ACTIVITY OF LATERAL-LINE SENSE ORGANS IN SWIMMING DOGFISH

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INTRODUCTION

The lateral lines are a conspicuous feature of fish anatomy and mark the location of a sensory system which is absent in adult terrestrial vertebrates. Although lateral-line structure varies considerably in detail in different fishes, in most cases the system consists of fluid-filled canals, lined by a sensory epithelium, which are arranged in a symmetrical pattern on the surface of the head and body. The sense organs (the neuromasts) are sufficiently similar in structure and development to the various receptors of the labyrinth for all these sense organs to be grouped together as the 'acoustico-lateralis sensory system', despite their different functions (Pumphrey, 1950). It is known that the semicircular canals detect angular movements, that the vestibular apparatus monitors static position and that the inner ear is a receptor for sound, but the functions of the lateral-line system are uncertain. Indeed there has been considerable debate, speculation and experimental work centred particularly around two properties of lateral-line organs, namely their sensitivity and biological significance (e.g. see papers in Cahn, 1967).

It is generally accepted that the lateral-line organ is a mechanoreceptor stimulated by water movements, although there are cases of chemosensitivity (Katsuki *et al.* 1969) and of electroreception (Suga, 1967). It is obvious that the great sensitivity to water displacements shown by the neuromasts should permit the recognition of the movements of nearby animals, and this information might be useful in a variety of situations such as the discovery of prey, enemies and sexual partners. Certainly there is clear evidence that the lateralis system is necessary for the detection of surface waves by surface-feeding fish (Schwartz & Hasler, 1966) and that it plays some role in the rheotactic reaction of fishes to water currents (Dijkgraaf, 1933). Less well established is the idea that lateral-line organs are important in schooling behaviour (Shaw, 1969), where the recognition of water displacements resulting from the locomotion of adjacent fish could be the basis for correct fish-to-fish spacing. The pattern of water disturbances generated by locomotory movements is unknown for most fishes, but Rosen (1959) found that each concave body undulation of a swimming *Brachydanio* was associated with a discrete spinning water vortex. Displacements of this kind might be detected by neighbouring fishes when schooling (Breder, 1965) or by the swimming fish itself, in which case the lateral line could function as a proprioceptor.

If the lateral line were activated by swimming movements it would provide the nervous system with a source of rhythmical input which might be useful in the timing of body movement. All lateral-line organs, whatever their position on the body, are

innervated by nerve fibres which project to the same part of the hind-brain (acoustico-lateralis centre), and so a comparison of the activity of adjacent neuromasts could easily be made and would provide an instantaneous picture of the locomotory wave-form.

However, although Cahn & Shaw (1965) have reported that movements of the cupulae of free neuromasts occur in swimming larval *Menidia*, and although Hoagland (1933 a), Sand (1937) and Katsuki, Yoshino & Chen (1950) all recorded sensory activity when the fish they studied moved vigorously, Kuiper (1967) believed that only for the fastest-moving fish would the water displacements produced during swimming be above threshold even for superficially situated neuromasts. The idea that the neuromasts could be a locomotory proprioceptor has also been discarded because swimming movements do not appear to alter after the lateral-line nerve has been cut (Dijkgraaf, 1933).

Two points need to be established before the neuromast can be designated as a proprioceptor. They are: (1) that the discharge of the lateral-line organ embodies quantitative information about the swimming movements; (2) that this information is used for locomotory co-ordination. The experiments described in this paper are an attempt to settle the first point by studying the actual behaviour of the lateral-line organs in a swimming fish. They were made on spinal dogfish which swim steadily for many hours (Gray & Sand, 1936 a, b), for in this preparation, which can be fixed firmly by the head, it is possible to monitor the activity of the nerves supplying the lateral-line organs while the body of the fish moves in a relatively normal manner. Only the activity of the posterior lateral line is described, as the behaviour of the head organs will be considered in another paper (Paul & Roberts, 1971).

METHODS

The experiments were performed on 20 large spinal dogfish, *Scyliorhinus canicula* L, weighing between 900 and 1010 g, which were prepared by destroying the brain and spinal cord for the anterior third of the body. The neuromasts of the body lateral-line canal are innervated from the lateral-line branch of cranial nerve X (vagus), which was exposed when an incision about 10 cm long was made dorsal to the canal and just behind the pectoral girdle. The nerve bundle was dissected free and cut centrally. All experiments were carried out on the lateral-line nerve on the left side of the fish.

The fish was placed in a tank of sea water, clamped firmly at the head and at the posterior edge of the incision, and artificially ventilated by passing sea water through the mouth and over the gills at a rate of $1 \cdot 0$–$1 \cdot 5$ l/min (Text-fig. 1). The level of sea water was adjusted so that most of the fish was immersed while the incision lay above the water. Because of the destruction of the brain and part of the spinal cord the anterior portion of the fish was inert and insensitive, but the remaining abdominal and caudal segments were responsive, and in most preparations this part of the fish performed rhythmical swimming movements, similar to those of intact fish, at a steady frequency (30–40 beats/min) for many hours. Further information about the properties of this experimental preparation is given in papers by Gray & Sand (1936a, b); Lissmann (1946a, b); Bone (1966) and Roberts (1969a).

The temperature of the sea water ranged from 11 to 17 °C, although it fluctuated by less than $0 \cdot 5$ °C in any one experiment.

