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THE POST-SYNAPTIC ACTION OF EFFERENT FIBRES IN THE LATERAL LINE ORGAN OF THE BURBOT *LOTA LOTA*

BY ÅKE FLOCK AND IAN J. RUSSELL*

From the King Gustav V Research Institute, S – 104 01 Stockholm 60, Sweden, and the Department of Otolaryngology, Karolinska sjukhuset, S – 104 01 Stockholm 60, Sweden

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SUMMARY

1. The post-synaptic action of efferent fibres on lateral line organs in the burbot was investigated with extracellular electrodes.

2. Selective excitation of efferent fibres or stimulation of the lateral line nerve causes a negative efferent potential in the epithelium, an increase in the microphonic potential, and inhibition of afferent nerve impulses.

3. Stimulation of the lateral line nerve causes antidromic impulses in the afferent fibres in addition to exciting the efferent fibres. However, stimulation of the lateral line nerve has no post-synaptic influence on lateral line organs when the efferent synapses are selectively blocked by gallamine.

4. The influence of efferent stimulation on the microphonic potential is greater at large amplitudes of mechanical stimulation than at low.

5. The similarities between the effects of efferent stimulation in the lateral line organ and in the cochlea suggest similar synaptic mechanisms.

INTRODUCTION

The sensory hair cells of the cochlea, vestibular apparatus and lateral line organs receive efferent and afferent nerve fibres which make synaptic contact with the hair cells at their base (Engström, 1958; Wersäll, 1960; Hama, 1962; Flock, 1965). In all cases where their action has been demonstrated, the efferent synapses have been found to be inhibitory. Stimulation of the crossed olivocochlear bundle, whose fibres terminate as efferent synapses on outer hair cells, and stimulation of the efferent systems of lateral line organs and the vestibular apparatus, causes inhibition of impulse activity in the afferent nerve fibres (Galambos, 1956; Fex, 1962; Russell, 1968; Llinás & Precht, 1969; Klinke & Schmidt, 1970).

* Neurobiology and Ethology Group, School of Biology, University of Sussex.

In the cochlea, stimulation of the crossed olivocochlear bundle causes a slow d.c. change in the endocochlear potential (Fex, 1967*a*). This change is negative when recorded above the apical surface of the hair cells and positive when recorded below the hair cells. In addition, stimulation of the crossed olivocochlear bundle causes an increase in the cochlear microphonic potential (Fex, 1962). These potential changes are believed to be a direct result of the post-synaptic action of the efferent fibres on the hair cells. Fex (1967*a*) found that stimulation of the uncrossed olivocochlear bundle, whose fibres do not terminate on hair cells but on the afferent nerve terminals of inner hair cells, does not cause changes in the endocochlear and microphonic potentials.

If the potential changes which Fex observed are a direct consequence of the post-synaptic action of efferent fibres on hair cells, then similar potential changes should be observed in the related vestibular apparatus and lateral line organs on stimulation of the efferent system. This paper is concerned with the potential changes produced by stimulation of the efferent innervation of lateral line organs in the fresh water cod, the burbot *Lota lota*.

METHODS

Forty specimens of the burbot *Lota lota* weighing 400–1000 g were used. They were anaesthetized in a 0·25% solution of Tricaine methane sulphonate (Sandoz), the brain was exposed and the forebrain was destroyed by cautery. The spinal cord was transected posterior to the medulla and destroyed by pithing the entire length. In all cases the blood supply to the lateral line canal organs remained in good condition for several hours provided the fish were adequately respired.

After exposure of the brain the fish were removed to a Perspex recording tank where they were held by head and body clamps and respired by perfusing tap water over their gills at 1·5 l./min. and at 12° C. Room temperature was 20° C. Canal organs in the supratemporal and supraorbital canals were revealed by removing the overlying skin and bone bridge. The supraophthalmic branch of the 7th nerve which supplies the organs in the supraorbital canal is easily accessible inside the brain case and requires little dissection (Jakubowski, 1967). Peripheral branches of the anterior and posterior lateral line nerve which supply canal organs in the supratemporal canal and body canal, lie adjacent to their respective canals, and skin and superficial muscle was removed to reveal them. The nerve was kept moist with Cautland saline (Wolf, 1963).

In some experiments the fish were immobilized by Flaxedil (gallamine triethiodide) 3–4 mg/kg injected I.M.

Concentric electrodes constructed from 25-gauge hypodermic needles and 40 gauge insulated stainless-steel wire were used to stimulate the medial longitudinal fasciculus on the floor of the 4th ventricle. Shock strengths were 1–4 V and 0·1 msec in duration. Bipolar platinum hook electrodes were used to stimulate, and to record from branches of the lateral line nerve. On some occasions impulses were recorded from nerves by micropipettes filled with 3 M-KCl. These had resistances of 4–10 MΩ measured in saline. They were connected to a high impedance amplifier. Microphonic and d.c.

potentials were recorded from the lateral line organ by a silver–silver chloride electrode placed close to the sensory epithelium.

