Stimulus Filtering and Electroreception:
Tuberous Electroreceptors in Three Species
of Gymnotoid Fish

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Summary. Electroreceptive neurons in the posterior branch of the anterior lateral line nerve of three species of electric fish (Gymnotoidei): *Sternopygus macrurus*, *Eigenmannia virescens*, and *Apteronotus albifrons*, show species-specific differences in the filtering of electrical stimuli. All of the tuberous electroreceptor fibers of an individual are tuned to the same frequency: that of the electric organ discharge (EOD) of the species, more specifically, to that of the individual. The fibers in *Sternopygus* are tuned to 50–150 Hz; those in *Eigenmannia* to 250–500 Hz, and those in *Apteronotus* to 800–1,200 Hz (Figs. 3, 5, 8). Two classes of organs in *Sternopygus* and *Eigenmannia*, P and T units, respond to sinusoidal stimuli at the unit's best frequency (BF) with a phase-locked partially-adapting (P), or tonic (sustained) (T) discharge. T-units are more sharply tuned and are more sensitive than P-units. Only one class of organs, *P* or partially adapting units, have been found in *Apteronotus* and phase-locking is less evident than it is in other species.

Nerve section proximal to the recording site does not alter the tuning curves in *Sternopygus* (Fig. 18), but local warming and cooling of the cutaneous receptor site in both *Sternopygus* and *Eigenmannia* shifts the tuning curve to higher and lower frequencies, respectively (Fig. 17).

Species-specific differences in peripheral electroreceptor tuning are thought to play an important role in the functioning of electric communication and electro-location among gymnotoid fish.

Introduction

Because animal communication is a two-component process in which the behavior of one organism effects a change in the behavior of another, we may expect natural selection to affect a signaler's signs, as well as a receiver's mechanisms of perception so as to permit efficient signal exchange. Ethologists, long concerned

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with the mechanisms by which stimuli evoke species-typical responses in animals (Marler, 1961) are now finding physiological mechanisms specialized for the reception and recognition of stimuli relevant to its social communication (Frishkopf and Goldstein, 1963; Capranica, 1965; Capranica and Moffat, 1975; Nocke, 1972; Horch and Salmon, 1969; Schneider, 1974; Scheich, 1974). A recipient, usually being bombarded by stimuli—both relevant and irrelevant—is faced with a complex problem of interpreting signals in the presence of "noise" from other organisms and non-biological sources, and noise from distortion of its species' signals. The ways in which organisms filter stimuli, in peripheral receptors, in afferent pathways, in the CNS (Marler, 1961) may differ from one modality to another. This paper is concerned with the electrosensory modality and with the ways in which electrical stimuli are filtered by the peripheral structures in South American gymnotoid fish.

The wave-like *E*lectric *O*rgan *D*ischarge (EOD) of certain species of gymnotoid fish is a remarkably regular fixed action pattern. Measurements of the intervals between successive discharges in *Apteronotus* for example, with its mean interval of 1 ms, may show periods lasting several minutes during which the standard deviation of interval durations is 0.01 % of the mean (Bullock, 1969, 1970). Thus it is one of the least variable behavioral action patterns known. Since the EOD can be used in both exoteric (i.e. intraspecific) and solipsistic (electrolocation) communication (Black-Cleworth, 1970; Hopkins, 1974a; Lissmann and Machin, 1958) it is of considerable interest to consider how the receiving systems of these fish process incoming communication signals. Scheich's et al. (1973) analysis of tuberous electroreceptors in *Eigenmannia* acted as a stimulus to the work reported here, which will emphasize intraspecific variation in stimulus filtering, and compare three species of wave discharging gymnotoids.

Methods

Gymnotoid fish that had reportedly been collected in the Guyanas, Columbia or Peru, were obtained through tropical fish suppliers in Los Angeles and in San Diego. They were kept in 80 liter aquariums at temperatures ranging between 25–29 °C in a room with a 12:12 light-dark cycle, and were fed brine-shrimp (*Artemia*) or white-worms (*Enchytraeus*) each evening. Three species, comprising the majority of the experiments discussed here, were identified as: *Sternopygus macrurus* (Rhamphichthyidae), *Eigenmannia virescens* (Rhamphichthyidae), and *Apteronotus albifrons* (Apteronotidae). These three species are common over much of northern South America and are known to occur sympatrically in Guyana (Hopkins, 1972), frequently sharing the same habitat. I used an electronic counter (Hewlett-Packard 5211A) to measure the frequency of each experimental fish's electric organ discharge (referred to here as EOD) while the fish rested in water from its own tank. Each of the three species produce a continuous tone discharge that does not vary significantly with mechanical disturbances (Bullock, 1969; Hopkins, 1974a). I used light anesthesia (ethyl m-aminobenzoate f-methanesulphonate or "MS222") initially to subdue the fish (concentration = approximately 50 mg per liter). Subsequently the fish was immobilized with an intramuscular injection of the curare-like drug, Gallamine triethiodide (Davis and Geck), at a concentration of approximately 0.006 mg per gram body weight.

In addition to immobilizing the fish, Gallamine was effective in silencing the EOD in those species with muscle-derived electric organs (*Sternopygus* and *Eigenmannia*), but not in *Apteronotus* which is known to have a neurally-derived electric organ (Waxman et al., 1972). Because it was essential to have the EOD silenced for the work reported here, when working with *Apteronotus* I made an incision in the tail large enough to pass a fine wire into the spinal column. When most of the spinal cord was destroyed with this fine wire, the EOD became unsynchronized and reduced in amplitude; it usually persisted for as long as one hour, at which time it was possible to begin an experiment.
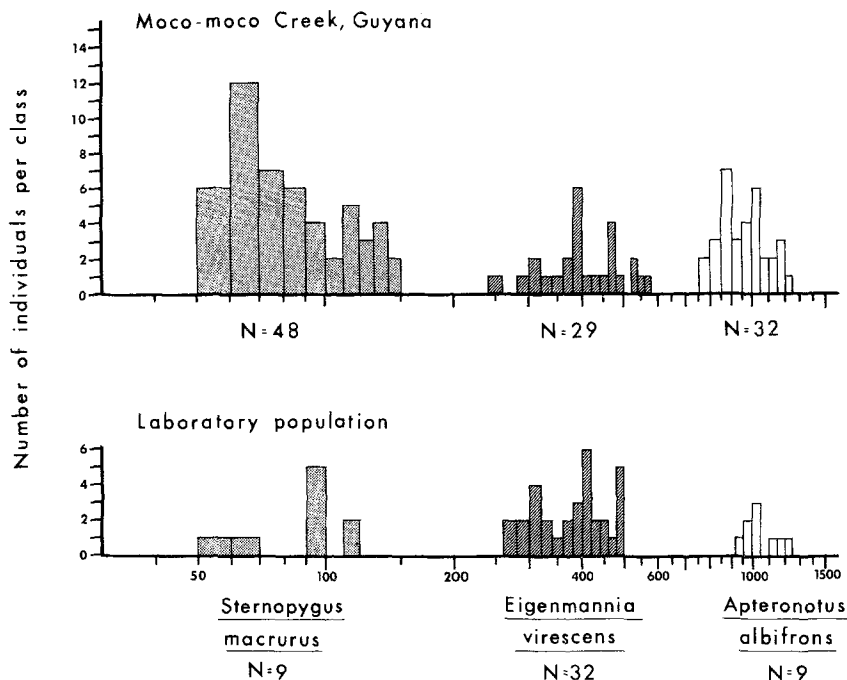
Fig. 1. Distribution of discharge frequencies of wave-discharging gymnotoids used in this study. The upper histogram shows frequencies of individuals captured in Moco-moco Creek in Guyana (from Hopkins, 1974), and the lower histogram shows frequencies from the laboratory populations. All frequencies were measured at 25 °C or were corrected to this temperature using a Q_{10} factor of 1.5

The fish was placed on its side on a small Plexiglas table and was held in place with two rubber bands cushioned by sponge rubber pads. The table was suspended at an angle in a large Plexiglas bath ($43 \times 20.5 \times 8$ cm) so that the fish was completely submerged except for a small region near the operculum from which recordings were made. Freshly aerated water (no MS 222) flowed through the glass tube affixed in the mouth of the fish. The conductivity of the bath and respirating water was always adjusted to 2.0 kOhm · cm using dilute fish saline.

The posterior branch of the anterior lateral line nerve (NLLa) was exposed at a point where it comes close to the surface of the skin to go around a rib bone slightly dorsal to and posterior from the gill slit (see Szabo, 1965). The nerve with its sheaf left intact was bathed with Forster and Taggart's (1950) saline solution periodically. I used a pair of fine-tipped forceps held in a micromanipulator to hold the rib directly under the nerve in order to mechanically stabilize and to electrically ground the preparation.

Extracellular nerve spikes could be recorded using 3 M NaCl fiber-filled glass micropipets connected to a differential preamplifier (Grass P-15). A fine silver wire used for the indifferent electrode was placed between the ground forceps and the recording micropipette in order to minimize stimulus artifacts. Electrical stimuli were applied to the bath homogeneously using two silver-silver chloride plates, 1 cm × 10 cm, located on each end of the bath at the same depth as the fish so that current lines ran parallel to the longitudinal axis of the fish. Stimuli generated by an IEC-F33 function generator were isolated from circuit ground using an isolation transformer (Argonaut LIT069). The field strength of the applied stimulus was measured with two silver wire electrodes placed 1 cm apart positioned near the fish. The signal across these electrodes was amplified with a Tektronix 122 preamplifier and measured using an Hewlett-Packard 403 AC volt meter. A voice commentary, nerve spikes, the stimulus, and stimulus synchronization pulses, were recorded on a 7-channel tape recorder (Ampex FR 1300) at 7.5 IPS for later analysis.

The EOD frequencies of the experimental fish are shown in Figure 1 (laboratory population). Because the measure of frequency were all made at different temperatures between 23 °C and 28 °C, and because EOD frequency is known to change with temperature (Enger and Szabo, 1968), frequencies were "corrected" to their presumed values at 25° using a Q_{10} factor of 1.5. Figure 1 also shows data collected from the same species of fish occurring sympatrically in a small stream in Guyana, South America (from Hopkins, 1974a). Both in the field, and in the laboratory, individuals of these three species occupy distinctive frequency ranges, covering between 0.8 and 1.5 octaves, with close similarity between laboratory and field samples.

These three species of fish produce electric discharges in which the pulse duration is relatively long compared to the interval between pulses, and in which the frequency is stable. Known as "tone" or "wave" discharges, this type contrasts with that of other major class of species of gymnotoids which produce "pulse" EODs (pulses are short compared to the interval between pulses, and the EOD frequency is variable).

Results

I. Afferent Fiber Types

Records obtained from single fibers in the posterior branch of the anterior lateral line nerve (NLLa) permitted analysis of the action of the electroreceptor organ complex, consisting of receptor cells, synapses, and an afferent neuron, but not of its component parts. "Electroreceptor", used here, will refer to this complex. Two major classes of electroreceptor fibers are represented in the NLLa of gymnotoids. Those belonging to the first class (ampullary, see below), of which there appears to be but a single type, are most responsive to electrical stimuli with spectral energy between 5 and 50 Hz. The two types of electroreceptor fibers known for the second class (tuberous) are responsive to comparably higher frequencies, with the peak sensitivity at 50 Hz or more. Because the two classes of cutaneous organs appear fundamentally different in anatomical structure and in mechanisms of action, but more important because they differ in the range of frequencies over which they are sensitive or functional, they have been called "low-frequency" and "high-frequency" electroreceptors (Bullock, 1973 and 1974).

Figure 2 represents oscilloscope tracings from a low- and from a high-frequency electroreceptor fiber in the gymnotoid, *Eigenmannia virescens*. While the low-frequency receptor unit, shown in the lower part of Figure 2, emits a regular train of impulses in the absence of electrical stimulation, spike frequency is modified by weak, low frequency electrical stimuli. Here a 4 Hz 0.27 mV/cm sine wave evokes nearly sinusoidal fluctuations in the frequency of the train of spikes, from low frequency to high, at a modulation rate which closely approximates the stimulus. They are unaffected by water motion or mechanical vibration. Low-frequency receptors will not be dealt with further here; an extensive linear systems analysis of the tuning properties of ampullary electroreceptors in another gymnotoid fish, *Gymnotus carapo*, has been conducted by Dunning (1973).

High-frequency electroreceptors (upper part of Fig. 2) are similarly unaffected by mechanical stimulation; however, at rest they can be silent or can show spontaneous erratic firing, but when stimulated with high frequency sinusoidal stimuli (greater than 50 Hz), spikes tend to be phase-locked to the stimulus. They are usually insensitive to low-frequency electrical stimuli.
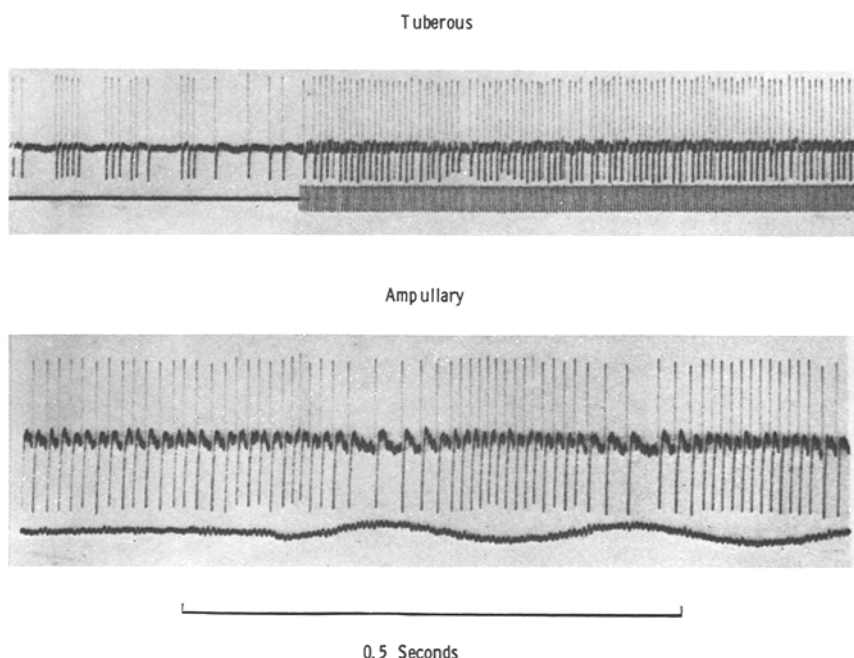
Tuberous

Ampullary

0.5 Seconds

Fig. 2. Typical spike trains from a tuberous receptor (upper example) and from an ampullary receptor (lower example) in *Eigenmannia virescens*. In each, the upper trace shows spikes recorded from the posterior branch of anterior lateral line nerve and the lower trace shows the stimulus. The tuberous receptor responds to the 350 Hz, 1.24 mV/cm stimulus with phase-locked spikes at an approximately 0.5 probability; the ampullary receptor responds to the 4 Hz, 0.27 mV/cm sine wave stimulus with a frequency-modulated spike train

Electroreceptors also fall into two principal groups on the basis of structure (Szabo, 1965; Lissmann and Mullinger, 1968) and combined physiological-histological studies have provided convincing evidence that electroreceptors that are "ampullary" in structure, are "low-frequency" in response sensitivity; those that are "tuberous" in structure, are "high-frequency" in function (Bennett, 1967; Suga, 1967). The terminology for the different receptor types varies in the literature, but is summarized in a review by Szabo (1974).

