J. exp. Biol. **102**, 223–238, 1983

THE EFFECT OF EFFERENT STIMULATION ON THE PHASE AND AMPLITUDE OF EXTRACELLULAR RECEPTOR POTENTIALS IN THE LATERAL LINE SYSTEM OF THE PERCH (*PERCA FLUVIATILIS*)

BY I. J. RUSSELL AND D. A. LOWE

School of Biological Sciences, University of Sussex, Brighton, BN1 9QG, Sussex

(*Received 3 June 1982—Accepted 14 September 1982*)

SUMMARY

1. Microphonic and summating potentials were recorded extracellularly from lateral line organs in the suborbital canal of the perch in response to sinusoidal movements of canal fluid.

2. These potentials were changed in amplitude, shape and phase, relative to the mechanical stimulus, by electrical stimulation of efferent fibres in the lateral line nerve.

3. The receptor potential amplitude/stimulus intensity relationships for the microphonic and summating potentials saturated at high levels of stimulation, and at progressively lower amplitudes with increasing frequencies of mechanical stimulation. Efferent stimulation tended to reduce this rate of saturation.

4. Amplitude versus frequency relationships plotted at different stimulus intensities for the microphonic potential showed that the lateral line organs were most sensitive to frequencies between 35–65 Hz (centre frequency), and at these frequencies efferent stimulation caused the greatest increase in amplitude.

5. Analysis of the second order and third order harmonic components of the microphonic showed that these were reduced by efferent stimulation and that the strongest reduction occurred at the centre frequency.

6. The phase of the receptor potential led that of the mechanical stimulus at very low frequencies by nearly 90°. This changed to zero phase at the centre frequency and to a phase lag at higher frequencies. Efferent stimulation caused no change in phase of the microphonic relative to the control state at the centre frequency, but caused a progressive phase lead and lag as the frequency was decreased and increased respectively about the centre frequency.

7. In the linear response range, the lateral line organs responded as critically damped low frequency resonators to the velocity of the stimulus. Efferent stimulation appeared to alter the damping of this resonance. The possibility is discussed that efferent stimulation can alter the mechanical properties of the lateral line hair cells.

INTRODUCTION

The majority of sense organs in the acoustico-lateralis system receive an efferent innervation. In the lateral line organs of fishes and aquatic amphibians, the efferent

Key words: Efferent, receptor potentials, lateral line.

fibres form synapses with the hair cells (Flock, 1965; Harris & Flock, 1967) and are inhibitory (Russell, 1968; Flock & Russell, 1973*a*). They are active just before and during any active movement made by the animal (Russell, 1971*a*; 1976; Roberts & Russell, 1972), and their proposed role is to suppress activity in the afferent fibres which might be elicited by the animal's own movements. This is achieved by a presynaptic effect on the hair cell. Brief electrical stimulation of the efferent fibres causes long lasting inhibitory post-synaptic potentials and conductance increases in the hair cells. This leads to a reduction in the amplitude of the excitatory post-synaptic potentials recorded in the terminals of the afferent fibres (Flock & Russell, 1976). Associated with these intracellular events is an increase in the microphonic and summating potentials (Flock & Russell, 1973*b*), which are the extracellularly recorded receptor potentials of lateral line organs (Kuiper, 1956; Flock, 1965).

In response to sinusoidal mechanical stimulation, the microphonic potential recorded from lateral line organs is roughly sinusoidal, but twice the frequency of the stimulus. Flock (1965) attributed this frequency doubling to the presence of two populations of hair cells in lateral line organs. These have their kinocilia located on opposite sides of the stereocilia bundles, and are, thereby, morphologically polarized in opposite directions. In the hair cells of the frog sacculus, Hudspeth & Corey (1977) demonstrated a physiological correlation for this morphological polarization, in that only displacement of the stereocilia towards the kinocilium caused an excitatory response. This finding supported Flock's proposal that each population of lateral line hair cells generated asymmetrical receptor potentials which were 180° out of phase with respect to each other, and that the double microphonic was due to the algebraic sum of these two potentials. More recent intracellular studies of lateral line hair cells also tend to support this view (Flock, Jørgensen & Russell, 1973). The asymmetrical voltage response of the lateral line hair cells gives rise to a d.c. potential or summating potential. The polarity of the microphonic and summating potentials depends on the configuration of the recording electrodes, but they represent an inward flow of current across the apical membranes of the hair cells. Thus their increase during efferent inhibition is believed to be due to an increased inward flow of current across the apical membranes of the hair cells caused by their hyperpolarization (Flock & Russell, 1976). However, there is increasing evidence that hair cells in the acoustico-lateralis system may have an active, rather than a passive, role in transduction, and that efferent fibres may regulate this activity. The idea stems from the discovery of the contractile proteins actin and myosin in the stereocilia and apical regions of hair cells (Flock & Cheung, 1977; De Rosier, Tilney & Egelman, 1980; Macartney, Comis & Pickles, 1980). More recently Mountain, Hubbard & Geisler (1980), Mountain (1980) and Siegel & Kim (1980) have shown that stimulation of the crossed olivo-cochlear bundle alters the generation of distortion products in the microphonic potential and sound pressure measured in the cochlea and at the tympanic membrane respectively. They attributed these effects to changes in the mechanical properties of the outer hair cells with which fibres of the crossed olivo-cochlear bundle form synaptic contact (Smith, 1968). In this paper we show that electrical stimulation of the efferent fibres in lateral line canal organs causes changes in the phase and harmonic distortion of the microphonic potential and we discuss the possibility that these are due to changes in the mechanical properties of the hair cells.

METHODS

A total of 43 perch, 6–7 in long were used in this study. They were each anaesthetized with intraperitoneal injections of 18–20 mg/kg Saffan (Glaxovet) (Oswald, 1978) and then transferred to a specially constructed Perspex tank where they were held rigidly on their sides, and respired artificially by a flow of tap water through a plastic mouth-piece.

The orbit was exposed to reveal the branch of the anterior lateral line nerve supplying the sense organs of the sub-orbital canal. This was exposed and placed over a pair of platinum-iridium hook electrodes and covered with mineral oil. The electrodes were used to record from the nerve, and to electrically stimulate it. When the electrodes were used for stimulating they were fed from a stimulus isolator with voltage pulses of 0·05 ms duration at frequencies up to 200 pulses s^{-1} in bursts between 80 ms and 30 s long.

Extracellular receptor potentials were recorded from lateral line organs in the sub-orbital canal by inserting a silver wire for a distance of about 1 mm into one of the pores. The wire was 100 μm diameter and insulated except for a 50 μm exposed tip which was chlorided. The indifferent electrode was a silver-silver chloride electrode inserted into the body musculature. Signals from these electrodes were amplified, displayed on an oscilloscope and stored on an F.M. tape-recorder for future analysis.

