled into a single trunk. The nerve lies free on the vestibular wall, and, when it has been severed at its utricular end and ligatured, it can be lifted clear of the surrounding tissue and placed upon an electrode. On the average 2 or 3 mm. of nerve were available.

The dogfish can survive for several hours out of water, and it was not found necessary to provide a respiratory current to the gills of our urethanised fishes during the experiment. Control tests showed that 3 hours after the beginning of an experiment respiratory movements recommenced when the fish was immersed in water.

The action potentials were recorded with a condenser coupled amplifier and Matthews' oscillograph. A loud speaker with auxiliary power stage was connected in the output circuit. This gave acoustical information which was of great value in the conduct of the experiments. The electrodes were silver wires, the nerve being connected to the grid electrode, while the earth electrode was inserted into the tissues in the floor of the orbit. In order to minimise vibrational disturbances during rotation, and also to facilitate the adjustment of the nerve on the electrode, a micro-manipulator was designed with mechanical movement in three planes, which was rigidly bolted to the brass plate on which the fish was secured. In this way the fish and electrodes formed a rigid system which could be shaken or jarred without causing any appreciable electrical artifacts. The plate carrying the fish and electrodes was placed horizontally inside a screened box, which rested on a metal turn-table 1 metre square, revolving on ball bearings. Connection between the electrodes and the input of the amplifier was achieved by means of two annular mercury troughs mounted on the central shaft of the turn-table with a stationary amalgamated copper wire dipping into the mercury (Fig. 1). Slight microphonic oscillations from the ball race could not be entirely eliminated, but they were greatly reduced by mounting the preparation on rubber pads, and by enclosing the screened input leads in rubber tubing. In order to obtain a synchronised record of the angular velocity and acceleration and the activity of the nerve during rotation, an electromagnetic signal was employed. An oscillograph mirror was mounted on the end of the pointer, and was placed close to the oscillograph so that it reflected an additional image of the slit into the camera. The signal was in circuit with a spring key, which was opened on being struck by a rod projecting vertically down-

wards from the edge of the turn-table. Four such rods were mounted one at each corner of the turn-table, so that each quarter turn was marked on the record. In order to avoid interference from the electromagnet it was necessary to have a shunt resistance in the circuit. The speed of the camera was calibrated with a 50 ~ tuning fork.
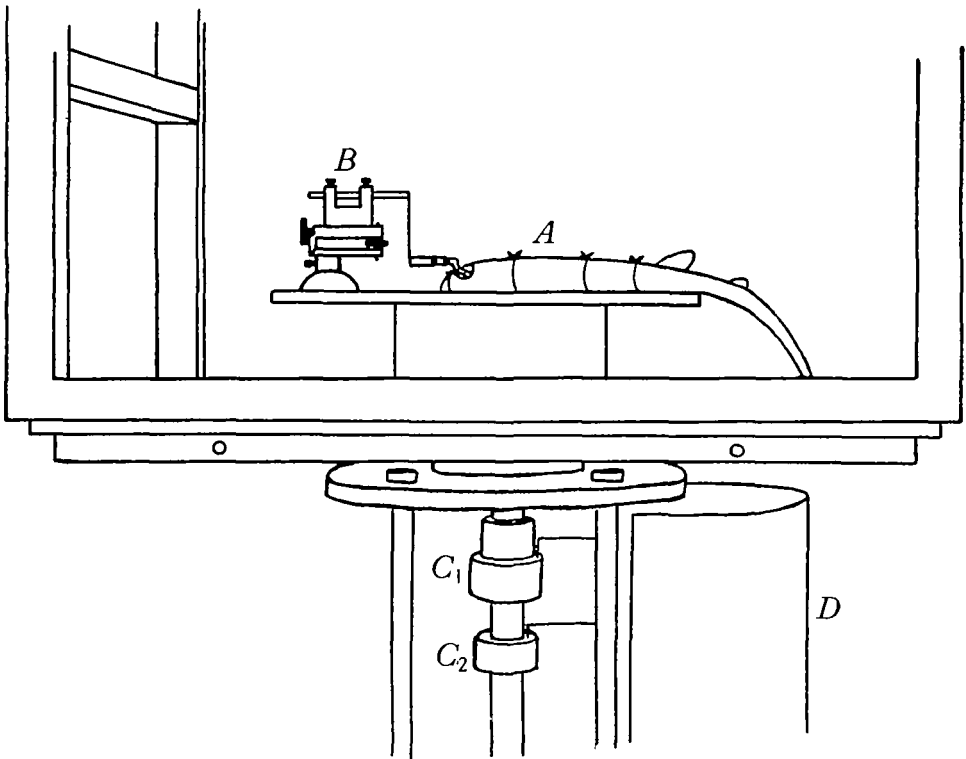