Mechanoreceptive neurons, identified by extremely sensitive responsiveness to vibrations or to surface ripples were rare in the posterior branch of NLLa, and were only recorded from one species, *Sternopygus macrurus*. The predominant afferent pathway for mechanical receptors is found in the posterior, rather than anterior, lateral line nerve in gymnotoids (Szabo, 1965; Maler, Finger and Karten, 1974). There were numerous unidentified spontaneously-active neurons in the lateral line nerve of gymnotoids which could be stimulated neither electrically nor mechanically.

II. Species Differences in Electroreceptor Tuning

Because of the large degree of geographical divergence and local species-specificity in the discharge frequency of several gymnotoid fish with wave discharges (Stein-

bach, 1970; Hopkins, 1974a), it is of considerable interest to know something of the frequency specificity of electroreceptor mechanisms. Tuberous electroreceptor tuning was examined in the NLLa of three species of gymnotoids: *Sternopygus*, *Eigenmannia*, and *Apteronotus*.

A. *Sternopygus macrurus*

An 100 Hz tone-burst sine wave of approximately 10 mV/cm peak to peak was applied periodically to the electrodes in the test chamber as the microelectrode was advanced through the nerve in search of active neurons. A fiber from a tuberous receptor was identified as one that fired spikes in phase with the stimulus waves. Criteria for a threshold response were difficult to standardize from one unit to the next, and especially from one species to the next because of differences in spontaneous discharge activity, and in rates of adaptation to continuous tone stimulation. I attempted, therefore, to use several methods of stimulating the receptor organ so that different criteria could be compared separately.

In these first series of experiments, I used Scheich's et al. (1973) criterion for threshold as the minimum electric field strength which evoked a single nerve spike for *each* stimulus period. Figure 3 shows plots of these one-to-one (1:1) thresholds as a function of the stimulus frequency for eleven units in a single *Sternopygus* (male, length = 23.8 cm). The curves clearly cluster into two populations, one representing the sensitive organs (low-threshold), and the other being less-sensitive (high threshold). The difference in sensitivity is on the order of a factor of ten. By analogy with the units known for *Eigenmannia* (Scheich et al., 1973) we can call sensitive electroreceptors, "T-units," and the less sensitive ones, "P-units." All of the neurons from this individual were clearly tuned preferentially to a single frequency (approximately 130 Hz) regardless of their overall sensitivity.

Sensitive (T) units appeared to be tuned more sharply than the less-sensitive (P) units, largely because of the threshold slopes on the low-frequency end of the spectrum. The average 1:1 threshold for the six sensitive units (T) in this individual drops by 17.9 ± 6.4 db per octave on the low frequency side of the minimum- or best-frequency (BF), and increases at a rate of 69.3 ± 18.1 db per octave on the high side. In contrast, the six less-sensitive units (P) filtered at an average of 10.3 ± 4.3 db per octave on the low-frequency side of the BF and 32.2 ± 15.3 db per octave on the high-frequency side. The frequency range to which this individual is sensitive corresponds very well to the range of EOD frequencies observed for *Sternopygus macrurus*, in our laboratory populations and in wild populations from Guyana, South America (Fig. 1). Even more interesting, the BF of each of these units is uniformly well matched to the discharge frequency of this particular individual's own electric organ (arrow in Fig. 3) as recorded prior to curarization of the animal and silencing of its discharge.

Eight other *Sternopygus macrurus* yielded results similar to those represented in Figure 3. Of the 111 fibers recorded from NLLa in the 9 *Sternopygus*, 98 of them, or 88 % were identified as coming from tuberous or high-frequency receptors, 7 % were from ampullary or low-frequency receptors, 0.9 % from mechanical receptors, and 4 % were unidentified. All of the high frequency electroreceptors
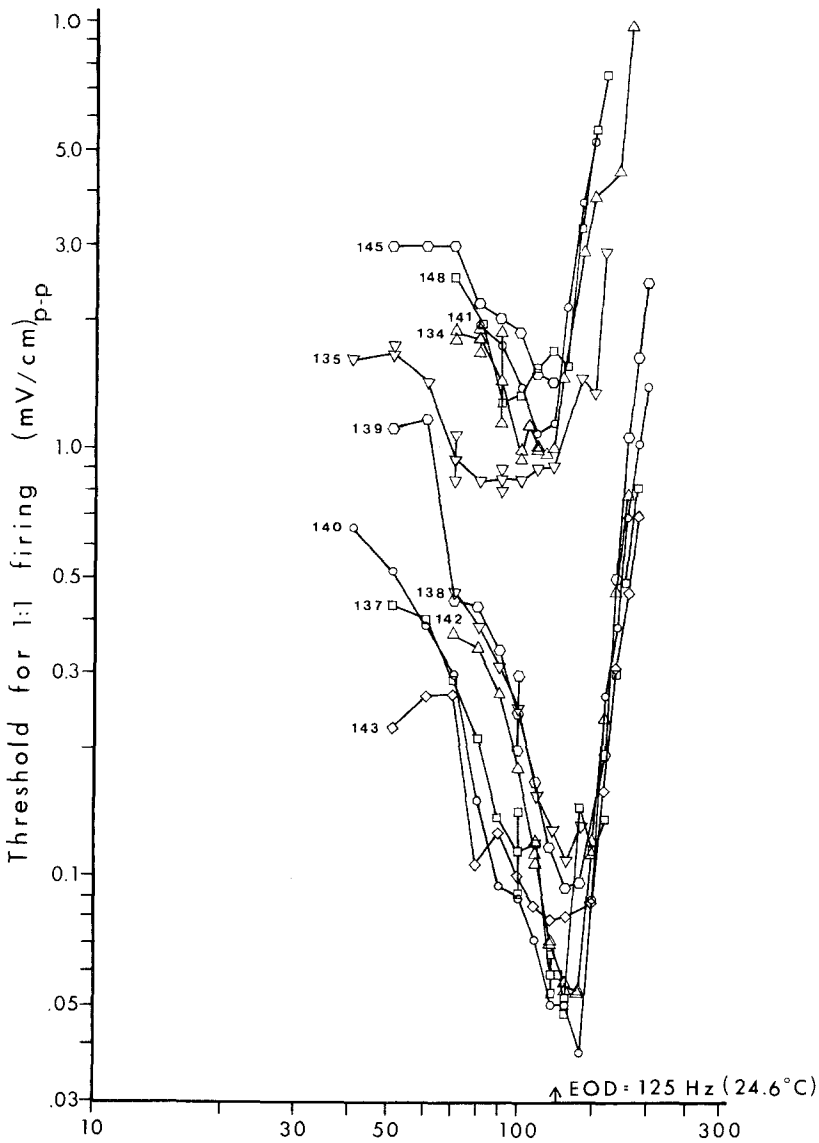
Sternopygus macrurus (42)

Fig. 3. Tuning curves for tuberous (high-frequency) electroreceptors from a single *Sternopygus macrurus*. Each curve represents a single fiber; numbers give its identity. Peak to peak thresholds were determined by measuring the minimum electric field required to elicit one spike on each stimulus period (1:1 firing). The arrow shows this fish's EOD frequency prior to the experiment. The population of cells with low threshold (lower cluster) are all T-units; those with high-threshold are P-units. Duration of stimuli: 2 s
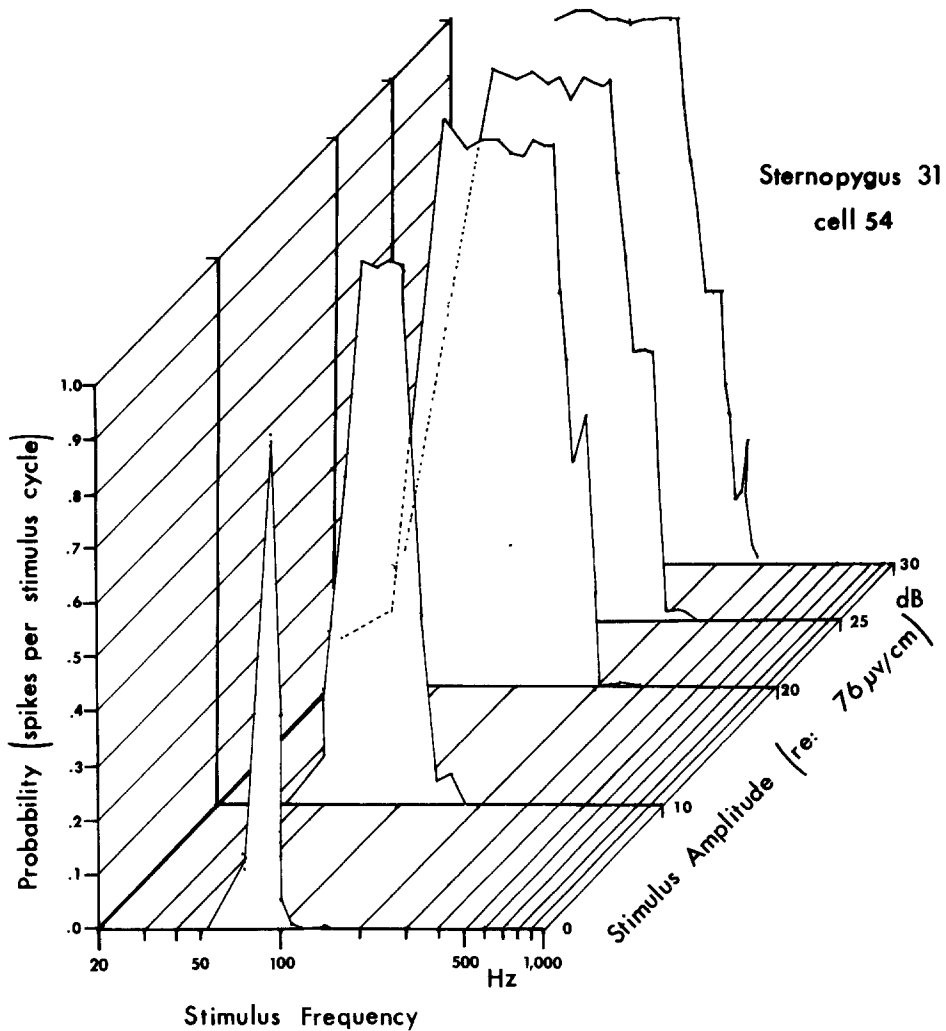
Fig. 4. Spike probability of a T-unit from *Sternopygus macrurus* as a function of sinusoidal stimulus frequency and amplitude. Amplitudes, in db, are referred to 76 μV/cm. Probability is the spike frequency divided by the stimulus frequency

in *Sternopygus*, were found to be tuned only to the EOD frequency of the individual prior to the experiment, although I made several attempts to search for other types of fibers using 300–1,000 Hz test stimuli.

It is also possible to use electroreceptor firing frequency as an indicator of tuning properties and the results are only slightly different from those obtained from the 1:1 threshold experiments. Figure 4 shows the probability of a sensitive (T) unit firing a spike (number of spikes divided by the number of stimulus periods) as a function of both the stimulus frequency and the stimulus intensity. All stimuli were 2.0 s sine wave tone bursts. Low amplitude stimuli (0 db ≡ 76 μV/cm) evoke spikes with a high probability when the stimulus frequency is 85 Hz, but the

response is highly selective to this one frequency. At higher stimulus intensities, the spike probability saturates at $p = 1.0$ over a range of frequencies around the 85 Hz peak; then it drops rapidly. One observes a slight increase in probability of firing for frequencies at approximately 170 Hz and a small shoulder occurs at approximately 240 Hz. These two plateaus, at twice and three times the BF of the unit represent a stable firing pattern. At one octave above the BF, the plateau is at $p = 0.5$; thus, spikes still occur at BF. Confirmation of this stable firing pattern is seen in dot diagrams of instantaneous firing frequency in Figure 14 to be discussed below.

Sternopygus macrurus is an especially interesting species from the viewpoint of a "tuned" receptor system because, upon reaching sexual maturity, males and females appear to adopt different electric organ discharge frequencies, with males discharging at 50 to 100 Hz and females at 100 to 150 Hz (Hopkins, 1972). The question arises whether males are more sensitive to other males' or to females' EODs. Unfortunately, even under field conditions, sexual maturity is not attained until individuals reach approximately 300 mm in length, and large specimens such as this were not available in the laboratory at the time of this study. Two, sexually immature males having EOD frequencies of 127 Hz and 60 Hz had all of their tuberous electroreceptors tuned to their own respective frequencies. There were no apparent differences in threshold, filter specificity, or other characteristics, except best frequency, between these two individuals.