The lateral line canal organs were stimulated mechanically by the movements of a glass probe with a spherical tip about 200 μm in diameter. This was lowered until it contacted the surface of the canal lymph in the pore adjacent to the one from which recordings were being made (Fig. 1). The probe was attached to a piezoelectric bimorph (Corey & Hudspeth, 1980) which vibrated the probe along a line parallel to the long axis of the canal, with amplitudes not exceeding about 20 μm. The bimorph was driven with sinusoidally varying voltage signals from a Wavetek function generator, and their amplitude was attenuated by a Hewlett-Packard attenuator. The motion of the probe was monitored by reflecting a laser beam from a small mirror (about 50 μm square), attached close to the probe tip, onto an opal screen, behind which were a pair of photodiodes coupled differentially to the input of an amplifier.

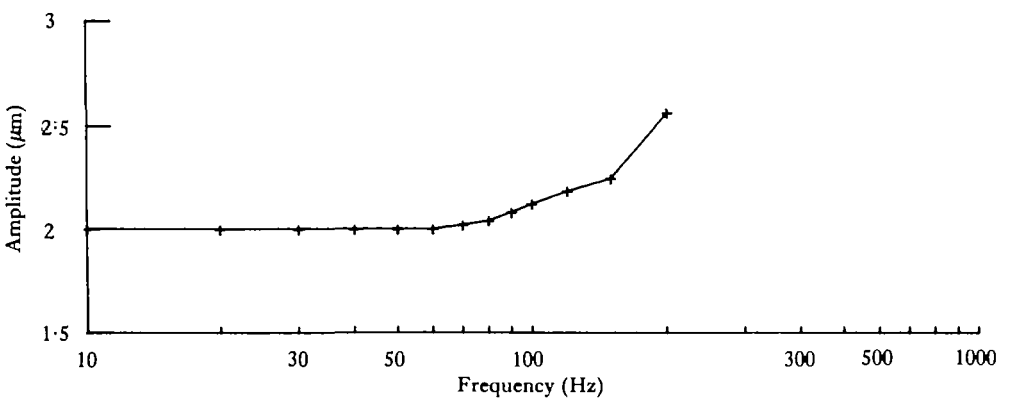

Fig. 1. Frequency response of the stimulus probe to a 10 V driving voltage.

This optical lever device was used to measure the frequency characteristics of the probe and its piezoelectric driver (Fig. 2), the amplitude of its movement (not more than 20 μm) and its linearity. In fact the system was found to be linear over its working range which was 30 to -60 dB relative to 2 μm displacement.

Signal averaging was performed by either a Biomac 1000 signal averager or a PDP 1103 microprocessor. Amplitude and zero crossing phase measurements were made from averaged records in the majority of instances, but on the few occasions when prolonged efferent stimulation was used, phase and amplitude measurements were made with a pair of Brookdeal SC905 lock-in amplifiers fitted with an Omniphase module. The summating potential was measured as the difference between the recording base line and the half peak to peak amplitude of the microphonic potential. Harmonic distortion of the waveform was measured with a Princeton 4512 spectrum analyser.

RESULTS

The effect of electrical stimulation of the lateral line nerve on the amplitude of the microphonic and summating potentials

Microphonic and summating potentials were recorded from organs in the suborbital canal in response to small sinusoidal water displacements adjacent to the canal pores. From the onset of an intense mechanical stimulus, the summating potential grew to a maximum within about 15 ms and then decreased progressively over the next 100–150 ms to reach a relatively steady state (Figs 3, 4). When the summating potential was at its largest, the microphonic was small and clipped in the negative, or inward directed phase, but it became larger and more symmetrical as it approached the steady state. At the cessation of mechanical stimulation there was a slow positive or outward potential, which lasted for about 100–120 ms. However, at lower levels of mechanical stimulation, the onset and offset potentials were reduced (Fig. 4).

In these experiments we did not attempt to discover the origins of the potential changes associated with the onset and offset of the mechanical stimulus. They may have represented adaptation of the hair cell transduction process or a changing membrane conductance associated with it. However, these onset and offset changes have been found to be absent, or nearly absent, when the cupulae of lateral line organs are driven directly (Flock, 1965; Flock & Russell, 1973*b*). It is thus likely that the potential changes arose from the movements of canal lymph associated with the onset and offset of vibration of the stimulus probe. The inaccessibility of the lateral line canal organs, which are located in their narrow, fluid-filled canals, prevented us from monitoring the motion of the cupulae.

Electrical stimulation of the branch of the anterior lateral line nerve supplying the organ caused an increase in the peak to peak amplitude of the microphonic potential and an increase in the amplitude of the negative summating potential (Figs 3, 4). The time courses of these changes were identical and rather slow. The increases in the microphonic and summating potentials reached their maximum after 25–50 ms and returned to their prestimulus levels about 350 ms after cessation of the electrical stimulation. The effectiveness of the electrical stimulation of the lateral line nerve on the extracellular receptor potentials and the adaptation of its effect was dependent on

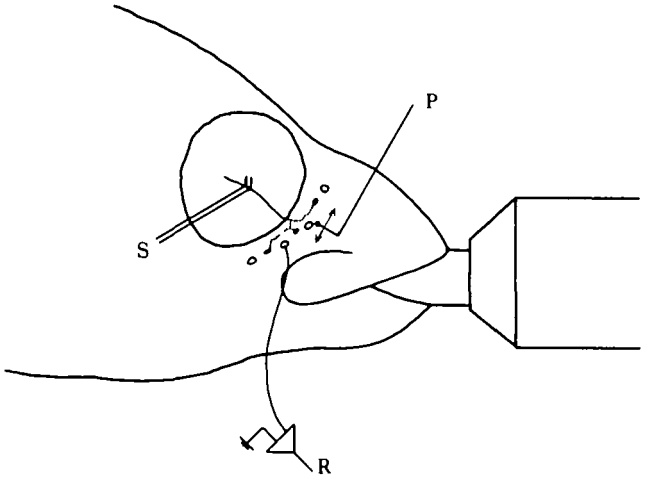

Fig. 2. The experimental arrangement showing the direction of movement (arrows) of the mechanical stimulus probe (P), and the locations of the recording (R) and stimulating electrodes (S). The approximate locations of the canal pores (open circles) and canal organs (solid circles) are shown for the suborbital canal. The course of the branch of the anterior lateral line nerve supplying these organs is shown as a dotted line.