In some experiments efferent impulses were recorded by hook electrodes from fine branches of the lateral line nerves which supplied single organs and contained only a few efferent fibres. By careful manipulation of the electrodes it was possible to effectively isolate the discharges of a single fibre by making its impulses appear larger than those of the other fibres. If successive impulses were closely similar in size and shape and did not coincide with each other, then they were assumed to be from a single fibre. The impulses were then fed into a variable threshold discriminator whose levels were set to exclude the impulses of other fibres recorded by the hook electrodes. The nerve impulses whose amplitudes were above the limit set on the discriminator triggered short pulses which intensified the beam of a storage oscilloscope. Each impulse was then indicated as a dot on the oscilloscope screen. The sweep of the storage oscilloscope was triggered by stimulus events and successive stimulus presentations produced successive lines on this dot pattern display (Wall, 1959).

The lateral line organs were mechanically stimulated by a glass pipette with a tip 100 μm in diameter which was brought into contact with the cupula and which displaced it sinusoidally in the direction of maximum sensitivity. The source of the sine wave was a gated oscillator, and the signal from this was then passed through a decade attenuator. Signals and dot displays were photographed from a storage oscilloscope. Histograms were compiled on a special purpose computer (DIDAC 4000).

RESULTS

Efferent impulse activity

In burbot which had been immobilized with Flaxedil efferent impulses were recorded from the proximal portions of lateral line nerves which had been severed from their peripheral connexions. The responses of the efferent fibres to natural stimulation were very similar to those found in the lateral line efferent systems of *Xenopus laevis* (Russell, 1971*a*) and dogfish (Roberts & Russell, 1972). For example, the efferent system in burbot is insensitive to airborne sound or lateral line stimulation, unless the stimuli are of a kind which would normally cause a fish to perform a movement, when the efferent fibres discharge throughout the movement. In this respect the lateral line efferent fibres in burbot fire vigorously after mechanical stimulation of the vestibular apparatus, due to movement which such stimulation usually causes; the efferent fibres often discharge impulses at frequencies as high as 100/sec. Fig. 1 shows a vigorous increase in firing rate of the efferent fibres to vibration of the labyrinth at 70 Hz, and also a post-stimulation depression which is clearly seen in Fig. 1*b*.

Excitation of efferent fibres

A means of selective excitation of the lateral line efferent system in *Xenopus* is to stimulate electrically the medial longitudinal fasciculus (Russell, 1971*a*). This method of stimulating efferent fibres was also tried

in the burbot which were first immobilized by Flaxedil. A brief electrical shock (0·5 V and 0·1 msec duration) delivered by bipolar electrodes placed on the medial longitudinal fasciculus in the 4th ventricle excites the efferent fibres. This is seen in branches of the lateral line nerve as a burst of action potentials of variable latency (7–15 msec). In fish which have not

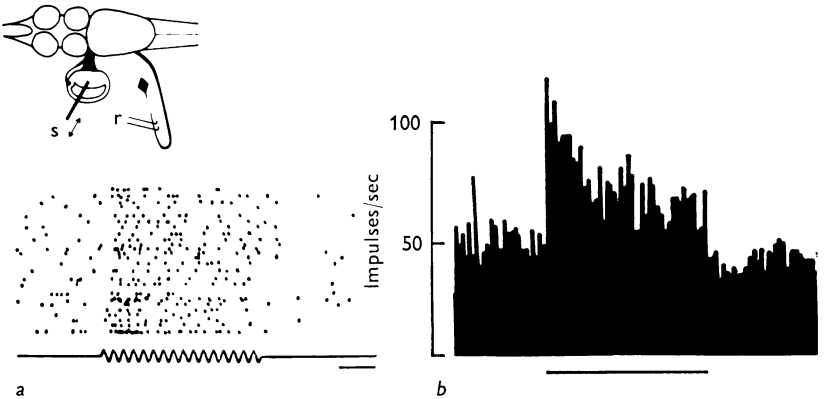

Fig. 1. Response of single efferent fibre in the branch of the posterior lateral line nerve supplying an organ in the supratemporal canal to vibration of the vestibular system. The diagram in this and the following figures shows dorsal view of brain and nerves, points of stimulation (s) and recording (r).

a, Dot display; successive responses are shown as successive lines with cell discharges indicated by dots. Below is a monitor of the 70 Hz vibration applied to the labyrinth. Time bar: 50 msec.

b, Corresponding time-histogram. Note reduced activity following excitation during horizontal bar.