Electrical recording

The activity of the neuromasts was monitored by recording from the lateral-line nerve, which was cut centrally and split into filaments until single-unit records were obtained. The filaments were periodically moistened with saline solution (NaCl 291·6; KCl 3·24; $CaCl_2$ 1·8; $MgCl_2$ 2·16; Na_2SO_4 3·52; urea 450 mM/l (Bone, unpublished)), and covered with mineral oil during recording. The recording arrangements were conventional, and the impulses, recorded with bipolar platinum electrodes,
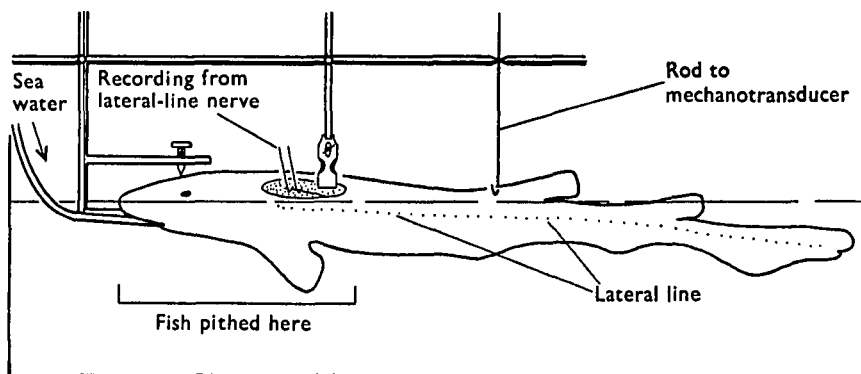
Text-fig. 1. Diagram of the experimental preparation for the recording of lateral-line activity in swimming dogfish.

were stored on magnetic tape or photographed from the oscilloscope. The pulses stored on tape were later analysed using a voltage gate in conjunction with an instantaneous rate meter and a Biomac 1000 signal analyser; the resulting histograms were written on an XY plotter. In some fish electromyograms were taken from the red musculature with concentric needle electrodes, as a monitor of movement.

Mechanical recording

The amplitude and frequency of the swimming movements were recorded by supporting the body from a light rod which was attached to a linear, wire-wound potentiometer whose output was displayed on an oscilloscope channel. The rod was fixed to the body at the base of the first dorsal fin and so the transducer only indicated the movement of the body in this region, which was not necessarily the site of the sense organ. In most records therefore the transducer trace and the electrical record are out of phase.

A photographic technique was sometimes used to give a better idea of the relationship between the discharge of a sense organ and its position. A sense organ was located and marked with an indian ink spot by recording from the lateral-line nerve while the canal was mechanically probed, and then recordings were taken as the fish swam. A 35 mm camera with a 50 mm lens was suspended over the experimental tank and focused on the swimming animal. The shutter was left open and the room was kept totally dark, except at selected intervals when illumination was provided by one electronic flash gun. This was triggered by pulses from a rate meter into which the

potentials from the located sense organ were fed. The resulting photographs showed
the exact position of the body at selected moments in the sensory discharge.

RESULTS

The posterior lateral-line nerve bundle contains about 900 myelinated nerve fibres
which range in diameter from 2 to 25 μm (Roberts & Ryan, 1971). Some of the smaller
fibres, conducting at 12 m/sec, are efferent in nature (Roberts & Russell, 1970) and
were not studied in the present experiments. The real significance of the efferent
system is not yet known, but it is possible to inhibit the sensory discharge by exciting
the efferent fibres. Therefore it is important to realize that the data reported in this
paper were obtained from de-efferented neuromasts, isolated from the efferent neurones
located in the hind-brain. The results are based on a study of 45 units in detail.
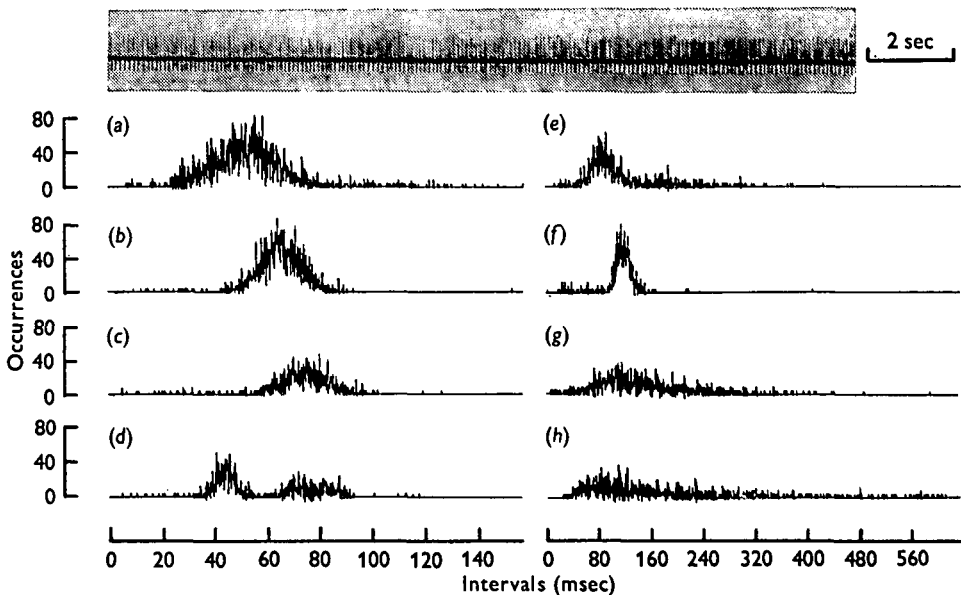
Text-fig. 2. Histograms of intervals between impulses recorded from neuromasts in non-
swimming dogfish. The histograms in the left-hand column are plotted on a different time scale
from (e) to (h). In each case 1000 consecutive impulses were sampled. The top trace is a typical
record of a spontaneously discharging unit.

