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THE ACTIVITY OF LATERAL-LINE EFFERENT NEURONES IN STATIONARY AND SWIMMING DOGFISH

BY B. L. ROBERTS AND I. J. RUSSELL*

The Laboratory of the Marine Biological Association, Plymouth and Department of Zoology, University of Cambridge

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INTRODUCTION

The hair cells of the acoustico-lateralis sensory system receive both afferent and efferent innervation. This dual innervation was first demonstrated in the case of the organ of Corti, where the efferent nerve fibres constitute the olivo-cochlear bundle (Rasmussen, 1942). An efferent pathway has also been traced along cranial nerve VIII to the vestibular system (Rasmussen & Gacek, 1958; Gacek, 1960; Rossi & Cortesina, 1963) and in the frog it has been shown that these efferent fibres originate from Purkinje cells in the auricular lobe of the cerebellum (Hillman, 1969; Llinás & Precht, 1969).

The function of the efferent system has not been established, although it is generally agreed that efferent fibres can exert an inhibitory effect on the sense organs which they innervate (Galambos, 1956; Fex, 1959; Sala, 1965; Llinás & Precht, 1969). The idea of an inhibitory function was developed from experiments in which the efferent fibres were stimulated synchronously with trains of pulses, but it is difficult to judge the significance of these results because of the lack of information about the activity patterns of efferent neurones under natural conditions. In this paper the natural pattern of efferent activity is described in the case of the lateral-line sensory system of dogfish. A preliminary report of this work has already been published (Roberts & Russell, 1970).

The lateral-line organ of fishes and amphibia is the simplest example of an acoustico-lateralis receptor; it lies on the body surface or just beneath it in a fluid-filled canal and is sensitive to 'near-field' water displacements (Harris & van Bergeijk, 1962). Electron-microscopical studies have shown that efferent synapses similar to those found at the base of hair cells in the ear (Engström & Wersäll, 1958) are also present at the base of hair cells in lateral-line organs (Hama, 1965; Flock, 1965, 1967) including those of sharks and dogfish (Hama, 1970; Roberts & Ryan, 1971). As in other acoustico-lateralis receptors, electrical stimulation of lateral-line efferent nerve fibres suppresses impulses in the afferent pathway (Katsuki, Hashimoto & Yanagisawa, 1968; Russell, 1968; Russell & Roberts, 1972).

Dogfish were chosen for this study because of the relative ease with which lateral-line activity can be monitored from a swimming preparation (Roberts, 1972).

* Present address: School of Biology, University of Sussex, Falmer, Sussex.

METHODS

Preparation. The experiments were performed on 41 dogfish, *Scyliorhinus canicula* L., which were kept in large tanks of sea water until required. These fish, which weighed between 500 and 1000 g, were anaesthetized by immersion of the head alone in a solution of 0·05% ethyl *m*-aminobenzoate methane sulfonic acid (Tricaine; Sigma Ltd.) for 10–15 min until all reflexes were abolished. The brain case was opened, the large blood vessels were cauterized and the forebrain was removed following a transection made rostral to the optic lobes. Further details of this preparation are given by Paul & Roberts (1972).

The efferent nerve fibres which innervate the lateral-line organs of the body of the fish are grouped with the sensory fibres in a special lateral-line branch of cranial nerve X. This nerve bundle was exposed on the left side of the body behind the pectoral girdle for 5–10 cm and dissected free from connective tissue. The fish was then placed in a tank of sea water with its head held firmly in a head holder (Fig. 1). The body was clamped just behind the incision and also at times near to the second dorsal fin. Sea water was passed into the mouth and over the gills at a rate of 1·0–1·5 l/min and the sea-water level was adjusted so that as much of the fish as possible was immersed. The temperature of the sea water, which ranged from 10 to 15 °C, varied little during the course of an experiment.

A number of experiments were carried out on fish in which most of the spinal cord had been destroyed to stop all movement, and in some of these a Perspex plate was placed under the fish to give additional support. In other experiments the spinal cord was left intact and the fish was able to move the unclamped posterior portion of the body, which was supported only by a thread from the base of the first dorsal fin. Such preparations did not swim steadily, however, because of the inhibiting effect of the anterior clamps, and only made violent movements in response to stimulation. The influence of the clamps was overcome in a number of preparations by the subcutaneous injection of 1 ml of 2% procaine (with adrenaline) solution beneath the clamps. After the anaesthetic had taken effect, 9 of the 12 fish prepared in this way began, when stimulated, to swim steadily in an apparently normal fashion, at tail-beat frequencies of 30–40/min. Although one preparation swam steadily for nearly 6 h, in most cases it was necessary to stimulate the fish periodically to sustain movement. The movements of the fish were monitored by taking electromyograms from the red and white muscle fibres with 0·2 mm diameter copper wire, insulated except for the tip, or with concentric needle electrodes. In a few experiments body movement was monitored by a displacement transducer coupled to the first dorsal fin.

Recording. The posterior lateral-line nerve was cut peripherally and placed over bipolar platinum recording and stimulating electrodes. Although descending efferent activity could be recorded from whole bundles, most records were obtained from thin filaments which were teased from the main bundle, after it had been de-sheathed, by fine razor-blade scalpels. It was found that the efferent fibres were easily damaged if the bundle was stretched. The fibres were moistened periodically with a saline solution (Roberts, 1972) and covered with mineral oil during the experiment. The recording arrangements were conventional and impulses were stored on magnetic tape or photographed from the oscilloscope.