There is good correspondence between the physiological properties of the two classes of tuberous, or high-frequency electroreceptor units in Sternopygus with those in another Rhamphichthyid, Eigenmannia virescens, as studied by Scheich et al. (1973; also see Scheich and Bullock, 1974, p. 217). Physiological properties of the two types of fibers are described further in Section III below, but it should be noted that in Eigenmannia, too, one class of fibers, called Phase Coders or "T" receptors, showed an overall lower threshold and a steeper low-cutoff filter than did the other class, which Scheich et al. called Probability Coders, or "P" receptors. I use the "T" and "P-unit" terminology here because, in some cases it is difficult to make comparisons of the absolute sensitivity of an electroreceptor organ. Bennett (1965) demonstrated, for example, that overall sensitivity to a longitudinal electric field stimulus, was affected by the receptor's location on the skin. Whether the cell adapts to sustained sine wave stimuli or not, is a more reliable indicator of the type of unit, as described in Section III below.

B. *Eigenmannia virescens*

I used 300–500 Hz sine wave bursts as test stimuli while searching for electroreceptor fibers in the posterior branch of NLLa of *Eigenmannia virescens*. Eighty-five of the 96 units recorded from 37 fish were found to be from tuberous electroreceptors, while 11 were from ampullary. The experimental fish were electrically silent, and while stimulated with sine wave bursts lasting for 2.0 s, thresholds were determined for 1:1 firing for the duration of the stimulus. Figure 5 shows representative tuning curves from 12 tuberous electroreceptor fibers in one of these fish.
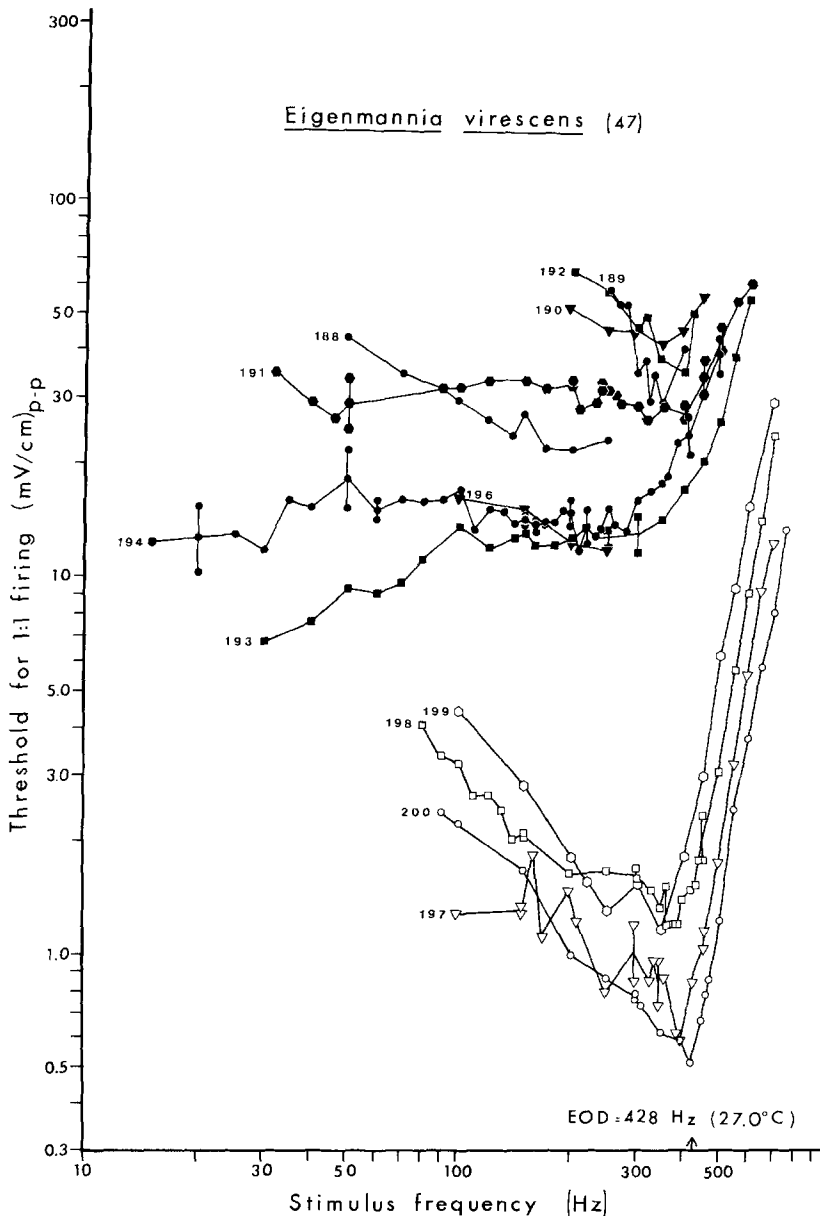
Fig. 5. Tuning curves for tuberous electroreceptors from an *Eigenmannia virescens*, measured in the same way as in Figure 1. Solid symbols are P-units, open symbols are T-units. Duration of stimuli: 2 s

Two populations of tuberous electroreceptors are clearly apparent, the differences between them being based upon the overall sensitivity of the unit and the sharpness of tuning on the low-frequency side of the BF. The physiological properties of these two populations of units correspond closely with the descriptions given by Scheich et al. (1973). The sensitive units (open symbols), are "T"

receptors, and the less sensitive units (closed symbols) are "P" receptors. All are sensitive only to the range of EOD frequencies typical for the species in the laboratory and field populations (Fig. 1) matching closely the EOD frequency of the individual prior to curarization (arrow). T-receptors ($n = 4$) filter at 6.0 ± 0.5 db per octave on the low-frequency side of the BF and 31.0 ± 4.7 db per octave on the high side. P-receptors ($n = 8$) filter at 2.2 ± 5.5 db per octave on the low side, and at 22.5 ± 14.2 db on the high side.

Many tuberous organs in *Eigenmannia* were spontaneously active, discharging at frequencies ranging from fewer than 2 to over 185 spikes per s, others were completely silent. Spontaneous firing was usually irregular or bursty, and showed a highly variable distribution of intervals between spikes. While it is not known why some units showed a high degree of spontaneous activity and others did not, spontaneous activity was apparently reduced in several experiments for which I had employed MS 222 as anesthesia. Previous research on tuberous electro-receptors in *Eigenmannia* which reported the absence of spontaneous activity was also conducted utilizing MS 222 (Scheich et al., 1973; Bullock and Chichibu, 1965; Hagiwara and Morita, 1963), but Bennett (1967) did not use it, nor did he report significant spontaneous activity. An example of typical spontaneous firing in a tuberous electroreceptor from a curarized but unaesthetized fish is shown in Figure 2.

High levels of spontaneous activity sometimes interfered with determination of the BF. If a weak stimulus is applied to a fish while recording from a unit with spontaneous activity, there may be no effect upon the firing frequency of the unit. A plot of firing frequency vs. stimulus frequency would show constant firing, but a plot of *response probability* (the average response spike frequency divided by the stimulus frequency) vs. stimulus frequency would yield a hyperbolic curve which, in either case would not show the obvious entrainment or phase-locking to the stimulus at the preferred frequency. Stronger stimuli may evoke an increase in the firing frequency at the "best" frequency of the unit, but lower stimulus frequencies could depress or inhibit the spontaneous rate because responses tend to be phase-locked. Thus, a unit spontaneously-active at 100 spikes/s might fire at 90 spikes/s in response to a 90 Hz sine wave stimulus.

Figure 6 shows a plot of spike probabilities as a function of the stimulus frequency for a tuberous electroreceptor fiber in *Eigenmannia*. Three curves are shown in this graph: 1) The *observed probability*, or the number of spikes recorded during the 2.2 s stimulus divided by the number of stimulus cycles. 2) The *spontaneous probability*, or the average spontaneous spike frequency (98.8 spikes/s) divided by the stimulus frequency. 3) The *observed-spontaneous probability*, or the frequency of spikes recorded during the stimulus period minus the frequency recorded during the control period immediately preceeding the stimulus, divided by the stimulus frequency. These curves show that observed responses closely follow the spontaneous responses except at a range of preferred frequencies at 350 to 400 Hz, where the response probability is significantly increased. Note the slight depression or inhibition of the spontaneous firing frequency at 280 Hz which is due to phase locking to the stimulus. No inhibition of firing frequency was ever seen for frequencies greater than the best frequency; the spontaneous discharge continued as if uninterrupted.
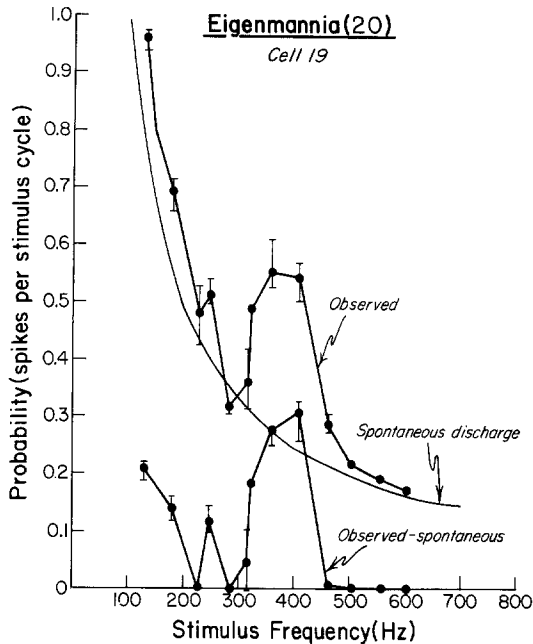
Fig. 6. Probability of firing as a function of stimulus frequency for an *Eigenmannia* tuberous receptor with a high rate of spontaneous discharge. For the unit firing at its spontaneous rate, one expects a probability curve shown by the hyperbola. The observed probability peaks at the unit's BF, however and by subtracting the spontaneous discharge rate from the observed data, the peak in the unit's sensitivity is shown clearly

Another unit (#24) from another specimen of *Eigenmannia*, which had a very low rate of spontaneous firing (2.5 spikes/s), showed a very sharp peak in observed probability at frequencies between 250 and 300 Hz and it was not necessary to subtract the spontaneous rate of discharge. When 1.8 mV/cm stimuli were applied to this unit, the response probability achieved 1.0 at 300 Hz, but fell rapidly to 0.1 at 460 Hz on the high side, and to 0.8 at 175 Hz on the low side. Thus, tuning filters abruptly cut off the high frequencies, and less sharply the low frequencies.

C. *Apteronotus albifrons*

Of the 42 units recorded from 9 different specimens of *Apteronotus albifrons*, 37 (88%) were identified as arising from tuberous receptors and 5 (12%) from ampullary. After silencing the neurally-derived EOD by making lesions in the spinal cord with a fine wire and after individuals were curarized to prevent movements, electroreceptor fibers were isolated in the NLLa as with other species. Stimuli on the order of 1 kHz were so similar to the spectra of nerve spikes, that stimulus artifacts were a serious problem, especially at high intensities. It was important to manipulate the indifferent electrode and ground electrode to reduce
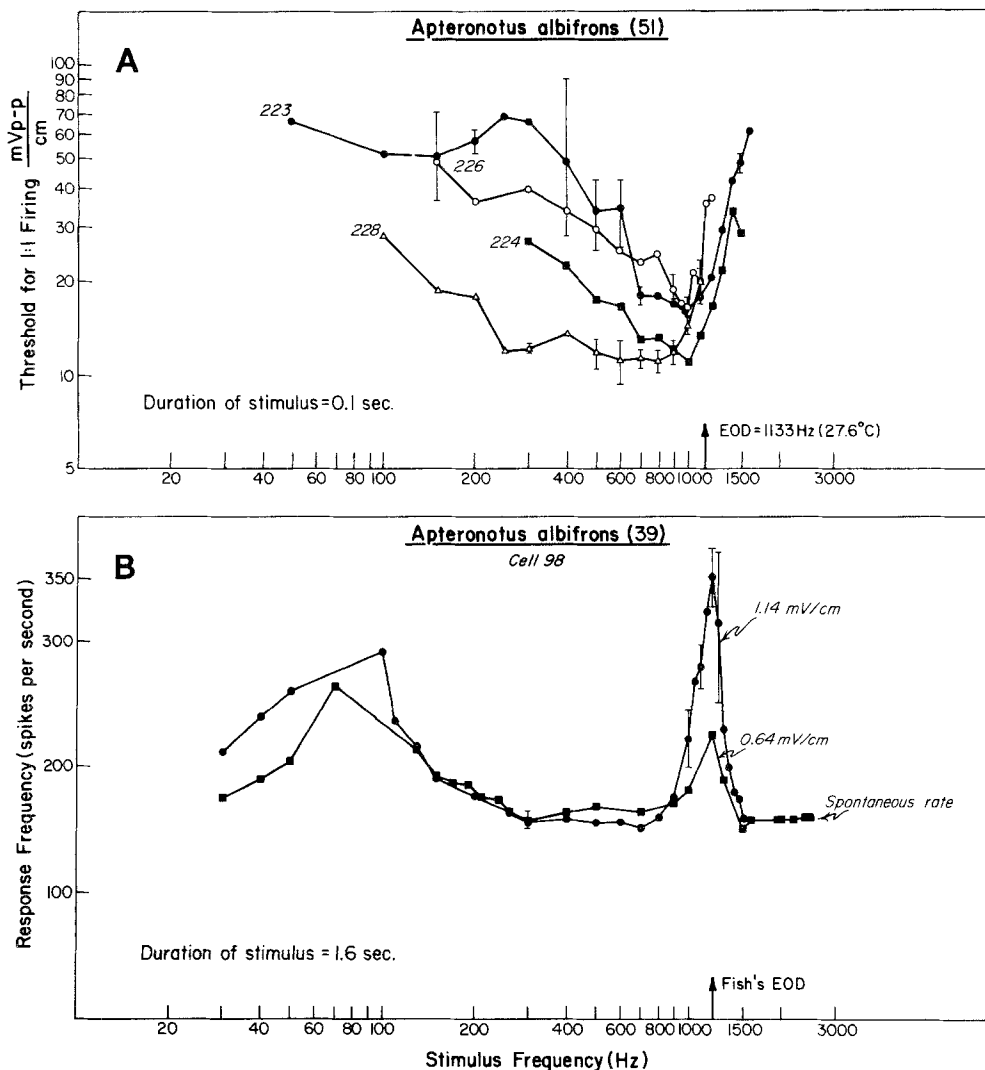
Fig. 7. A Thresholds for 1:1 firing of tuberous electroreceptors in an *Apteronotus albifrons*. Duration of sinusoidal tone bursts: 100 ms. **B** Mean firing frequency of a tuberous electroreceptor in an *Apteronotus* as a function of stimulus frequency. Stimuli were 1.6 s in duration; two stimulus amplitudes are shown

artifacts, and it was also necessary to localize the receptor on the skin so that it could be stimulated with a small wire probe, insulated except at the tip, placed near the receptor opening (a single pore centered on a scale). The sensitivity of the receptor stimulated in this way was calibrated against a longitudinal stimulus, by determining the amplitudes necessary for evoking a threshold response with both the gross stimulus, and with the local probe.