Spontaneous activity in non-swimming spinal dogfish

Hoagland (1933 a, b, c, d) was the first to show that the unstimulated lateral-line
organ is spontaneously active, and this important observation has been repeated on a
number of fishes (Sand, 1937; Katsuki et al. 1950) and amphibia (Dijkgraaf, 1956).
Hoagland was uncertain whether the discharge had any significance, but shortly after-
wards a similar feature was recorded from the receptors of the semicircular canals
(Lowenstein & Sand, 1936), where it is believed to have a tonic function (Lowenstein,
1937).

Recordings from whole lateral-line bundles in non-swimming dogfish revealed con-
siderable neural activity, and most of the single units examined showed steady spon-

aneous activity when the fish was stationary. A number of these units were studied in detail, and some interval histograms are provided (Text-fig. 2) to illustrate the various patterns of activity. In each case the abscissa is the interval between successive impulses (in msec) and the ordinate is the number of these intervals. Some units discharged steadily, at a frequency of about 18 impulses/sec, while others showed grouped discharges. The discharges of most receptors produced unimodal histograms (mode 60–100 msec), while in a few (Text-fig. 2*d*) the histograms were distinctly bimodal. Long intervals (500 msec and larger) were rarely seen.
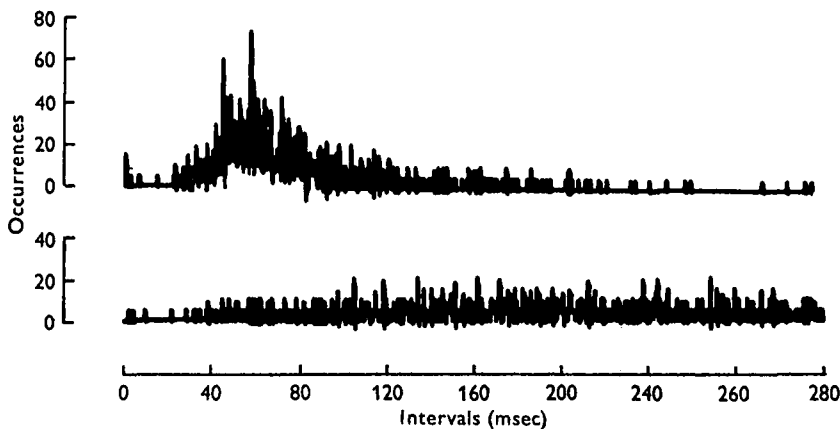
Text-fig. 3. Histograms of the inter-spike intervals recorded from the same sense organ at different times during the course of an experiment. The bottom histogram is based on a record taken 2 h after the record used for the top histogram. One thousand impulses were recorded in each case.
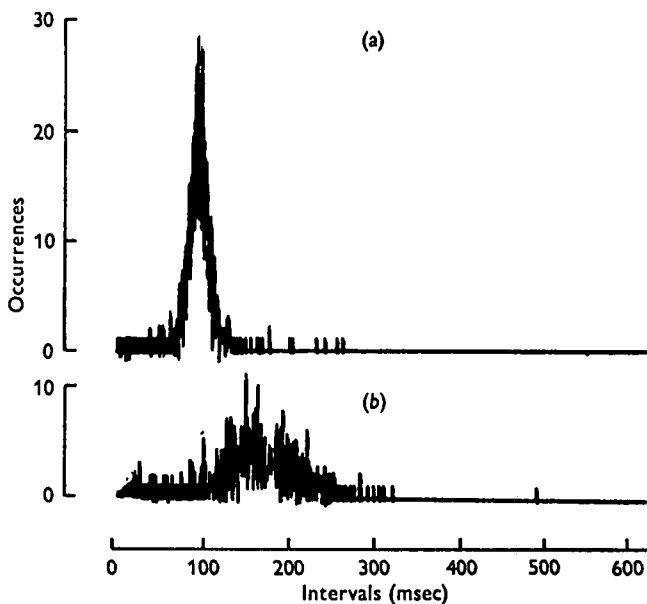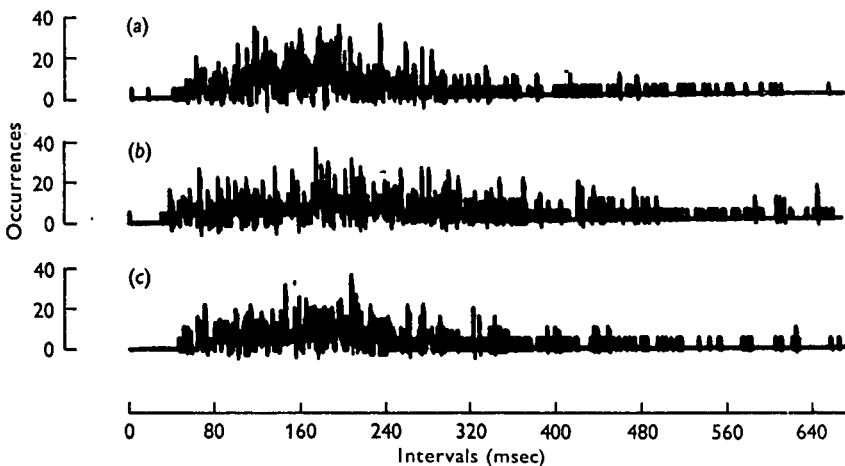

Text-fig. 4. Histograms of 1000 inter-spike intervals recorded from the same sense organ immediately before (*b*) and after (*a*) strong stimulation.