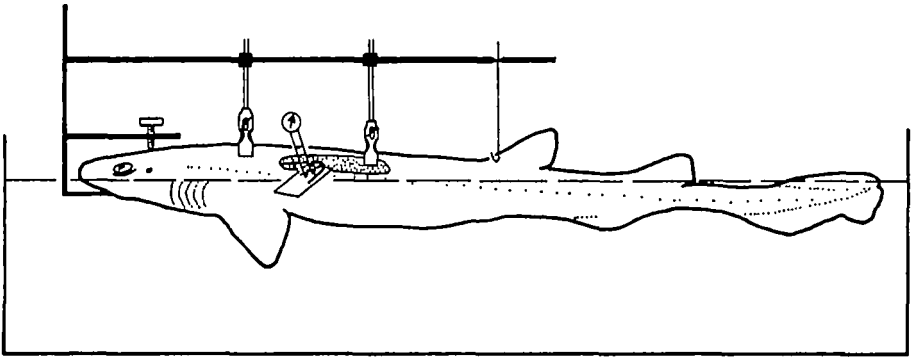

Fig. 1. Diagram of the experimental preparation for studying lateral-line efferent activity in a swimming fish. A decerebrate dogfish is clamped firmly at the head and suspended in a tank of circulating sea water. Cranial nerve X is exposed and teased into fine branches which are placed over recording electrodes.

Stimulation. Natural stimuli were provided by pipetting water at the lateral-line canals on the head and body, by scratching the skin with pointed instruments, and by tapping the head-holding frame. Repetitive transient water displacements of varying amplitude and frequency were generated by a vibrator (Goodman Ltd.) which moved a Perspex rod, terminating in a disk of area 50 mm^2, through distances of 0·1–0·5 mm. The rod was placed at variable distances from the lateral-line canals.

Electrical stimuli to the lateral-line nerve bundle were 0·05 msec pulses delivered at varying frequencies. The stimulus thresholds were established by monitoring the afferent volleys.

RESULTS

Lateral-line efferent activity in stationary dogfish

Descending impulses, conducted at 12 m/sec (14 °C) were recorded from fibres in the posterior lateral-line nerve bundle in all preparations, but only when the animal was stimulated in some way. Simple sectioning experiments showed that these fibres originated from cell bodies which were located in the hind-brain. The absence of spontaneous efferent activity is in contrast to the steady discharge of impulses (at about 18 imp./sec) present in many afferent nerve fibres even when the fish is unstimulated (Roberts, 1972). Immediately after dissection of the nerve bundle a few efferent fibres were found to be active for a short while, discharging initially at a high rate but rapidly dropping to zero. In a few cases, and again usually soon after dissection, efferent responses were recorded in time with gill movements. Continuous activity was recorded from all the efferent fibres in a number of fish in which the hind-brain was damaged, or in which a blood clot was present under the choroid plexus. Spontaneous activity of the efferent neurones ceased when this clot was removed.

Stimulation of the efferent neurones

Efferent discharges could be recorded from the posterior lateral-line nerve when the fish was mechanically stimulated, e.g. by stroking the head. This stimulus is complex and involves a variety of modalities – tactile, vestibular and lateral line. The efferent

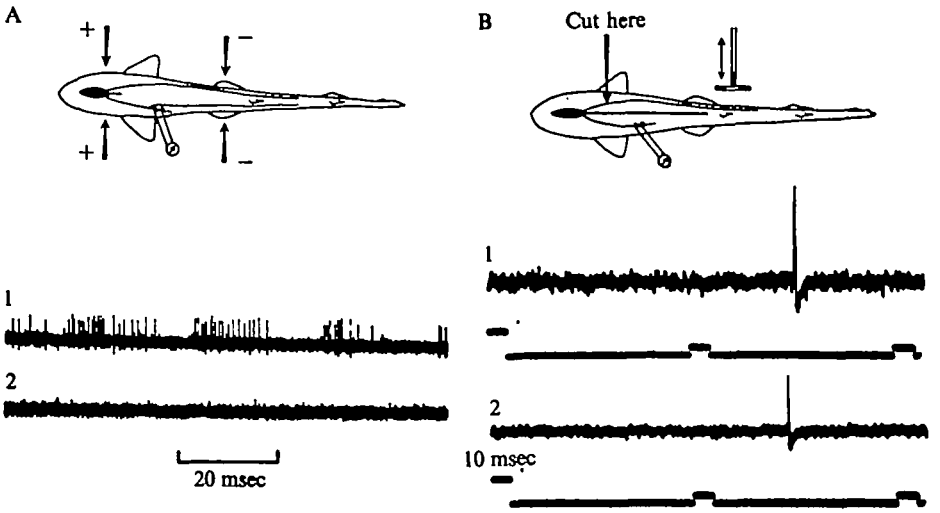

Fig. 2. The absence of efferent activity in response to lateral-line stimulation. The diagrams show dorsal views of the experimental preparations.

(A) The upper record (A 1) shows a recording taken from efferent fibres in the left lateral-line nerve while the head was stroked (+ stimulus). The lower record (A 2) is recorded from the same fibres while the body was stroked (− stimulus).

(B) The upper record (B 1) shows an efferent response obtained in the lateral-line nerve when a single water displacement was made by a disk moved on the right side near to the lateral-line. The lower record (B 2) shows that this response persisted even after the right lateral-line nerve had been cut.

response was monitored as each type of stimulus was presented in turn so as to see which was the most effective.

Lateral-line stimulation. Efferent nerve activity was recorded while the lateral-line receptors on the head and body were stimulated by water movements produced by a Pasteur pipette or by a disk pulsating close to the fish.