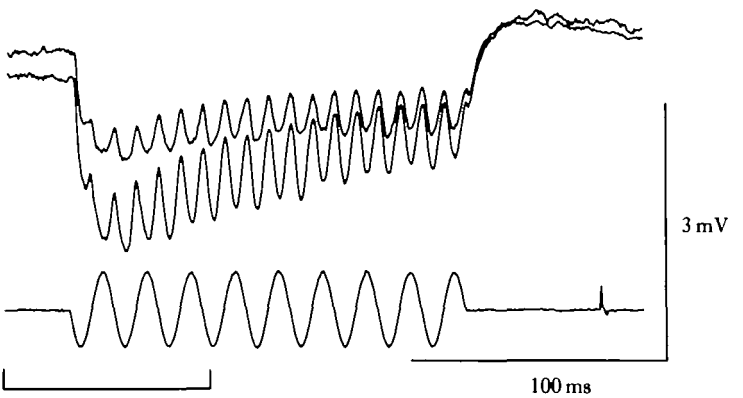

Fig. 3. The influence of electrical stimulation of the lateral line nerve on extracellularly recorded receptor potentials recorded from the suborbital canal. Upper trace, the microphonic and summating potential recorded in response to a 60 Hz mechanical stimulus of 2 μm amplitude. Bottom trace, the voltage input to the piezoelectric bimorph. Middle trace, microphonic and summating potential recorded during electrical stimulation of the nerve supplying the suborbital canal organs. The duration of the stimulus is indicated by the bar in the bottom left hand corner of the record, i.e. 80 ms at 60 pulses s^{-1}. Each trace is an average of eight records.

the state of the animal. In animals whose physiological condition was judged to be excellent no adaptation was seen after 5 s of continuous electrical stimulation of the lateral line nerve (Fig. 10) at frequencies about twice that required to produce a maximum change in the microphonic and summating potentials. These effects on the extracellular receptor potentials were abolished when 'Flaxedil' was released from an indwelling catheter inserted into the body musculature. The amount of Flaxedil required for this was small (5 mg/kg) and it did not block the afferent fibres, which continued to respond normally to mechanical stimulation of the end organ. It is

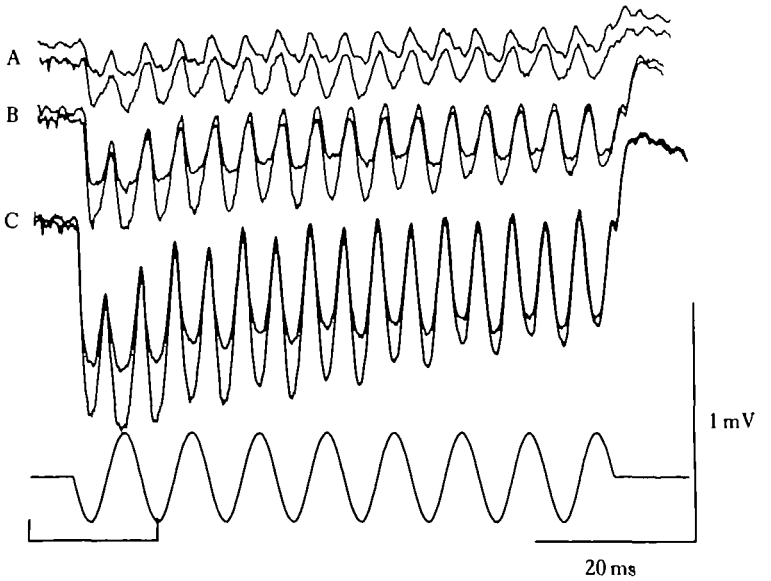

Fig. 4. Extracellular receptor potentials recorded from the suborbital canal in response to 25 Hz mechanical stimulation at −20 dB(A), −10 dB(B) and 0 dB(C) relative to a 2 μm displacement of the stimulus probe. In each pair of traces the lower is the response during electrical stimulation of the lateral line nerve. The duration of this stimulus, at 70 pulses s^{-1}, is indicated by the bar in the bottom left-hand corner. Each trace is the average of eight records. Bottom trace, voltage input to piezoelectric stimulus probe.

presumed that the changes observed in the microphonic and summating potential during electrical stimulation of the lateral line nerve were due to the efferent fibres whose synapses are blocked by agents which interfere with the release of acetylcholine or compete for receptor sites for this transmitter (Russell, 1971*b*).

Changes in the amplitude-intensity relationships of the extracellular receptor potentials during efferent stimulation

The relationship between the amplitude of the extracellular receptor potential and stimulus intensity was dependent upon the frequency of the mechanical stimulus and tended to saturate at progressively lower amplitudes as the frequency was increased (Fig. 5). This tendency was demonstrated most strongly by the microphonic and the trend continued above the most sensitive frequency of the lateral line canal organ (centre frequency), which is about 50 Hz in Fig. 5.

When the efferent fibres were electrically excited, the receptor potentials were augmented, and this had the effect of shifting the amplitude-intensity relationships to the left of the controls (Fig. 6). Electrical stimulation of the efferent fibres appeared to have the most potent effect on the negative summating potential at low levels of mechanical stimulation (Fig. 6). However, this is presumably because stimulation of the efferent fibres causes an efferent potential due to the inward flow of current through the apical surface of the sensory epithelium caused by the hyperpolarization of the hair cells (Flock & Russell, 1973*b*). This potential is large relative to the negative summating potential caused by low levels of mechanical stimulation, and its