The discharge pattern of the neuromasts was not fixed but varied even during the course of an experiment (Text-fig. 3) and was noticeably altered after the neuromast had been stimulated (Text-fig. 4).

This might account for the differences seen between the histograms prepared from steadily discharging units, for it is possible that the discharges were not always truly spontaneous. It was difficult to be certain that there had been no external stimulation of any kind for there was always the possibility of unnoticed water-borne stimuli, vibrations of the fish-holding frame, or even of small movements of the fish itself. Certainly the interval histogram changed noticeably when there was a slight movement, with the type of change depending on the duration and direction of the movement.

Directional response of the sense organ

It is now generally recognized that hair cells of the acoustico-lateralis system show directional sensitivity in their responses (Dijkgraaf, 1963). The initial demonstration of this was Sand's (1937) discovery that some receptors of the lateral-line canal of *Raja* discharged more rapidly when fluid was perfused down the canal, and were inhibited when the flow was up the canal, while other receptors showed the opposite response.

Text-fig. 5. Histograms of inter-spike intervals for a neuromast when the overlying part of the body was bent through the same arc to the right and left sides of the mid-line. The record in (*b*) is when the body was not bent; (*a*) was when the body was bent to the right and (*c*) when it was bent to the left. In all cases 1000 impulses were sampled.

In the experiments described in this paper twofold responses were obtained from the neuromasts of *Scyliorhinus* when the part of the fish overlying the receptors was moved in different directions. For example, the unit illustrated in Plate 1, fig. 1 showed a pronounced accelerated discharge when the body was bent in one direction and stopped discharging when the body was moved towards the opposite side. Neither the increase nor the decrease in discharge continued for long after the movement had stopped, and soon the receptor discharge had returned to a steady spontaneous level. Thus histograms of the response of an organ when the fish was bent to the right and kept there do not differ markedly from those obtained when the body was kept bent

to the left (Text-fig. 5), for the receptor could not maintain a steady increased or decreased discharge which was proportional to the amount of bending (unlike proprioceptors in the body (Roberts, 1969 *b*)). However, while the body was moving, the increase in excitation or the inhibition of the discharge was maintained (Plate 1, fig. 1). Another unit can be seen in Plate 1, fig. 1 which discharged when the body was bent to the right and was inhibited when the body moved to the left; i.e. the responses of the two units alternated. Thus each receptor showed a specific sensitivity to the direction of movement of the part of the body where the receptor was located, some being enhanced by movement to the animal's left, whereas others were inhibited by movement in this direction.

The experiments in which photographs of the swimming fish were taken by electronic flash (see Methods) also provided evidence for a bi-directional response of the lateral-line receptors, for in some cases the maximum discharge of the unit took place when the part of the body overlying the receptor was concave, while the maximum discharge of other units was when that part of the body was convex. These results show that each organ is sensitive to a changing rather than to a static stimulus.

Rhythmical activity in swimming spinal dogfish

It follows from these results that the discharge pattern recorded from spontaneously active neuromasts will change when a fish begins to swim, the nature of the change depending on the directional sensitivity of each hair cell. Recordings taken from the lateral-line bundle showed that the moment a spinal dogfish began to swim the continuous spontaneous activity was replaced by grouped discharges which were coincident with the frequency of the swimming movements. In the example shown in Plate 1, fig. 2 the rhythmical movements were infrequent and of small amplitude and the receptor discharged continuously but with a periodic quickening of the discharge in time with the swimming rhythm. When the movements increased in amplitude and frequency, the discharges became grouped and alternated with silent periods, so that in a fish swimming normally (30–60 beats/min) the receptor discharge was always grouped and locked in phase with the swimming frequency (Plate 1, fig. 3). The change in the discharge pattern is shown in the interval histograms of Text-fig. 6. The top histogram shows the distribution of impulse intervals when the fish was kept stationary by being clamped hard about the tail. Most of the inter-spike intervals were 80 msec long. The fish began to swim when it was released from the clamp, and the pattern of lateral-line activity changed at once. The histogram became displaced, as most of the intervals were short (37 msec) and bimodal, with a small peak at 400 msec due to the silent period between the bursts. The rhythm is evidently not produced by a periodic interruption of the background spontaneous discharge, and both the discharge and the silent period must be actively produced.

The phasic response of the neuromast was obtained whatever the frequency of body movement. In a few experiments the body was gripped anteriorly and made to oscillate (see Roberts, 1969 *a*) at frequencies higher than those naturally obtained during swimming, to see whether the sense organ would follow bending movements of the body at high frequency. The records (Plate 2, fig. 1) show that at frequencies even as high as 200 cyc./min the rhythmical sensory discharge was obtained.