Fig. 1. Dogfish on turn-table, inside screen box. A = dogfish; B = electrode holder; C_1, C_2 = annular mercury contacts; D = screening of the turn-table stand, folded back to show contacts. The wiring has been omitted for the sake of clarity.

III. EXPERIMENTAL RESULTS

Operations were performed on twenty-four fishes. In seventeen of these electrical responses to rotation occurred. The failure of the remaining seven was due to damage during manipulation or insufficient length of nerve. In three of the seventeen fishes that gave results an additional operation was performed with a view to determining the effect on the behaviour of the ampulla of exposing, ligaturing and cutting the semicircular canal. The results obtained were inconclusive, but they clearly demonstrated the fact that the extremely delicate ampullary mechanism is seriously damaged by interference of this kind. Of the remaining fourteen fishes, twelve gave a consistent picture which we are convinced represents the normal

behaviour of the ampulla, and which will be described in detail below. The other two showed a somewhat different behaviour, which we have reason to regard as abnormal, and which also will be dealt with later. All the experiments were carried out on the left horizontal ampulla.

When the fish was set up in the normal horizontal position with the nerve connected to the amplifier, a spontaneous asynchronous discharge of impulses from the ampulla was observed. This spontaneous discharge persisted as long as the experiment was continued (2 or 3 hours), or until the nerve was killed. The action potentials were of the order of 10–20 microvolts and varied somewhat in different fishes owing to variation in length and thickness of nerve. Comparison with the base line after the nerve had been killed with toluol Ringer clearly demonstrated the physiological origin of these potentials.

Ipsilateral rotation (anticlockwise) immediately evoked a strong increase in the discharge of impulses (Fig. 2). The ampulla was remarkably sensitive to this stimulus,
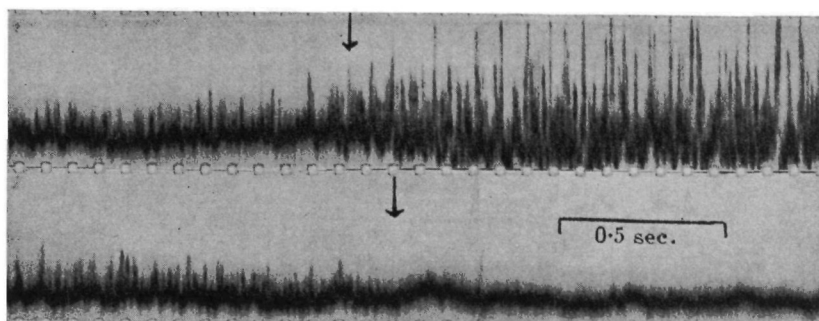

Fig. 2. Oscillograph records from the nerve branch from the left horizontal ampulla of the dogfish. Above: response to ipsilateral rotation (anticlockwise). Below: response to contralateral rotation (clockwise). The arrows mark the beginning of rotation. Note the spontaneous discharge before rotation commences. Records read from left to right.

and a marked increase in the discharge was observed at an average angular velocity as low as 22° per sec. during the first 90° of rotation. On the assumption that the angular acceleration was uniform during the quarter turn, the threshold acceleration was of the order of 11° per sec² During continuous rotation (10 revolutions) an angular velocity of 120° per sec. was not exceeded. There is no evidence in the records that at a constant velocity of rotation the discharge returns to its resting level, but the conditions of our experiments do not permit a final conclusion on this point. The large turn-table was revolved by hand, and, although the rotation signal frequently showed a constant velocity during several consecutive quarter turns, the method of driving the table was such that within each 90° of revolution there was a slight slowing and quickening of angular speed. In view of the very great sensitivity of the ampulla the possibility cannot be excluded that these small fluctuations were adequate to provide repetitive stimulation. When, however, the angular velocity was deliberately varied within wide limits during a prolonged rotation, the records clearly show fluctuations in the intensity of the discharge