The records provided in Fig. 2A were taken from the efferent fibres in the left lateral-line nerve, in which the majority of afferent fibres were left intact. In this preparation, in which most of the spinal cord had been destroyed, vigorous water jets on to the lateral line, large to and fro water movements and stroking movements along the denervated portion of the body failed to excite the efferent fibres. But in contrast, stroking movements, although not water jets, anterior to the pithed region, where both tactile and lateral-line receptors were still innervated, evoked efferent activity (Fig. 2A 1,). Water jets aimed at the right lateral line also failed to excite the efferent fibres, as did water movements about the head of the type known to stimulate strongly the anterior lateral-line sense organs (Paul & Roberts, 1972).

The records in Fig. 2B show the efferent response recorded in the left lateral-line nerve in response to a water displacement which would be expected to stimulate the lateral-line organs. This response, however, was not being detected by the lateral-line sense organs for it persisted even after the right lateral-line nerve had been sectioned (Fig. 2B, 2).

It appeared from these experiments that lateral-line stimulation was not followed by activity in the efferent system.

Table 1. *Effect of cutting selected cranial nerves on efferent nerve activity*

(The table shows whether, after selected cranial nerves had been cut, a certain type of stimulus (defined as stimulating either tactile, lateral-line or vestibular sense organs) led to activity in the efferent fibres in the posterior lateral-line nerve.)

	Stimulus						
	Touch				Lateral-line	Vestibular	
Nerve cut	Eye	Gill	Back	Snout	Pipette under eye	Tap to head bar	Head up and down
None (Control)	+	+	+	+	+	+	+
Left superficial ophthalamic V	+	+	+	−	+	+	+
Right superficial ophthalamic V	+	+	+	−	+	+	+
Left VIII	+	+	+	−	+	+	+
Right VIII	+	+	+	−	+	−	−
Spinal cord	+	+	−	−	+	−	−
Left ophthalamic VII	+	+	−	−	+	−	−
Left maxillary V and buccal VII	−	−	−	−	+	−	−
Right maxillary V and buccal VII	−	−	−	−	−	−	−

Tactile stimulation. In contrast, the efferent neurones were easily activated by tactile stimulation. The most sensitive areas were on the head, where even a gentle touch was followed by a brief efferent discharge. Stimulation on the body was less effective, and the efferent neurones were normally only excited by stimuli which were sufficiently strong to excite the animal to move vigorously, when the efferent discharge would also be vigorous.

Vestibular stimulation. The efferent system was easily activated when the head supports were tapped, when the head-holding frame was rocked, or when other vestibular stimulation was presented. But airborne sound of moderate intensities was ineffective.

Chemical stimulation. Considerable activity was recorded from the lateral-line efferent neurones when small volumes of 4 M-NaCl or 3 M-KCl were pipetted through the spiracle into the buccal cavity. These stimuli were accompanied by vigorous gill contractions and forcible exhalations of water. In contrast, similar quantities of sea water applied through the spiracle had no effect.

Visual stimulation. The efferent neurones were not excited by visual stimuli. When light flashes 300 msec long were delivered at 1 Hz from a 6 V lamp bulb which was focused on to the dark-adapted eye to stimulate an area of retina equivalent to an external field subtending several degrees at the eye, no efferent response was observed.

The effects of cutting selected cranial nerves

The experiments described so far indicated that tactile stimulation was more effective in eliciting efferent responses than was lateral-line stimulation. Further evidence on this point was obtained from experiments in which the efferent response to various stimuli was monitored after certain cranial nerves had been sectioned, for the

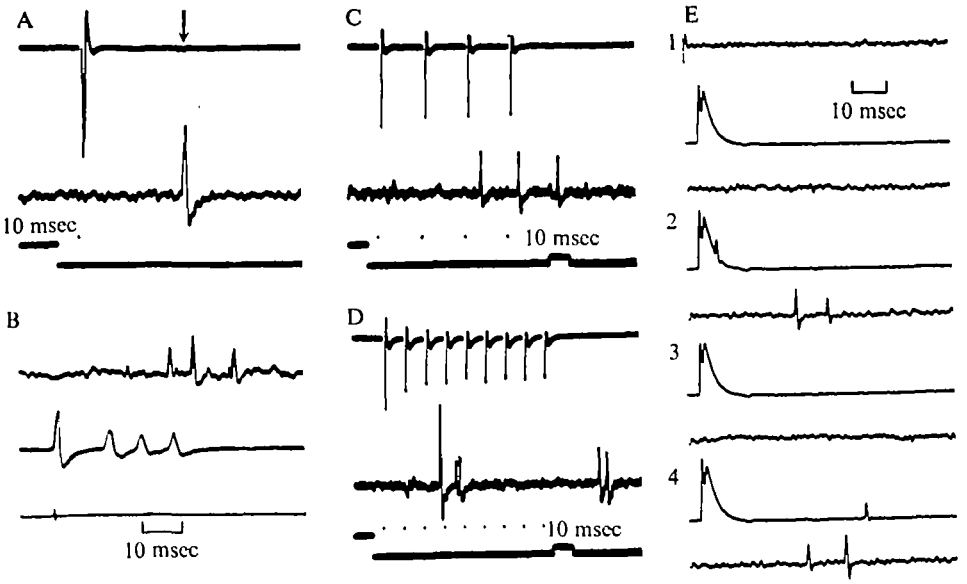

Fig. 3. Reflex efferent activity in response to electrical stimulation of cranial nerves.