The frequency of impulses making up each rhythmical group is variable and dependent on the form of the body movement. The movements of fishes are not easy to describe quantitatively, and most workers have followed Gray (1933) in considering the undulatory movement as being a propagated muscular wave to be described in terms of the frequency, amplitude and wavelength. These are not independent variables and the relationships between them have yet to be studied. In the spinal dogfish the form of the locomotory movements can be modified by stimulation – for example, by pinching the fins or by stroking the body – and these changes are accompanied by alterations in the discharge pattern of the neuromasts.
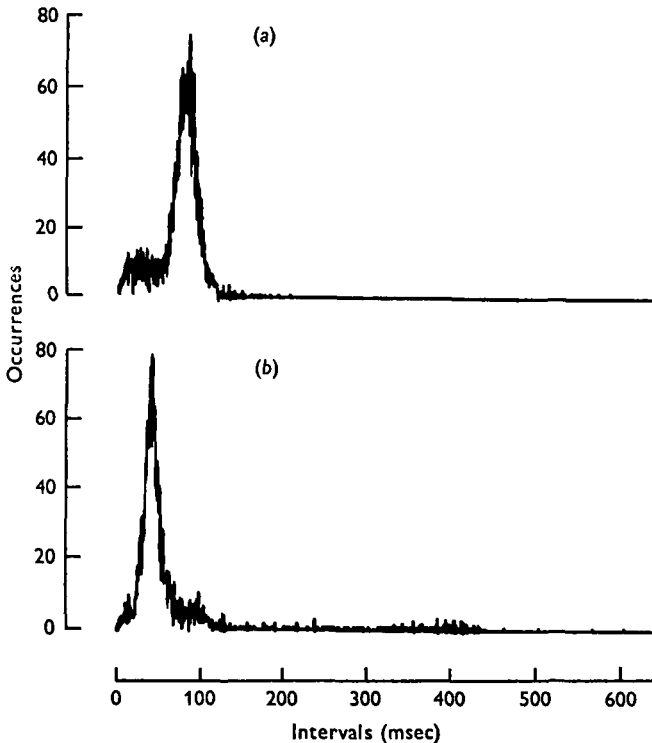

Text-fig. 6. Histograms of intervals between impulses from a neuromast in (a) stationary fish; (b) swimming fish. Five thousand impulses were sampled for each histogram.

However, even when the swimming movements seemed to be very consistent in size and frequency, the pattern of discharge in each rhythmical burst was quite variable. Most usually, as shown in Plate 2, fig. 2, there was a gradual increase in discharge frequency to an initial peak, then a slight decline before a second higher peak was reached, followed by a rapid drop and a silent period. The distinction into two peaks in the impulse frequency was particularly clear when the movements were rapid or large but sometimes the separate groups were less apparent (Plate 2, fig. 2a).

Changes in the frequency of swimming produced particularly noticeable changes in the pattern of receptor discharge. For example, it was found that the time between the points of maximum impulse frequency in successive discharges was correlated with the frequency of swimming (Text-fig. 7), and a measurement of this interval would

give the fish an indication of the frequency of its body movements. The duration of the discharge was also related to the frequency of swimming, each burst becoming shorter as the swimming frequency increased (Text-fig. 8*a*). There was also an increase in impulse frequency with rising swimming frequency (Text-fig. 8*b*).
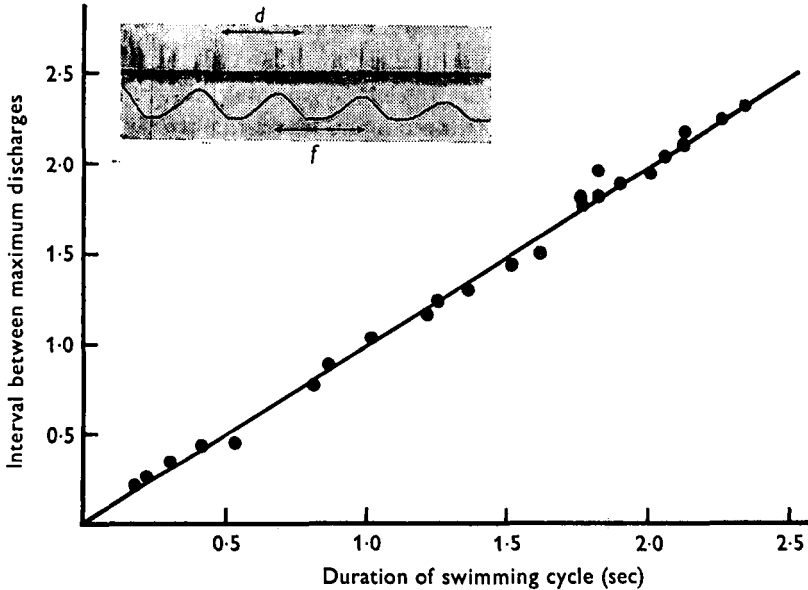
Text-fig. 7. The relationship between the duration of each swimming cycle and the interval between the maximum impulse discharges in consecutive bursts for a single unit. The inset shows how the measurements were made: d = inter-burst interval; f = duration of each cycle.
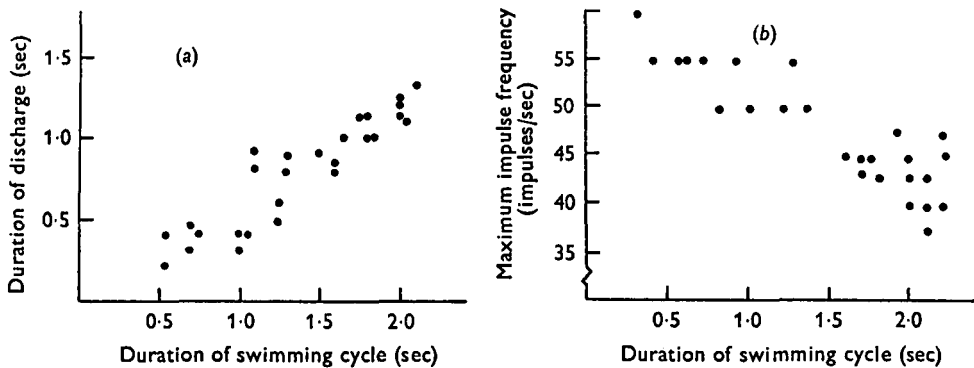
Text-fig. 8. The relationship between the swimming frequency and (*a*) the duration of each rhythmical discharge and (*b*) the highest impulse frequency. The points are from a single unit.