Tuberous electroreceptors can respond with 1:1 firing even at stimulus frequencies as high as 1 kHz. Figure 7A shows plots of the 1:1 threshold as a function of frequency. Stimuli lasted 0.1 s and were spaced apart by 5 s or more.

The electric field strengths are a factor of 10 higher than for *Eigenmannia*, but it was difficult to drive the electroreceptor to fire at such a high frequency. The stimuli required to do this may even be outside the physiological working range of the receptors. Yet Figure 7A shows that there appears to be only *one* population of electroreceptor fibers for *Apteronotus* in contrast to two for *Eigenmannia* and *Sternopygus*. The fibers are not sensitive, and other physiological criteria, to be discussed below, strongly suggest analogy with P receptors rather than T-receptors in the other two species. A. Feng (pers. comm.) recently found T-units in *Apteronotus* to be rare (only 10 % of tuberous units for *A. leptorrhynchus*), which may account for my not encountering them here. The threshold curves in Figure 7A filter at 4.2 ± 2.2 db per octave on the low-frequency side, and 22.5 ± 5.7 db per octave on the high frequency side of the best frequency.

Units from *Apteronotus albifrons* were usually spontaneously active at frequencies ranging as high as 100 spikes/s. Because of this and because of rapid sensory adaptation, 1:1 firing was sometimes achieved only with very strong stimuli. I decided to use a different criterion for threshold for *Apteronotus*. By monitoring average spike frequency using a passive low-pass filter as an integrator, it was possible to judge a minimum stimulus for observing a perceptible or "just noticeable difference" in the spontaneous firing frequency. I used 100 ms duration sine wave bursts as stimuli to prevent habituation, and recorded the average spike frequency on a recording oscillograph to obtain a visual record that was useful in making reliable judgements. Figure 8 (insert) illustrates the type of neural responses. Here, using an integrator time constant of 50 ms and using pulsed stimuli 100 ms in duration, spike frequency is plotted against time with the amplitude of successive stimuli being varied until threshold is determined. Spontaneous discharge frequency in this unit was approximately 100 spikes/s.

Plots of threshold for perceptible change in firing frequency as a function of stimulus frequency are shown in Figure 8 for a series of 8 units from a single fish. All of the units were maximally sensitive to frequencies corresponding to the fish's own EOD frequency (1048 Hz), but all units appeared to be of the same type, showing a large spread in the sensitivity from 0.03 mV/cm (p − p) to 1.0 mV/cm at the BF which is considerably greater than the spread of thresholds for units in other species. The eleven units shown in Figure 8 filter at 33.6 ± 20.3 db/octave on the low side, and 37.9 ± 13.9 db/octave on the high frequency side of the best frequency. All *Apteronotus* units adapt to continuous tone stimuli, and most showed a definite increase in sensitivity for frequencies at twice their most sensitive frequency. All *Apteronotus* units adapted to continuous tone stimuli, and most above the most sensitive frequency. The octave sensitivity was not seen when attempting to drive the units with 1:1 firing, presumably due to rapid adaptation.

While electroreceptors in *Apteronotus albifrons* exhibited a high rate of spontaneous activity, stimuli around the BF tended to evoke the strongest response. Plots of receptor response frequency as a function of stimulus frequency (Fig. 7B) show a marked increase in firing frequency above the spontaneous rate, for stimuli around the BF.

It is also very interesting to note that many units in *Apteronotus* were responsive to low frequency stimuli as well (80–100 Hz) as is shown in Figure 7B. At low frequencies of stimulation, *Apteronotus* cells tended to be more strongly phase-
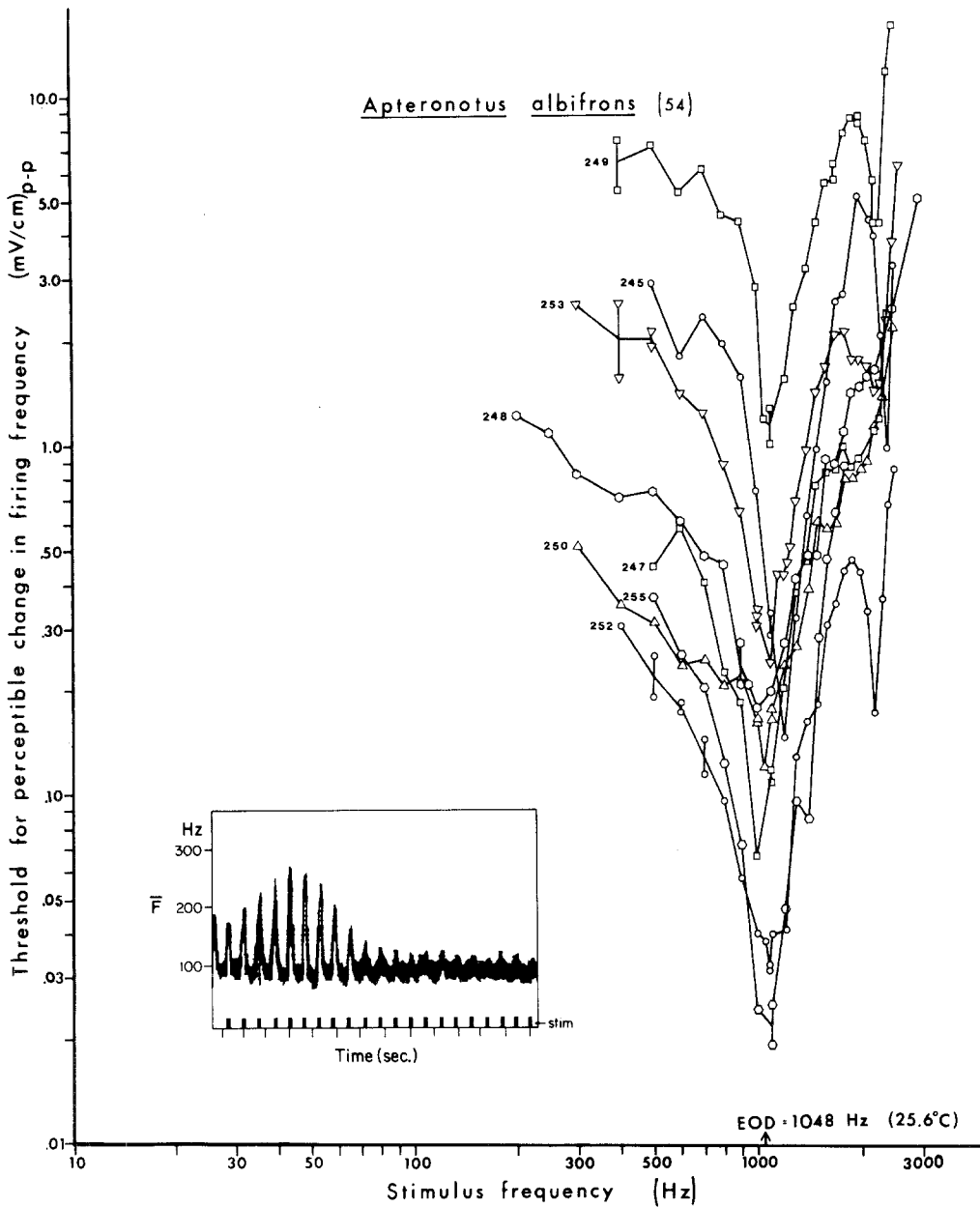
Fig. 8. Oscillograph records of average spike frequency of an *Apteronotus albifrons* unit firing in response to tone burst stimuli, 100 ms in duration. Each stimulus burst is indicated by a tic mark. The amplitude (not shown) of the stimulus was continuously varied until average spike frequency was barely perceptible. Time constant of integrator = 50 ms. Threshold for provoking a noticeable difference in firing frequency of tuberous electroreceptors in an *Apteronotus albifrons*. Each curve represents a different unit. The arrow shows the EOD frequency of this fish before the experiment (stimulus duration = 100 ms)
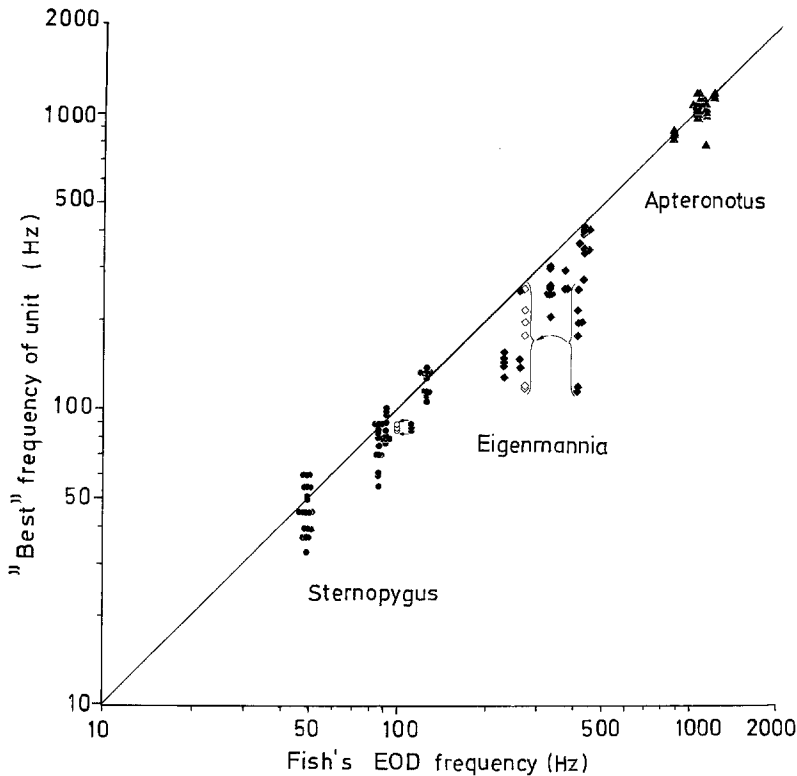
Fig. 9. Plot of tuberous electroreceptor best frequencies (BFs) as a function of the EOD frequencies of the fish from which units were recorded. *Sternopygus* units are represented as circles, *Eigenmannia*'s as diamonds, *Apteronotus*' as triangles. In cases for two experiments in which the temperatures of unit recordings were different from the temperatures used to measure the EOD frequency, the EOD frequency is translated according to a Q_{10} of 1.5 to a new value, and is shown as an open symbol. The diagonal line shows perfect correspondence between EOD frequency and BF

locked to the stimulus than at the BF. It was also remarkable to note that at extremely low frequencies of stimulation (1–5 Hz) P-units in *Apteronotus* behaved like ampullary receptors, and encoded the slow stimulus as frequency-modulated spontaneous discharge (Fig. 12b). Thus *Apteronotus* P-receptors may be able to encode a wide range of frequencies, but are maximally sensitive to those near its own EOD frequency.

D. Summary: Species Differences in Receptor Tuning

Figure 9 summarizes data from all of the electroreceptors in the three species for which I was able to determine the unit's BF by one of the methods outlined above: 1:1 firing, threshold for perceptible frequency change, or greatest spike response frequency. The BF of the unit is plotted against the EOD frequency of the individual fish prior to the beginning of the experiment. Each point on the graph represents a single unit, and the diagonal line indicates perfect correspondence between the best frequency of the unit and the EOD frequency of the fish.

Table 1. Comparison of tuning characteristics of tuberous electroreceptors of three species of gymnotoid fishes

Species	Cell Type	Filter characteristics db/octave		BF(Hz)	$Q_{(5)}$ [c]
		Low cutoff	High cutoff		
Sternopygus macrurus	T [b]	17.9 ± 6.4	69.3 ± 18.1	100	2.9
	P [b]	10.3 ± 4.3	32.2 ± 15.3	100	2.1
Eigenmannia virescens	T [b]	6.0 ± 0.5	31.0 ± 4.7	500	1.4
	P [b]	2.2 ± 5.5	22.5 ± 14.2	500	0.9
Apteronotus albifrons	P [a]	33.6 ± 20.3	37.9 ± 13.9	1,000	3.2
	P [b]	4.2 ± 2.2	22.5 ± 5.7	1,000	1.2
	T	—	—	—	—

[a] Threshold determined using the minimum stimulus for causing a just-noticeable difference in spontaneous activity

[b] Threshold determined for causing 1:1 response firing

[c] $Q_{(5)} = f_c/(f_2 - f_1)$. Where f_c is the best frequency, f_2 and f_1 are the upper and lower frequencies at which threshold has increased by 5 db in comparison to the threshold at the best frequency

During several experiments, in which temperature regulation was not very accurate, the best frequency of the unit was measured at a temperature different from that used to measure the EOD frequency. It is known that near 25 °C EOD frequency changes with temperature according to a Q_{10} factor of 1.5 (Enger and Szabo, 1965). Thus, for two cases, I have calculated what the EOD frequency would have been at the experimental temperature. Because both sets of replotted points (Fig. 9) were in closer correspondence with the straight line agreement between EOD frequency and unit BF, it strongly suggests that tuning of electroreceptors may be temperature compensated. This question is addressed in Section IV A below.

Comparisons between electroreceptors of different species can be facilitated by adopting a measure, $Q_{(5)}$, of the sharpness or quality of the electroreceptor tuning curve, defined as: $f_c/(f_2 - f_1)$, where f_c is the BF, and $(f_2 - f_1)$ is the bandwidth at the BF threshold plus 5 db (Kiang et al., 1965). High $Q_{(5)}$ values indicate that the unit is very sharply tuned (has a narrow spread of frequencies compared to the best frequency), whereas low $Q_{(5)}$ values indicate a unit with broad tuning.