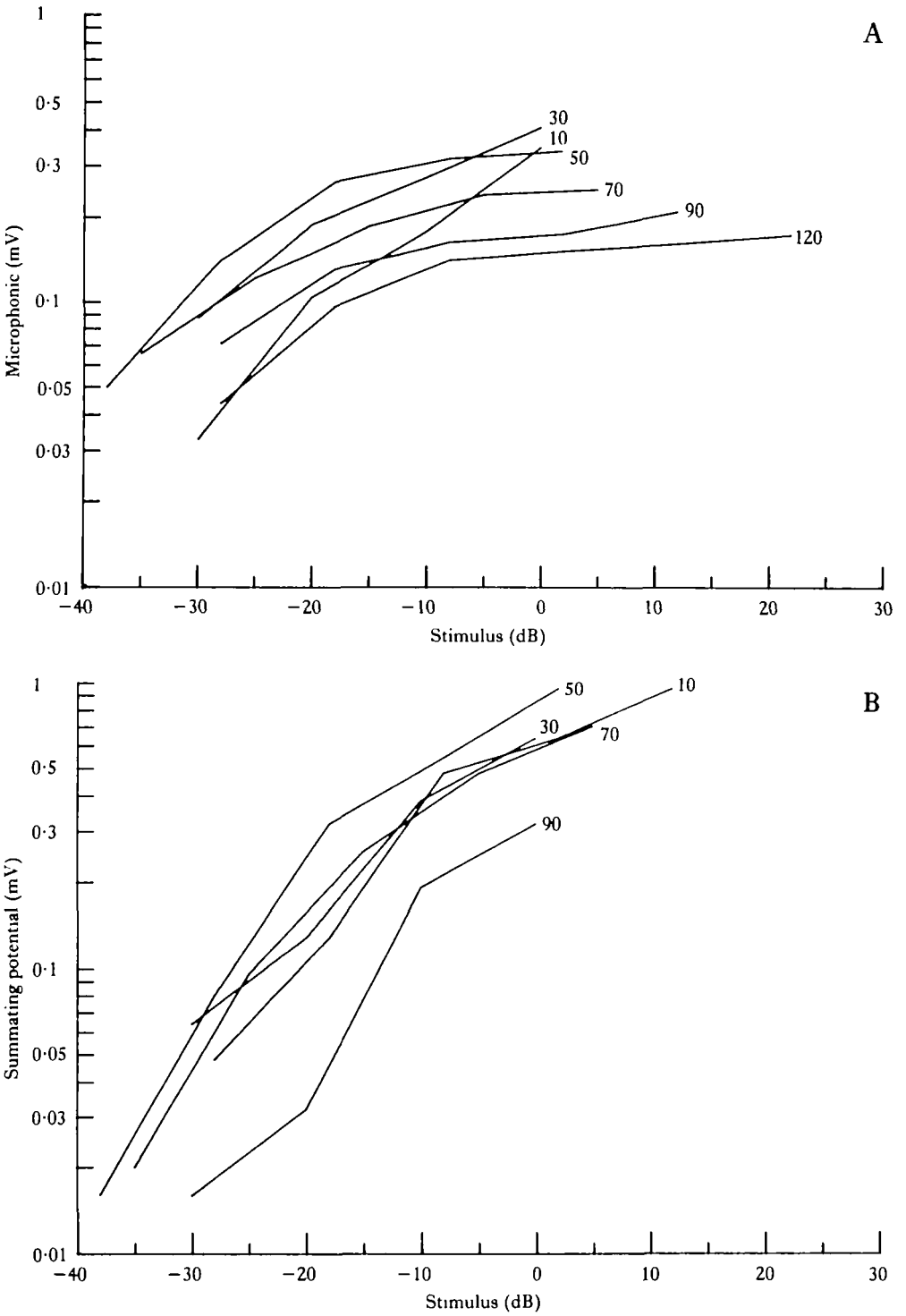

Fig. 5. The relationships between the intensity of the stimulus and the microphonic potential (A) and summating potential (B) for a single preparation at the different stimulus frequencies indicated in Hz against each trace. The stimulus intensity is expressed in dB relative to a 2 μm displacement of the stimulus probe.

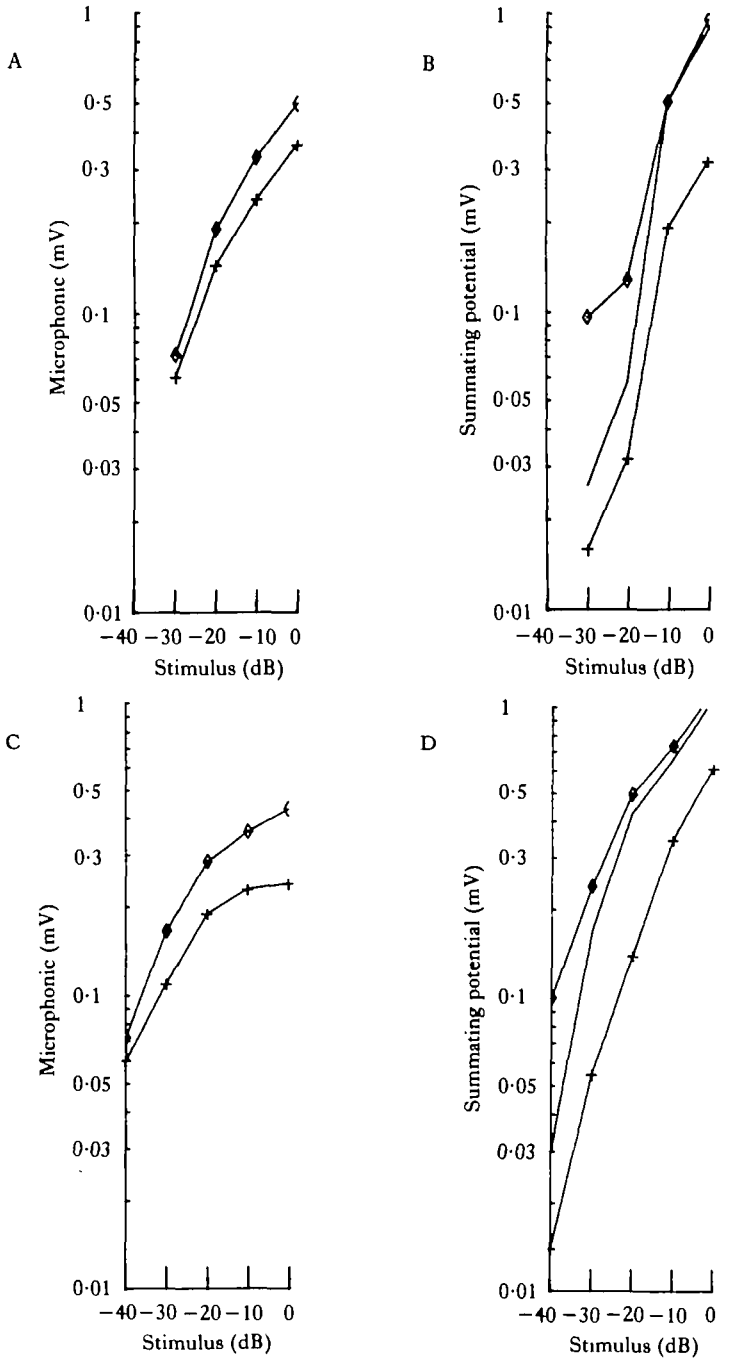

Fig. 6. The relationships between the stimulus intensity and the microphonic potential (A, C) and summating potential (B, D) in a single preparation at two stimulus frequencies: A, B (20 Hz); C, D (60 Hz). + Marks the control and ◇ the response during efferent stimulation at 60 pulses s^{-1} for 180 ms. The curves without symbols in B and D show the change in the amplitude of the summating potential after the deduction of the efferent potential of 0·07 mV.

relative contribution to the summating potential becomes progressively smaller when the stimulus amplitude is increased.

The amplitude-intensity relationships of the microphonic potential were also altered by efferent stimulation in that they tended to reduce the strong saturation of these potentials which occurred at high stimulus intensities and frequencies (Fig. 6C).

Changes in the harmonic composition of the microphonic, following stimulation of the efferent fibres

A close examination of the waveform of the microphonic showed that electrical stimulation of the lateral line nerve caused it to appear more symmetrical in response to sinusoidal mechanical stimulation. The effect was most noticeable at high intensities, when the microphonic was saturating (Figs 3, 4C), but it occurred at all stimulus intensities, including those within the linear region of the lateral line organ's response properties (Fig. 4A, B). The change in the waveform of the microphonic was also revealed as a change in its harmonic distortion, which was reduced by stimulation of the lateral line nerve. This distortion, and its reduction by the action of the efferent fibres, was frequency dependent. In Fig. 7 is shown the relationship between the