corresponding to acceleration and deceleration in the revolution of the turn-table. In Table I we give an analysis of two records taken at an interval of 1 hour from the same fish, during ipsilateral rotation with a fluctuating angular velocity. It is to be noted that there is no *absolute* relation between angular velocity and the intensity of the discharge, for in both records deceleration brought about a diminution of the discharge to the resting level at an angular velocity which, at the beginning of rotation, produced a clear increase. When the turn-table was allowed to come to rest gradually, as in Table I, the discharge declined to the resting level, and continued as the spontaneous discharge after rotation had ceased. When, however, the table was brought to rest fairly suddenly, there followed a period, which we may designate as the negative after-effect, during which the discharge from the ampulla was actually less than the normal spontaneous discharge.

Table I. *Response of the left horizontal ampulla during five ipsilateral revolutions at varying speeds*

Quarter turns	1 hour after operation		2 hours after operation	
	Average speed degrees per second	Response	Average speed degrees per second	Response
----	0	×	0	×
1st	43	× ×	45	× ×
2nd	73	× × × ×	72	× × ×
3rd	82	× × ×	72	× × ×
4th	88	× × × ×	77	× × × ×
5th	88	× × ×	86	× × × ×
6th	77	× ×	84	× × × ×
7th	64	×	72	× ×
8th	53	×	61	× ×
9th	40	×	49	×
10th	49	× ×	42	×
11th	65	× × ×	57	× ×
12th	71	× × ×	74	× × ×
13th	77	× × ×	84	× × × ×
14th	78	× × ×	84	× × ×
15th	80	× × ×	86	× × ×
16th	88	× × × ×	82	× × × ×
17th	75	× × × ×	68	× ×
18th	62	× × ×	57	×
19th	51	× ×	45	×
20th	38	×	31	×
—	0	×	0	×

×, spontaneous discharge; × ×, increased discharge; × × ×, strongly increased discharge; × × × ×, very strongly increased discharge.

Contralateral (clockwise) rotation reduced the spontaneous discharge from the ampulla (Fig. 2). In some cases the discharge was completely abolished, in others it was markedly diminished. The effect was strikingly reproduced by the loud speaker. The rumble of the spontaneous discharge was instantly silenced when the table was turned to the right. It is clear from the records that the diminution of the discharge during contralateral rotation is quantitatively less than the increase during ipsi-

lateral rotation, which implies that there exists a peripheral asymmetry in intensity of response to rotation in the two directions. The threshold for the contralateral response is of the same order as for the ipsilateral, and a clear reduction of the spontaneous discharge has been observed at an angular acceleration of 11° per sec² As in the case of the ipsilateral response, so with the contralateral, the discharge during prolonged rotation follows variations in speed of revolution, but in the reverse manner. When the speed is diminished the discharge increases, and may attain the level of the spontaneous discharge; when the speed is increased again the discharge shows a corresponding diminution.

When prolonged contralateral rotation is arrested the intensity of the discharge rises well above the level of the resting spontaneous discharge, and is maintained as an after-discharge for a considerable period of time (Fig. 3). We have not investigated the relation between the duration of contralateral rotation and the duration of after-discharge except in one experiment, where ten clockwise revolutions lasting 45 sec. were followed by an after-discharge of 35–40 sec. duration.

The spontaneous discharge was abolished when the nerve was irrigated with toluol Ringer, and all responses to rotation likewise disappeared. As a control, however, such a procedure was unnecessary, for the silencing of the spontaneous discharge on contralateral rotation itself furnished strong evidence that the electrical phenomena under consideration were physiological. But the most complete and conclusive test was provided by observations on an inverted fish (ventral surface upwards). In this position clockwise rotation of the turn-table is ipsilateral with respect to the left horizontal ampulla and anticlockwise is contralateral. It must be pointed out that the inverted position is highly abnormal, and probably creates internal conditions within the ampulla which do not occur naturally. It is therefore not surprising, perhaps, that the spontaneous discharge was weakened or abolished in this position. But in response to rotational stimuli the ampulla continued to function normally, and a discharge of impulses was evoked by ipsilateral, not by contralateral rotation (Fig. 4). Thus the conditions of this experiment were such that the observed electrical phenomena were now associated with mechanical movements of the apparatus which were exactly opposite to the corresponding movements in experiments with the fish in the normal position. No control could, in our opinion, be more conclusive.