Table 1 lists $Q_{(5)}$ values, estimated from the average sensitivity fall off curves for high and low frequencies determined for each species. Q values are higher for T receptors than for P receptors, and are generally higher for Sternopygus than for Eigenmannia. Apteronotus has a high $Q_{(5)}$ when tested with brief, non-adapting stimuli, but has low values when tested with adapting stimuli.

III. Other Physiological Properties of Tuberous Receptors

A. Adaptation to Continuous Tone Stimuli

P units in Eigenmannia, Sternopygus, and all cells in Apteronotus partially adapt to a continuous sine wave stimulus at their BFs whereas T cells continue to fire
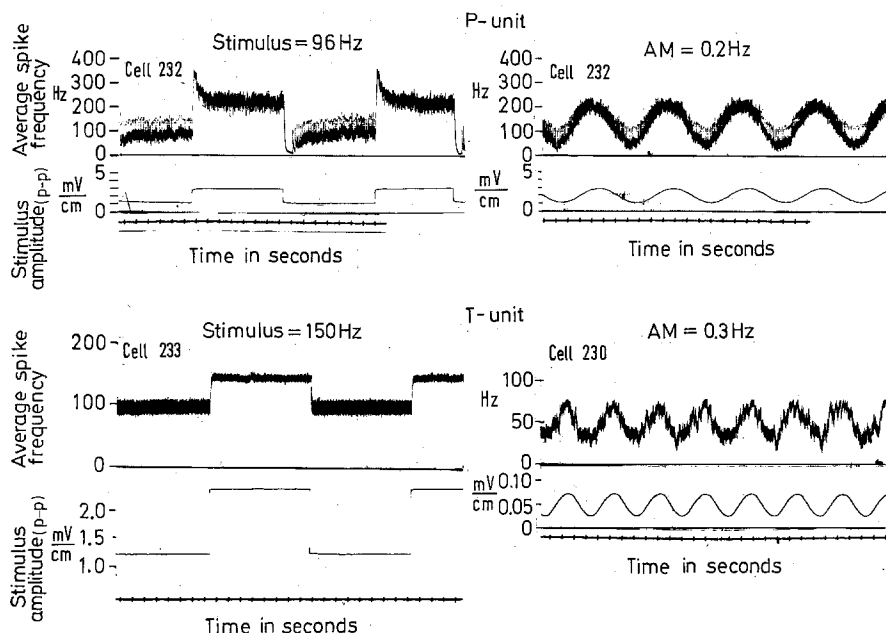
Fig. 10. Oscillograph recordings of average spike frequency of a P-unit and two different T-units from *Sternopygus*, being stimulated by an amplitude-modulated sine wave (sine wave frequency = 96 Hz for the P-unit; 150 Hz for both T-units). Modulations are either rectangular (left) or sinusoidal (right), and the stimulus amplitude is recorded in the lower trace in each example. P-units show partial adaptation to amplitude modulations whereas T-units do not. Adaptation in P units causes the spike frequency to phase-lead the sinusoidally amplitude-modulated stimulus

at a sustained rate. Figure 10 is an oscillograph record illustrating this for a P unit and a T unit from *Sternopygus macrurus*. Stimuli are amplitude-modulated sine waves; responses are standard pulses triggered by spikes that have been integrated with an R − C circuit with 50 ms time constant to show average spike frequency. When the amplitude of the 150 Hz sine wave stimulus is suddenly increased, the T unit changes firing from about 100 spikes/s to 150 spikes/s, i.e. commences 1:1 firing. T units are tonic, or non-adapting, therefore, to amplitude-modulated sine waves of the appropriate frequency (BF). The P unit in the same individual, by contrast, responds to an increase in the stimulus amplitude with a partially-adapting increase in the spike frequency. When the stimulus amplitude is suddenly lowered there is an undershoot in spike frequency which gradually increases back to a resting frequency. The P units are characteristically phasic in response to AM sinewaves at the BF. Both T and P units are more sensitive to intermediate frequencies of amplitude modulation.

Figure 11 illustrates typical patterns of adaptation in a P-receptor in *Eigenmannia*. Three different frequencies of stimulation, all at 3.4 mV/cm peak to peak amplitude, are shown. In each case, the unit initially responds with 1:1 firing, but then begins to fire at a reduced frequency. Adaptation is relatively rapid for the 500 Hz stimulus compared to the 300 Hz stimulus. At 300 Hz,
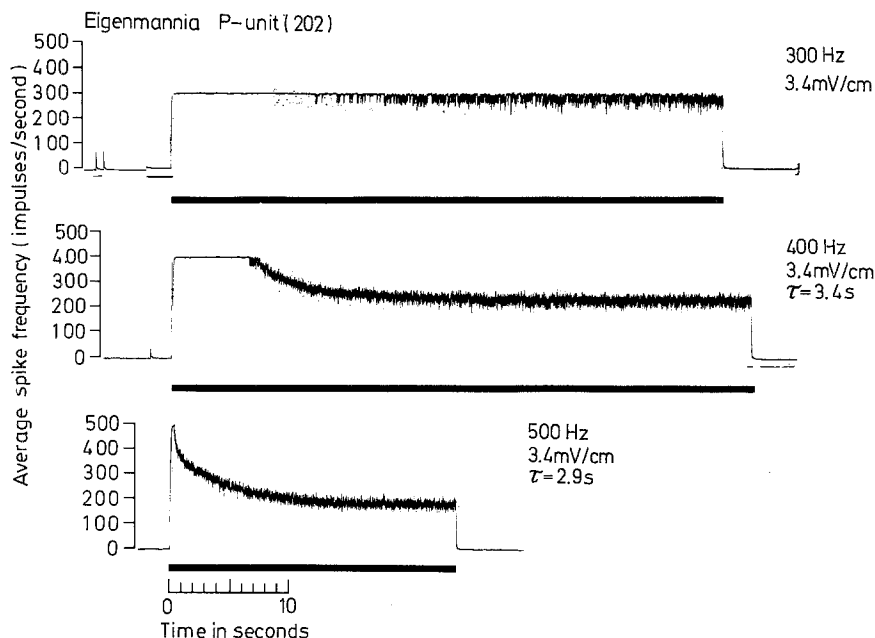
Fig. 11. Oscillograph recordings of average spike frequency of a P-unit from *Eigenmannia virescens*. Stimulus frequency and amplitude indicated at right, stimulus duration indicated as a dark bar below each graph

adaptation begins only after a delay: i.e. it is not expressed as a decrease in firing frequency until after 7 to 12 s have passed. Once the cell begins missing stimulus cycles (sputtering) the average firing frequency decreases exponentially. Adaptation occurs with a time constant of 3.4 s and 2.9 s for the 400 and 500 Hz stimuli, respectively.

Determinants of adaptation time courses were complex in this and in other units in *Eigenmannia*. While there is an apparent decrease in time constant with increasing firing frequency, slight changes in the stimulus amplitude also causes changes in the adaptation time constant. For example, a 2 mV/cm stimulus at 500 Hz applied to the same unit as above causes very rapid adaptation ($\tau = 0.2$ s compared to $\tau = 2.9$ s for a 3.4 mV/cm stimulus). The adaptation may result from the interaction of several variables: the stimulus frequency, the firing frequency of the unit, its previous history, etc.

Adaptation in an *Apteronotus* unit is shown in Figure 12A. Here, a computer-generated plot of instantaneous frequency vs. time illustrates the same principle: rapid adaptation after the onset of the stimulus to a steady-state level, and a decrement in the spontaneous activity following the termination of the stimulus. The inter-spike intervals are highly variable in *Apteronotus*, both during spontaneous activity, and after the onset of the stimulus.

To gain further understanding of the time course of adaptation of tuberous electroreceptors of the P variety, Figure 13 shows the time constant of adaptation (determined from slope on a semi-logarithmic plot) for 10-s bursts of stimuli
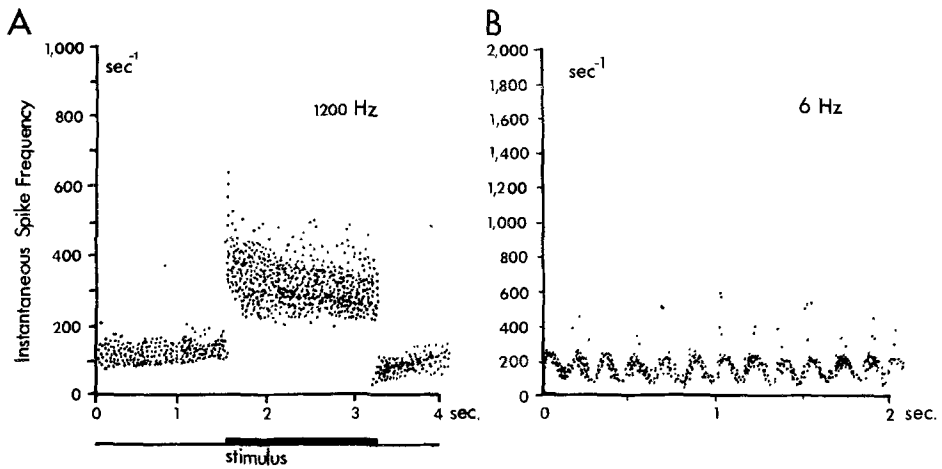
Fig. 12. Computer-generated display of instantaneous spike frequency (reciprocal inter-spike interval) of a tuberous unit from *Apteronotus albifrons* stimulated with tone bursts at 1,200 Hz, 2.32 mV/cm (left) and at 6 Hz, 16.4 mV/cm (right). Stimulus duration is indicated for the 1,200 Hz stimulus as a black bar below the figure. Partial adaptation is apparent when stimulating at the BF of the unit. The spontaneous discharge is frequency-modulated by low frequency stimuli much as in an ampullary receptor
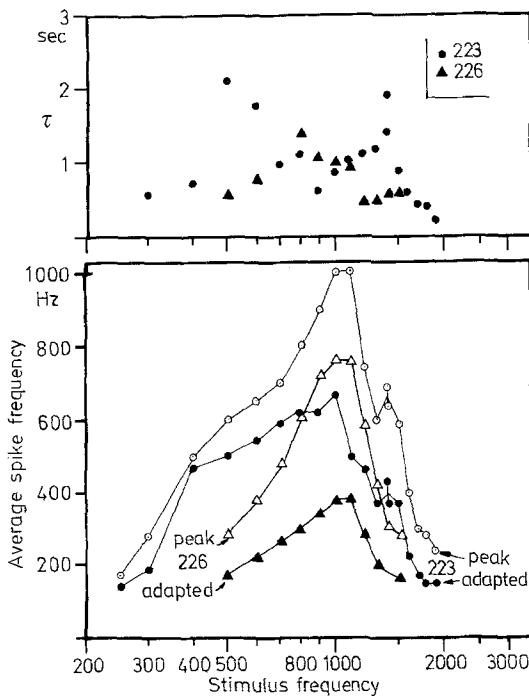

Fig. 13. Average spike frequency vs. stimulus frequency of two tuberous receptors in an *Apteronotus albifrons* (lower graph). Both the peak and the adapted spike frequency are shown. Adaptation time constants for the same two receptors are plotted as a function of stimulus frequency (upper). Stimulus amplitude = 1.77 mV/cm for cell 226; 27.6 mV/cm for cell 223

delivered to two different units in the same *Apteronotus albifrons*. Plotted below is the peak average firing frequency and the adapted average firing frequency as a function of the stimulus frequency. Adaptation time constants are highly variable, but show a general trend in both units, for long adaptation times in the stimulus frequency range of 500–1,200 Hz — which is approximately the range of discharge frequencies of the fish itself. Thus, while there is variability, these two units appear to adapt slowest to frequencies to which they are themselves most sensitive. Both units give weak responses and adapt rapidly to high frequency stimuli. Other units showed long (1–2 s) adaptation times to low frequency stimuli. Both are maximally responsive to 1,100 Hz stimuli; the EOD frequency of this fish prior to the experiment was 1,133 Hz.

Adaptation time constant, although related to stimulus frequency, showed no clear relationship with firing frequency of the unit. In plots of peak firing frequency of the unit, vs. the adaptation time constant (irrespective of the stimulus frequency), adaptation time was found to be positively correlated with firing frequency in unit 226, with a linear regression slope of $+1$ ms/Hz ($R=0.537$; D.F. $=17$; $0.05 \geq P \geq 0.01$). A second unit, #228, also showed a positive slope, 1.14 ms/Hz, but the linear regression was not significant at the 5% level ($R=0.226$, D.F. $=13$, $p>0.05$), and a third, #223, was 0.9 mV/Hz ($R=0.42$, D.F. $=17$, $p>0.05$). The fact that the time constant of adaptation increases rather than decreases with increasing firing frequency, suggests that the adaptation may occur pre-synaptically. Depletion of synaptic transmitter is a possible mechanism, for example, but as yet the phenomenon is not understood.

The adaptation time course is of utmost importance to understanding the response of the tuberous electroreceptors to time-varying amplitude-modulated signals; recovery time constants are equally important. A fast adapting cell will respond best to high frequency A.M., and in non-linear systems such as these, it will also respond to combination tones in which the beat frequency is high. Slowly adapting fibers, on the other hand, will be better at sensing low frequency A.M. or summed signals with low-frequency beats. Every encounter between one individual and another of its species results in superposition of waveforms from two individuals, and the resulting signal, modulated at the "beat" or difference frequency, may be perceived as a time-varying amplitude modulation the fish's own EOD. Fibers, such as the T-receptors in *Eigenmannia* and in *Sternopygus*, that do not appear to adapt at all, are suitable for detecting very slow changes in the amplitude of a stimulus, but the P receptors may be better adapted for AM signals or beats.