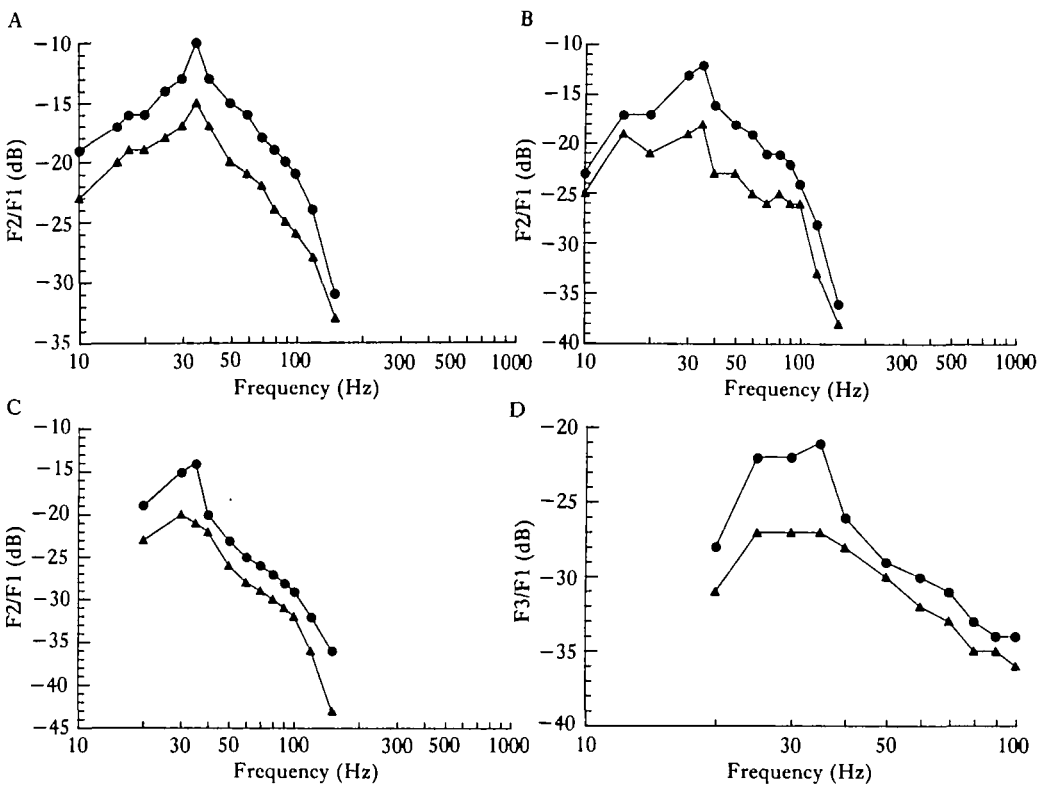

Fig. 7. A, B and C. The ratio of the second order harmonic component relative to the fundamental frequency of the microphonic potential (4th order relative to the stimulus frequency) versus frequency at 0; −10, and −20 dB respectively relative to a 2 μm displacement of the stimulus probe. D. Third order harmonic component of the microphonic versus frequency at 0 dB. ●, Control; ▲, during maximal electrical stimulation of the lateral line nerve at 80 pulses s^{-1} for 320 ms.

ratios of the second and third order harmonic components of the microphonic and its fundamental (fourth, sixth and second order, respectively, relative to the mechanical stimulus) and the frequency of mechanical stimulation, for responses recorded at a single location in the suborbital canal at several intensities. The distortion increased relative to the fundamental at a rate of about 6 dB/octave from low frequencies to a maximum at the centre frequency of the organs (30–40 Hz in the example illustrated) and declined at this rate above the centre frequency. Electrical stimulation of the lateral line nerve reduced this distortion at all levels of mechanical stimulation and, most noticeably, at the centre frequency.

Amplitude and phase relationships of the microphonic

Families of curves were constructed which depicted the change in amplitude of the microphonic with stimulus frequency at different intensities (Fig. 8). The curves, in effect, describe the filter properties of the mechanism responsible for generating the microphonic. At the lowest intensities, when the microphonic increases linearly with intensity, it can be seen that the relationship between the amplitude of the microphonic and the stimulus intensity resembles a broad band pass filter (Fig. 9A, B). The centre frequencies of this relationship were found to vary between 35 Hz and 65 Hz in 11 preparations with a mean of 53·5 Hz (S.E., 8·3). When the efferent fibres were electrically stimulated, the amplitude of the microphonic was increased over the entire frequency range, but the largest changes occurred around the centre frequency.

The amplitude changes, which were caused by electrical stimulation of the lateral line nerve, were also associated with small changes, usually less than 10° and never more than 25°, in the phase of the receptor potential relative to the mechanical

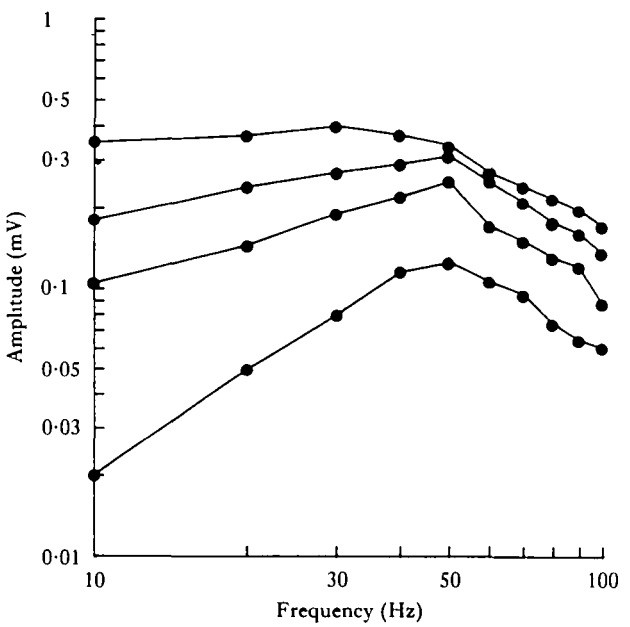

Fig. 8. Amplitude-frequency relationships of the microphonic potential recorded from a single location on the suborbital canal. In descending order, the curves show responses to 0 dB, −10 dB, −20 dB and −30 dB intensities of stimulation relative to a 2 μm displacement of the probe.