(A) Stimulation of the posterior lateral-line nerve. The top trace shows the afferent compound potential and the very small ipsilateral efferent response (arrow) recorded from the whole nerve trunk on the right side in response to a stimulus to this nerve (marked on the bottom trace). The second trace is an efferent unit recorded from a single fibre on the left side.

(B) The middle trace is the compound afferent potential and succeeding efferent discharges recorded from the superficial ophthalamic branch of nerve VII in response to a stimulus. The top trace is the efferent response recorded from a fine filament.

(C, D) Stimulation of the posterior lateral-line nerve. The top trace in both records shows compound afferent potentials recorded from the whole nerve in response to an applied stimulus train; the middle traces show efferent activity in a filament of the contralateral lateral-line nerve. In (C) the nerve was stimulated at 50 Hz; in (D) at 100 Hz.

(E) Habituation of efferent activity in response to applied stimulation of nerve VII. The upper trace in 1 shows the stimulus; the second trace shows the compound afferent response recorded from nerve VII in response to an applied stimulus; the third trace is the record from an efferent fibre in the posterior lateral-line nerve. The reflex response had become habituated. In records 2, 3 and 4 the top trace is omitted. In records 2 and 4 the head of the fish was stroked as nerve VII was stimulated.

afferent nerve fibres from tactile and lateral-line organs pass to the brain in different cranial nerves (Norris & Hughes, 1920). The afferent fibres for the lateral-line system are carried in branches of cranial nerves VII, IX and X, whereas nerve V conveys no lateral-line information, although sensory nerves of other modalities are carried in it.

The results of the experiments in which cranial nerves V, VII and VIII were cut in turn are summarized in Table 1, which shows which stimuli were ineffective after each nerve had been sectioned. The most significant result was the loss of response to touch on the dorsal surface of the snout after the superficial ophthalamic branch of nerve V had been cut. This nerve carries no lateral-line information from the snout, for the lateral-line canals are innervated by the superficial branch of nerve VII. Although this nerve bundle was still intact all stimuli to the snout failed to excite the efferent system.

Electrical excitation of selected cranial nerves

The failure of lateral-line stimulation to evoke reflex activity in the efferent fibres was at first surprising and so we examined whether electrical synchronous stimulation of lateral-line sensory fibres was also ineffective. Efferent impulses were recorded from thin filaments of the posterior lateral-line nerve while branches of certain sensory cranial nerves were stimulated. The following branches were stimulated: superficial ophthalamic branches of nerves V and VII, nerve VIII, and the posterior lateral-line nerve (X) on the right side and the part of this nerve on the left side not used for efferent recording. Efferent discharges could be recorded from the left posterior lateral-line nerve, with a latency of 20–40 msec, when stimuli were above threshold for the sensory fibres in all these nerves. Some records of typical responses are provided in Fig. 3, which shows, for example, that stimulation of the posterior lateral-line nerve at regular intervals was accompanied by discharges of the posterior lateral-line efferent nerves (A). In a fresh preparation the efferent system followed stimulation with single shocks at frequencies up to 4 Hz, but responses to shocks delivered quicker than this rapidly waned. Habituation was obtained at even lower frequencies in other preparations and particularly as the condition of each preparation deteriorated. After the response had become habituated, touch to the head led to the reappearance of the response to lateral-line nerve stimulation (dishabituation) (Fig. 3 E).

As might be expected from these results, brief trains of stimulating pulses at frequencies of 50 Hz and above were not followed absolutely even when first presented (Fig. 3 C, D). Essentially similar responses were obtained whichever cranial nerve was stimulated, but in the one experiment in which a spinal nerve was stimulated no efferent response could be obtained.

Lateral-line efferent activity in moving dogfish

The results obtained from experiments with natural stimulation gave a clear impression that the type of stimulus which was successful in evoking efferent activity was followed by some movement of the fish. These movements depend on two muscle systems, which are brought into action at different times, according to the type of movement. Steady rhythmical movements are thought to involve only the peripheral red muscle system of the body whereas briefer, larger, unsustained movements (e.g. escape movements) utilize the white muscle fibres of the twitch type which make up the greater portion of the myotomes (Bone, 1966). It is likely that these two systems involve distinct groups of motoneurones which are regulated by separate central mechanisms (Roberts, 1969*a*). We have recorded efferent activity from the posterior lateral-line nerve during both types of movement.

Vigorous brief movements of the fish are a frequent response to strong tactile stimulation and are immediately preceded by and accompanied by activity of the efferent neurones. In fact, only stimulation to the body which was strong enough to evoke movements of this kind was followed by efferent activity. A few efferent impulses were recorded, however, when the head was gently stimulated even though there was no obvious movement of the body. But even in this case it is likely that some motor activity was involved because this stimulus to an intact stationary dogfish is followed by a brisk lateral movement of the head, a response which would not have