Because these *Apteronotus* units adapt so rapidly to high frequency stimulation (τ, less than 0.5 s) it is difficult to determine the threshold for responses using long-duration stimulation. At high frequencies, the unit adapts to the stimulus, and will not fire 1:1 except at very high intensities. The units in Figure 7A for which I determined the threshold of 1:1 firing using 0.1 s stimuli, have an extremely steep threshold slope on the high-frequency side of the BF compared to the low-frequency side. In Figure 8 (insert) in which the unit was tested using 100 ms duration stimuli efforts were made to prevent the unit from adapting from firing at a high frequency and is perhaps a clearer representation of the filtering characteristics of the receptor organ.
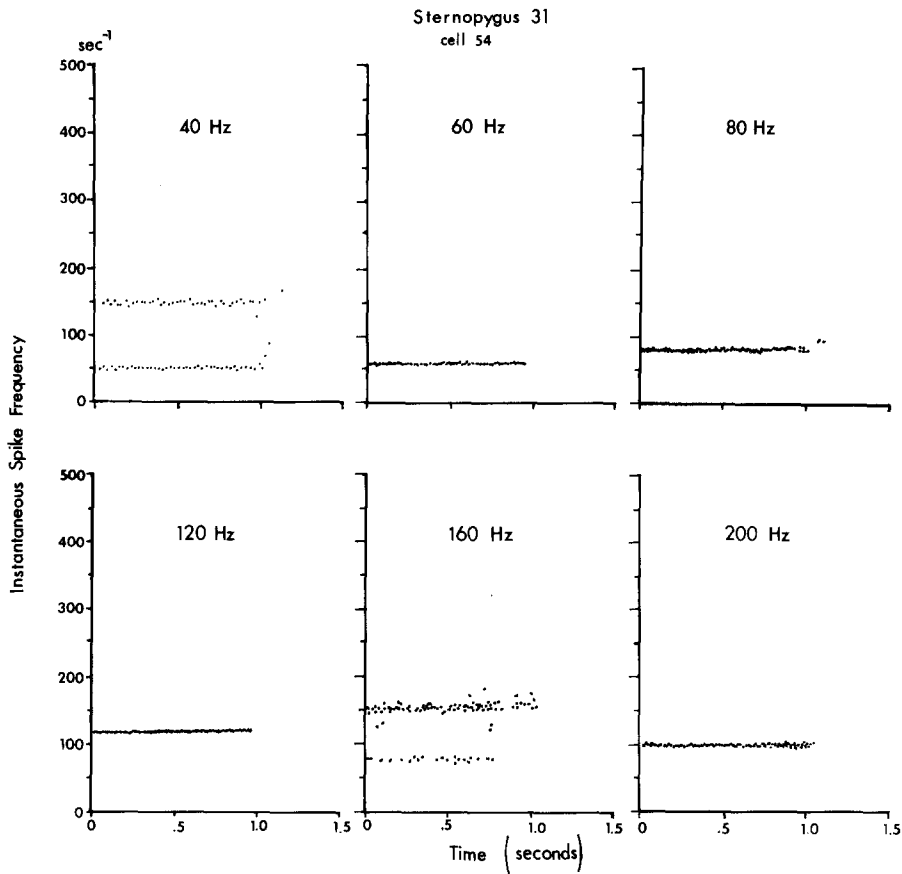
Fig. 14. Computer display of instantaneous spike frequency as a function of time, for a *Sternopygus* tuberous receptor responding to sine waves of various frequencies (all stimuli are 0.1 mV/cm p−p)

B. Phase Locking

Tuberous electroreceptors fire spikes which are phase-locked to the stimulus (Bullock and Chichibu, 1965; Hagiwara and Morita, 1963; Scheich, Bullock and Hamstra, 1973) thereby allowing stimulus intensity to be encoded as changes in the relative phase or latency of the spike response to the fish's own EOD. This characteristic is also shared by auditory fibers found in the auditory nerve (Anderson et al., 1971).

Phase locking may be seen for a unit from *Sternopygus* (EOD frequency = 94 Hz) in Figure 14 in which I have used the computer to generate a plot of instantaneous spike frequency (reciprocal interspike interval) vs. time for a series of stimuli at 0.1 mV/cm and at different frequencies. When low frequency stimuli (40 Hz) are used, this unit responds with two spikes per stimulus cycle. The two spikes come close to one another and this results in two bands on the frequency vs. time plot. The band at approximately 50 Hz results from the interval between the second spike on one phase and the first spike on the next phase. The high

frequency band at 150 Hz is the result of the interval between the first and second spikes for each period. Multiple firing is a typical characteristic of tuberous electroreceptors being stimulated at low frequencies, and has been noted previously (Scheich et al., 1973).

For intermediate stimulus frequencies, 60 through 120 Hz, this unit fires in perfect phase-synchrony to the stimulus, one spike for each cycle of the stimulus. At 160 Hz, however, which is approaching the upper frequency limit of responsiveness, the unit again fires unevenly, now intervals representing 160 Hz are seen mixed in with intervals representing one half that, or 80 Hz. Thus, the unit is now beginning to respond on an intermittent basis, missing some intervals. At 200 Hz stimulation, the unit fires on exactly *every other* stimulus cycle. The fact that the probability drops to exactly one half, still in phase with the stimulus, suggests that the unit always fires at a preferred or resonant frequency, and that stimuli an octave above the preferred stimulus can cause the unit to resonate (see also Fig. 4).

The receptor's ability to resonate in response to the second harmonic of BF is even more apparent in a series of stimuli delivered to an *Eigenmannia*. Shown in Figure 15, this unit phase-locks to stimuli as did the *Sternopygus* unit. It follows 1:1 for 120 and 160 Hz, but begins to skip cycles beginning at 200 Hz. When the frequency of stimulation is increased to 400 Hz, the unit skips a spike on every other stimulus cycle, so that the unit's firing frequency is reduced to one-half or 200 Hz. Increasing the stimulus frequency causes responses that, although phase-locked, are so disorganized that no pattern emerges in the instantaneous frequency plot. *Eigenmannia*, too, appears to be responding to the octave above its BF by a type of "resonance" response to the octave. In plots shown in Figure 4 for *Sternopygus*, the slight increase in responsiveness indicated at the octave above the BF is quite apparent.

Apteronotus demonstrated typical phase locking with low frequency (300 to 500 Hz) stimuli, but when stimulated at the EOD frequency for the species, phase locking was less apparent. There was merely a tendency toward phase-locking to the response as evidenced by a higher probability of certain response phases than others. This effect was also noted by Hagiwara et al., (1965) in their studies of *Apteronotus*.

C. Response Linearity

Electroreceptors appear to be highly nonlinear in their responses to different intensities of stimuli; however, for many units the log of the stimulus intensity plotted against the frequency or the probability of the response, shows an S-shaped response, such as that illustrated in Figure 16. There may be a short region of log-linearity in between a region of saturated firing and spontaneous activity. In Figure 16, plots of probability of firing vs. the log of the stimulus intensity for a T-receptor in *Eigenmannia* show a region of log linearity over about 8 to 10 db. Other T receptors in *Eigenmannia* are similar. *Sternopygus* responds similarly but in several examples the log-linear region spans only 6 db.
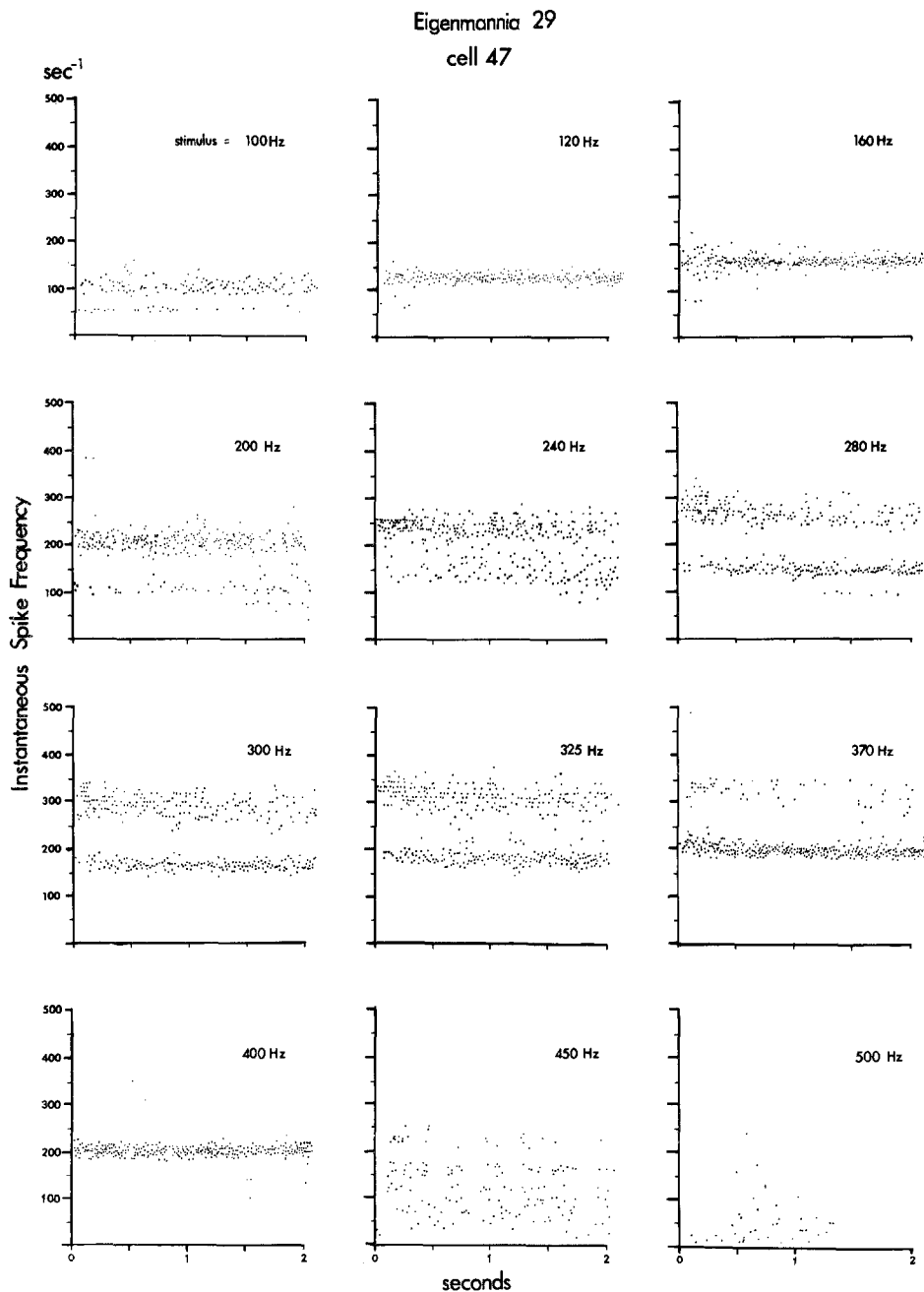
Fig. 15. Computer display of instantaneous spike frequency as a function of time for an *Eigenmannia* tuberous receptor in response to since waves of various frequencies (all stimuli are 0.71 mV/cm)
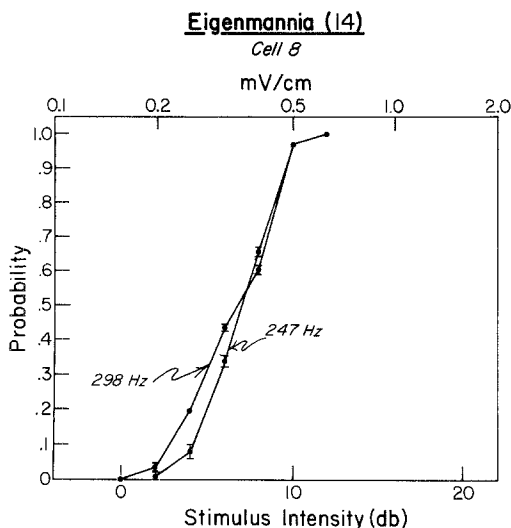
Eigenmannia (14)

Cell 8

Fig. 16. Response probability as a function of stimulus intensity for a tuberous receptor in *Eigenmannia virescens*. Two stimulus frequencies are shown

P-receptors in *Eigenmannia* were sensitive to a broader range of stimulus intensities, but did not show a straight-line region as did many of the T receptors. Usually, probability increases slowly with increases in the log of the stimulus intensity and finally levels off abruptly once $p = 1.0$. Curves of probability vs. log intensity usually show monotonic increases for a 15 to 20 db range of stimulus intensities.

Plots of probability vs. log intensity in *Apteronotus* all yield slowly increasing curves. It was difficult to generate the entire curve because many units would not fire 1:1 with the stimulus, but it was not uncommon to find the probability increasing monotonically for 20 db or more. Similar results were reported for *Eigenmannia* by Scheich et al., 1973. At certain stimulus frequencies, the response probability does not always monotonically increase. As Scheich et al. (1973) illustrate, certain response frequencies seem to be preferred; this results in a plateau in the intensity-probability curve. Such a situation is typically encountered when the unit is responding preferentially to every other stimulus cycle. As described before in the instantaneous frequency plots, this seems to represent a stable firing pattern which is difficult to disrupt.

IV. Can Receptor Tuning be Altered?

The enhancement of sensitivity to certain predictable signals such as those that fish produce themselves or to those that are likely to evolve for use in intraspecific communication, may occur only with a concomitant deterioration in the quality or sensitivity to other signals, especially when the selected enhancement or stimulus filtering takes place peripherally, rather than centrally. The following

two situations are cases in which it would appear necessary for an electric fish to have control over the tuning characteristics of its electroreceptors so as to prevent a mismatch between its own signals and its receptor tuning characteristics:

1) As a fish's body temperature changes in warm or cool water, its discharge frequency also changes according to the Q_{10} factor of 1.5 (Enger and Szabo, 1965). Imagine, e.g., an *Eigenmannia* which is subjected to a 5 °C temperature change from night to day (a temperature variation which is not uncommon in some small South American streams). If this fish's discharge were 350 Hz at night it would increase by 0.29 octaves (to 428 Hz) during the day. If the fish were maximally sensitive to its own discharge frequency during the nighttime, it would be approximately 7–9 db less sensitive during the daytime if its frequency sensitivity did not change to match the discharge frequency.

2) An individual fish might alter the frequency of its discharge during its lifetime, thereby necessitating a change in the BF of its electroreceptors. Sexually mature *Sternopygus macrurus* males, for example, have discharge frequencies between 50 and 90 Hz whereas females discharge at 100 to 150 Hz. Such differences between males and females are not apparent among immature fish, thus a change must occur with the onset of sexual maturity, perhaps with the beginning of each breeding season (Hopkins, 1972, 1974c).