The ampulla could not be stimulated by mechanical methods other than rotation. Vibrations imparted to the fish by shaking and percussion were without effect, and a tuning fork of 120 ∼ did not stimulate the organ, although it produced a microphonic effect which was unaltered when the nerve had been killed.

Prolonged rotations of several complete revolutions do not occur in nature, and it appeared to us of interest to record the activity of the ampulla under conditions which approximate to the movements of the head during swimming. In swimming a dogfish sways its head from side to side, and to imitate this movement we have swayed the turn-table slowly to the left and to the right through an arc of approximately 45°, at a speed of 3 or 4 sec. for each complete swing. The records show that
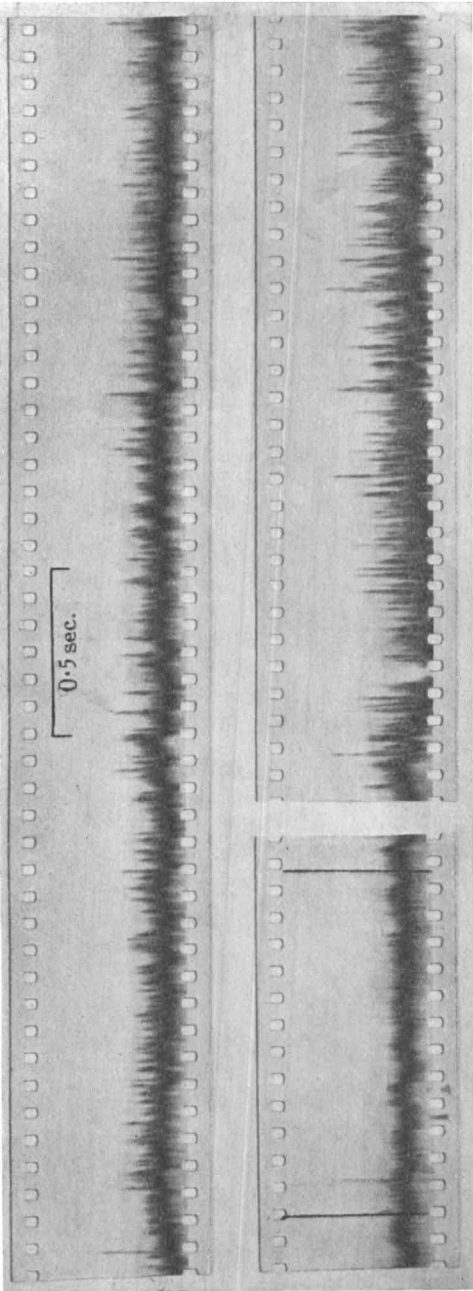
