INHIBITION OF SPONTANEOUS LATERAL-LINE ACTIVITY
BY EFFERENT NERVE STIMULATION

BY I. J. RUSSELL* AND B. L. ROBERTS
Department of Zoology, University of Cambridge,
and The Laboratory of the Marine Biological Association, Plymouth

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INTRODUCTION

In common with other acoustico-lateralis receptors, the hair cells of the lateral-line organs of fishes and amphibia receive efferent innervation. Ultrastructural studies have shown that efferent synapses similar to those found at the base of the hair cells in the cochlea (Engström & Wersäll, 1958) and vestibular system (Wersäll, 1956) exist also 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). Furthermore, efferent impulses have been recorded from lateral-line nerves in amphibia (Schmidt, 1965; Görner, 1967; Russell, 1971), in teleost fish (Hashimoto, Katsuki & Yanagisawa, 1970) and in elasmobranchs (Roberts & Russell, 1970).

In cases where the function of the efferent system has been studied, namely in the cochlea (Galambos, 1956; Fex, 1962), in the vestibular systems of fishes (Klinke & Schmidt, 1970), of amphibia (Gleissner & Henriksson, 1964; Linás & Precht, 1969; Goetmakers & Groen, 1970) and of mammals (Sala, 1965) and in the lateral-line systems of the eel, Astroconger myriaster (Hashimoto et al. 1970) and of Xenopus laevis (Russell, 1968, 1971), it has been shown that stimulation of the efferent fibres can lead to inhibition of impulse activity in the primary afferent fibres.

The experiments described in this paper were designed to show whether efferent fibres could be made to exert an inhibitory effect on the lateral-line sense organs of dogfish.

METHODS

These experiments were performed on 13 trawled dogfish, Scyliorhinus canicula; each weighing between 500 and 1000 g. They were quickly pithed and clamped by the head and dorsal part of the body to a Perspex plate. The gills were continuously irrigated with sea water at a temperature of 14 °C and a flow rate of 1.0–1.5 l/min and the body was kept wet by covering it with tissue paper soaked in sea water. The posterior lateral-line branch of cranial nerve X of one side, which was exposed for a distance of about 10 cm behind the gills, was cut and the peripheral end was placed on a glass plate moistened with saline solution (Roberts, 1972), where it was desheathed with a fine razor-blade scalpel.

A fine filament containing a single active afferent fibre or a few active afferent fibres was teased from the nerve bundle and each branch was placed over platinum

* Present address: School of Biology, University of Sussex, Falmer, Sussex.
electrodes, as illustrated in Fig. 1. The electrodes were then covered with mineral oil as a precaution against desiccation and also to prevent stimulus spread from the main bundle to the fibres in the fine filament.

It was assumed that the main bundle would contain efferent fibres which innervated end organs supplied by the afferent fibres included in the fine filament. The efferent fibres in the main bundle were stimulated at frequencies of 10–100 sec⁻¹ by gated pulse trains 1 sec long containing electrical pulses of 0.02 msec duration. In some cases as a check on successful stimulation the compound potential in the main bundle was monitored and stimulus amplitudes were increased until this potential was of maximum size. Stimulus strengths of 3–5 times this value were then used during the course of the experiment. The nerve impulses were recorded with conventional equipment and stored for later analysis on an FM tape-recorder. The preparations were used for 2–3 h, during which time the spontaneous afferent activity remained constant; after this time there was a decline in the frequency of afferent impulses.

RESULTS

The majority of afferent fibres were spontaneously active, discharging at a steady rate of 5–18 sec⁻¹ at 14 °C. Some afferent fibres, however, were inactive unless the sense organs they innervated were stimulated mechanically.

Most of the afferent units were unaffected by stimulation of the main bundle. When an effect of electrical stimulation of efferent fibres on afferent impulse activity was detected it was one of two kinds, depending on whether the afferent fibre was quiescent or spontaneously active.