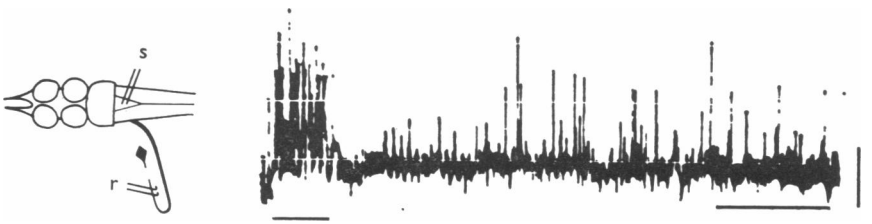

Fig. 2. Electric stimulation of the medial longitudinal fasciculus causes efferent fibres to fire. Stimulus: 9 shocks during first bar. Time bar: 100 msec. Vertical bar: 250 μV.

been immobilized by Flaxedil the electric shock to the floor of the 4th ventricle causes violent body movements. Furthermore stimulation of the floor of the 4th ventricle depresses any ambient activity of the efferent fibres for a period of 150 msec following the stimulus (Fig. 2). Post-stimulatory depression of efferent activity also follows reflex excitation of the efferent neurones (cf. Fig. 1*b*).

D.c. potentials in the lateral line canal evoked by stimulation of the lateral line nerve

Repetitive electrical stimulation of the lateral line nerve caused a negative potential change which was recorded between an electrode placed close to the sensory epithelium of the lateral line organs and an indifferent electrode inserted in the musculature behind the head (Fig. 3*a*). With trains of 0·1 msec pulses at 200/sec and lasting for 80 msec the maximum amplitude was 200 μV. The time taken for the potential to reach its peak from the onset of stimulation was 115–120 msec and the time taken for its decline measured from the peak to its disappearance was 250–370 msec.

Care was taken to exclude the possibility that the DC potential was an artifact of muscle movement caused by possible stimulus spread from the stimulating electrodes on the lateral line nerves. The nerve and electrodes were held clear from the body in a pool of mineral oil, and there was no apparent change in the shape or magnitude of the potential when the indifferent recording electrode was placed in an alternative site in saline soaked cotton-wool in the cranium. Finally, in several control experiments the lateral line nerve was crushed between the stimulating electrodes and lateral line organ. This presumably would not alter stimulus spread from the stimulating electrodes, but it abolished the potential. Thus we were convinced that the potential was due to the action of stimulated lateral line nerve fibres on the lateral line organ.

The potential recorded in the lateral line canal is similar to the change in the endocochlear potential which may be recorded in the cochlea as a result of repetitive stimulation of the crossed olivocochlear bundle (Fex, 1967*a*). However, electrical stimulation of the lateral line nerves not only excites the efferent fibres, but also evokes antidromic impulses in the afferent nerve fibres, and it may be that the antidromic afferent impulses contribute towards the negative potential. This was examined by selectively blocking the lateral line efferent synapse. The transmitter substance which is liberated at the afferent synapse is unknown, but atropine and D-tubocurarine chloride in small concentrations block the efferent synapses (Russell, 1968, 1971*b*) and there is evidence that the efferent synapses are cholinergic. Intramuscular injections of Flaxedil in concentrations just sufficient to immobilize burbot (3 – 4 mg/kg body weight) abolished the negative potential (Fig. 3*b*). Low concentrations of Flaxedil and other cholinergic blocking drugs seem not to influence either transmission of impulses in lateral line nerves (Russell, 1971*b*) or transmitter release at the afferent synapses (Flock & Russell, 1973). Therefore the negative potential may be attributed entirely to the action of the efferent fibres on the sensory epithelium.

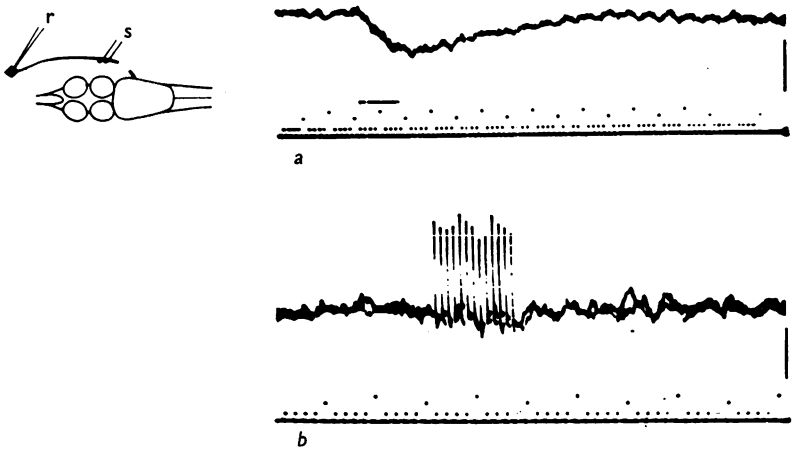

Fig. 3. D.c. potential in canal organ evoked by lateral line nerve stimulation. *a*, The upper trace records d.c. potential close to the sensory epithelium. Vertical bar: 250 μV. Lower trace marks 10, 50, 100 msec, and stimulus pulses delivered to the nerve. *b*, Same recording and stimulating conditions but after intramuscular injection of Flaxedil (3 mg/kg body wt). Period of nerve stimulation is indicated by shock artifacts. The amplification is the same as in *a* but the time scale is expanded.