Fig. 3. The after-discharge. Above: fish stationary, spontaneous discharge. Below: contralateral rotation and stopping. The vertical lines signal 90° of revolution. At break in record the turn-table is brought to rest. After-discharge begins.
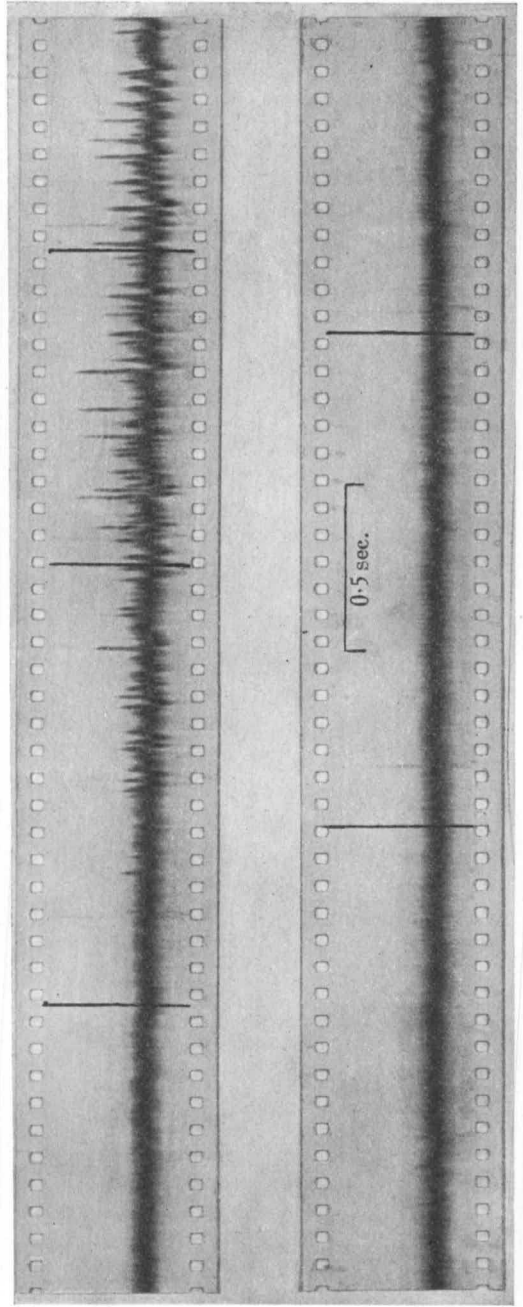
Fig. 4. Fish inverted. Spontaneous discharge absent. Above: at first vertical line ipsilateral (clockwise) rotation begins. Below: at first vertical line contralateral (anticlockwise) rotation begins. The vertical lines signal each 90° of revolution.
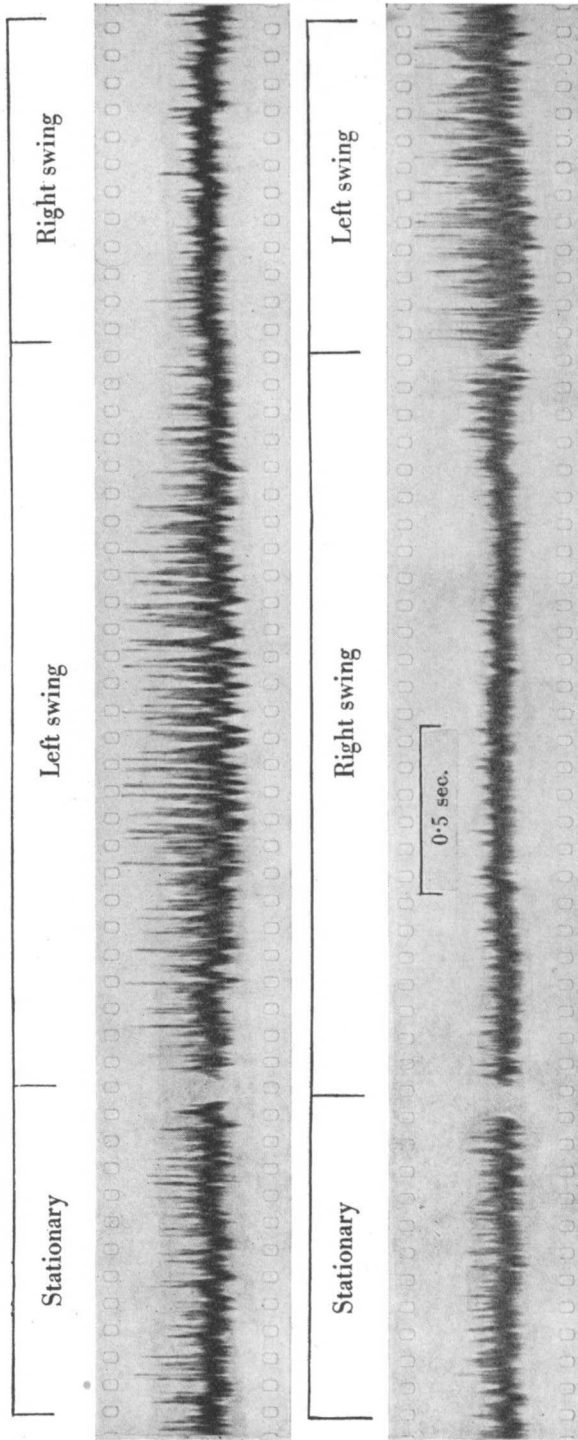
Fig. 5. Responses of the left horizontal ampulla to swaying from side to side. Above: an ipsilateral swing through an arc of 45° is followed by a contralateral swing. Below: a contralateral swing is followed by an ipsilateral one.

such very slight excursions of the head produce a strong increase and decrease in the spontaneous discharge on ipsilateral and contralateral rotation (Fig. 5).