Electrical stimulation of efferent fibres with trains of pulses at frequencies of 40–100 sec⁻¹ caused the non-spontaneous afferent fibres to discharge several impulses, usually 3–4 at a frequency of 6–7 sec⁻¹ (Fig. 2), which appeared 500–600 msec after the stimulus train. Trains of stimulating pulses at frequencies below 40 sec⁻¹ did not produce this effect.

In the second type of response, and the most frequently encountered, there was a decrease in the frequency of spontaneous impulses accompanying electrical stimulation. This is shown clearly in the example given in Fig. 3, where the spontaneous activity of a unit was totally inhibited when the efferent fibres were stimulated at 40 sec⁻¹. Inhibition continued for a further 150–200 msec following the inhibitory train and was not succeeded by an obvious post-inhibitory after discharge of the afferent fibre.
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Fig. 2. The afterdischarge of a non-spontaneously active lateral-line afferent fibre in response to stimulation of the efferent fibres. The stimulation periods, which are marked by the stimulus artifacts, occur every 5.5 sec. The pulses last 1 sec at 100 sec⁻¹.

Fig. 3. Total suppression of spontaneous afferent impulse activity by electrical stimulation of efferent nerve fibres. The upper trace is the record of afferent unit activity; the lower trace shows the stimulus given to the efferent fibres—a 1 sec train of pulses at 42 sec⁻¹ delivered every 3 sec. The time marks occur every second.

More commonly, electrical stimulation of efferent fibres was accompanied only by a reduction in the frequency of the spontaneous activity to values between one-third and two-thirds of the resting value, rather than total inhibition, as shown in Fig. 4. This effect was seen usually at relatively high frequencies of electrical stimulation (50–100 sec⁻¹), but in a few cases significant reduction in the frequency of spontaneous impulses was achieved at lower frequencies of stimulation. For example, one unit with a resting frequency of 5.4 ± 0.09 sec⁻¹ discharged at 4.8 ± 0.13 sec⁻¹ when stimulated at 20 sec⁻¹.

The response of spontaneously active afferent fibres to electrical stimulation of efferent fibres declined and showed variability with succeeding bursts of stimuli (Fig. 5). The inhibitory response to the initial stimulus train was usually greater than to successive bursts, but after a poor inhibitory response the next burst of efferent stimulation often caused a big reduction in spontaneous activity (e.g. compare stimuli 10 and 11 in Fig. 5).

Because of the declining effect of the applied efferent stimulus it was not possible in most cases to attempt more than a few variations of the stimulus parameters for any unit. The usual experimental procedure was to stimulate at first with trains of stimuli at frequencies of 50–100 sec⁻¹ and then, after an effect had been established, to drop to lower stimulus frequencies. In no case did single pulses appear to influence the spontaneous discharge and only trains at frequencies of 20 sec⁻¹ or higher were effective. Because of the difficulty in finding afferent fibres which were modified by efferent fibre stimulation, and because of the declining effect when a responsive unit was found, we were unable to investigate the impact of efferent activity on mechanically stimulated lateral-line organs.
Fig. 4. Reduction in spontaneous afferent activity caused by electrical stimulation of efferent nerve fibres. The top record is the unstimulated preparation. Stimulation at 10 sec\(^{-1}\) has little effect, but at 100 sec\(^{-1}\) (bottom two records) the impulse frequency declines during the stimulation period. The stimulus is marked on the time trace; the time marks occur every second.

Fig. 5. This graph shows the variability and decline in inhibitory effect brought about by electrical stimulation of efferent fibres delivered every 3 sec in trains 1 sec long at 100 sec\(^{-1}\). Complete inhibition (100%) indicates that the unit was totally inactive during the stimulation period; at 0% the fibre discharged at its resting frequency (15 sec\(^{-1}\)).