A. Effects of Temperature

Warm water dripped locally on a receptor site shifts the tuning curve toward higher frequencies. Thus, temperature compensation for tuning appears to be accomplished locally at each receptor. Figure 17 shows the results of an experiment using an *Eigenmannia virescens*. The fish was kept in water at 20° for one week prior to the experiment and the temperature of the fish in the recording chamber was kept at 20° by circulating water from an ice bath through the recording chamber. When a single unit had been isolated in the NLLa, its receptor was localized on the skin using a fine wire stimulus probe, insulated except at the tip. The precise spot on the skin could be found by reducing the strength of the stimulus in stages as the probe was brought nearer and nearer to the fish's skin. Once localized, a 1 mm diameter polyethylene tube was positioned over the receptor pore. Warm water, of conductivity equal to that of the main bath, was then allowed to pass through the tube, over the receptor pore, thereby locally warming the receptor organ. Stopping the flow allowed the skin temperature to drift back to the bath temperature. A glass-insulated thermal probe placed near the opening of the pore was used to record the temperature of the water in the vicinity of the pore, and to crudely assess the temperature of the receptor. Two different T-receptor organs are represented in Figure 17; both are from the same *Eigenmannia* and both are T-receptor organs, chosen because of their sharp tuning characteristics. This *Eigenmannia* had a low discharge frequency 273 Hz (25 °C) which was even lower (230 Hz) in the experimental chamber.

The first cell, 217, represented by squares in the figure, was repeatedly warmed and cooled through five separate determinations of tuning curves: two conducted
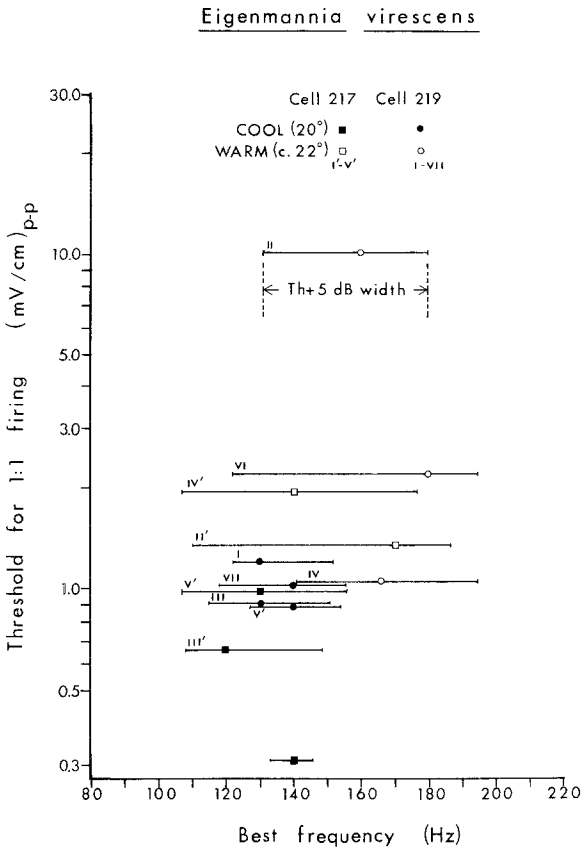
Fig. 17. Symbols represent the BFs as a function of threshold for 1:1 firing, and lines represent the bandwidths for threshold at BF plus 5 db for two cells in the same *Eigenmannia virescens*. Black symbols show the BFs of the two cells recorded at 20 °C; open symbols show BFs for the same cells recorded while the receptor organ was locally warmed to approximately 22 °C by passing a stream of warm water over the receptor. Roman numerals show the order in which the tuning curves were measured, first in cool water, then when warmed, then cooled, etc.

while warm, three while cool. A similar series is repeated for cell 219 through a sequence of seven tuning curves, three while warm and four while cool. Plotted in the figure is the BF of the unit, represented as a dot, vs. the threshold for 1:1 firing of the unit at the BF. Also indicated by a line is the 5 db bandwidth of each tuning curve. The results indicate that a cell's best frequency is generally lower at 20° than it is at approximately 22°. The experiment is complicated by the fact that the effects are not entirely reversible, possibly because of inaccurate temperature control, and by the fact that there are slight shifts in sensitivity during the course of the experiment, warmer receptors being slightly less sensitive than cool ones. Cool receptors clearly have lower frequency BFs than warmed ones, however. A plot of the BF vs. approximate temperature allows an approximation of Q_{10} temperature coefficient of these two cells: $Q_{10} = 2.8$ for receptor 219 and 3.0 for
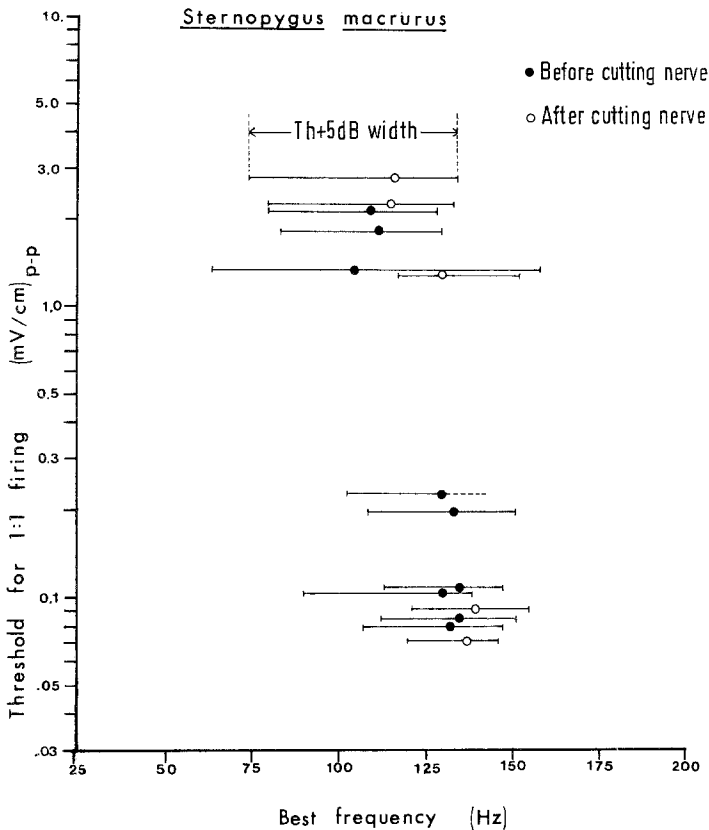
Fig. 18. BFs (symbols) and 5 db bandwidths (lines) of tuberous electroreceptors in a *Sternopygus macrurus*. Closed circles represent tuning curves taken as controls, open circles show the BFs for the other units measured after sectioning the lateral line nerve proximal to the recording site. No change can be observed in the BF or bandwidth of the units after nerve section

receptor 217 over the temperature range 20° to 22 °C. These temperature figures are a rough approximation because it is unknown how accurately the surface temperature probe measured the temperature of the receptor organ itself. These Q_{10} values are high in comparison with the Q_{10} of 1.5 known for the EOD frequency. I also conducted these experiments with *Sternopygus macrurus* and found essentially similar results. By recording from T and P receptors in *Sternopygus* before and after cooling the entire recording chamber, I found that receptor tuning curves were shifted to significantly higher frequencies in warm water compared to those in cool water. Thus, electroreceptor tuning changes with changes in the temperature of the water — a change which appears to be adaptive for matching the maximum sensitivity of the receptor with the EOD frequency of the fish's EOD. Local, temperature-dependent physiological changes appear adequate to account for this behavior.

B. Effects of Nerve Section

Lateral line detectors in elasmobranchs and in amphibians, are known to be innervated by centrifugal fibers which modulate sensitivity through efferent discharge activity (Flock, 1967; Collet, 1974; Russell and Roberts, 1972) but anatomical studies on electroreceptors have revealed only a single neuron innervating each electroreceptor organ. Presumed to be a chemical synapse, there are both pre- and post-synaptic vesicles as well as tight junctions in some species (Review in Szabo, 1974), but efferent connections have never been identified in the gymnotoid or mormyrid electroreceptors. The following experiment supports this view:

Tuning curves of nine different receptor complexes, three P units and six T units, were determined in a *Sternopygus macrurus*. Following this, the posterior branch of NLLa was severed proximal to the recording site, and tuning curves for five additional organs, three P units and two T units were determined. The results (Fig. 18) indicate that there is no change in the tuning characteristics, neither shape nor threshold, after cutting the lateral line nerve. Two other *Sternopygus*, tested similarly, had similar tuning curves prior to nerve section ($n=9$, $m=3$) and afterwards ($n=3$, $m=9$).

Discussion

I. Mechanisms of Electroreceptor Tuning

Several physiological processes in the tuberous electroreceptor complex which consists of receptor cells, synaptic junctions, and an afferent neuron, could contribute to the frequency-selective tuning reported here. While experiments have not yet been designed to distinguish between synaptic fatigue, afferent neuron refractory periods, and other possible frequency-dependent processes, Bennett (1965, 1967, 1971) has outlined a comprehensive theory of electroreceptor physiology that may account for the tuning characteristics reported here for NLLa. In Bennett's model, tuberous electroreceptor cells, enclosed within an ampulla lying under a layer of epithelial cells in the fish's skin, are composed of an outer face, which is oriented toward the exterior, and an inner face, which is closest to the site of synaptic contact. The outer surface area of the receptor cell, made appreciable by an extensive network of microvilli (Lissmann and Mullinger, 1968; Wachtel and Szamier, 1966; Szamier and Wachtel, 1970), acts like a capacitor in series with the remainder of the electrical circuit and blocks D.C. currents from flowing through the receptor cell. Long duration rectangular pulses applied to the receptor pore evoke spikes in the lateral line nerve both at the beginning and termination, but not during the stimulus. Other than contributing capacitance to the circuit, the outer face of the receptor cell is inactive, and does not fire spikes.

The inner face of the receptor cell is thought to be electrically excitable, but frequently functions below the threshold for spike initiation by producing oscillatory sub-threshold generator potentials. Microelectrodes placed near the unpigmented "pore" in the skin immediately overlying the receptor organ can be used to record these subthreshold, oscillatory potentials. In Bennett's (1967) experiments with *Gymnotus carapo* (Gymnotidae) rectangular currents applied

across the organ causes a damped oscillation voltage from the organ (oscillation potentials recorded outside the receptor pore do not originate from afferent nerve action potentials; they are still present when nerve spikes are blocked by Tetrodotoxin applied locally [Bennett, 1971] and they also occur after the lateral line nerve has degenerated but the receptor organ remains intact [Roth and Szabo, 1972; Bennett, 1971]). Oscillatory potentials in receptor cells have a high amplitude and are slowly damped when there is no resistive load; thus, in distilled water, when the receptor is out of water, or when a high-impedance load is applied artifically, the receptor "rings" for tens of milliseconds in response to a rectangular stimulus. In conducting water or with a low-impedance load, the oscillations are low amplitude and are rapidly damped.

Bennett (1967) also shows correlations between the frequency of receptor cell oscillations and the EOD frequency of several species of gymnotids. *Sternopygus* receptor cells oscillate at a much lower frequency than those in *Eigenmannia* or *Apteronotus*.

The fact that receptor cells ring at a resonant frequency suggests that membrane processes are acting as a band-pass filter with a high "Q". The Q value ought to be affected by the impedance of the load on the receptor cell, but tuning curves for spike generation in NLLa are not available for water of different conductivities to verify this. If the receptor cell membrane does act as a tuned oscillator, it could account for the sharp tuning characteristics of electroreceptor neurons reported here.

While the mechanisms underlying receptor cell oscillations are unknown, it seems worthwhile to point out that Hodgkin and Huxley's (1952) model of the squid axon membrane can mimic the damped, sub-threshold or "small signal" oscillations in membrane potential observed in squid axons which are depolarized by a constant current stimulus. Oscillations are due to voltage-dependent, time-varying conductance changes in the sodium and potassium sub-systems and can be modeled as phenomenological impedance (Mauro et al., 1970). The H-H model treated in this way, therefore, has a natural frequency of oscillation much like the electroreceptor. Changes in the temperature of the squid axon alters various parameters of these sub-threshold oscillations, including their natural frequency, but these effects can be accurately modeled by making changes in the first-order rate constants, α and β, in the H-H equations. In experiments and model, temperature exerts an effect upon oscillation frequency with a Q_{10} of 2.25 to 3 (Sabah and Leibovic, 1969; Guttmann, 1969). If oscillations in electroreceptor cells are due to Hodgkin-Huxley like membrane process, we might expect them to be temperature-dependent, behaving like the electroreceptor tuning curves did in the experiments outlined above.

Receptor cell oscillations are phase-related to nerve activity in NLLa, but not every oscillation produces a spike (Bennett, 1967, 1965). We might expect, therefore, since electric stimuli can induce oscillations, that nerve spikes should be phase-locked to stimuli.

To account for species differences in the best-frequencies of electroreceptors using Bennett's tuned oscillator model we must account for differences in the resonant frequencies of the inner membrane of the receptor cells. While there may be differences in molecular organization of the membrane, it is worthwhile

to point out that there are clear structural differences in the electroreceptors of different species of gymnotoids. Lissmann and Mullinger (1968) found that the diameter of the ampulla into which the receptor cells project is larger for high-frequency EOD gymnotoids than for low frequency species, for example. They also found that the number of discrete groups of receptor cells within an ampulla was greater for the high frequency species than for the low-frequency species. It is unknown how structural differences might affect tuning frequency, if at all. It is of interest once again to note that squid axon oscillation frequency is dependent simply on average membrane polarization voltage (Mauro et al., 1970), thus, differences in receptor cell tuning might be due solely to differences in polarization voltage, and might not even be expressed morphologically.

P and T-receptors were indistinguishable externally in my observations, and it is not known whether they differ internally, but Szabo (1965, 1974) presents criteria for distinguishing two types of tuberous electroreceptors in gymnotids (Type I and II) on morphological grounds, based upon the number of sensory cells in the ampulla, and on whether the afferent nerve leading from the receptor cells is myelinated near the nerve terminal.

