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Differential responses of two types of electroreceptive afferents to signal distortions may permit capacitance measurement in a weakly electric fish, *Gnathonemus petersii*

Gerhard von der Emde[1]* and Horst Bleckmann[2]

[1] Universität Regensburg, Zoologisches Institut, W-8400 Regensburg, Federal Republic of Germany
[2] Universität Bielefeld, Fakultät für Biologie II, Postfach 8640, W-4800 Bielefeld, Federal Republic of Germany

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Summary. *Gnathonemus petersii* discriminates between ohmic and capacitive objects. To investigate the sensory basis of this discrimination we recorded from primary afferents that innervate either A or B mormyromast sensory cells. Modified and natural electric organ discharges were used as stimuli. In both A and B fibres frequencies below the peak-power frequency (3.8 to 4.5 kHz) of the electric organ discharge caused minimal first-spike latencies and a maximum number of spikes. A fibres did not discriminate phase-shifted stimuli, whereas B fibres responded significantly with a decrease in first-spike latency if the phase shift was only $-1°$. In both A and B fibres an amplitude increase caused a decrease in spike latency and an increase in spike number; an amplitude decrease had the reverse effect. If stimulated with quasi-natural electric organ discharges distorted by capacitive objects, the responses of A fibres decreased with increasing signal distortion. In contrast, the responses of B fibres increased until amplitude effects began to dominate. *Gnathonemus* may use the physiological differences between A and B fibres to detect and discriminate between capacitive and purely ohmic objects.

Key words: Weakly electric fish – Electrolocation – Complex impedance – Object discrimination – Sensory physiology

Introduction

Weakly electric fish of the African family Mormyridae emit pulse-type electric organ discharges (EODs). In order to detect and discriminate nearby objects, mormyrids monitor their EOD with electroreceptors (mormyromasts) scattered all over their body surface. The electric fields caused by EODs are altered by objects placed in the vicinity of an electroreceptor (Schlegel 1975; Bastian 1986). Local amplitude changes of the EOD depend on the electrical impedance of the object: an impedance lower than that of the surrounding water leads to an increase in EOD amplitude, an impedance higher than that of the water has the reverse effect.

Natural objects such as plants or animals often have complex impedances, i.e. these objects have both ohmic and capacitive components (Schwan 1963; Heiligenberg 1973, 1977; von der Emde and Ringer 1992). Capacitive objects affect the local EODs in several ways (von der Emde 1990): (1) the peak-to-peak (p-p) amplitude of the EOD changes depending on the complex impedance which is negatively correlated with the capacitive value of the object. It should be noted that different combinations of resistors and capacitors can lead to identical amplitude changes of the EOD; (2) the spectral composition of single EODs is altered because the lower frequencies within the EOD are attenuated more strongly by a capacitive load than the higher frequencies. This leads to a shift of the peak-power spectral frequency of the EOD to higher values; (3) the waveform of the local EOD is distorted due to a frequency-dependent phase shift of the EOD. In the biphasic EOD of *Gnathonemus petersii* the relative amplitudes of the two main phases change, and a third phase may occur. These waveform changes constitute time-domain cues. All such changes of the local EOD depend on the capacitive value of the object under investigation. While the amplitude of the EOD monotonically increases with the capacity of the object, the pulse distortion (measured as the amplitude ratio of the main positive phase to the main negative phase) has – for water of a certain conductivity – a maximum around 1 nF. Pulse distortions decrease to both smaller and larger capacities.

Electrolocating mormyrids can detect and discriminate capacitive objects within a certain range which coincides with the range of capacitances which distort the local EOD waveform (von der Emde 1990). Within that range, mormyrids can also discriminate between capacitive and purely ohmic objects even if the magnitudes of the impedances of the objects under investigation are

* *Present address:* Robert S. Dow Neurological Science Institute, Good Samaritan Hospital and Medical Center, 1120 NW 20th Avenue, Portland, OR 97209, USA

Abbreviations: ELL, electrosensory lateral line lobe; EOD, electric organ discharge; LFS, local filtered signal; p-p, peak-to-peak

Correspondence to: G. von der Emde

identical (von der Emde 1990; von der Emde and Ringer 1992). While the p-p amplitudes of the local EODs may be similar, pulse distortions occur only in the presence of a capacitive object. From behavioural studies it was concluded that mormyrids not only measure the local EOD amplitude but also the pulse distortions caused by the capacitance of an object (von der Emde 1990; von der Emde and Ringer 1992).

There are at least two mechanisms the fish could use to identify a capacitive object: (1) the animal may sense a shift in the peak-power frequency of the local EOD, or (2) it may perceive changes of the EOD waveform, i.e. it may use time-domain cues (Heiligenberg and Altes 1978). In the latter case, the fish should be able to detect minute waveform distortions even if the frequency content, the amplitude and the duration of the EOD remain the same. In the context of communication, such abilities have been demonstrated for the mormyrid *Brienomyrus brachyistius* (Hopkins and Bass 1981) and the gymnotiform electric fish *Hypopomus artedi* (Heiligenberg and Altes 1978) which responded differently to electric stimulus pulses with identical spectral amplitudes but different spectral phase functions.

Gymnotiforms have tuberous organs called P and T units (Bennett 1971; Scheich et al. 1973). P units encode the signal amplitude, whereas T units, in contrast, are exact phase coders which react differently to capacitive versus resistive shunts having the same impedance (Scheich and Bullock 1974). Thus, a central comparison of P and T unit input may enable gymnotiform fish to detect capacitances unambiguously. In addition to mormyromasts, mormyrids have Knollenorgans and ampullary electroreceptors (Bennett 1967). Mormyrids, however, rely exclusively on mormyromast input for electrolocation (Bennett 1965; Szabo and Hagiwara 1967; Zakon 1986; Bell et al. 1989) for two reasons: (1) the perception of Knollenorgan input is centrally blocked by a corollary discharge during EOD emission (Bennett and Steinbach 1969; Zipser and Bennett 1976; Bell 1986; Bell and Grant 1989) and (2), the ampullary organs are low-frequency electroreceptors that do respond to the fish's own EOD but are only minimally affected by objects (Bell and Russell 1978a).

Mormyromasts are unique in having two morphologically distinct populations of receptor cells, called A and B cells (Szabo and Wersäll 1970; Bell et al. 1989). A and B cells, both of which encode the local stimulus amplitude by first-spike latency and by the number of spikes elicited per EOD, terminate in separate brain areas (Bell and Russell 1978b; Bell and Szabo 1986). Several physiological differences between A and B fibers have been described (Bell 1990). These include the threshold to square-wave stimuli, the maximal number of spikes per EOD, the tuning to single-cycle sine waves, and strength-duration curves. Despite these differences it appears that both A and B fibres are mainly amplitude coders which are not well suited for exact time measurements (Bell 1990).

If this is true, how can mormyrids discriminate between purely ohmic and purely capacitive objects in cases where these objects cause identical changes in EOD amplitude? There are only two possible explanations: either the fish has differentially tuned receptor cell populations, or some of its sensory cells are waveform-coders. Neither assumption is supported by the present literature. Therefore, we extended the study of Bell (1990) by stimulating mormyromast electroreceptors with various distorted and undistorted EODs while recording from their primary afferents.

This paper demonstrates that A and B fibres of *Gnathonemus petersii* indeed respond differently to biologically relevant distortions of the EOD: B fibres are extremely sensitive to pulse distortions caused by capacitive objects, whereas A fibres are mere amplitude coders, i.e. they do not encode the EOD waveform. A central comparison of the input from the two receptor cell populations should allow mormyrids to discriminate between capacitive and ohmic objects. A preliminary report of some of these results has previously been published (von der Emde and Bleckmann 1992).

Materials and methods

Animals. Fourteen male and female *Gnathonemus petersii* (Mormyridae) ranging in length (mouth to fork of tail) from 8 to 17 cm were used. Fish were maintained in aquaria (150–200 l) at 24–26 °C. Water conductivity was 150–300 $\mu S \cdot cm^{-1}$.