The impulse frequency also increased as the amplitude of the swimming movements became larger but the relationship was dependent on the rate of movement, the impulse frequency being higher when a large movement was executed rapidly than when the same movement was performed more slowly.

A few neuromasts were studied which showed no spontaneous activity when the fish

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was stationary but which discharged rhythmically when the fish swam (Plate 3, fig. 1). This type of unit was easily overlooked, because of the absence of spontaneous activity, and is possibly quite abundant.

The source of rhythmical stimulation

External water movements. Recordings from the lateral-line nerve of a swimming fish were made while the water in the tank was drained away, so that the fish, supported by the head and at the base of the dorsal fin, was left 'swimming' in air. The movements were similar both in air and in water, although the frequency was increased and the amplitude decreased when the fish was in air. Some records of these experiments are given in Plate 3, fig. 1 (*b*), from which it can be seen that the rhythmical activity of the sense organs remained essentially unchanged when the fish was in air. Evidently, the rhythmical activity recorded from a swimming fish arises from within the fish itself and is not evoked by water displacements generated by the movements of the fish.

Movements of fluid in the canal. The stimulus which Sand (1937) used in his elegant experiments on the neuromasts of rays was a flow of fluid along the lateral-line canal, and it seemed possible that there might be a flow of canal endolymph in the swimming dogfish which could stimulate the sensory endings. Smith (1930) has demonstrated a flow of sea water through the canals of some teleosts and Tester & Kendall (1968) found that a tripan blue solution penetrated along the canals of a young hammerhead shark when it was made to swim in the dye. If a flow of endolymph during swimming was the stimulus to the neuromasts, their activity would be modified by interference with the canal. But when the canal was cut or ligatured near to the neuromast, the rhythmical discharge in a swimming fish was not modified even though any net flow of endolymph would have been prevented; it is unlikely therefore that there is any longitudinal flow of endolymph in time with the body movements. Because the canal is small it was not possible to study the actual endolymph movement in swimming fish, but movements of dyes injected into the large vein which lies just below the lateral-line canal were observed, and as expected the dye particles did not show a longitudinal movement but oscillated to and fro in time with locomotion. A similar movement of canal endolymph would excite the neuromasts.

Large-amplitude swimming movements

Although lateral-line receptors do not respond to external water movements generated by the steadily swimming dogfish, they are excited when the fish moves violently. For example, when a dogfish is pinched on the tip of the dorsal, anal or caudal fins, very rapid, large-amplitude movements are often performed which cause considerable disturbance in the surrounding water. In this case the water movements do stimulate the lateral-line receptors and continue to do so even after body movements have stopped.

The detection of external water displacements

It is generally agreed that the lateral-line sense organs are very sensitive to nearby water displacements, which are detected as a change in the frequency of lateral-line spontaneous activity (Dijkgraaf, 1963). But it is shown here that in a swimming fish the pattern of lateral-line activity consists not of a steady discharge but of a rhythmical

series of bursts. The problem therefore arises of whether in a swimming dogfish the detection of external signals is seriously affected by the sensory activity evoked by movement, because, as we have seen, the sensitivity of a unit is depressed shortly after it has been stimulated (see Text-fig. 4). This problem will be examined more closely in a subsequent paper; but one solution might be to have two classes of sense organ, one of which included units responding only to movements of the body whereas the other group would be sensitive to externally generated displacements. But the record in Plate 3, fig. 2(*a*) shows that units which discharge rhythmically when the fish is swimming are also stimulated by external disturbances. If these are sufficiently large and frequent, they override the rhythmical discharge produced during movement (Plate 3, fig. 2*a*), but smaller stimuli evoke impulses which become superimposed on the locomotory rhythm (Plate 3, fig. 2*b*).

DISCUSSION

The function of the rhythmical discharge

The experiments described in this paper were designed to test whether lateral-line sense organs are stimulated by the locomotory movements of fishes. It has been shown that the neuromasts of swimming dogfish discharge rhythmical bursts of impulses in a pattern which depends on the form of the locomotory movements and that the stimulus for this rhythm comes from within the fish itself and is not the result of external water movements. The neuromasts could function as proprioceptors and provide data which might be useful in locomotory co-ordination, because the burst length, repetition, impulse frequency and number of impulses are all correlated with the swimming movements.

It is now recognized that many proprioceptors function in two ways: by triggering specific reflexes and by exerting a general tonic effect on the central nervous system (Lissmann, 1950). This is well illustrated by the receptors of the labyrinth, which are involved in the labyrinthine reflexes and which, by virtue of their spontaneous activity, are also responsible for muscle 'tone'. As lateral-line sense organs are related to those of the labyrinth they might be expected to act in an analogous way. However, no specific locomotory reflexes have been attributed to lateral-line stimulation, although synchronous excitation of posterior lateral-line nerve fibres evokes gulping movements in *Scyliorhinus* and re-sets the respiratory rhythm (Paul & Roberts, 1971).

In dogfish the lateral line is unlikely to provide timing cues for locomotion because the swimming movements of spinal dogfish, in which the hind-brain has been separated from the spinal cord, do not differ markedly from those of intact fish, while in other fishes no observable locomotory defects have been reported after the lateral-line nerves have been cut (Dijkgraaf, 1933; Hoagland, 1933*d*). It is more likely therefore that the lateral line plays a more subtle role in co-ordination, perhaps by exerting a tonic effect on descending spinal systems, and this kind of action will not be revealed by ablation experiments but only by electrophysiological recording made from central neurones.