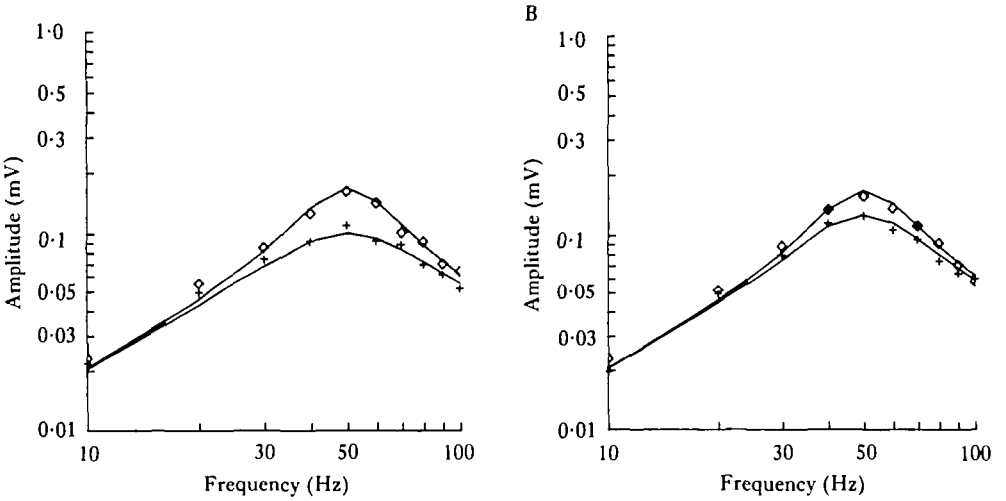

Fig. 9. The effect of electrical stimulation of the efferent fibres on the amplitude-frequency relationships of the microphonic potential in response to a −30 dB mechanical stimulus. A and B are from two different preparations. +, Control; ◇, measurements during efferent stimulation at 60 pulses s^{-1} for 180 ms. The theoretical curves drawn through the points are for the responses of a velocity detector with a low pass resonance at 50 Hz whose amplitude characteristics are given in equation (1). In (A) the damping factor is changed from 1 (control) to 0·6 (efferent stimulation) and in (B) from 1 to 0·8.

stimulus. In Fig. 10, the upper trace shows the effect of a 5 s burst of electrical stimulation of the lateral line nerve on the microphonic potential elicited in response to a continuous 60 Hz sinusoidal mechanical stimulus at an intensity within the linear response region of the lateral line organ. The middle and lower traces show the amplitude and phase changes, respectively, of the fundamental frequency of the microphonic (twice the stimulus frequency), caused by efferent stimulation. These traces represent the modulus and phase outputs of a pair of lock-in amplifiers set to measure only the fundamental frequency of a complex waveform, and in quadrature. The time courses of these measurements are limited by the time constants of the amplifiers (about 3 ms) and the electronics of the Omniphase (about 2 s for a step change in phase). In the linear operating region of each lateral line organ, from which measurements were taken, phase changes in the microphonic potential relative to the mechanical stimulus were not observed when the stimulus intensity was increased to produce an increase in the amplitude of the microphonic to match that caused by efferent stimulation.

A more comprehensive attempt was made in several lateral line organs to relate the phase of the microphonic, with and without electrical stimulation of the lateral line nerve, to that of the mechanical stimulus at different frequencies. It was the general case that at frequencies below the centre frequency of the organ, electrical stimulation of the lateral line nerve caused a phase lead of the microphonic, and above it, a lag (Figs 11, 12). There was no apparent phase change at the centre frequency.

A model to fit the observations

An attempt was made to find a model which fitted the linear responses of the microphonics to mechanical and efferent stimulation. An inspection of the amplitude

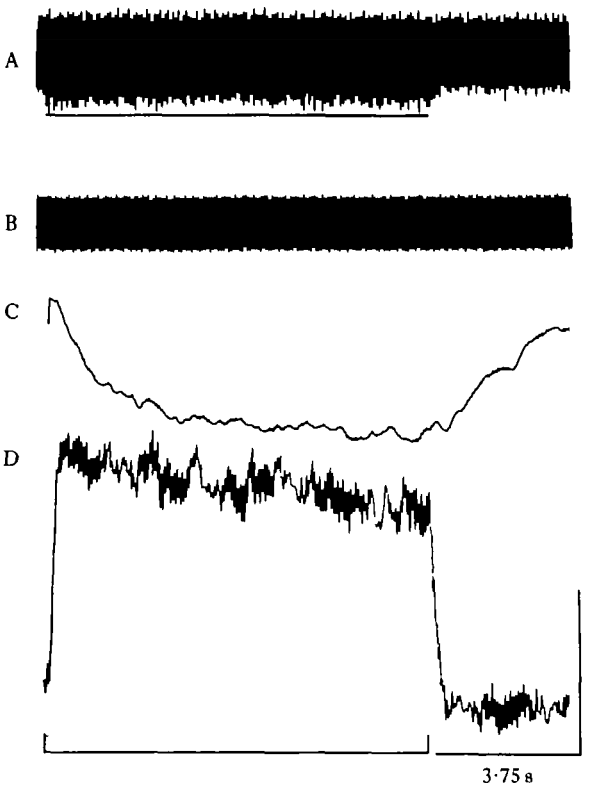

Fig. 10. Phase and amplitude changes in the microphonic potential caused by electrical stimulation of the lateral line nerve. Trace A, microphonic potential recorded in response to a constant 50 Hz mechanical stimulation with a 2 μm displacement. The bar indicates the 5 s period for which the efferent fibres were driven at 120 pulses s^{-1}, which is twice the rate necessary to produce a maximum change. Trace B, mechanical stimulus. Traces C and D show the phase and amplitude changes in the microphonic measured with lock-in amplifiers and omniphase module respectively. The time constant of the lock-in amplifier was 3 ms, and the response time of the Omniphase to a step change in phase is about 2 s. Vertical bar is 600 μV for A, 12·5° for C and 50 μV for D.

and phase relationships of the microphonic potential with respect to the mechanical stimulus, and reference to previous models of the lateral line system (Kuiper, 1956; Kroese, van der Zalm & van den Berken, 1978) indicated that the lateral line canal organ was coupled by viscous drag to the motion of the stimulating sphere, and that it also behaved as an approximately critically damped, low pass resonator.

The amplitude characteristics of a low pass resonance are given by

$$y = \left[\frac{1}{\left(1 - \frac{\omega^2}{\omega_0^2}\right)^2 + T^2 \frac{\omega^2}{\omega_0^2}} \right]^{\frac{1}{2}} \quad (1)$$

where y is the amplitude gain of the low pass resonance, ω_0 is the natural cut-off frequency and T is the damping factor (Bendat & Piersol, 1971). In a mechanical system ω_0 is determined by the elasticity and mass of the vibrator and T is determined by 'friction' or resistance to movement. The effect of increasing T is to decrease the frequency selectivity of the resonance and to shift the maximum amplitude of vibration to a frequency below ω_0. When T is equal to one, the system is critically damped.