Surgery. Surgery was done under anaesthesia (ethyl *p*-aminobenzoate, 0.003%) and consisted of carefully exposing a small part of the dorsal branch of the posterior lateral line nerve just behind the cranium (afferent fibres from the dorsal electroreceptors were selected because the dorsal electroreceptors can be easily identified and recorded from under the operating microscope). A piece of plastic was glued to the skin around the ventral part of the small wound to retain mineral oil over the nerve. After surgery the fish were immobilized (Pancuronium, 0.1–0.2 µl/g) and placed in the experimental tank. Water conductivity was between 200 and 300 $\mu S \cdot cm^{-1}$ and temperature was maintained between 24 and 27 °C. Aerated fresh water was passed at a rate of about 50 $ml \cdot min^{-1}$ over the fish's gills by use of polyethylene tubing inserted into the mouth. All animals survived the experiments.

Recording. The action potentials of single mormyromast afferents were recorded by lifting fine bundles of nerve fibres from the exposed nerve on a small hook electrode made of either a chlorided silver wire or a fine steel (insect) needle. The nerve bundle was always cut just proximal to the recording electrode, i.e. between the brain and the recording electrode. In this way antidromic spikes were not recorded (Slesinger and Bell 1985). The reference electrode was a chlorided silver wire placed in the muscle near the exposed lateral line nerve. The electrode signal was amplified (DAM 80), and spikes routed to a digital tape recorder (Biologic, DAT 1800) for back-up and to a computer data acquisition system (GW Instruments MacAdios II; Apple Macintosh IIci) for real-time display and subsequent analysis.

Stimuli. In order to obtain quasi-natural stimuli, local EODs were recorded differentially prior to the experiments by two carbon electrodes (diameter 0.3 mm, distance between electrode tips about 2 mm) positioned at an angle of 90° close (< 1 mm) to the pore of a mormyromast organ of a *G. petersii*. Local EODs were also recorded in the presence of objects with various electrical properties. This was done by positioning a dipole-object (Fig. 1A) at a distance of about 2 mm from the recording electrodes. The electrical properties of the object could be changed by introducing electronic elements into the circuit between the poles (cf. von der Emde 1990).

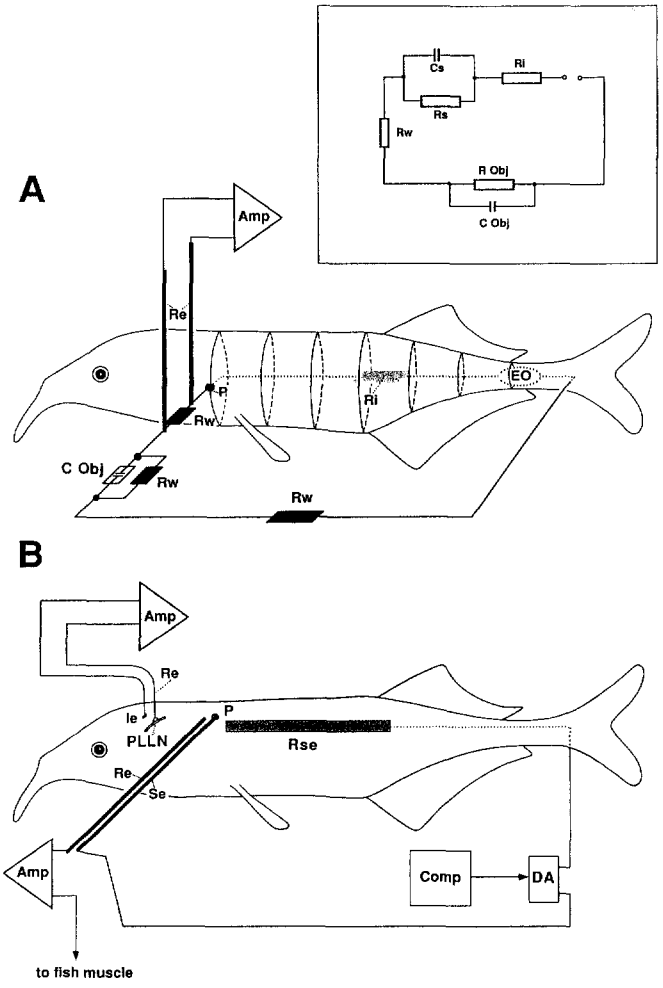

Fig. 1. A Experimental arrangement for recording of fish-generated EODs. In the case shown the EOD was altered by a capacitive object *(C Obj)* placed within a few millimetres of the fish. *Inset:* simplified circuit diagram of fish, water and capacitive object. **B** Experimental arrangement for the application of artificial electric stimuli or of quasi-natural, pre-recorded EODs. *Abbreviations:* Amp, amplifier; Comp, computer; C Obj, capacitive object; Cs, skin capacity of fish; DA, digital to analog converter; EO, electric organ; Ie, indifferent electrode; P, pore of mormyromast; PLLN, dorsal branch of the posterior lateral line nerve; Re, recording electrode; Ri, inner resistance of fish; R Obj, resistance of object; Rs, resistance of fish's skin; Rse, reference stimulation electrode behind fish; Rw, water resistance; Se, stimulation electrode

The recorded signals were digitized at 2 MHz (Digital oscilloscope DSO 3335, Krenz Electronics) and stored on the hard disk of an IBM computer.

Besides natural local EODs, EODs manipulated by computer were also used as stimuli. Custom-made software written in Turbo-Pascal together with a Pascal version of the subroutine FFT842 of the package FAST (Bergland and Doland 1979) were used for digital signal processing. The waveform of the local EOD (without an object present) was altered by retarding the phase angle of all positive frequencies of the FFT phase spectrum by a constant angle, while the negative frequencies were advanced by the same angle (Heiligenberg and Altes 1978; Hopkins and Bass 1981; Hopkins and Westby 1986). In this way the EOD waveform was phase-shifted in a similar way to that effected by a capacitive object. This method guarantees that the power spectrum and the duration of the EODs are left unchanged. A phase shift of 0° (or 360°) represented the natural EOD, a shift of −180° its negative version (Fig. 2). EODs subjected to phase-shifts between 0 and −30° resembled EODs altered by capacitive objects.

Outside-positive square waves 10 ms long were used as stimuli to discriminate between A and B fibres as described by Bell (1990). Two criteria were used: 1) threshold intensity to 10 ms outside-positive square pulses and 2) maximal spike number to a large amplitude stimulus. With these two criteria A and B fibres could be discriminated unequivocally. Thresholds were taken as the stimulus voltage that just evoked 1:1 following to the stimulus by an afferent spike. When EODs were used as stimuli during threshold measurements, p-p voltages were taken. Stimulus amplitude was measured at the receptor pore by a saline-agar electrode with reference to an internally placed silver wire electrode (Bell 1990) so that stimulus intensities were in terms of voltage drops across the skin.

The stored stimulus pulses were played back by an IBM computer with a digital-to-analog converter (CompuGen 840, Gage Applied Sciences Ltd.) operating at a sampling rate of 2 MHz. The output of the converter was passed through a custom-made dB-attenuator for amplitude adjustment and through a stimulus isolation unit to isolate the stimuli from ground. Electrical stimuli were delivered through a small carbon rod (diameter 0.3 mm) which was insulated except for 2 mm from the tip. DC between the electrodes was blocked by capacitor coupling. The tip of the stimulus electrode was positioned close (about 1 mm) to the electroreceptor pore. The reference stimulation electrode was a larger carbon rod (diameter 6 mm, length 5 cm) which was placed parallel to the contralateral body side of the fish (Fig. 1B).

Each mormyromast afferent encountered was first identified as an A or B fibre and then tested with several series of stimuli. During a series, each stimulus was provided 15 times at a rate of 2 Hz. Before switching to the next stimulus, a 2-s break was inserted. Before ending a series the first stimulus was played back to control for changes in the physiological condition of the fibre under test. Therefore in Figs. 5 to 9 two responses to the first stimulus (i.e. the unshifted EOD, see below) sometimes become visible. If not otherwise stated the amplitude of the first stimulus within a series was adjusted to 1, 2 or 3 dB above threshold. In this way the fibres were prevented from being driven into saturation.