It is also possible that the information about the swimming movements provided by the neuromasts is ignored by the nervous system. Certainly one possibility is that the rhythmical activity of the sense organs is suppressed by the action of efferent fibres which project from the hind-brain on to the neuromasts (Roberts & Russell, 1970).

At the moment the proper function of the efferent system is not understood, although it is known that the efferent fibres can be made to exert an inhibitory effect on the neuromasts and that the efferent neurones discharge rhythmically in bursts in swimming dogfish at the same frequency as the swimming movements (Russell & Roberts, 1971). But until the role of the efferent system has been elucidated it is not possible to say whether the hind-brain regards the rhythmical activity of the lateral-line afferents in the swimming fish as being 'noise' or as being a source of information for the co-ordination of movement.

SUMMARY

1. The activity of lateral-line sense organs was studied in swimming spinal dogfish by recording from filaments of the lateral-line nerve dissected in an anterior immobile part of the fish, the rest of the fish being free to move.

2. In a non-swimming fish most of the receptors were spontaneously active, discharging at 15–20 impulses/sec.

3. When the part of the body overlying the receptor was flexed, the impulse frequency was either enhanced or depressed, depending on the direction of movement.

4. In swimming spinal dogfish the sense organs discharged in bursts at the same frequency as the swimming rhythm.

5. The lateral-line receptors could provide information which would be useful in locomotory co-ordination, for the burst length, frequency, discharge frequency and number of impulses in the rhythmical discharge could all be correlated with the swimming movements.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Bi-directional response of a lateral-line sense organ. The records show the response of a sense organ in a stationary fish when the part of the body immediately overlying the receptor was bent to the right or to the left of the mid-line. The large unit discharged faster when the body was bent to the left and was inhibited when the body was bent to the right. In contrast, the smaller unit (marked by arrows in (b)) accelerated when the body was bent to the right and was inhibited when the body was moved to the left. The record in (c) shows the response of the large unit to a slow movement to the left.

Fig. 2. Continuous record of impulse activity in a fish which was almost stationary. At the point marked by the arrow the body was touched and the fish swam more strongly, as is shown by the transducer trace.

Fig. 3. (a) Another record of the typical rhythmical discharge recorded from neuromasts in swimming dogfish. (b) This record shows that the discharge alters if the form of the locomotory movement changes. In (a) the arrows mark the division of the discharge into two groups.
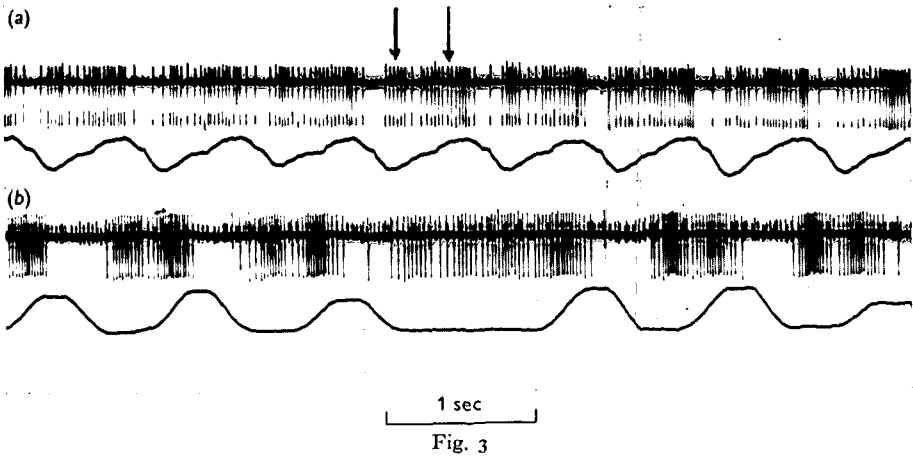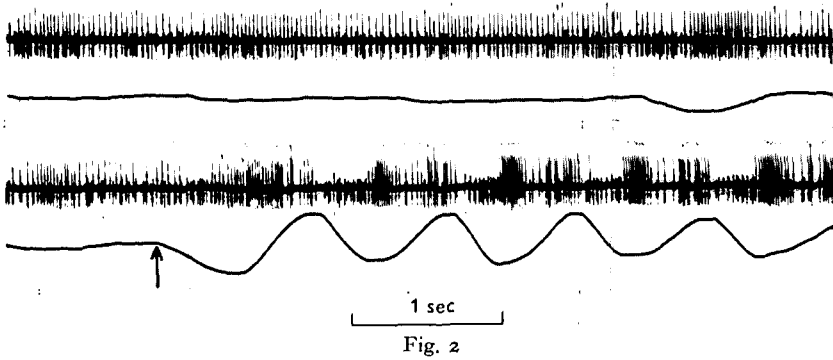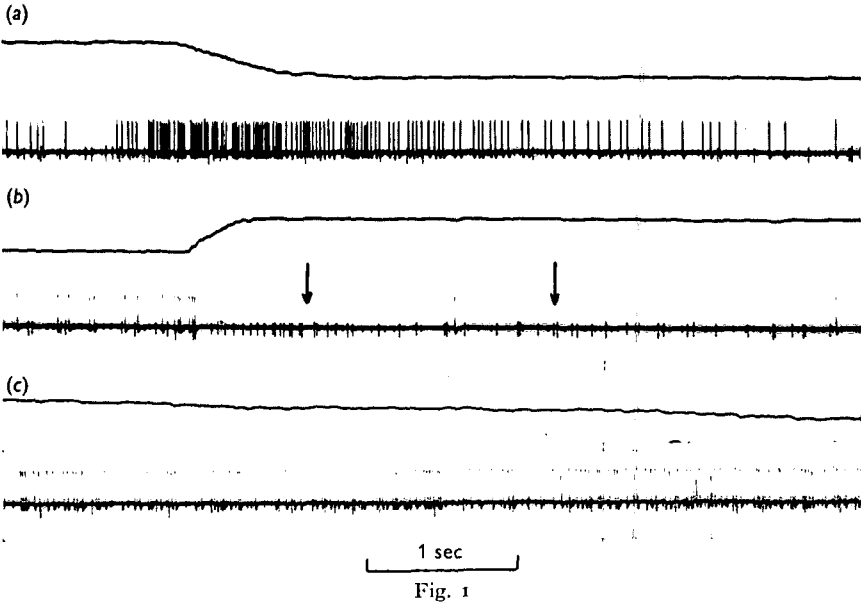
PLATE 2