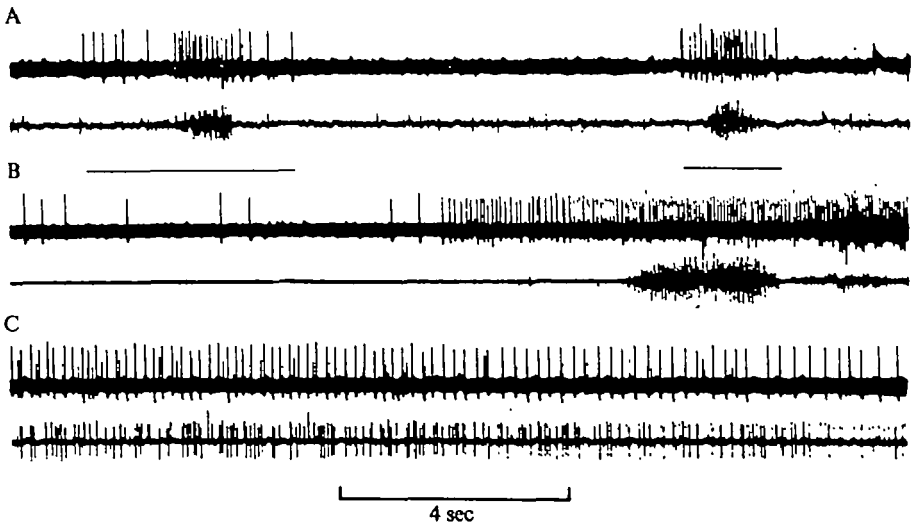

Fig. 4. Efferent activity accompanying body movement. In all three records the top trace is recorded from efferent fibres in the left posterior lateral-line nerve and the bottom trace is the electromyogram recorded from white muscle fibres in a segment close to the first dorsal fin.

(A) Efferent responses and motor activity recorded in response to tactile stimulation to the body (stimulus duration marked by lines).

(B) Vigorous continuous tactile stimulation to the body is accompanied by large movements and efferent discharges of high frequency.

(C) The efferent discharge is sustained if the fibres contract tonically.

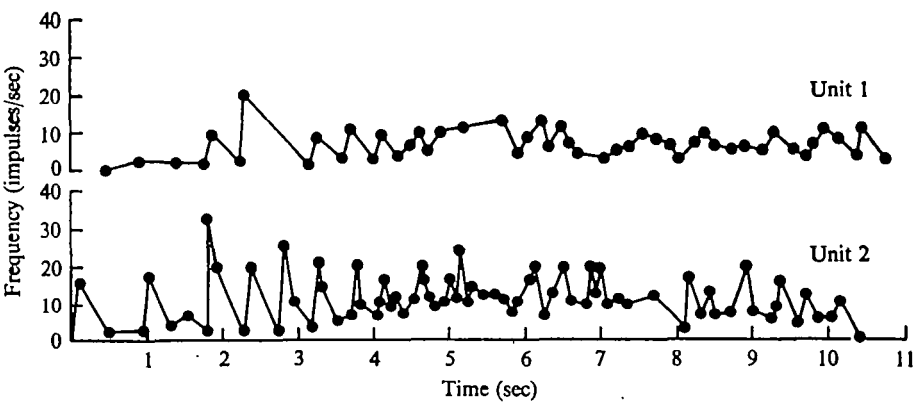

Fig. 5. The instantaneous frequency of impulses recorded from two efferent units in response to the same tactile stimulus.

been obvious in our preparations in which all head movements were prevented by the head-holder.

An example of the efferent discharge produced during vigorous body movement is shown in Fig. 4, in which lateral-line efferent activity is compared with the electromyogram taken from the white musculature of a body myotome situated near to the first dorsal fin. The movement, evoked by stroking the body, was accompanied by a discharge of the efferent fibres, which increased in frequency as the muscular wave

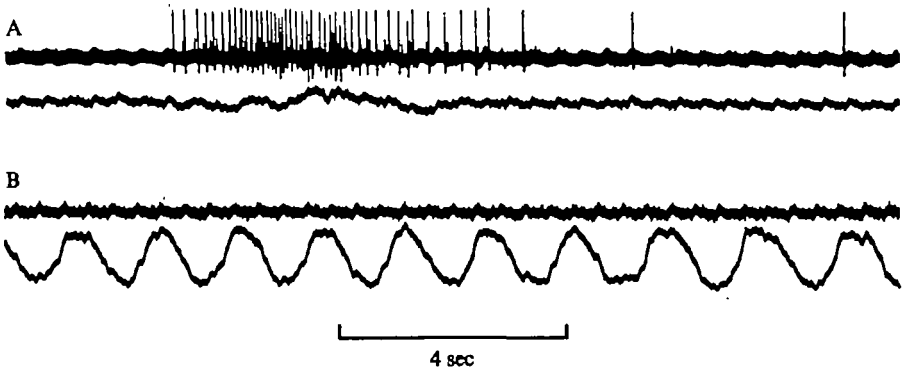

Fig. 6. In A and B the top trace is recorded from efferent nerve fibres and the bottom trace is body movement registered by a transducer fixed to the base of the first dorsal fin. (A) When the fish moves in response to a stimulus the efferent fibres are also active. (B) When the body is moved by the observer the efferent fibres are inactive.

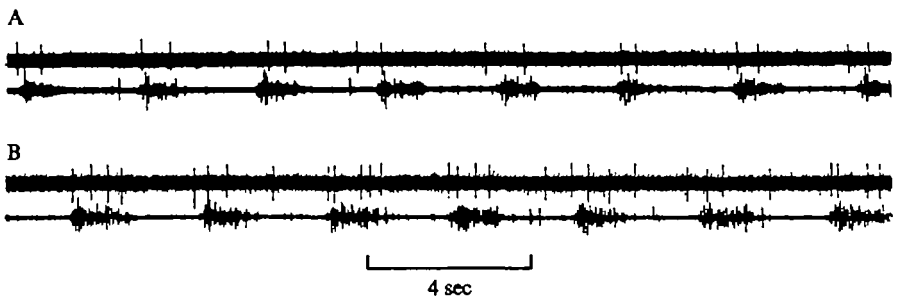

Fig. 7. Rhythmical activity of the efferent system accompanying steady swimming movements recorded from two fish. In both A and B the top trace is recorded from an efferent fibre and the bottom trace is the electromyogram recorded from a segment close to the first dorsal fin.