**DISCUSSION**

These experiments have demonstrated that it is possible to bring about a decrease and even total inhibition of the spontaneous activity of the lateral-line organs of dogfish by stimulation of the efferent nerve fibres; however, with our present technique the inhibitory effect was seen only occasionally. One possible reason for this might be that if the afferent and efferent nerve fibres lie close together in the lateral-line nerve it would be difficult to separate them into two bundles for recording and stimulation. Another possibility is that only a few of the lateral-line hair cells actually receive an efferent innervation. Although this seems improbable it was noticed in electron-microscope studies on the lateral-line organs of *Scyliorhinus* that afferent endings were easier to find than were efferent synapses (Roberts & Ryan, 1971). In experiments on the mammalian cochlea (Wiederhold & Kiang, 1970) reduction in the activity of spontaneously active auditory nerve fibres during stimulation of the efferent fibres of the crossed olivo-cochlear bundle (COC B) was also infrequently obtained, but in this case the effect of COC B stimulation was found to depend on the level of external...
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It would seem to be important therefore to examine the effect of efferent fibre stimulation on mechanically stimulated lateral-line organs in order to see whether insensitivity to efferent fibre stimulation is confined only to spontaneously active, unexcited afferent units; this kind of experiment, however, would be impracticable using the present technique.

The inhibition of spontaneously active lateral-line fibres in dogfish is similar to the inhibition of spontaneously active primary auditory fibres produced by tetanic stimulation of the COC B (Wiederhold & Kiang, 1970) but is unlike the suppression of spontaneously active lateral-line fibres in Xenopus (Russell, 1968, 1971) and of acoustically excited fibres in the mammalian auditory nerve (Wiederhold & Kiang, 1970), where the inhibitory period is followed by a brief post-inhibitory after-discharge.

Impulse traffic along spontaneously active afferent fibres in the dogfish lateral-line nerve was suppressed for 150–200 msec following a train of stimuli to the efferent nerve fibres. This is at least twice as long as in Astroconger (Hashimoto et al. 1970), where suppression continues for only 40–70 msec. In dogfish total suppression of spontaneously active afferent impulses was sometimes achieved by stimulating the efferent fibres at 40 sec⁻¹, which means that individual efferent impulses were capable of maintaining the impulse-generating mechanism of the lateral-line organ in a sub-threshold state for at least 25 msec.

Two features of these results are puzzling in view of the presumed inhibitory function of the efferent system. First, although significant changes in afferent activity could be produced when the efferent nerves were stimulated by trains of pulses at frequencies between 20–100 sec⁻¹, the inhibitory effect was variable and subject to fatigue, possibly because the efferent synapses were over-stimulated. Secondly, in most cases changes in afferent activity were seen only when the efferent fibres were stimulated at or above the maximum frequencies at which they had been observed to discharge naturally. Thus it was found when recordings were made from efferent nerves in decerebrate dogfish (Roberts & Russell, 1970, 1972) that the efferent fibres did not discharge spontaneously and that they discharged only a few impulses at low frequency even when the fish was stimulated sufficiently to evoke body movement. Although vigorous movements were accompanied by efferent activity of up to 30 sec⁻¹, steady swimming movements were associated with rhythmical efferent bursts discharging at impulse frequencies as low as 5–10 sec⁻¹. Our experiments have shown that at these frequencies of efferent nerve activity complete inhibition of spontaneous afferent impulses would not be achieved.

SUMMARY

1. Efferent nerve fibres innervating the lateral-line sense organs of the dogfish Scyliorhinus were stimulated with trains of stimuli while spontaneous afferent activity was monitored.

2. Significant changes in spontaneous impulse frequency could be produced when the efferent nerves were stimulated by trains of pulses at frequencies between 20–100 sec⁻¹; lower stimulus frequencies had no visible effect. The impulse frequency decreased or was totally inhibited during the stimulus period and for 150–200 msec.
following it. The inhibitory effect was very variable and declined with repetitive stimulation.

3. Stimulation of the efferent nerves to inactive afferent units was followed after 500 msec by a brief low-frequency discharge.

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