In two exceptional fishes it was found that an increased discharge of impulses occurred during contralateral rotation. The frequency of the discharge was considerably lower than during ipsilateral rotation, and the spontaneous discharge was either absent or doubtful. One of these fishes gave an after-discharge after contralateral rotation, the other did not. Experiments on ligaturing and cutting the canal, and also tests after decapitation and destruction of the brain, have shown that the activity of the labyrinth is profoundly affected by drastic treatment of this kind. In general, the ampulla loses its discriminative capacity, and develops an abnormal sensitivity to every kind of mechanical disturbance. Although we are unable to specify any precise damage to the labyrinth in the two exceptional cases under consideration, we are inclined to believe that some such damage existed, and that, therefore, the results obtained from these two fishes cannot be regarded as representing the normal activity of the ampulla.

IV. DISCUSSION

A spontaneous discharge of impulses in the lateral line nerve of fishes has been observed by Hoagland (1932–3, 1933–4) and confirmed by one of us (A. S., unpublished), and Hoagland (1935) has developed the thesis that "discharges from the lateral line receptors may perform a tonic reinforcing role in postural and swimming reflexes in addition to serving as pressure receptors". A tonus function was attributed to the semicircular canals of the labyrinth by Ewald (1892) which was interpreted as being due to a hypothetical spontaneous ciliary activity. From experiments with the pneumatic hammer Ewald concluded that a flow of endolymph in one direction increased the effect of the ciliary activity, while a flow in the opposite direction inhibited it, with corresponding effects on the muscle tonus. Further experimental evidence for a tonus function of the semicircular canals in vertebrates has been recently reviewed by one of us (Löwenstein, 1936).

Without prejudice to the question of the internal ampullary mechanism, our observations clearly demonstrate that the ampullary sense cells are in fact spontaneously active. This activity would serve to account for the tonic effects of canal elimination recently described by Tait and McNally (1934), since the centre is thereby robbed of an afferent inflow which is a constant element of its normal functional state.

But the maintenance of tonus is not the only function of the spontaneous activity of the ampullary receptors. An organ which is designed to respond to a biphasic physical change can do so either by possessing two functionally differentiated types of elements, or by being capable of a two-way modification of its basic activity. The latter possibility presents itself when the unstimulated receptor displays a level of spontaneous activity which can be either increased or decreased. Our records show that a single horizontal ampulla does in fact respond to rotation in both directions, and that one phase of rotation (ipsilateral) increases the

sensory excitation, while the opposite phase (contralateral) diminishes and may even abolish it. Thus the remarkable fact is revealed that a spontaneous activity may have a special significance in a certain type of receptor, and may endow it with the power of signalling to the centre the occurrence of two equal and opposite physical changes. So far as we are aware no other case of an adequate stimulus causing a *decrease* of afferent discharge has been as yet demonstrated.

When the activity of the horizontal ampulla is reviewed, it presents the picture of a damped pendulum with a very slow natural period. If it is assumed, as in Fig. 6, that in the resting state the pendulum is maintained in such a position that it induces a moderate excitation of the sense cells (position *a*), and that displacement in one direction increases the excitation, while displacement in the opposite direction reduces it, the phenomena of after-discharge on stopping contralateral rotation, and negative after-effect on stopping ipsilateral rotation become intelligible. The arrest of rotation is physically equivalent to acceleration in the opposite direction. Acceleration to the left (Fig. 6) will cause a displacement of the pendulum
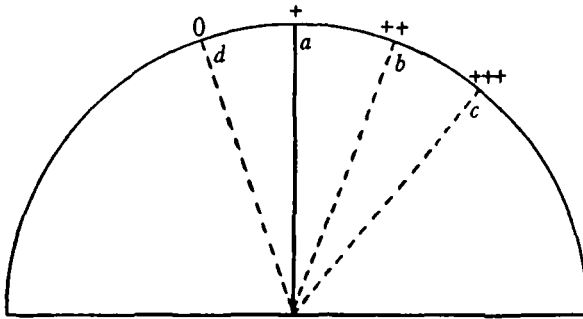