passed along the body; an enhanced after-discharge of the efferent neurones was never observed to follow white muscle activity. Although all the efferent neurones showed similar behaviour to this stimulus they differed in detail and in discharge frequency (Fig. 5). Repetitive movements and efferent discharges were obtained if the stimulus was sufficiently noxious and there was a general correlation between the frequency of efferent activity and the amplitude of movement, for smaller movements were accompanied by efferent discharges of lower frequency than were larger movements (Fig. 4B). The efferent impulses discharged steadily and did not become fatigued during sustained contractions of the white musculature (Fig. 4C). The movement of the body alone was not sufficient to stimulate the efferent system because passive body movements, which are known to drive proprioceptive spinal circuits (Roberts, 1969*b*), were not accompanied by efferent activity (Fig. 6B); some higher motor centre is therefore essential.

Rhythmical swimming movements involving the action of the red musculature were frequently observed in preparations in which procaine had been injected under the body clamps. The efferent neurones were spontaneously active during these movements, discharging a few impulses at low frequency (5–10 imp/sec). Sometimes these impulses appeared to be unrelated in time to the swimming rhythm but in other

examples clear rhythmical efferent activity, at the swimming frequency, was seen (Fig. 7). The bursts comprised few impulses (1–3) discharging at low frequencies (5–10 imp/sec). At slow swimming speeds the efferent neurones discharged for longer periods but with a frequency of discharge similar to that occurring at faster swimming speeds. Because of the short inter-burst silent period, the efferent rhythm was less obvious than in faster-moving fish.

The efferent neurones stopped discharging rhythmically in time with locomotion after the spinal cord had been transected at a high level even though the fish continued to swim. In these preparations the lateral-line organs would have been stimulated by the swimming movements (Roberts, 1972), and the information about the swimming movements would reach the brain on the right side of the body where the lateral-line nerve was intact; nevertheless the efferent neurones remained inactive. The rhythmical pattern of the efferent neurones recorded from the swimming fish clearly depends, therefore, on the connexion of the medulla with the spinal cord.

DISCUSSION

The main conclusion from these experiments is that the activity of efferent neurones of the lateral-line system is not linked specifically to any particular type of stimulus but to the movements which the dogfish makes either in response to various stimuli or spontaneously. Unlike the sense organs which they innervate the efferent neurones are not active in an unstimulated stationary dogfish and cannot therefore maintain any tonic influence on the hair cells. Stimulation of the lateral-line sense organs, even if sustained, is not followed by efferent activity although efferent discharges follow tactile, vestibular and chemical stimuli if these elicit movements from the fish.

While natural stimulation of lateral-line organs shows that there is normally no direct action of lateral-line stimuli on efferent neurones, electrical stimulation of the posterior lateral-line nerve reflexly excites the efferent neurones. This indicates the existence of a connexion between afferent and efferent neurones which has been unmasked by synchronous volleys in the lateral-line nerve. But we believe that this connexion has no natural significance because electrical excitation of other cranial nerves, including those containing no lateral-line fibres, also reflexly drives the efferent neurones. In fact, lateral-line efferent neurones are more readily excited by electrical stimulation of some cranial nerves, e.g. V and VIII, than of others, e.g. X. These strongly excitatory nerves innervate sense organs (tactile and vestibular) which when naturally stimulated cause reflex movements and elicit impulses from lateral-line efferent neurones.

It is probable that the efferent neurones are indirectly connected to sensory fibres via motor centres in the hind-brain which receive a variety of inputs. Until more is known about the central locations of the efferent neurones and about the nature and position of the neurones involved in the control of movement little more can be said about the central pathways, but it is evident from the absence of any clear-cut effect of lateral-line stimulation that the efferent system is not part of a regulatory closed feedback loop to the lateral-line sense organs. This conclusion is contrary to that of Hashimoto, Katsuki & Yanagisawa (1970), who reported that the efferent system of the lateral-line organs of the eel was excited by stimulation of the sense organs. They

concluded that efferent discharges evoked by probing the body wall were obtained because the lateral lines were being stimulated, but we suggest that their results depended on the stimulation of tactile endings. Certainly responses of the kind they reported are abolished in dogfish after the spinal cord has been sectioned and the efferent system has thereby been isolated from tactile stimulation (Fig. 2). The failure of lateral-line stimulation to excite the efferent neurones is understandable because a dogfish does not respond reflexly to lateral-line excitation by moving, even though it might subsequently decide to move on the basis of the information derived from lateral-line activity. However, noxious and tactile stimulation are followed reflexly by body movements and so appear to be directly coupled to the efferent system.

The auditory efferent neurones are believed to act principally as a feedback system (Fex, 1962, 1965) but technical difficulties have prevented an examination of the natural activity patterns of these neurones and it is not known to what extent they are influenced by extra-auditory activity. But in the lateral-line system (Schmidt, 1965; Görner, 1967; Russell, 1971) and in the vestibular system (Schmidt, 1963; Llinás & Precht, 1969; Klinke & Schmidt, 1970; Precht, Llinás & Clarke, 1971), including the mammalian vestibular system (Dichgans, Wist & Schmidt, 1970), the efferent neurones have been shown to receive multimodal input.