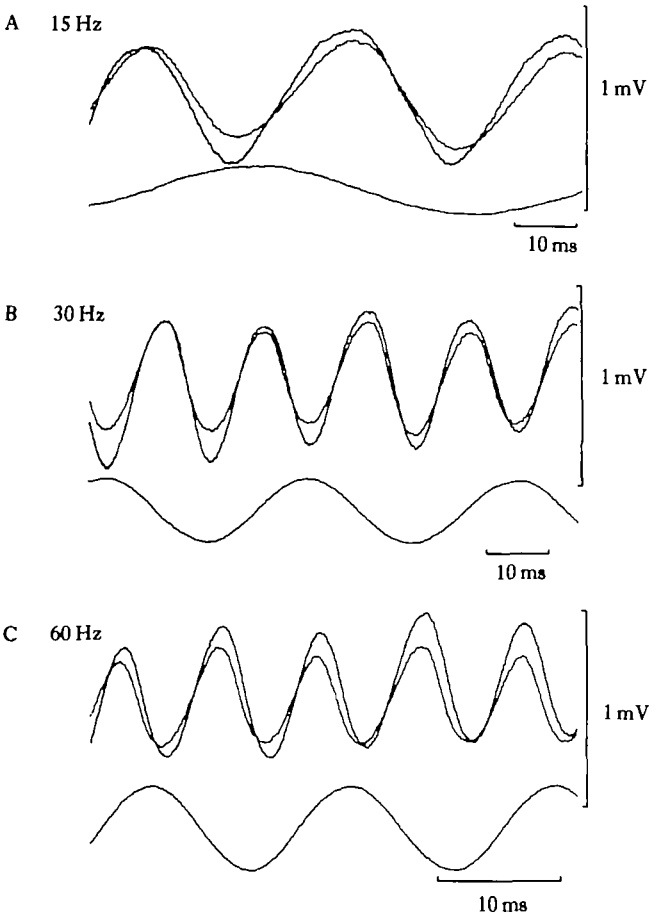

Fig. 11. Microphonic potentials recorded from a single preparation with A, 15 Hz; B, 30 Hz; and C, 60 Hz mechanical stimulation at 0 dB relative to a 2 μm displacement of the stimulus probe. Thin trace, control; thick trace, during electrical stimulation of the lateral line nerve at 60 pulses s^{-1} for 180 ms. Lower trace voltage input to stimulus probe. Each trace is the average of 16 sweeps.

and in this condition it shows little frequency selectivity and, if mechanically disturbed, it returns optimally to its mean position without oscillation.

The phase of the low pass resonator is given by:

$$p = \tan^{-1}\left[\frac{-\left(\frac{\omega}{\omega_0}\right)\cdot T}{1-\left(\frac{\omega^2}{\omega_0^2}\right)}\right] \qquad (2)$$

At frequencies well below the natural frequency, ω_o, the forced oscillation is in phase with the driving force and lags the driver by $\pi/2$ at ω_o and by π radians at frequencies well above this. This phase change takes place over a short frequency range either side of ω_o if the damping is light, but occurs smoothly, without transition, if the system is critically damped.

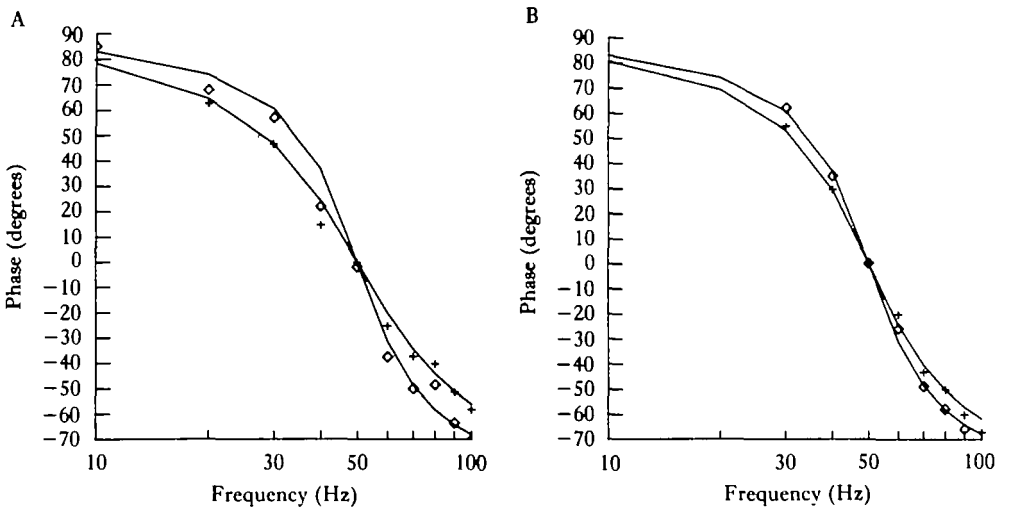

Fig. 12. The phase of the microphonic relative to that of the stimulus probe versus frequency measured at an intensity −30 dB relative to a 2 μm displacement of the stimulus probe for two preparations. +, Control; ◇, during electrical stimulation of the lateral line nerve at 60 pulses s^{-1} for 180 ms. The theoretical curves are for a velocity detector with a low pass resonance at 50 Hz whose phase characteristics are given in equation (2), which changes its damping factor from 1 to 0·6 (A) and from 1 to 0·8 (B).

Values for the natural frequency of the damped, low pass resonance and the damping factor were estimated from the data in the linear regions of the response characteristics. These values were used in equations 1 and 2 to fit theoretical curves to the measured amplitude and phase characteristics of microphonic potentials recorded in response to low intensity stimuli when the lateral line organs are operating in their linear range.

It is particularly interesting to observe that when this model is used to describe the change in the amplitude of the microphonic with frequency, in response to low amplitude water displacements, it is necessary to change only one parameter in order to account for the changes observed when the efferent fibres are stimulated. This is the damping factor of the low pass resonance, and in the examples illustrated in Fig. 2, this decreased by about 0·2–0·4 of the nearly critically damped control state when the efferent fibres were stimulated.

DISCUSSION

The experiments described in this paper have revealed that electrical stimulation of efferent fibres in the lateral line nerve caused frequency dependent increases in the microphonic and summating potentials recorded from sub-orbital canal organs in the perch, and changes in the phase and harmonic composition of the microphonic waveform.

In their linear operating range, the sub-orbital canal organs of the perch behave as critically damped, low pass resonators coupled to the viscous flow of fluid in their environment. These observations are in agreement with Kuiper's (1956) discovery that the cupulae of the ruff, *Acerina cernua*, behaved as critically damped resonators

when they were driven directly and with the demonstration by Kroese *et al.* (1978) that cupulae of the superficial lateral line organs in *Xenopus* were coupled to the velocity of water movement in their immediate environment. In the perch, electrical stimulation of the efferent fibres causes frequency dependent phase and amplitude changes in the microphonics which are consistent with the hypothesis that it is the damping factor of the low pass resonance which is altered. If the frequency dependent characteristics of the microphonic potential are due to the mechanical properties of the lateral line organs, then the efferent fibres have in some way altered them to reduce the damping between the movements of the cupula and the responses of the hair cells. There is a precedence for this proposal based on changes in the non-linear behaviour of cochlear microphonic and middle ear mechanics following stimulation of the efferent system in the mammalian auditory system (Mountain, 1980; Siegel & Kim, 1980).

It may be that the frequency-dependent properties of the microphonic potential, which are modified by efferent stimulation, are due to the electrical properties of the hair cells. For example, Crawford & Fettiplace (1981) have attributed the frequency tuning of hair cells in the turtle cochlea to an electrical resonance in their membrane properties. However, the possibility of similar electrical resonances occurring as a property of hair cell membranes in lateral line receptors has yet to be explored.