Fig. 6. Scheme to illustrate the pendulum-like action of the cupula of the left horizontal ampulla. Explanation in text.

to the right (incremental), while acceleration to the right will displace the pendulum to the left (decremental). Referring to the left horizontal ampulla, ipsilateral rotation would correspond to displacement from position *a* to *b* or *c*, depending on the degree of angular acceleration, while contralateral rotation would correspond to displacement from position *a* to position *d*. Now the arrest of rotation would cause in each case a displacement in the opposite direction, and therefore on stopping ipsilateral rotation the pendulum would swing back from *c* or *b* to *a*, and, if the displacing force is strong enough, may even overshoot the resting position and reach *d*, or at least some intermediate position between *a* and *d*, before equilibrium at *a* is finally attained. A temporary decremental phase, corresponding with the negative after-effect, would then occur. On stopping contralateral rotation the pendulum would swing back from position *d* and, if it overshoots the position of equilibrium at *a*, would cause an incremental phase at some intermediate position between *a* and *c*, before coming to rest at *a*. This would correspond to the after-discharge. In view of the comparatively strong forces required to evoke the negative after-effect, and its relative insignificance when evoked, and in view also

of the prominence of the after-discharge and its long duration, it is necessary to postulate a greater freedom of movement in one direction than in the other. We have, therefore, in Fig. 6, represented a greater maximum displacement of the pendulum to the right than to the left. It is generally held that the cupula, the gelatinous auxiliary structure resting upon the crista, undergoes such displacement during rotation, and Steinhausen (1933) has actually confirmed this view by direct observation of the exposed horizontal ampulla in the pike, *Esox lucius.* We are not primarily concerned here with the actual mechanism of the ampullary organ, but, so far as our observations shed any light on this problem, they appear to lend support to the conception of a pendulum-like cupula whose displacement causes changes in the excitation of the sense cells.

We have discussed hitherto the activity of a single ampulla. When the reflex behaviour of the intact animal is considered, it is necessary to bear in mind that the left and right ampullae are both simultaneously active, and that they work antagonistically. When the animal is at rest the centre receives an equal afferent discharge from each side. On turning to the left the discharge from the left side is increased, while the discharge from the right is simultaneously reduced, and *vice versa*. The quantitative effect of a rotational stimulus is therefore much greater at the centre than it is at the peripheral sense organ on one or the other side. This is clearly seen in Fig. 5, which shows the responses of the left horizontal ampulla to swaying from side to side. This figure may serve equally well to illustrate the simultaneous activity of the left ampulla (upper record) and the right ampulla (lower record) in response to a left swing followed by a right swing. In the lower record we have a response to contralateral rotation followed by a response to ipsilateral rotation, and these are equivalent to left swinging and right swinging with respect to the right horizontal ampulla. Thus the two records together serve to show, first, the spontaneous discharge from the left and right when the head is still, then the increased discharge from the left (above) and the diminished discharge from the right (below) during a swing to the left, and, lastly, the diminished discharge from the left (above) and the increased discharge from the right (below) when the head swings back to the right.

Although our observations have shown that a single ampulla is capable of responding to rotation in both directions, it is not to be assumed that a unilateral elimination must necessarily leave a reflex mechanism which can function normally in all respects. The abolition of the afferent discharge on one side must effect a profound disorganisation at the centre, and it is of great interest to note that a number of investigators have observed in fishes, birds and mammals that the reflex response to contralateral rotation in the horizontal plane only makes its appearance after a period of recovery. It may be suggested that during this period central accommodation to a unilateral discharge has occurred.

V. SUMMARY

1. Oscillographic records from the horizontal ampulla of the dogfish show:

(*a*) A spontaneous discharge of impulses when the fish is stationary in the normal position.

(*b*) An increased discharge during ipsilateral rotation.

(*c*) A diminution of the spontaneous discharge during contralateral rotation.

(*d*) A prolonged after-discharge on stopping contralateral rotation.

2. The threshold for the responses is an angular acceleration of the order of $11°$ per sec.^{2}

3. This mechanism provides a means of signalling to the centre equal and opposite phases of a biphasic physical change.

4. The two opposite ampullae work antagonistically, and the reflex responses of the normal fish depend upon the balance of the afferent discharges from the left and right labyrinths.

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