A correlation has been reported between sudden movement and efferent activity to the lateral-line of *Xenopus* (Görner, 1967; Russell, 1971) and to the vestibule of goldfish (Klinke & Schmidt, 1970). In our experiments we have now shown that regular active movements of the fish, similar to normal swimming movements, are also accompanied by regular bursts of efferent activity. Thus the role of the efferent system is obviously related to the behaviour of lateral-line organs during movement, because it is only at these times that the efferent neurones are active. Locomotory movements are a source of prolonged and sometimes excessive stimulation to the lateral-line organs, for recordings made from swimming spinal dogfish (in which the efferent system is inoperative) have shown that the afferent fibres discharge bursts of impulses at high frequency in time with locomotion and that during violent movements many of the afferent fibres discharge concurrently (Roberts, 1972). Virtually continuous high-frequency stimulation of the sense organ might lead to fatigue and to a period of post-stimulatory depression.

The lateral-line efferent system might act to stop short-term fatigue occurring in the receptors, by limiting the flow of impulses generated at the afferent synapse so that the lateral-line system would be fully responsive immediately any movement stopped (Russell, 1971). The action of the efferent system might also produce a change in the range of sensitivity of the sense organs so that they would be matched to the amplitudes of water displacements generated by vigorous swimming movements, for there is a correlation between the amplitude of movement and the frequency of the efferent discharge. In either case we would expect, as has been reported, that the sensitivity of the sense organs would decrease while the animal was moving (Schwartz, 1967; Russell, 1969).

The lateral-line efferent neurones of dogfish and *Xenopus* (Russell, 1971) are not spontaneously active, unlike other acoustico-lateralis efferent neurones, and cannot exert a tonic influence on the hair cells. Furthermore, the neurones all become active together and exert a similar influence over the entire lateral-line system. In this they

differ from the efferent neurones of the cochlea, which have individual response characteristics (Fex, 1962, 1965; Klinke, Boerger & Gruber, 1969) and from vestibular efferent neurones which appear to act in a bilaterally antagonistic manner (Sala, 1965; Klinke & Schmidt, 1970). Because of the overall action of lateral-line efferent neurones it is unlikely that they function in information processing, as has been suggested for the auditory efferent neurones (Klinke *et al.* 1969; Nieder & Nieder, 1970), nor is it likely that they enhance the directional properties of the hair cells, as has been suggested for the vestibular efferent system (Precht *et al.* 1971). This is because lateral-line efferent neurones in *Xenopus* innervate hair cells in the same and different organs without regard for their directional sensitivity (Russell, 1971) and it is probable that there is a similar innervation pattern in dogfish.

Many of the functions which have been suggested for efferent neurones in acousticolateralis systems could be carried out centrally using simple neural circuitry, but a protective action of the kind we suggest could not be performed centrally, as the synapses to be protected from overload are located at the periphery.

SUMMARY

1. The activity of efferent neurones innervating lateral-line organs on the body of dogfish was followed by recording from filaments of cranial nerve X in 41 decerebrate preparations.

2. The efferent nerves were not spontaneously active.

3. Tactile stimulation to the head and body, vestibular stimulation and noxious chemical stimulation were followed by activity of the efferent nerves.

4. In contrast, natural stimulation of lateral-line organs (water jets) did not reflexly evoke discharges from the efferent fibres.

5. Reflex efferent responses were still obtained to mechanical stimulation even after the lateral-line organs had been denervated.

6. Electrical stimulation of cranial nerves innervating lateral-lines organs was followed by reflex activity of the efferent fibres. But similar stimuli applied to other cranial nerves were equally effective in exciting the efferent system.

7. Vigorous movements of the fish, involving the white musculature, were preceded and accompanied by activity of the efferent fibres which persisted as long as the white muscle fibres were contracting.

8. Rhythmical swimming movements were accompanied by a few impulses in the efferent fibres grouped in bursts at the same frequency as the swimming movements.

9. It is concluded that the efferent neurones cannot contribute to a feedback regulatory system because they are not excited by natural stimulation of the lateral-line sense organs. The close correlation found between efferent activity and body movement suggests that the efferent system might operate in a protective manner to prevent the sense organs from being over-stimulated when the fish makes vigorous movements.

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REFERENCES

BONE, Q. (1966). On the function of the two types of myotomal muscle fibre in elasmobranch fish. *J. mar. biol. Ass. U.K.* **46**, 321–49.

DICHGANS, J., WIST, E. R. & SCHMIDT, C. L. (1970). Modulation of spontaneous activity of neurons in the vestibular nerve by oculomotor impulses in the rabbit. *Pflügers Arch. ges. Physiol.* **318**, R154–5.

ENGSTRÖM, H. & WERSÄLL, J. (1958). The ultrastructural organization of the organ of Corti and the vestibular sensory epithelia. *Expl Cell. Res.* **5**, 460–92.

FEX, J. (1959). Augmentation of cochlear microphonics by stimulation of efferent fibres to the cochlea. *Acta oto-lar.* (Suppl.) **50**, 540–1.

FEX, J. (1962). Auditory activity in centrifugal and centripetal cochlear fibres in the cat. *Acta physiol. scand.* (Suppl.) **189**, 1–68.

FEX, J. (1965). Auditory activity in uncrossed centrifugal cochlear fibres in cat. A study of a feedback system: II. *Acta physiol. scand.* **64**, 43–57.

FLOCK, A. (1965). Electron microscopic and electrophysiological studies on the lateral-line canal organ. *Acta oto-lar.* (Suppl.) **199**, 1–90.

FLOCK, A. (1967). Ultrastructure and function of the lateral-line organs. In *Lateral Line Detectors* (ed. P. H. Cahn), pp. 163–97. Bloomington: Indiana University Press.