Frequency tuning. A stimulus series was designed to determine the frequency tuning of the fibres. The first stimulus was an initially negative-going single-period sine wave with a duration of 2 ms (500 Hz). While the stimulus frequency was increased in the following stimuli in 500-Hz steps until a fibre ceased to respond, the p-p voltage was held constant. Thus, the energy content and the duration decreased as the frequency increased.

Phase-shifted EODs. Two series with natural EODs whose positive frequency components were phase-shifted relative to the negative components by a fixed-phase angle with the aid of the computer were used as stimuli. EOD phase angles were shifted in steps of −5° from 0 to −45° and in steps of −15° from −45 to −90° in the first series. Stimulus duration, p-p amplitude and the amplitude spectra of the stimuli were not altered within this series. Because a phase shift of −5° was sufficient for a significant response in B fibres (see Results), a second series was conducted in which phase shifts increased in steps of −1° from 0 to −10° (Fig. 2).

Signal distortions caused by capacitive objects. In order to determine the sensitivity of fibres to biologically relevant signal distortions, EODs prerecorded in the presence of capacitive objects were also used as stimuli. Capacitive values of the objects changed from 100 nF, which caused only minor waveform distortions, to 1 nF which caused strong changes in waveform. To separate the effects caused by wave amplitude (voltage), the p-p amplitude of the EODs was held constant throughout the first series. In a second series the stimulus voltage was allowed to change by the same amount as with natural capacitive objects. Capacitive values varied between 50 nF (highest amplitude) and 0.1 nF (weakest amplitude). In a third series the stimulus amplitude was allowed to change as in the second series; however, in this series the stimulus waveform was kept constant. Thus, the effect of amplitude change alone could be measured.

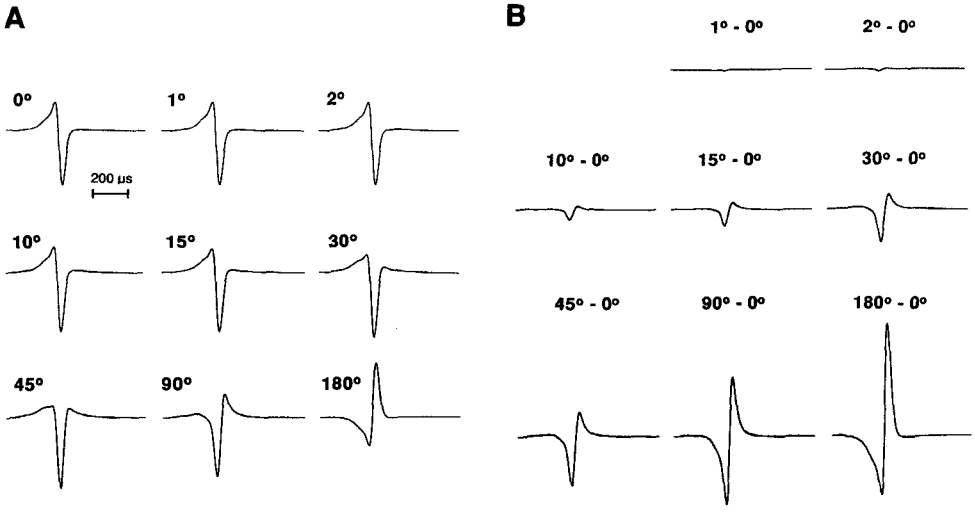

Fig. 2. **A** The EOD of *G. petersii* (*top left record;* inside positive is up) and examples of transformations obtained by subtracting the indicated degrees from the spectral phases of all positive frequencies while advancing those of the negative frequencies by the same phase angle. All pulses have identical amplitude spectra (Fourier transform magnitudes) and duration. Maximal spectral power of a single EOD is near 3900 Hz. **B** The differences between the undistorted EOD (*top left* in **A**) and EODs distorted by the indicated phase shifts. The signals were obtained by subtracting the undistorted EOD from the phase-shifted stimuli

Results

Besides 50–60 Knollenorgan afferents, a total of 86 fibres that innervated mormyromast electroreceptors were recorded. An unequivocal differentiation between A and B sensory cell input (cf. Bell 1990) was possible in 78 fibres.

Response thresholds

Square pulses. Measurement of thresholds to outside-positive 10-ms square pulses confirmed (Bell 1990) two classes of fibres with low (between 1 and 15 mV) or high (between 18 and 200 mV) amplitude thresholds. The maximum spike number caused by a single EOD also differed in these two classes: 5–8 spikes in the low-threshold group and 1–5 spikes in the high-threshold group (Table 1). According to Bell (1990) the low threshold group innervates B sensory cells and the high-threshold group innervates A sensory cells.

Phase shifted EODs. In A fibres thresholds to natural EODs were not affected by phase shifts between 0 and $-30°$ (Fig. 3A). In some A fibres, however, thresholds started to decrease slowly at phase shifts larger than $-30°$. In most B fibres threshold curves were different in that they started to decrease at a phase shift of $-5°$ (Fig. 3B). There was one B fibre that behaved differently: thresholds of this fibre increased up to a phase shift of $-10°$ and then started to decrease.

EODs distorted by capacitive objects. Thresholds to natural EODs distorted by capacitive objects (for signal examples see Fig. 7, left bottom trace) were not well separated in the two fiber types (Fig. 3B, D and Table 1). Thresholds of A fibres varied between 15 and 450 mV p-p amplitude; in B fibres the corresponding values were 10–175 mV. Because of this threshold overlap the response differences between A and B fibres were not significant (Table 1).

It should be noted that the threshold of a given A fiber

Table 1. Comparison of some physiological properties of A and B fibres

	Max. spike number to EOD	Best frequency (kHz)	Average threshold (mV) to a		Amplitude range (dB) which caused		Number of fibers			
							Phase sensitive		LFS-sensitive	
			positive square pulse	local EOD	a latency change of first spike	a change in the number of spikes	Decrease in latency	No decrease in latency	Decrease in latency	No decrease in latency
A cells	3.3 ± 0.89 $n=54$	2.0 ± 0.35 $n=5$	58.8 ± 50.6 $n=29$	202 ± 227 $n=23$	5–11 $n=24$	2–6 $n=24$	2 $n=33$	31	0 $n=42$	42
B cells	5.92 ± 0.72 $n=24$	2.1 ± 0.22 $n=5$	6.72 ± 4.2 $n=11$	63 ± 54 $n=9$	5–7 $n=9$	1–3 $n=10$	15 $n=16$	1	18 $n=20$	2
	$P<0.001$	$P>0.1$	$P<0.01$	$P>0.1$	$P<0.001$	$P<0.001$	$P<0.00001$		$P<0.00001$	

In the first four columns mean values $\pm$ SD are given. The seventh and eighth columns give the number of fibres that did or did not respond with a decrease in first spike latency to phase shifted EODs of constant amplitude. The last two columns give the number of fibres that did or did not respond positively to constant amplitude EODs distorted by capacitive objects. The LFS (local filtered signal) is the local EOD measured close to a receptor pore in the presence of a capacitive object. The last row of the table indicates whether the compared responses of A and B fibres are significantly different (Columns 1–6 *t*-test; columns 7–10: Fisher four-fold table test)