The effect of lateral line stimulation on the microphonic potential

As in the cochlea an externally recorded receptor potential, the microphonic potential, may be recorded from close to the lateral line sensory epithelium in response to mechanical stimulation of the organ. Repetitive electrical stimulation of the lateral line nerve causes an augmentation of the microphonic potential and this effect is blocked by I.M. injections of Flaxedil (Fig. 4). The latency and duration of the augmentation of the microphonic and the negative potential are the same and the amplitude of the augmentation is dependent upon the frequency of shocks to the lateral line nerve. Both the negative potential and augmentation of the microphonic increase progressively with the frequency of shocks to the lateral line nerve and reach a maximum at about 200/sec (Fig. 5). Even very low frequencies of stimulation at 10–20/sec produce observable negative potentials and changes in microphonic potential.

The input–output curve of the lateral line microphonic to vibration at 70 Hz becomes steeper and is shifted to the left by stimulation of the lateral line nerve. The extent of the shift and the steepness of the curve are both dependent upon the intensity of the tone burst and are greatest during points of maximal displacement of the lateral line organs (Fig. 6).

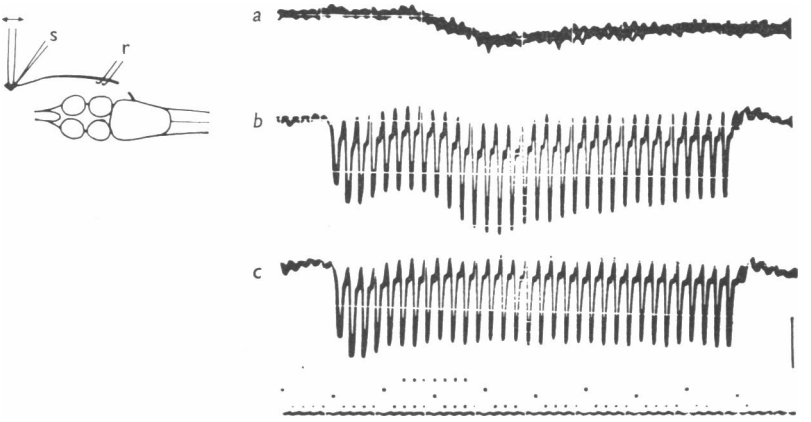

Fig. 4. Effect of nerve stimulation on microphonic potential. *a*, Monitor of d.c. change cf. Fig. 3*a*. *b*, The microphonic potential evoked by driving the cupula with a 70 Hz vibration is augmented by electrical stimulation of the nerve. *c*, This effect is blocked by intramuscular injection of Flaxedil (cf. Fig. 3*b*). Vertical bar applies to all records: 250 μV. Nerve stimulation is marked above time scale. Time scale marks 10, 50 and 100 msec.

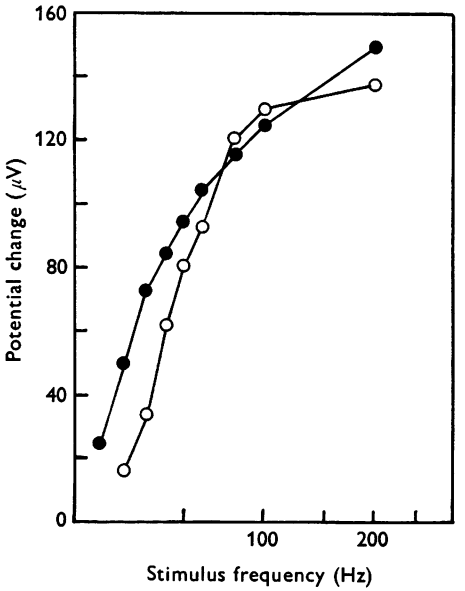

Fig. 5. Increase of negative potential (○—○) and microphonic potential (●—●) with increasing frequency of lateral line nerve stimulation.