GACEK, R. R. (1960). Efferent component of the vestibular nerve. In *Neural Mechanisms of the Auditory and Vestibular Systems*, ed. G. L. Rasmussen and W. F. Windle. Illinois: Thomas Springfield.

GALAMBOS, R. (1956). Suppression of the auditory nerve activity by stimulation of efferent fibres to the cochlea. *J. Neurophysiol.* **19**, 424–37.

GÖRNER, P. (1967). Independence of afferent activity from efferent activity in the lateral-line organs of *Xenopus laevis*. In *Lateral Line Detectors* (ed. P. H. Cahn), pp. 199–216. Bloomington: Indiana University Press.

HAMA, K. (1965). A study of the fine structure of the lateral-line organ of the Japanese sea eel *Lycozymba nystromi*. *J. Cell Biol.* **24**, 193–210.

HAMA, K. (1970). In Katsuki, Y., Hashimoto, T. & Yanagisawa, K. (1970). The Lateral line organ of shark as chemoreceptor. *Advan. in Biophys.* Vol. 1. pp. 1–51.

HARRIS, G. G. & VAN BERGEIJK, W. A. (1962). Evidence that the lateral-line organ responds to near-field displacements of sound sources in water. *J. acoust. Soc. Am.* **34**, 1831–41.

HASHIMOTO, T., KATSUKI, Y. & YANAGISAWA, K. (1970). Efferent system of lateral-line organ of fish. *Comp. Biochem. Physiol.* **33**, 405–21.

HILLMAN, D. E. (1969). Light and electron microscopical study of the relationships between the cerebellum and the vestibular organ of the frog. *Expl Brain Res.* **9**, 1–15.

KATSUKI, Y., HASHIMOTO, T. & YANAGISAWA, K. (1968). Information processing in fish lateral-line sense organs. *Science, N.Y.* **160**, 439.

KLINKE, R., BOERGER, G. & GRUBER, J. (1969). Studies on the functional significance of efferent innervation in the auditory system: afferent neuronal activity as influenced by contralaterally applied sound. *Pflügers Arch ges. Physiol.* **306**, 165–75.

KLINKE, R. & SCHMIDT, C. L. (1970). Efferent influence on the vestibular organ during active movements of the body. *Pflügers Arch ges. Physiol.* **318**, 333–52.

LLINÁS, R. & PRECHT, W. (1969). The inhibitory vestibular efferent system and its relations to the cerebellum in the frog. *Expl Brain Res.* **9**, 16–29.

NIEDER, P. & NIEDER, I. (1970). Stimulation of efferent olivocochlear bundle causes release from low level masking. *Nature, Lond.* **227**, 184–5.

NORRIS, H. W. & HUGHES, S. P. (1920). The cranial, occipital and anterior spinal nerves of the dogfish, *Squalus acanthias*. *J. comp. Neurol.* **31**, 293–404.

PAUL, D. H. & ROBERTS, B. L. (1972). Activity in the lateral-line lobe of the dogfish hind brain in response to afferent inputs from the lateral-line nerves. (In the Press.)

PRECHT, W., LLINÁS, R. & CLARKE, M. (1971). Physiological responses of frog vestibular fibres to horizontal angular rotation. *Expl Brain Res.* **13**, 378–407.

RASMUSSEN, G. L. (1942). An efferent cochlear bundle. *Anat. Rec.* **82**, 441.

RASMUSSEN, G. L. & GACEK, R. R. (1958). Concerning the question of an efferent fiber component of the vestibular nerve of the cat. *Anat. Rec.* **130**, 361.

ROBERTS, B. L. (1969*a*). Spontaneous rhythms in the motoneurones of spinal dogfish (*Scyliorhinus canicula*). *J. mar. biol. Ass. U.K.* **49**, 33–49.

ROBERTS, B. L. (1969*b*). The co-ordination of the rhythmical fin movements of dogfish. *J. mar. biol. Ass. U.K.* **49**, 357–78.

ROBERTS, B. L. (1972). Activity of lateral-line sense organs in swimming dogfish. *J. exp. Biol.* **56**, 105–18.

ROBERTS, B. L. & RUSSELL, I. J. (1970). Efferent activity in the lateral-line nerve of dogfish. *J. Physiol.* **208**, 37*P*.

ROBERTS, B. L. & RYAN, K. P. (1971). The fine structure of the lateral-line sense organs of dogfish. *Proc. R. Soc.* B **179**, 157–69.

ROSSI, G. & CORTESINA, G. (1963). Research on the efferent innervation of the inner ear. *J. Lar. Otol.* **77**, 202.

RUSSELL, I. J. (1968). Influence of efferent fibres on a receptor. *Nature, Lond.* **219**, 177–8.

RUSSELL, I. J. (1971). The role of efferent fibres in the lateral-line system of *Xenopus laevis*. *J. exp. Biol.* **54**, 621–41.

RUSSELL, I. J. & ROBERTS, B. L. (1972). Inhibition of spontaneous lateral-line activity by efferent nerve stimulation. *J. exp. Biol.* **57**, 77–82.

SALA, O. (1965). The efferent vestibular system. *Acta oto-lar.* (Suppl.) **197**, 4–34.

SCHMIDT, R. S. (1963). Frog labyrinthine efferent impulses. *Acta oto-lar.* **56**, 51–64.

SCHMIDT, R. S. (1965). Amphibian acoustico-lateralis efferents. *J. cell. comp. Physiol.* **65**, 155–62.

SCHWARTZ, E. (1967). Analysis of surface wave perceptions in some teleosts. In *Lateral Line Detectors* (ed. P. H. Cahn), pp. 123–34. Bloomington: Indiana University Press