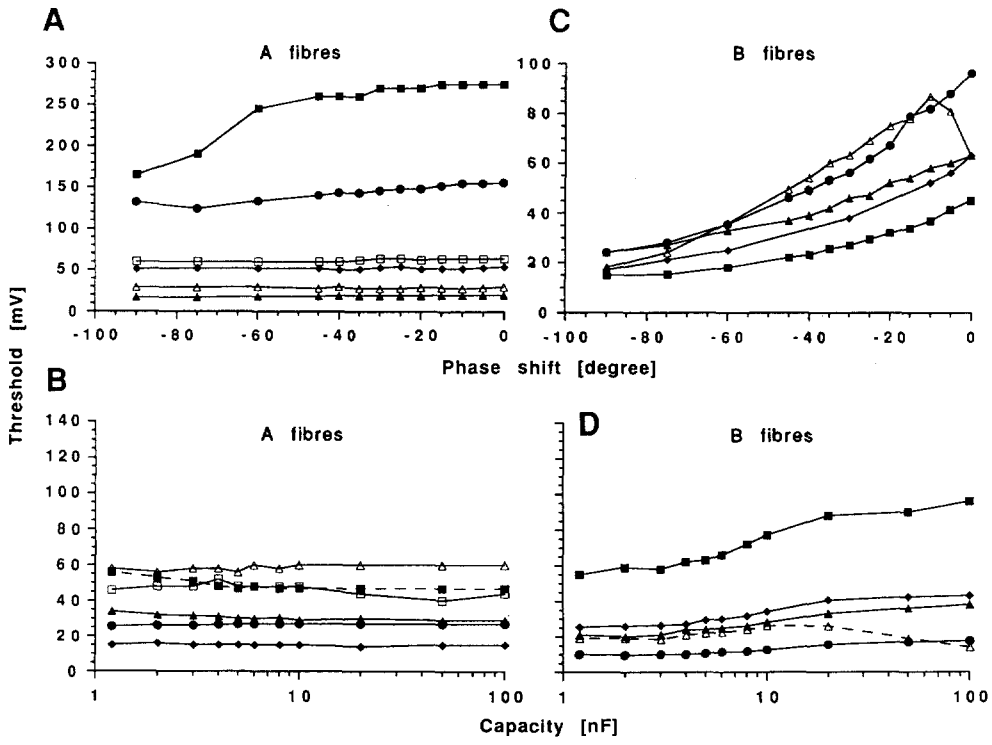

Fig. 3. Examples of the threshold of A fibres *(left)* and B fibres *(right)* to phase-shifted EODs with constant amplitude (**A, C**) and to EODs distorted by capacitive objects (**B, D**). Different symbols represent different fibres. Note that maximum pulse distortions occur at a phase shift of −90° *(top)* and a capacity of 1.2 nF *(bottom)*, respectively (cf. Figs. 2, 7, *left bottom trace*)

was almost constant irrespective of whether the EOD was distorted by a capacitive object or not (Fig. 3B). This was different in most B fibres: except for one fibre, thresholds decreased with decreasing capacitive values of the object (test range 100–1.2 nF; Fig. 3, right). Thus, B fibres were more sensitive to waveform-distorted EODs than to undistorted EODs.

Amplitude range

The dynamic amplitude range of the two fibre types differed significantly (Table 1). B fibres had a smaller amplitude range than A fibres, irrespective of whether changes in latency or maximal spike numbers were used as a criterion. Nevertheless, as already described (Szabo and Hagiwara 1967; Kramer-Feil 1976; Bell 1990), both fibre types showed basically the same response to an increase in stimulus amplitude. Up to a certain level, increasing amplitudes caused an increase in spike number and a decrease in spike latencies. An increase in stimulus intensity beyond saturation often caused an increase in latency and a decrease in spike number, i.e. a response reduction (Bennett 1965; Bell 1990).

Frequency tuning

Spike latencies were measured in 39 fibres with initially outside-negative sine wave stimuli at frequencies between 500 and 7000 Hz. All fibres reacted similarly to a single-period sine wave stimulus (Fig. 4). They were tuned very broadly and it was difficult to determine an exact best frequency. There was a minimal spike latency (and a maximum spike number) at an average frequency of 2.0 kHz in A fibres and at 2.1 kHz in B fibres (Table 1). Because of the broad tuning of both fibre types this difference in best frequency was not significant (cf. Table 1). If one considers that the peak power in the FFT amplitude spectra of a single cycle sine wave actually is about 70% lower in frequency than a sine wave of several periods [Viancour (1979) and personal observation], then the best frequencies of A and B fibres were between 1.4 and 1.5 kHz. The sensitivity of A and B fibres to both lower and higher frequencies decreased with respect to peak voltage. Our curves are similar to the threshold curves given by Bell (1990) who also found maximal sensitivities at frequencies well below the peak-power frequency of the EOD, which was between 3.8 and 4.5 kHz for the fish used in this study. At those frequencies the threshold curves are rising, i.e. fibres react less well if the stimulus frequency of the local EOD increases.

Responses to phase-shifted EODs

Thirty-three A fibres and 16 B fibres were tested with phase-shifted EODs of constant duration, amplitude spectra, and p-p amplitude. Due to the fact that the p-p amplitude of the EODs was held constant, the energy content of the signals slightly increased with increasing phase shifts (the energy increase was about 0.23% at −1° and 3.97% at −10°). Thus, within this series there was almost exclusively a change of waveform cues. First, the fibres were tested with stimuli phase-shifted in steps of −5° up to −45° and in steps of −15° up to −90°. Because a phase shift of −5° was sufficient for a significant latency shift in B fibres, a second series was con-

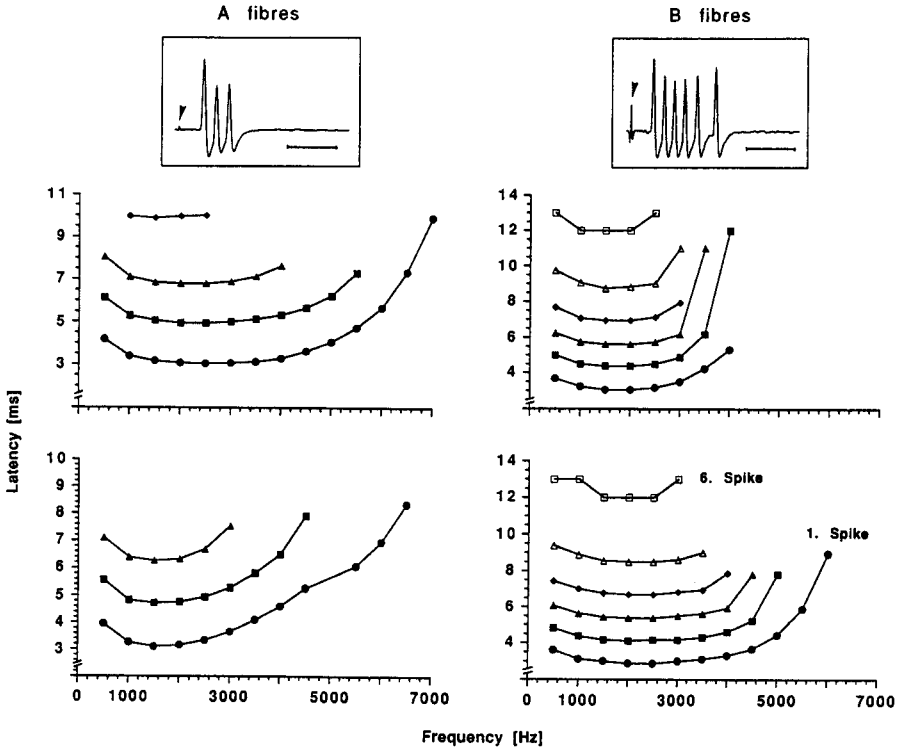

Fig. 4. Examples of tuning curves based on spike latencies of two A fibres *(left)* and two B fibres *(right)* to single-period sine-wave stimuli of different durations. In all cases analysed, the standard deviation (SD) of first-spike latency was below 0.065 ms (in one case 0.12 ms). Hence, the SD of the latencies are not shown in this figure and in Figs. 5–9. The peak-power of the EODs of the fish used for the experiments was between 3.8 and 4.5 kHz. In this figure and in Figs. 5–9, each latency value gives the mean of ten responses. ● first spike latency; ■ second spike latency; ▲ third spike latency; ◆ fourth spike latency; △ fifth spike latency; □ sixth spike latency; ○ seventh spike latency; ◇ eighth spike latency (a seventh and eighth spike occur only in some of the recordings shown either in Figs. 5, 6 or 8). *Insets:* the insets show the response of an A fibre *(top left)* and a B fibre *(top right)* to the pre-recorded EOD of *Gnathonemus petersii*. In both cases stimulus intensity was adjusted such that the fibres responded with the maximum number of spikes. *Arrowheads* indicate stimulus artefacts. *Bar scales* equal 5 ms