The non-linear properties of the intracellular receptor potentials recorded from lateral line organs – in particular, their saturation and harmonic distortion – are also influenced by efferent stimulation. Outside their linear range the extracellularly recorded receptor potentials share a property in common with intracellularly recorded potentials from inner hair cells in the mammalian cochlea. From frequencies well below their centre frequency, the responses of the hair cells saturate at increasingly lower amplitudes with increasing stimulus frequency (Russell & Sellick, 1978). When the efferent fibres are stimulated, the rate of saturation of the lateral line microphonic and summating potentials tends to be reduced, although the frequency-dependent trend in their saturation remains. Efferent stimulation also reduces the harmonic distortion of the waveform, making it appear more symmetrical in the depolarizing direction (Fig. 7) and this reduction is also frequency dependent. It may be that the efferent fibres have altered the electrical properties of the hair cells in such a way as to reduce the voltage sensitivity of the cells' membrane conductance. Current-voltage studies of hair cells in the isolated frog sacculus by Corey & Hudspeth (1979) showed that they became strongly rectified when polarized or depolarized. If the rectification is virtually instantaneous, then it could account for our observations. However, the time courses of the conductance changes underlying their observations have not been described and similar conductance changes operating in lateral line hair cells may be too slow to account for the saturation of the microphonic and summating potentials. If saturation is due to limitations in the motion of stereocilia, then they behave as if they offer progressively increasing resistance to displacements towards the kinocilium. If this is so, then efferent stimulation appears to change their behaviour as hardening springs and make them more linear. The precise nature of the post synaptic action of efferent fibres on hair cells must await further intracellular and micromechanical studies.

We thank Dr J. Ashmore for his helpful discussion and comments on the manuscript and Mrs E. M. Cowley for her skilled technical assistance. This work was supported by a grant from the M.R.C.

REFERENCES

BENDAT, J. S. & PIERSOL, A. G. (1971). *Random Data: Analysis and Measurement Procedures*. New York, Chichester, Brisbane & Toronto: Wiley-Interscience.

COREY, D. P. & HUDSPETH, A. J. (1979). Ionic basis of the receptor potential in a vertebrate hair cell. *Nature, Lond.* **281**, 675–677.

COREY, D. P. & HUDSPETH, A. J. (1980). Mechanical stimulation and micromanipulation with piezoelectric bimorph elements. *J. Neurosci. Methods* **3**, 183–202.

CRAWFORD, A. C. & FETTIPLACE, R. (1981). An electrical tuning mechanism in turtle cochlear hair cells. *J. Physiol, Lond.* **312**, 377–412.

DE ROSIER, D. J., TILNEY, L. G. & EGELMAN, E. (1980). Actin in the inner ear: the remarkable structure of the stereocilium. *Nature, Lond.* **287**, 291–296.

FLOCK, Å. (1965). Electron microscopical and electrophysiological studies on the lateral line canal organ. *Acta oto-laryngol., Stockh. Suppl.* **199**, 1–90.

FLOCK, Å. & CHEUNG, H. C. (1977). Actin filaments in sensory hairs of inner ear receptor cells. *J. Cell Biol.* **75**, 339–343.

FLOCK, Å., JØRGENSEN, J. M. & RUSSELL, I. J. (1973). The physiology of individual hair cells and their synapses. In *Basic Mechanisms in Hearing*, (ed. A. R. Møller), pp. 273–302. New York, London: Academic Press.

FLOCK, Å. & RUSSELL, I. J. (1973*a*). Efferent nerve fibres: Postsynaptic action on hair cells. *Nature, Lond.* **243**, 89–91.

FLOCK, Å. & RUSSELL, I. J. (1973*b*). The post-synaptic action of efferent fibres in the lateral line organ of the burbot *Lota lota*. *J. Physiol., Lond.* **235**, 591–605.

FLOCK, Å. & RUSSELL, I. J. (1976). Inhibition by efferent nerve fibres: action on hair cells and afferent synaptic transmission in the lateral line canal organ in the Burbot, *Lota lota*. *J. Physiol., Lond.* **257**, 45–62.

HARRIS, G. G. & FLOCK, Å. (1967). Spontaneous and evoked activity from the *Xenopus laevis* lateral line. In *Lateral Line Detectors*, (ed. P. Cahn), pp. 135–161. Indiana University Press.

HUDSPETH, A. J. & COREY, D. P. (1977). Sensitivity, polarity and conductance change in the response of vertebrate hair cells to controlled mechanical stimuli. *Proc. natn. Acad. Sci. U.S.A.* **74**, 2407–2411.

KROESE, A. B. A., VAN DER ZALM, J. M. & VAN DEN BERKEN, J. (1978). Frequency response of the lateral line organ of *Xenopus laevis*. *Pflugers. Arch. ges. Physiol.* **375**, 167–175.

KUIPER, J. W. (1956). The microphonic effect of the lateral line organ. Ph.D. thesis. Rijksuniversiteit te Groningen.

MACARTNEY, J. C., COMIS, S. D. & PICKLES, J. O. (1980). Myosin in the cochlea – a basis for active mobility. *Nature, Lond.* **288**, 491–492.

MOUNTAIN, D. C. (1980). Changes in endolymphatic potential and crossed olivocochlear bundle stimulation alter cochlear mechanisms. *Science, N.Y.* **210**, 71–72.

MOUNTAIN, D. C., HUBBARD, A. & GEISLER, C. D. (1980). Voltage-dependent elements are involved in the generation of the cochlear microphonic and sound induced resistance changes measured in scala media of the guinea pig. *Hearing Res.* **3**, 215–229.

OSWALD, R. L. (1978). Injection anaesthesia for experimental studies in fish. *Comp. Biochem. Physiol.* **60**C, 19–26.

ROBERTS, B. L. & RUSSELL, I. J. (1972). The activity of lateral line efferent neurones in stationary and swimming dog fish. *J. exp. Biol.* **57**, 435–448.

RUSSELL, I. J. (1968). Influence of efferent fibres on a receptor. *Nature, Lond.* **219**, 177–178.

RUSSELL, I. J. (1971*a*). The role of the lateral line efferent system in *Xenopus laevis*. *J. exp. Biol.* **54**, 621–641.

RUSSELL, I. J. (1971*b*). The pharmacology of efferent synapses in the lateral line system of *Xenopus laevis*. *J. exp. Biol.* **54**, 643–658.

RUSSELL, I. J. (1976). Amphibian lateral line receptors. In *Frog Neurobiology*, (eds R. Llinas & W. Precht), pp. 513–550. Berlin, Heidelberg: Springer-Verlag.

RUSSELL, I. J. & SELLICK, P. M. (1978). Intracellular studies of hair cells in the mammalian cochlea. *J. Physiol., Lond.* **284**, 261–290.

SIEGEL, J. H. & KIM, D. O. (1980). Efferent synaptic activity modifies cochlear mechanics seen in ear canal acoustic distortion products. *Neurosciences* **6**, 18.1.

SMITH, C. A. (1968). Electron microscopy of the inner ear. *Ann. Otol. Rhinol. Laryngol.* **77**, 269–284.