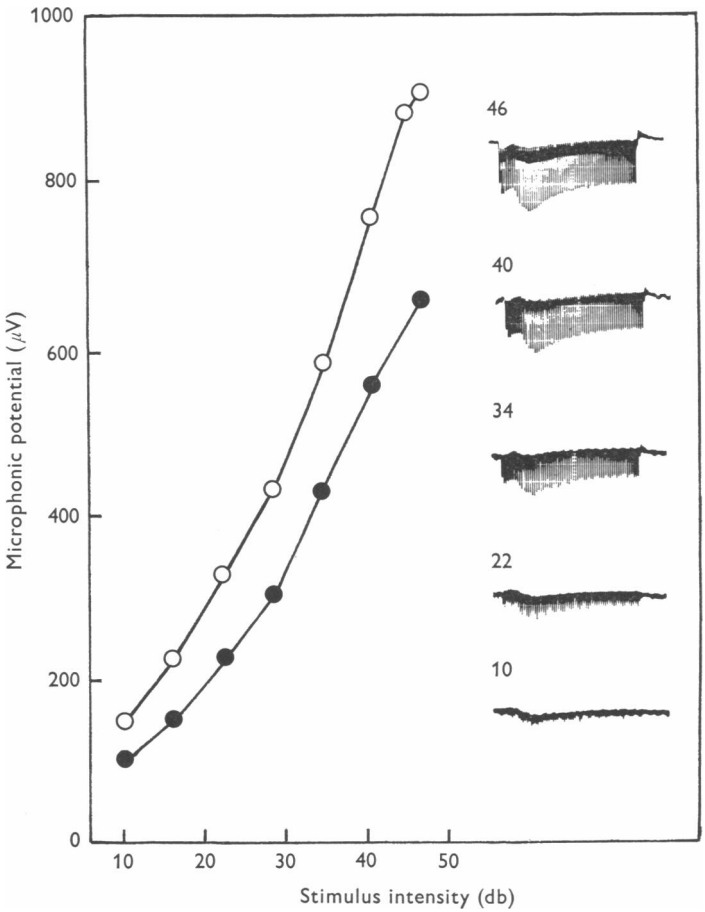

Fig. 6. Input–output curve of microphonic potential in response to a 70 Hz vibration. ○—○ is at the summit of augmentation caused by nerve stimulation, illustrated to the right by samples of records at intensities indicated. ●—● plots the amplitude of the microphonic potential without nerve stimulation. The ordinate shows the amplitude of the microphonic potential in μV. The abscissa is stimulus intensity plotted in db units relative to an empirically determined threshold for single unit fibres.

The effect of lateral line nerve stimulation on afferent activity

Impulse traffic in the afferent nerve fibres is inhibited by repetitive electrical stimulation of the lateral line nerve. A train of impulses at 200/sec, lasting 80 msec, caused inhibition of spontaneous afferent impulses for 200–250 msec (Fig. 7*a*). Inhibition is blocked by I.M. injection of Flaxedil (4 mg/kg body wt.) (Fig. 7*b*). It is known that antidromic invasion of afferent nerve fibres resets the threshold for impulse iniatition

(Harris & Flock, 1967), but the resetting period is small compared with that of the efferent inhibition.

In the absence of efferent inhibition, stimulation of the lateral line nerve appears to excite the afferent fibres (Fig. 7*b*). The cause of this excitation is unknown. It may be that antidromic invasion of the afferent nerve terminals causes a prolonged depolarization but there is no evidence to date to support this hypothesis (Harris & Flock, 1967). An alternative possibility is that the fine unmyelinated fibres which are found in the lateral line nerve (Flock, 1965) have been simultaneously excited with the afferent fibres, and that they have an excitatory action on them. However, the destination of the unmyelinated fibres remains to be discovered.

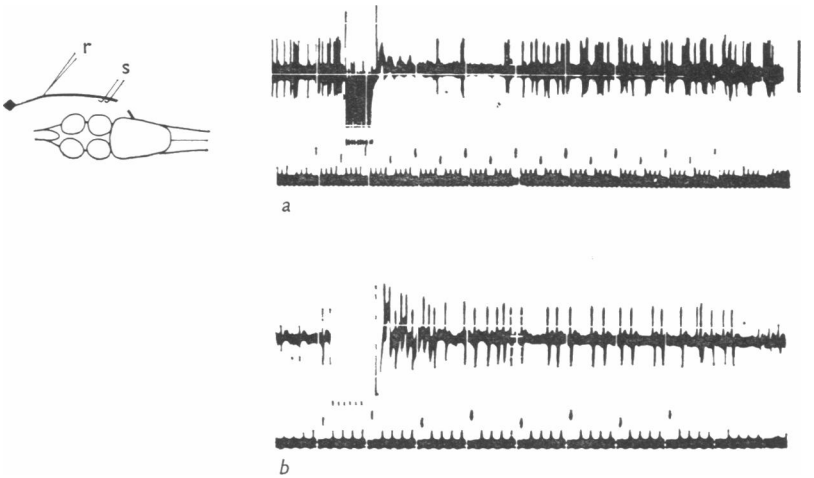

Fig. 7. The effect of nerve stimulation on the spontaneous discharge of an afferent fibre. The period of nerve stimulation is indicated by the artifact in the upper trace and row of dots above time base in lower trace. *a*, Afferent discharge is inhibited for a period following nerve stimulation. Time scale: 10, 50 and 100 msec. Vertical bar: 5 mV. *b*, Inhibition is absent when tested 10 min after I.M. injection of Flaxedil.