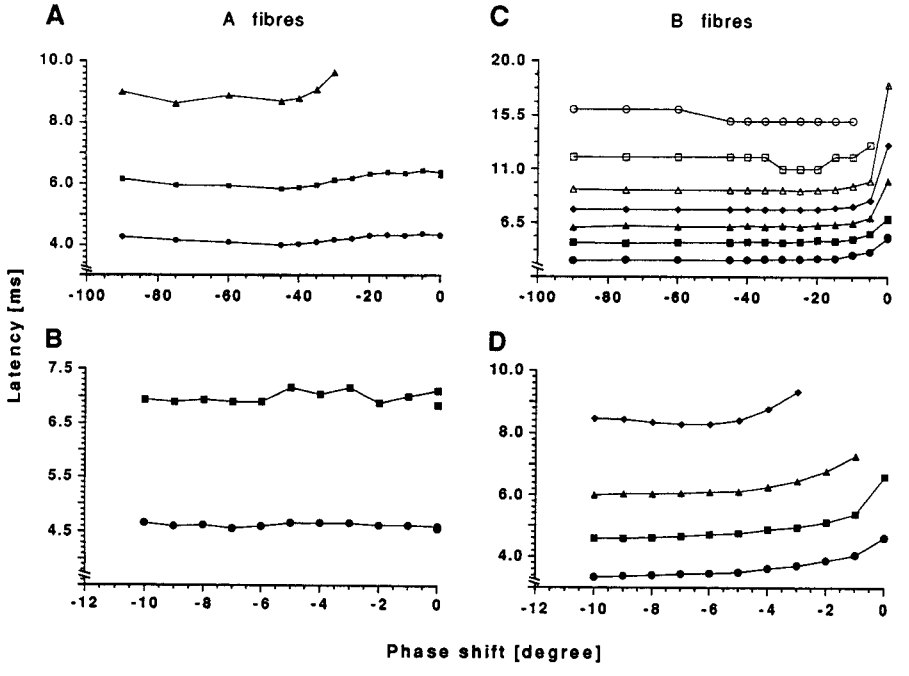

Fig. 5A–D. Examples of the responses of two A fibres *(left)* and two B fibres *(right)* to phase-shifted EODs. The *abscissa* gives the phase shift of the stimulus, the peak latencies of the spikes elicited by a given stimulus are shown on the *y*-axis. The first stimulus always was an unshifted EOD, the phase shifts increased in steps from right to left up to $-90°$ *(top)* or $-10°$ *(bottom)*. Different symbols represent different spikes of the same fibre

ducted during which the phase was shifted from 0 to $-10°$ in steps of $-1°$.

A and B fibres responded differently to phase-shifted EODs: the response of A fibres was either not affected or only slightly affected by phase shifts up to -20 or $-30°$ (Fig. 5A, B). Only with larger phase shifts did spike latencies start to decrease (Fig. 5A) and spike numbers to increase. In contrast, B fibres responded strongly to small phase shifts of the EOD, usually reaching a minimal spike latency (and maximal spike number) at phase shifts between -15 and $-20°$. Because the fibres were driven into saturation by stronger phase shifts, no further reduction in spike latencies occurred (Fig. 5C). This was true even if the amplitude of the unshifted EOD was adjusted such that it was barely above threshold. In five B fibres we tested whether a phase shift of $-1°$ was sufficient to cause a significant neural response. In all five fibers spike latencies decreased significantly (t-test, $P<0.0001$) and spike numbers increased when the stimulus changed from the unshifted EOD to a $-1°$ phase-shifted EOD (Fig. 5D). A $-1°$ phase shift of an EOD that lasts about 300 µs corresponds to a change in the timing of zero crossing of the main EOD transient of 500 ns. In contrast, the average change in first-spike latencies of B fibres to a $-1°$ phase shift was 350 ± 200 µs, which is 700 times as much. This decrease in first-spike latency is probably not due to an increase in signal energy, which was only 0.23%. To achieve a 350-µs first-spike latency shift in B fibres the signal energy must be increased by more than 83% [calculated according to data given by Bell (1990)]. Figure 2 shows that the negativity of the waveform increases for phase shifts from 0 to $-45°$. Apparently, this negativity is an important stimulus component.

Responses to EODs distorted by capacitive objects

Natural EODs distorted by capacitive objects are not only phase shifted but their amplitude spectra also shift to higher frequencies. Furthermore, the p-p amplitude of these EODs is altered depending on the complex impedance of the object (von der Emde 1990). In order to separate waveform cues from amplitude effects, two different series with naturally occurring pulse distortions, caused by capacitive objects with values decreasing from 100 to 1.2 nF, were conducted. In the first series, pulse distortions increased while the p-p amplitude of the EOD was held constant with aid of the computer. Decreasing capacitive values between 100 and 1.2 nF cause both increasing phase shifts and a shift of spectral power to higher frequencies (von der Emde 1990).

A fibres responded with a slight increase in spike latencies and a decrease in spike number when the capacitive value of the objects decreased from 100 to 1.2 nF (Fig. 6, left), i.e. the responses were similar to those caused by a decrease in EOD amplitude. B fibres responded in the opposite way: their spike latencies decreased and their spike numbers increased with increasing pulse distortions (Fig. 6, right). This response resembled the response caused by an increase in signal amplitude. The response to EODs altered by capacitive

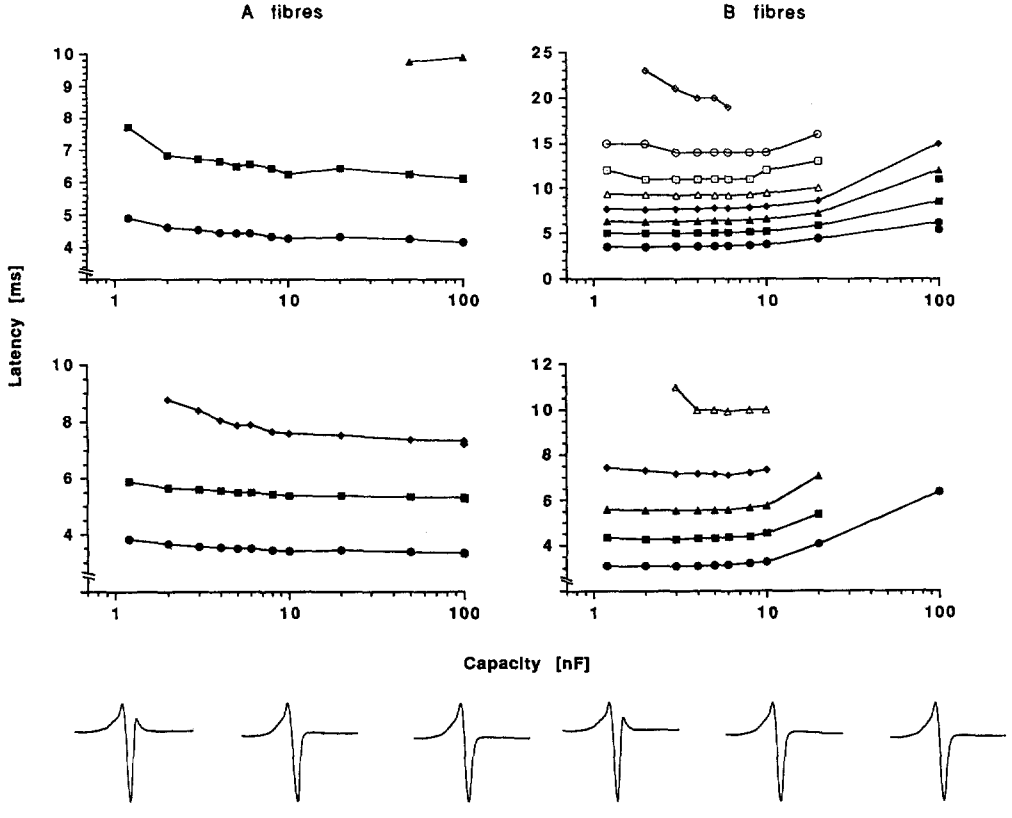

Fig. 6. Examples of the responses of two A fibres *(left)* and two B fibres *(right)* to EODs distorted by capacitive objects (see *bottom traces*). Different symbols represent different spikes of the same fibre. The p-p amplitude of the distorted EODs were adjusted such that they were identical with the p-p amplitudes of the undistorted EOD. In each case the *bottom line* shows the EODs altered by objects which had a capacity of 1.2 nF *(left)*, 10 nF *(middle)*, and 100 nF *(right)*