Fig. 1. Records of lateral-line activity at different frequencies of body bending. In (a) the fish was swimming naturally; in (b) and (c) the body was bent by hand.

Fig. 2. Examples of unit activity in a swimming fish, with rate-meter records (top traces) to show variations in burst composition. The unit shown in (a) discharges at a steady frequency; in (b) the unit shows a division into two groups which is clearly seen in (c). The unit in (d) is unusual in beginning each burst at high impulse frequency.

PLATE 3

Fig. 1. (a) Record of rhythmical activity from a unit which is non-spontaneous when the fish is stationary. (b) Rhythmical afferent activity recorded from a fish which was 'swimming' in air. The top trace is the electromyogram recorded from the red musculature.

Fig. 2. External stimulation in a swimming dogfish. (a) Large-amplitude water movements along the body generated by to and fro motion of a rod produce bursts of afferent activity which obliterate the response to body movement. (b) Small water movements generated by a rod pulsing at 10 Hz produce afferent impulses which are superimposed on the rhythmical discharge. The frequency of stimulation is indicated on the bottom trace, which also shows the body movements.
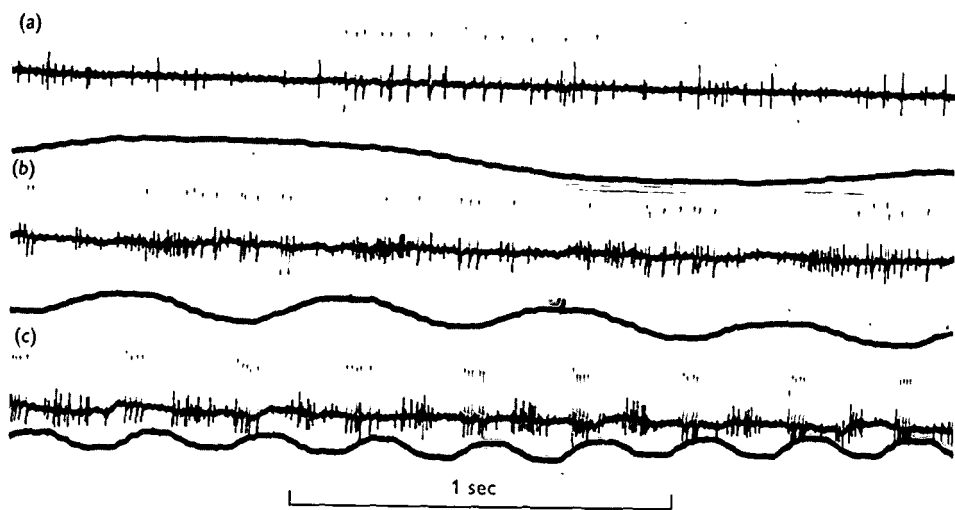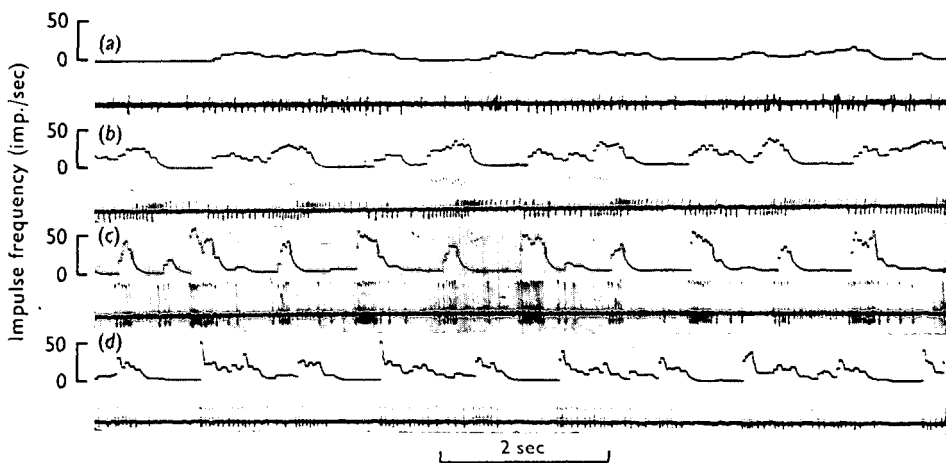
(a)

(b)

(c)

1 sec

Fig. 1

1 sec

Fig. 2

(a)

(b)

1 sec

Fig. 3

B. L. ROBERTS

(a)

(b)

(c)

1 sec

Fig. 1

Impulse frequency (imp./sec)

50

0 (a)

50 (b)

0

50 (c)

0

50 (d)

0

2 sec

Fig. 2

B. L. ROBERTS

(a)

(b)

|_____ 4 sec _____|

Fig. 1

(a)

(b)

|_____ 4 sec _____|

Fig. 2

B. L. ROBERTS