The influence of efferent activity on the lateral line organs

In order to be certain that the potential changes that had been observed were due entirely to the post-synaptic action of the efferent fibres on hair cells, it was necessary to stimulate the efferent fibres without simultaneously exciting the afferent fibres. This was done by electrical stimulation of the floor of the 4th ventricle. Furthermore, the fish had to be immobilized without the use of Flaxedil to avoid the gross body movements which accompanied this form of stimulation. To achieve this all of the motor nerves from the central nervous system were sectioned.

In all but one out of seven burbot which were immobilized by sectioning

the motor nerves, the lateral line efferent fibres were vigorously active (Fig. 8), and discharged at high frequencies. In the one case where the resting activity of the lateral line efferents was low, it was possible to observe a compound action potential in the lateral line nerves in response to electrical stimulation of the medial longitudinal fasciculus (Fig. 9).

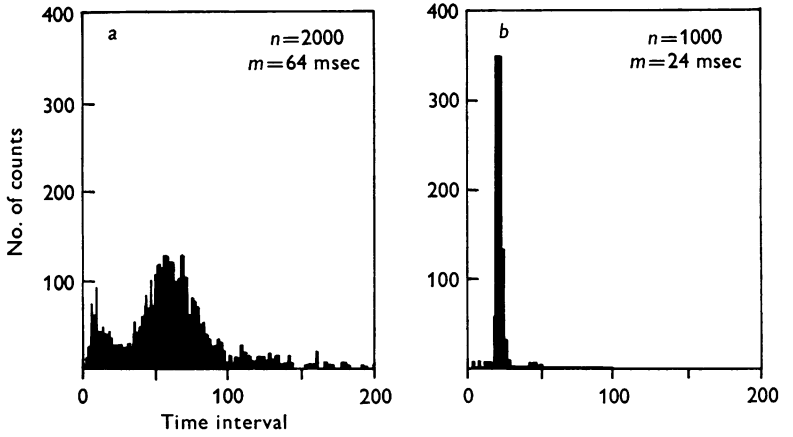

Fig. 8. Interval histograms of spontaneously firing efferent fibres. Abscissa: interval between successive spikes. Ordinate: number of counts per bin. *a*, An efferent fibre firing at a moderate frequency has a mode of most common intervals at 64 msec. *b*, In an animal where all cranial motor nerves were sectioned the efferent fibres fired at a high frequency; this fibre has a mode at 24 msec.

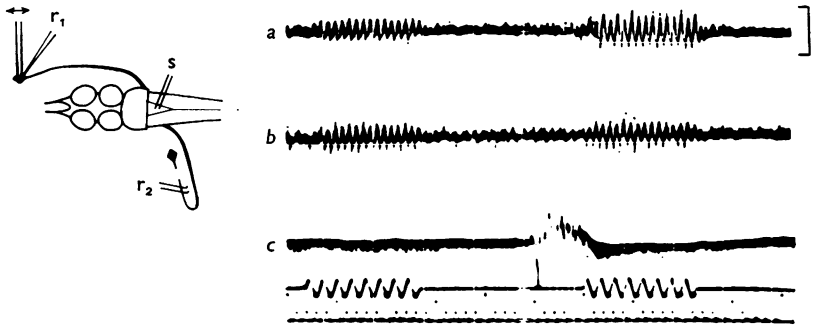

Fig. 9. The effect of selective stimulation of efferent fibres by shocks to the floor of the 4th ventricle on the microphonic potential. The top two traces record the microphonic potential (r_1) when the lateral line organ is stimulated twice by a 70 Hz vibration monitored below. *a*, Just before the second stimulus the efferent fibres are fired. As a result the microphonic potential is increased. *b*, Control without efferent excitation. *c*, Compound efferent action potential monitored by electrode r_2. Time scale 10, 50 and 100 msec. Vertical bar: 250 μV.