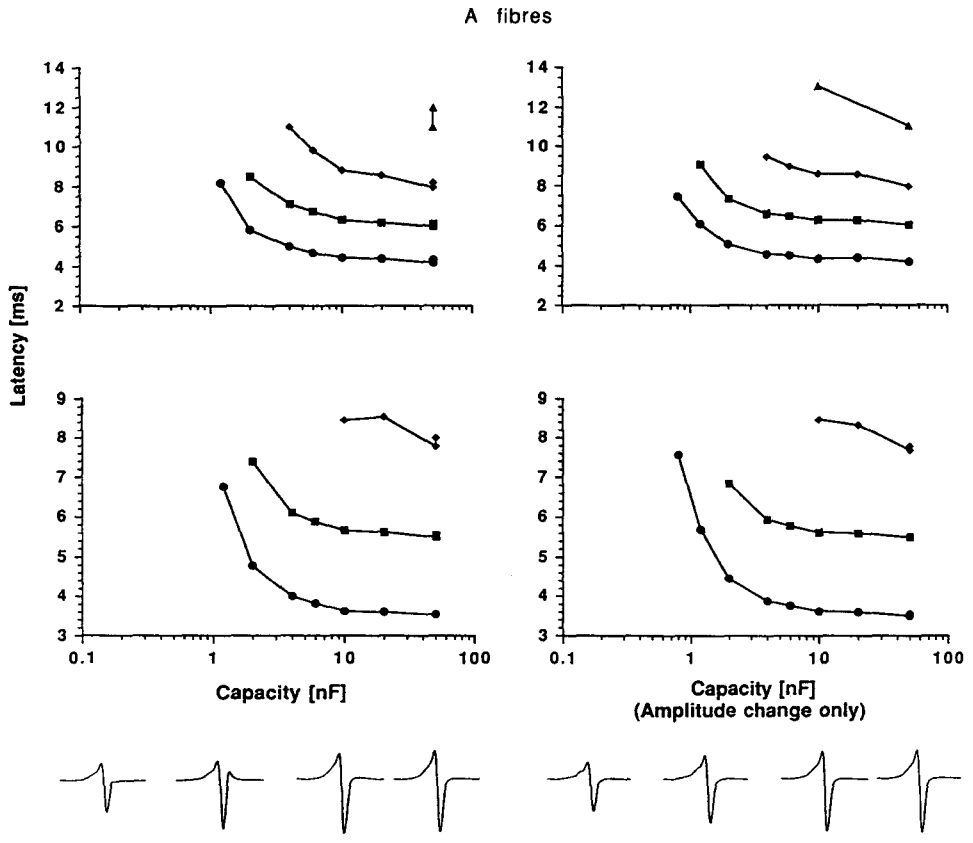

Fig. 7. Examples of two A fibre responses to EODs distorted by capacitive objects *(left)*. The *right side* shows the responses to EODs which were not phase shifted by a capacitive object but had the same amplitudes as the EODs used in the series shown on the *left side*. In this figure and in Figs. 8 and 9 the *left bottom trace* shows the EODs distorted by the capacities 0.1, 1.2, 10, and 50 nF *(left)*. Note that maximum pulse distortions occur around 1 nF, whereas the amplitude of the EOD monotonously increases from 0.1 to 100 nF. The *right bottom traces* show EODs altered by a 50-nF capacitor. Note that the amplitudes of these EODs were adjusted such that they were identical to those of the EODs shown on the *left*. Different symbols represent different spikes of the same fibre

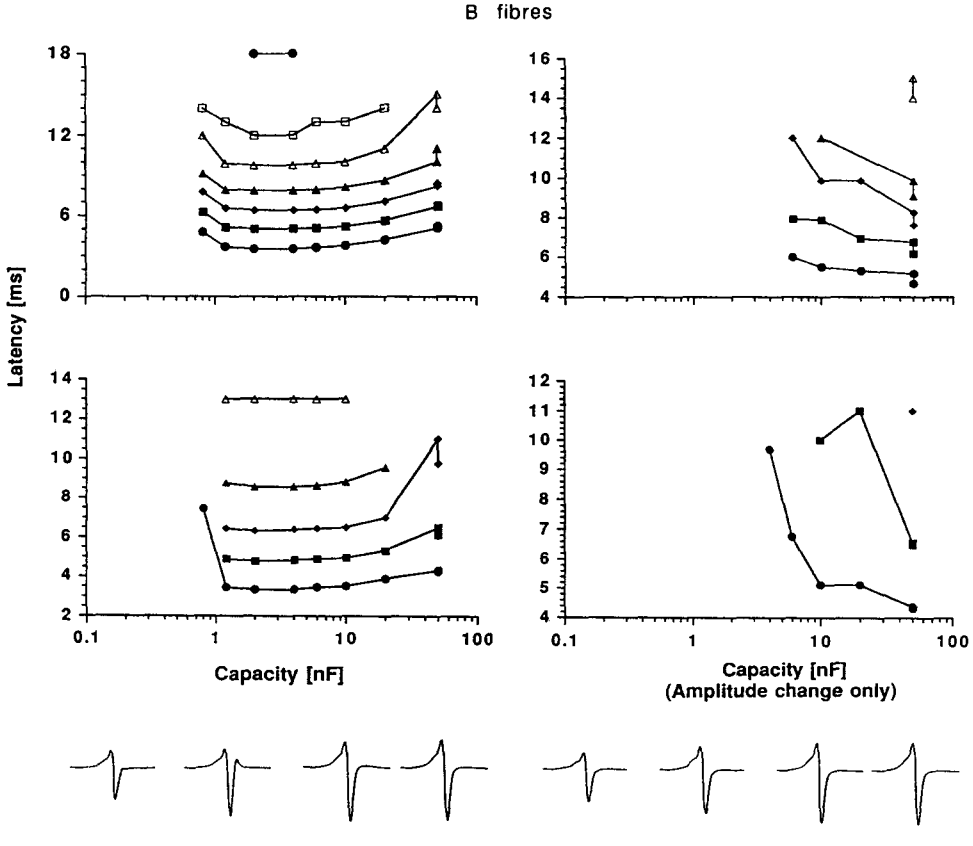

Fig. 8. Examples of the responses of two B fibres to EODs distorted by capacitive objects *(left)*. The *right side* shows the responses of the same fibres to EODs which were not phase shifted by a capacitive object but had the same amplitudes as the EODs used in the series shown on the *left side*. Different symbols represent different spikes of the same fibre. The *left bottom line* shows EODs altered by objects which had, from left to right, a capacity of 0.1, 1.2, 10, and 50 nF, respectively