Fig. 9 also shows the augmentation of the microphonic potential in the nasal organ of the right-hand supraorbital canal caused by electrical stimulation of the floor on the 4th ventricle. In another experiment microphonic potentials were recorded from a supraorbital canal organ in which the efferent neurones were vigorously active (Fig. 10*a*). Sectioning of the supraorbital branch of the 7th nerve which supplies this organ removed the tonic influence of the constantly active efferent fibres, and simultaneously caused a reduction in the amplitude of the microphonic potential (Fig. 10*b*). Fig. 11*c*, *d* and *e* shows the response of an afferent fibre in the intact supraophthalmic branch of the 7th nerve to mechanical stimulation of the lateral line organ it supplied. In this fish the lateral line

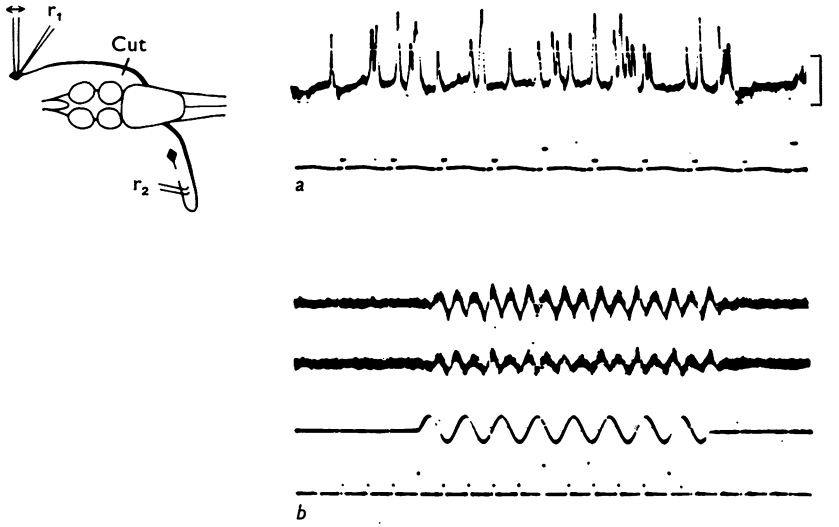

Fig. 10. Effect of withdrawal of tonic efferent influence on microphonic potential. *a*, Vigorous efferent activity recorded by electrode r_2. Time scale: 10 and 50 msec. Vertical bar: 250 μV. *b*, Top trace is the microphonic potential in response to mechanical stimulus monitored in the third trace. Second trace is the microphonic potential after the central connexion has been cut.

efferent fibres were vigorously active. Electrical stimulation of the supraophthalmic branch of the 7th nerve augmented the microphonic potential (Fig. 11*b*). Flaxedil was injected intramuscularly into the fish without mechanically disturbing the lateral line organ. This was done by injecting the Flaxedil through Teflon cannulas which were placed in the muscles of the gill region at the beginning of the experiment. The blocking action of the Flaxedil on the efferent synapse was monitored by observing the point at which the augmentation of the microphonic potential was abolished

(Fig. 11*b*). At this point it was assumed that the efferent synapses were blocked, and the response of the afferent fibre to mechanical stimulation of the lateral line organ was re-examined. The sensitivity of the afferent fibre increased and there was a greater probability of its firing to the first and second cycles of the sinusoidal mechanical stimulation of the cupula (Fig. 11*e*).