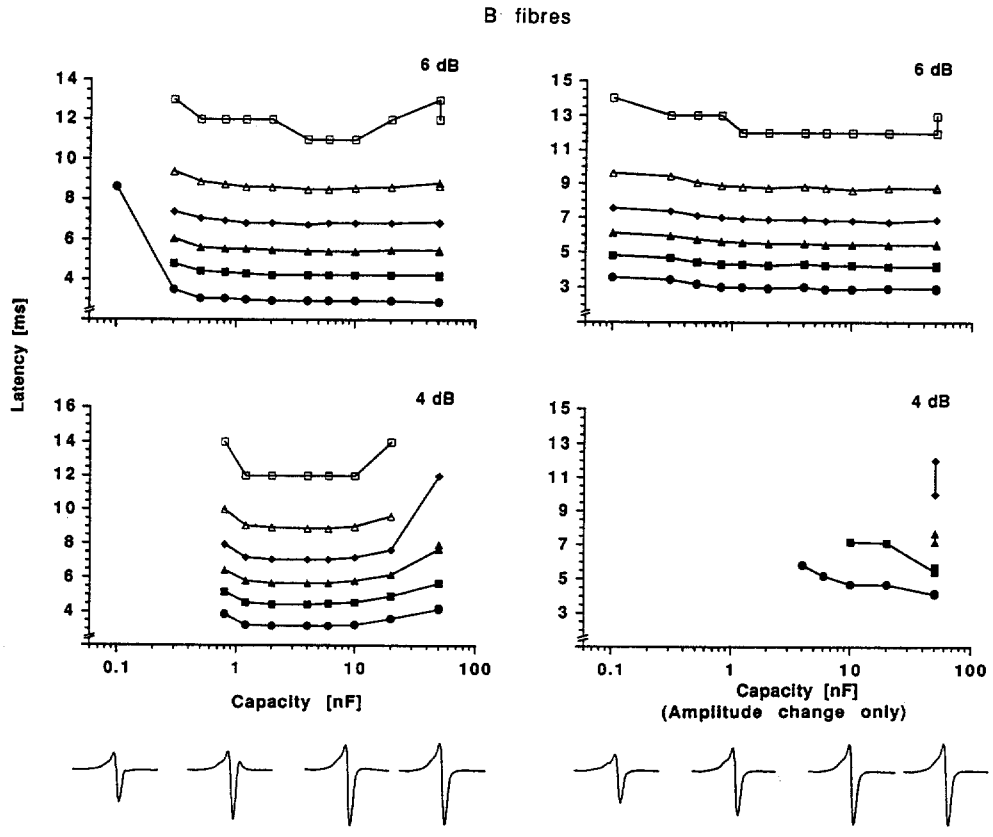

Fig. 9. Examples of the responses of two B fibres to EODs distorted by capacitive objects *(left)*. The *right side* shows the responses to EODs which were not phase-shifted by a capacitive object but had the same amplitudes as the EODs used in the series shown on the *left*. The stimulus amplitudes were 6 dB *(top)* or 4 dB *(bottom)* above threshold. Different symbols represent different spikes of the same fibre. The *left bottom line* shows EODs altered by objects which had, from left to right, a capacity of 0.1, 1.2, 10, and 50 nF, respectively

objects was strong in B fibres: they usually reached saturation (i.e. the shortest spike latency and the maximum number of spikes) at a capacitive value of 10 nF.

In the second series, EODs distorted by capacitive objects were again used as stimuli; however, signal amplitude was allowed to decrease by the same amount as in the presence of real objects. Capacitive values changed from 50 nF (little waveform distortions and high amplitudes) through 1.2 nF (maximum waveform distortions and medium amplitude) to 0.1 nF (again little waveform distortion but low stimulus amplitude). This means that the increasing waveform distortions between 50 and 1.2 nF were accompanied by a decrease in signal amplitude, whereas between 1.2 and 0.1 nF both waveform distortions and EOD amplitude decreased (Figs. 7, 8, 9; left bottom traces). The series with pulse distortions caused by capacitive objects was compared with another series with identical signal amplitudes as in the former series. In the third series, however, pulses remained undisturbed (Figs. 7, 8, 9; right bottom traces).

A and B fibres again responded differently. A fibres responded with an increase in spike latency and a decrease in spike number when either of the two series described above was used, irrespective of whether additional pulse distortions occurred (Fig. 7, left) or not (Fig. 7, right). A fibres obviously "ignored" the waveform distortions of the EOD. A fibres usually stopped responding if the capacitive values reached about 1.2 nF, probably because the stimulus amplitude became too small. The capacity at which A fibres ceased to respond depended on the initial EOD amplitude chosen.

B fibres responded with a decrease in spike latency and an increase in spike number, i.e. with a positive response if EODs distorted by capacitive objects were used as stimuli (Figs. 8, 9; left). This means that they responded as if the amplitude had increased even though it actually decreased. The signal distortions were obviously strong enough to override the effect caused by the decreasing stimulus amplitude. In the second series, which contained signals of decreasing amplitude without waveform distortions, B fibres responded in the following way: spike latencies increased and spike numbers decreased with decreasing EOD amplitude (Figs. 8, 9; right). This response resembled that of A fibres to the same series of stimuli.

The significance of the initial stimulus amplitude

The response change of B fibres depended on the amplitude of the first stimulus in a series. If the stimulus amplitude was 6 dB or more above threshold then the particular fibre was driven into saturation. This led to a constant response by the fibre to decreasing capacitive values until signal amplitude and pulse distortion became smaller at capacitive values below 1.2 nF. Finally, the fibre stopped responding (Fig. 9, top left). When the amplitude of the first stimulus was only 0.5, 1 or 4 dB above threshold (Figs. 8, 9) the fibre was able to decrease its spike latencies with increasing pulse distortions. In this case, the different responses of A and B fibres became obvious.

Discussion

Recent experiments have shown that mormyrids can discriminate between capacitive and ohmic objects (von der Emde 1990). Surprisingly all electrophysiological studies done so far (e.g. Szabo and Hagiwara 1967; Bell 1990) give no hints as to how the sensory periphery enables mormyrid fish to do this. Therefore, we extended the physiological work done by Bell (1990) in focusing on the questions of whether and how mormyromast input is sufficient to discriminate between capacitive and ohmic loads.

Amplitude and frequency sensitivity

We confirmed (Szabo and Hagiwara 1967; Bell 1990) that over a certain range both A and B fibres respond to an amplitude increase of the EOD with a decrease in spike latencies and an increase in spike number. If square pulses are used as stimuli, B fibres have lower thresholds than A fibres (Bell 1990). There are some indications that the thresholds of B fibres to natural EODs are also lower than those of A fibres, but the observed difference between the two fibre types was not significant (Table 1).

Both A and B fibres were most sensitive to single-cycle sine waves at frequencies below the peak frequency of the EOD power spectrum. At this frequency the response curves were rising (Fig. 4). According to Bell (1990), A fibres have minimal thresholds at 1–2 kHz, while B fibres have minimal thresholds at 100–500 Hz. The differences between our threshold curves and Bell's data may be due to the methods used: we applied stimuli several decibels above threshold and looked at first-spike latency changes, whereas Bell used the absolute thresholds of the fibres as response criteria.

Responses to phase-shifted EODs

B fibres always changed their responses if the EOD was phase shifted by at least $-1°$, whereas A fibres usually changed their responses only with unnaturally strong phase shifts (larger than $-30°$; Fig. 5). Because both the amplitude spectra and the p-p amplitudes of the EODs were held constant and the signal energy changed only slightly, response changes could only be due to time-domain cues. The relevant EOD parameter for the response of a B type receptor cell may be its positive- or negative-going main transient and/or the ratio of the amplitude of the positive phase of the EOD to the amplitude of the negative phase. In a $-1°$ phase-shifted EOD this transient changed by 500 ns relative to the undistorted EOD (Fig. 2). The response of a B fibre consisted of a 350-μs latency decrease, which is 700 times as much as the change of timing of the transient. Thus, the positive response of B fibres to a slightly distorted EOD constitutes a strong amplification of the stimulus changes.

It is not clear why B fibres responded to small phase shifts. It is tempting to assume, however, that the difference in wave-form sensitivity is caused by the morphological differences between A and B receptor cells (Szabo and Wersäll 1970; Bell et al. 1989). A cells are embedded between supporting cells and only a small piece of the outer membrane is exposed to the electric current during an EOD. In contrast, almost the whole body of B cells projects into a cavity of the electroreceptor organ. Thus, the free outer membrane of B cells is much larger in area and probably has a smaller resistance and larger capacitance than the membrane of A cells (C.C. Bell, personal communication). This should influence the behaviour of B cells towards alternating currents. Morphological differences between A and B cells might translate into differences in physical properties, e.g. their electrical conductances and time constants.