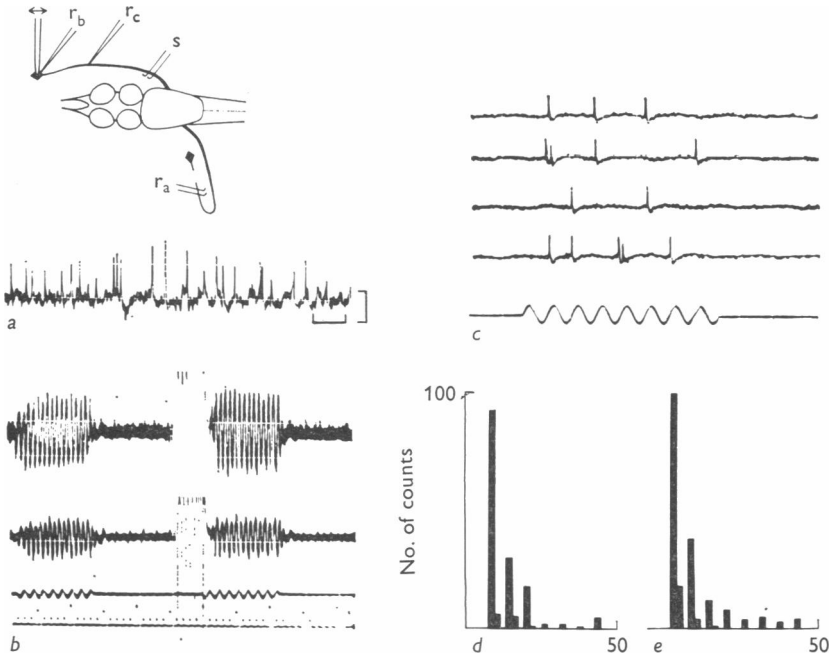

Fig. 11. Effect of withdrawal of efferent influence on evoked afferent discharge. Time bar: 20 msec for records *a* and *c*. Vertical bar: 250 μV for record *a*, upper traces in *b* and *c*, 500 μV for middle trace in *b*. *a*, Efferent activity recorded by electrode r_a. *b*, Microphonic potential monitored by electrode r_b. In the top trace the response to the second stimulus is augmented by electrical stimulation of the nerve (s). In the second trace augmentation fails after Flaxedil injection. *c*, The response of a single afferent fibre to the first stimulus is recorded by the glass micro-electrode r_c. *d*, Time histogram of the fibre responding in *c*. *e*, Time histogram of the same fibre when Flaxedil blockade of efferent synapses has been judged effective by monitor in *b*. In *d* and *e* abscissa = time in msec from beginning of the sinusoidal mechanical stimulation. In *e* the fibre fires more often than *d* to each cycle of the stimulus.

DISCUSSION

Selective excitation of the lateral line efferent fibres by stimulation of the 4th ventricle, or electrical stimulation of the lateral line nerve causes an increase in the lateral line microphonic potential, an evoked 'efferent' potential, and inhibition of impulse activity in the afferent fibres. These potentials occur simultaneously and share the same protracted time course. In addition it has been established, by selectively blocking the efferent synapses with Flaxedil, that the potential changes produced by electrical stimulation of the lateral line nerve are due entirely to the efferent fibres and not to antidromic invasion of the afferent fibres. This is in agreement with ultrastructural observations of the lateral line afferent nerve terminals which show that they are not electrically coupled to the hair cells (Flock, 1965) as they might be in Type I hair cells of the vestibular systems of reptiles, birds and mammals (Spoendlin, 1965; Wersäll & Lundquist, 1966). Furthermore, post-synaptic potentials have never been recorded from hair cells in fish immobilized with Flaxedil (Flock & Russell, 1973).

The sensitivity of the efferent synapses to Flaxedil is remarkably high. The latency and time course of the block are the same at the efferent synapse and neuromuscular junction, therefore both synapses must be equally permeable and sensitive to Flaxedil. Flaxedil is known to block the post-synaptic action of acetylcholine at the neuromuscular junction and there is good reason to believe that acetylcholine is released at the lateral line efferent synapse (Russell, 1971*b*) and at the efferent synapse of the cochlea (Fex, 1967*b*; Bobbin & Konishi, 1971).

In dogfish *Scyliorhinus canicula* the lateral line organs are strongly excited by body movements during locomotion (Roberts, 1972). It has been suggested that the role of the efferent system is to attenuate input from the lateral line organs during locomotion and vigorous movement (Russell, 1971*a*, *b*; Roberts & Russell, 1972). The function of the attenuation may be either to shift the range of the sensitivity of the lateral line organs to match those of the displacement caused by its own movements, or to protect the afferent synapses from fatigue. Our observations are compatible with these ideas. First, the amplitude of the efferent post-synaptic potential changes in the lateral line organs increase with the frequency of stimulation of the efferent fibres (Fig. 5). Since efferent fibres fire more vigorously during violent movements than during slow swimming (Roberts & Russell, 1972), the efferent fibres will exert their greatest post-synaptic action on hair cells during violent movements. Furthermore, the way in which the efferent fibres influence lateral line organs is also dependent upon the amplitude of the mechanical stimulation of the lateral line organs. The post-synaptic potentials produced by efferent activity are

largest during maximum amplitudes of mechanical stimulation (Fig. 6). This will increase the effectiveness of the lateral line efferent fibres in attenuating lateral line input during violent body movements.

In all respects the potential changes recorded in the lateral line organs in response to stimulation of the efferent fibres resemble those produced in the cochlea in response to stimulation of the crossed olivocochlear bundle (Fex, 1967*a*). It thus seems reasonable to presume that efferent fibres have similar post-synaptic actions on hair cells in the cochlea and lateral line organs. This has lead to the selection of the lateral line organ for an intracellular study of the post-synaptic action of efferent fibres on hair cells (Flock & Russell, 1973) because it is possible to make intracellular recordings from lateral line hair cells (Harris, Frischkopf & Flock, 1970; Flock, 1971). Lateral line organs offer further advantages for intracellular study in that antidromic invasion of the afferent fibres has no apparent post-synaptic influence on hair cells. This greatly simplifies the means of stimulating the efferent fibres; they can be stimulated by electrical stimulation of the lateral line nerve. Furthermore, the post-synaptic action of efferent fibres on hair cells in lateral line organs appears to be especially potent. Although the potential changes are maximal when the lateral line nerve is stimulated at 200/sec, observable changes in the microphonic and efferent potentials are seen at stimulus frequencies as low as 10/sec. The crossed olivocochlear bundle has to be stimulated at much higher frequencies to produce changes in the cochlear microphonic and endocochlear potentials (Fex, 1967*a*).

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