Responses to EODs distorted by capacitive objects

A fibres responded with an increase in first-spike latency and a decrease in spike number to constant amplitude EODs distorted by capacitive objects (Fig. 6, left). This may be due to the fact that the capacitive objects caused a frequency shift of the EOD to higher values. When the increase in pulse distortion and pulse frequency was accompanied by a decrease of pulse amplitude, the response of A fibres became even weaker (Fig. 7, left). Apparently the effects of both stimulus parameters were cumulative so that the fibres ceased to respond even sooner.

B fibres were extremely sensitive to waveform distortions caused by capacitive objects (Fig. 6, right). When natural waveform distortions were traded against decreasing EOD amplitudes (Fig. 8, left), the positive effects upon B fibre responses to waveform distortions overrode the negative effects caused by amplitude decrements. Only when the capacity decreased below 1.2 nF did the responses of B fibres start to decrease and then finally failed altogether (Fig. 8, left).

As already mentioned, both A and B fibres are more sensitive to sine waves whose frequencies are below the peak-power frequency of the EOD. Such a difference between receptor tuning and EOD peak-power frequency may be common in pulse-type electric fish. In six out of eight gymnotiform species studied, the steepest slope of the tuning curves overlies the range of peak-power frequencies found within the species (Bastian 1976; Hopkins and Heiligenberg 1978; Watson and Bastian 1979; Shumway and Zelick 1988). This provides a frequency resolution which might be used to discriminate the EODs of neighbouring fish (Shumway and Zelick 1988). It also may enable the discrimination between capacitive and ohmic objects for the following reason: within the biologically relevant range, any capacitive object will cause an increase in the peak-power frequency of the EOD (von der Emde 1990). In A fibres this leads to a decrease in response. In B fibres the response to positive phase shifts will override the negative, frequency-dependent effect, i.e. irrespective of the increase in EOD peak-power frequency, B fibres will respond more strongly to such a stimulus. The mismatch between receptor tuning and species-specific peak-power frequency thus helps to increase the response difference between A and B fibres.

Our results suggest how electrolocating mormyrids discriminate between capacitive and ohmic loads. A fibres mainly encode the amplitude and the frequency

content of the local EOD. Thus, they respond similarly to the presence of a capacitive or resistive object of the same magnitude of impedance, i.e. when both objects cause identical amplitude changes of the local EOD. However, B fibres respond differently to purely ohmic and purely capacitive loads of identical magnitude of impedance by reacting much more strongly to the capacitive load. A central comparison of the input of the two fibre types might be the basis for the observed behavioural discrimination (von der Emde 1990): if both fibre types respond similarly to an object it is purely resistive. If, however, B fibres of a given mormyromast respond more strongly than A fibres, then the object of interest has distorted the local EOD and therefore must have a capacitive component that corresponds in size to the mismatch of the A and B fibre responses.

It is not known in which part of the brain A and B fibre inputs are compared. Afferents of A and B fibres terminate in separate zones of the electrosensory lateral line lobe (ELL) cortex (Zipser and Bennett 1976; Bell et al. 1989). Each of these two zones, the medial zone for A fibres and the dorsolateral zone for B fibres, contains somatotopic maps (Bell and Szabo 1986). There are intrinsic connections within the ELL, in particular ipsilateral interzonal connections and contralateral commissural connections (Bell et al. 1981). Efferent neurons of all zones and of both sides of the ELL project to the same topographic point in the torus semicircularis. The regions in the zones that project to the same point in the torus receive their primary afferent input from identical skin areas (or a mirror image skin area of the opposite body side). It is not known, however, where convergence occurs at the cellular level (Bell and Szabo 1986). The morphological findings suggest that comparison of A and B fibre input may take place either in the ELL or at the level of the lateral torus semicircularis. In gymnotiforms, the torus semicircularis contains a time-comparison circuit which enables these fish to sense small (400-ns) phase differences between EODs at different points of the body surface (Rose and Heiligenberg 1985; Carr et al. 1986). These fish employ this phase information to perform a correct "jamming avoidance response" (Heiligenberg 1986) and are able to discriminate between foreign signals differing only in their phase spectra but not in their amplitude spectra (Kramer and Otto 1991).

Although behavioural tests are lacking, physiological studies indicate that gymnotiform wave species also have the sensory prerequisites to discriminate between capacitive and purely ohmic objects (Scheich et al. 1973). In contrast to mormyrids, however, gymnotiform wave fish have two types of electroreceptor organs, both of which are active during electrolocation (Szabo 1970; Scheich et al. 1973; Zakon 1986): (1) P units which encode the EOD amplitude by mean firing rate independently of phase shifts due to the presence of a capacitive object, and (2) T units which are exact time coders which fire phase locked to the stimulus waveform. They thus respond differently to capacitive and resistive objects because primarily capacitive objects cause phase shifts in the EOD. As in mormyrids, it must be assumed that a central integrator compares the two types of sensory inputs in order to discriminate between capacitive and ohmic loads (Scheich et al. 1973).

Discrimination of EODs elicited by neighbouring fish

Mormyrids use the Knollenorgans (Bennett 1965) to analyze the EOD of neighbouring fish during electrocommunication (Hopkins and Bass 1981). Independent of stimulus amplitude, Knollenorgans fire a single spike of fixed latency to outside negative-to-positive voltage transitions in foreign EODs (Bennett 1971; Szabo and Fessard 1974). Knollenorgans at opposite body sides thus respond to different phases of a foreign stimulus pulse because the polarity of the EOD experienced by opposite body sides is inverted. By employing this mechanism, some mormyrids may be able to discriminate between EODs of different species or different sexes (Hopkins and Bass 1981) and also between the slightly different EODs of the same species (Graff and Kramer 1989). For reasons given above, Knollenorgan input can not be used during electrolocation.

Gymnotiforms also have exact time coders which phase-lock to a particular EOD parameter: T units in wave species and M units in pulse species (Szabo 1974). The input of T or M units can be used in addition to the amplitude coding P units (or B units in pulse species) during electrolocation. The pulse-type gymnotiform *Hypopomus artedi* responds differently to EODs of identical power spectra but different phase functions (Heiligenberg and Altes 1978) possibly by employing its two types of electroreceptors. If frequency changes are involved, they may also be used. In a combined behavioural and electrophysiological study Shumway and Zelick (1988) concluded that the pulse-type gymnotiform *Hypopomus* is capable of discriminating male from female EOD pulse shape by using both temporal and spectral cues, but that frequency discrimination based on spectral tuning of electroreceptors is the most likely neuronal mechanism.

Recently, a third possible method of signal analysis in pulse gymnotiforms – called "scan sampling" – was proposed (Hopkins and Westby 1986). According to this theory a fish "scans" the signal of another fish by letting its own pulses successively overlap with the foreign EODs and then analyses the pronounced amplitude- and phase-modulated summed signals. In all cases mentioned, electric fish probably employ two types of electroreceptor organs, with one type always acting as a phase coder.

Mormyrids use only one type of electroreceptor organ (mormyromasts) during electrolocation, they nevertheless detect distortions of their own EOD. The explanation of this unexpected finding lies in the fact that each mormyromast contains two types of electroreceptive cells with only one type (B cells) being sensitive to waveform distortions. Even though mormyromasts are not exact time coders, such as Knollenorgans or T units, mormyrids have the remarkable ability to detect small temporal EOD disparities. Instead of encoding the waveform by phase locking (as do Knollenorgans or the T or M units of gymnotiforms), they rectify small waveform changes of the stimulus. This phenomenon is called "waveform tuning". The waveform analysis of mormyrids employed during electrolocation seems to be as efficient as its alternative, which is realized by the same fish during electrocommunication.

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