II. Tuning in Other Electric Fish

If the patterns of receptor cell oscillations or action potentials can be taken as an indicator of the best frequency of the receptor organ, then it appears that most electroreceptors are tuned to a specific range of frequencies. The pulse gymnotoids, such as *Gymnotus carapo*, typically exhibit receptor cell oscillations at approximately 1 kHz (Bennett, 1967) — which corresponds to the spectral energy peak of this brief triphasic pulse. The tuberous electroreceptors in Mormyrids also exhibit oscillatory behavior (Fessard and Szabo, 1961; Szabo, 1962; Bennett, 1965; Roth and Szabo, 1972; Harder, 1968), dependent on the impedance of the environment, on the temperature (Roth and Szabo, 1972) and on the species of the fish. The oscillations in mormyrids usually take on large voltages and are rather spike-like. Although the frequency of the "spikes" varies widely under different environmental conditions there may still be underlying resonate oscillatory frequencies that are obscured by the large potentials recorded from the surface of the fish. Some species of Mormyrids, such as *Petrocephalus*, which exhibit discharges only 0.2 msec in duration, show oscillatory frequencies up to 3,000 Hz (Harder, 1968).

III. Behavioral Evidence for Tuning

The electrophysiological results reported here show that fibers innervating electroreceptors are tuned to a specific range of frequencies when tested using single frequency sine waves. Isolated sine waves approximate the natural situation when the fish stimulates its receptors with its own EOD, but it may not necessarily be representative for the filtering of other external stimuli, added to its own EOD. But Knudsen (1974) conditioned both *Eigenmannia virescens* and *Apteronotus*

albifrons to swim through a plastic ring for a food reward upon presentation of a sinusoidal stimulus, and found that the fish were markedly sensitive to their own EOD frequency, and to the species range. With the exception of very low-frequency sensitivity (especially in *Apteronotus*) which may be accounted for by ampullary receptors, Knudsen's threshold sensitivity curves parallel very closely the sensitivity profiles of the individual tuberous receptor neurons in NLLa. Interestingly, Knudsen found that *Apteronotus* shows behavioral sensitivity to the octave above the BF, and a slight increase in sensitivity to frequencies at 100 Hz, in direct correspondence with the receptor physiology.

Certain natural responses to electrical stimuli can also be used to assess electroreceptor tuning, but there may be difficulties in interpretation of the results whenever a particular frequency has a biological significance to the individual. For example, Black-Cleworth (1970) determined the threshold for evoking attack from captive *Gymnotus carapo* on a dipole stimulator emitting different frequencies of sine waves, and found a best frequency at about 1 kHz. This corresponds well with the spectral energy of *Gymnotus*'s EOD, and to its receptor cell oscillation frequency (Bennett, 1967), and may represent the behavioral sensitivity of the species.

Eigenmannia will attack and electrically "threaten" (give a display that usually preceeds attack) a dipole Plexiglas model playing tape recordings of its own species. They will also attack and threaten the model playing sine waves of frequencies between 200 and 800 Hz. During the breeding season, male *Eigenmannia* will also give electrical courtship displays toward models playing sine waves of 200–800 Hz (Hopkins, 1974 b). These results parallel the response sensitivity results of the primary receptor and raise the possibility that *Eigenmannia*'s response preferences might be explained by the stimulus filtering processes that are occurring in the periphery. But not all response profiles are explained by the receptor sensitivity. *Sternopygus* males give electrical "courtship song" in the presence of females or sine waves of the female range of frequencies (100–150 Hz), while the male's own receptors, if tuned to their own EOD, would be tuned to 50–100 Hz (Hopkins, 1972, 1974c). And the Jamming Avoidance Response (JAR) known for *Eigenmannia* and *Apteronotus* (Bullock, 1970; Bullock et al., 1972) shows a marked frequency sensitivity, much more sharply tuned than the primary receptors.

IV. Stimulus Filtering and Response Selection

Filtering of external stimuli is a characteristic of all sensory modalities, but the specificity or the complexity of the filter varies widely. Peripheral filtering mechanisms play varying roles in the selection of relevant stimuli for responses; while it would be too simplistic to assume that a peripheral filter, such as an electroreceptor, could explain frequency preferences in an electric fish's behavior, obviously the peripheral filter is one important part of the response selection or releasing mechanism. A more realistic view would be a distributed system of filters engaged for response selection (Hinde, 1970). Recent comparative data on several behavioral responses in a variety of organisms have indicated a wide

range of information processing in peripheral receptors, and for those involving communication, there are many parallels with electroreceptor filters.

The simplest type of response selection is usually correlated with communication signals that show little temporal variation, and which consist of a single spectral factor — such as a single color, sound frequency, or chemical. The male mosquito's antenna appears to mechanically resonate to sound frequencies of 400 Hz (Roth, 1948) thereby filtering all but the relevant flight sound of females of the same species. Species-specific sex attractant odors similarly appear to trigger orientation behavior in male silk-worm moths by their action on peripheral receptor organs in the male's antenna (review in Schneider, 1974).

Peripheral auditory receptors in crickets are known to be highly sensitive to a selective range of carrier frequencies (Nocke, 1972; Katsuki and Suga, 1960), but the tuning curves for releasing phonotactic responses in female crickets (*Teleogryllus commodus*) are more sharply tuned than are the physiological auditory thresholds (Hill, 1974). Thus, one must conclude that additional frequency-specific filtering or response selection goes on in the CNS of the cricket. Temporal analysis also appears to occur centrally (Nocke, 1972; Huber, 1974).

Communication signals composed of several spectral factors may be analyzed in stages, both centrally and by ascending afferent pathways. A number of studies of the auditory system of various species of frogs and toads have shown two or three types of units in the auditory nerve responsive to specific ranges of frequencies. Correlations exist between the spectral peaks in the male's territorial calls and the best frequencies for the units in the periphery (VIIIth nerve) for the bullfrog, *Rana catesbeiana* (Capranica, 1965; Frishkopf and Goldstein, 1963; Feng, Narins and Capranica, 1975), for toads, *Scaphiopus couchi* (Capranica and Moffat, 1975), and for several other anurans. Interesting shifts in the tuning characteristics of auditory units occur in a species of *Acris* which shows correlated geographical shifts in the spectrum of the male's call (Capranica, Frishkopf and Nevo, 1973).

Calling may be evoked from male bullfrogs by playing sounds imitating other males, but synthesized sounds must be composed of all of the dominant spectral peaks to evoke calling (Capranica, 1965). Thus, a central mechanism, responsive to simultaneous input from the different populations of peripheral receptors is implied; but as yet, the only suggestion of a central filtering mechanism like this is seen in the dorsal thalamus of *Rana pipiens* in which evoked potentials from two tones presented simultaneously exceed the expected sum of the tones presented alone (Mudry, Constantine-Paton and Capranica, 1975).

While stimulus filtering in peripheral electroreceptors is frequency-sensitive and is clearly adaptive for perceiving stimuli relevant for species-specific communication, additional afferent mechanisms must be involved in the evocation of some behavioral responses. Electric fish are capable of responding to certain frequencies within their response range while not responding to others (i.e. *Sternopygus* males, Hopkins, 1974c). This capability is possible because information about stimulus frequency, encoded as phase-locked nerve spikes, is preserved in the CNS. In anuran auditory systems, phase-locking is less evident (Frishkopf, Capranica and Goldstein, 1968) so that frequency information is apparently lost within a tuned afferent pathway. Interestingly, all available physiological studies

of central neurons in electric fish for which tuning curves have been measured (e.g. Bastian, 1974, for cerebellum) show filter characteristics that can be explained by the peripheral receptors. The only known case where additional filtering, or filtering at a non-EOD frequency is known from the gymnotoid CNS occurs in the torus semicircularis of the midbrain, where Scheich (1974) found cells that were most sensitive to sine wave stimuli with frequencies within ± 2 to ± 5 Hz of its own EOD. These cells were thought to be critical for recognizing the very narrow frequency range of stimuli that evoke the Jamming Avoidance Response (see Bullock, 1969).

V. Electric Communication and Noise

The principle difficulty in communicating at a distance using any sensory modality results from noise in the communication channel. Electrical "noise" has a variety of origins, obviously other individuals or species of electric fish sharing the same habitat are major contributors, but non-biological sources are probably also important. Kalmijn (1974) reviews a number of important possible noise sources, but the key source of non-biological noise in the 20 Hz to 10 kHz frequency range arises from distant lightning activity — which is unusually common in South America where gymnotoids occur (Hopkins, 1973; Crichlow et al., 1971) and which travels long distances because of ionosphere reflections (Helliwell and Morgan, 1959). By narrowing their sensitive bandwidths, electroreceptors offer an improvement of the signal to noise ratio for species-specific signals and thereby increase the maximum distance of communication. Filtering will also improve the signal-to-noise ratio for perceiving cues in electrolocation, but this is probably less critical than it is for communication. Stagge and Schief (1966) tested the jamming effect of white noise on Mormyrid communication and electrolocation and concluded that electric communication was affected more severely by noise than was electrolocation. Conclusions about the adaptive significance of stimulus filtering in the periphery, for communication, for electrolocation, or for response selection, will have to await further investigations.

References

Anderson, D.J., Rose, J.E., Hind, J.E., Bruggee, J.F.: Temporal position of discharges in single auditory nerve fibers within the cycle of a sine wave stimulus: Frequency and intensity effects. J. acoust. Soc. Amer. **49**, 1131–1139 (1971)

Bastian, J.: Electrosensory input to the corpus cerebelli of the high frequency electric fish *Eigenmannia virescens*. J. comp. Physiol. **90**, 1–24 (1974)

Bennett, M.V.L.: Electro-receptors in mormyrids. Cold Spr. Harb. Symp. quant. Biol. **30**, 245–262 (1965)

Bennett, M.V.L.: Mechanisms of electroreception. In: Lateral line detectors (ed. P. Cahn), pp. 313–393. Bloomington: University Indiana Press 1967

Bennett, M.V.L.: Electroreception. In: Fish physiology (eds. Hoar, W.S., Randall, D.J.), pp. 493–574. New York: Academic Press 1971

Black-Cleworth, P.: The role of electric discharges in the non-reproductive social behavior of *Gymnotus carapo*. Anim. Behav. Monogr. **3**, 1–77 (1970)

Bullock, T.H.: Species differences in effect of electroreceptor input on electric organ pacemakers and other aspects of behavior in gymnotid fish. Brain, Behav. Evol. **2**, 85–118 (1969)

Bullock, T.H.: The reliability of neurons. J. gen. Physiol. **55**, 565–584 (1970)

Bullock, T.H.: Seeing the world through a new sense: electroreception in fish. Amer. Sci. **61**, 316–325 (1973)

Bullock, T.H.: Essay on the discovery of sensory receptors and assignment of their functions together with an introduction to electroreceptors. In: Handbook of sensory physiology, Vol. III/3 (ed. A. Fessard), pp. 1–12. New York: Springer 1974

Bullock, T.H., Chichibu, S.: Further analysis of sensory coding in electroreceptors of electric fish. Proc. nat. Acad. Sci. (Wash.) **54**, 422–429 (1965)

Bullock, T.H., Hamstra, R.H., Jr., Scheich, H.: The jamming avoidance response of high frequency electric fish. I. General features. J. comp. Physiol. **77**, 1–22 (1972)

Capranica, R.: The evoked vocal response of the bullfrog. Cambridge: Massachusetts Institute of Technology Press 1965

Capranica, R.R., Moffat, A.J.M.: Selectivity of the peripheral auditory system of spadefoot toads (*Scaphiopus couchi*) for sounds of biological significance. J. comp. Physiol. **100**, 231–249 (1975)

Capranica, R.R., Frishkopf, L.S., Nevo, E.: Encoding of geographic dialects in the auditory system of the cricket frog. Science **182**, 1272–1275 (1973)

Collett, Th.: The efferent control of sensory pathways. In: The biology of brains (ed. W.B. Broughton), pp. 11–42. New York: John Wiley & Sons 1974

Crichlow, W.Q., Davis, R.C., Disney, R.T., Clark, M.W.: Hourly probability of world-wide thunderstorm occurrence. Inst. for Telecomm. Sci. Res. report 12, U.S. Gov't. Print. Off. Stock No. 0300–0317 (1971)

Dunning, B.B.: A quantitative and comparative analysis of the tonic electroreceptors of *Gnathonemus, Gymnotus* and *Kryptopterus*. Ph.D. Thesis, U. of Minn. Grad. School. Minneapolis, Minn. 1973

Enger, P.S., Szabo, T.: Effect of temperature on discharge rates of the electric organ of some gymnotids. Comp. Biochem. Physiol. **27**, 625–627 (1968)

Feng, A.S., Narins, P.M., Capranica, R.R.: Three populations of primary auditory fibers in the bullfrog (*Rana catesbeiana*): their peripheral origins and frequency sensitivities (to ear is human, to frogive is devine). J. comp. Physiol. **100**, 221–229 (1975)

Fessard, A., Szabo, T.: Mise en évidence d'un récepteur sensible à l'électricité dans la peau des Mormyres. C. R. Acad. Sci. (Paris) **253**, 1859–1860 (1961)

Flock, A.: Ultrastructure and function in the lateral line organs. In: Lateral line detectors (ed. P. Cahn), pp. 163–197. Bloomington: Indiana Univ. Press 1967

Forster, R., Taggart, J.: Use of isolated renal tubules for the examination of metabolic processes associated with active cellular transport. J. cell. comp. Physiol. **36**, 251–270 (1950)

Frishkopf, L., Goldstein, M.H.: Responses to acoustic stimuli from single units in the eighth nerve of the bullfrog. J. acoust. Soc. Amer. **35**, 1219–1228 (1963)

Guttman, R.: Temperature dependence of oscillation in squid axons: comparison of experiments with computations. Biophys. J. **9**, 269 (1969)

Hagiwara, S., Morita, H.: Coding mechanisms of electroreceptor fibers in some electric fish. J. Neurophysiol. **26**, 551–567 (1963)

Hagiwara, S., Szabo, T., Enger, P.: Electroreceptor mechanisms in a high frequency weakly electric fish, *Sternarchus albifrons*. J. Neurophysiol. **28**, 784–799 (1965)

Harder, W.: Die Beziehungen zwischen Elektrorezeptoren, elektrischem Organ, Seitenlinienorganen und Nervensystemen bei den Mormyridae (Teleostei, Pisces). Z. vergl. Physiol. **59**, 272–318 (1968)

Helliwell, R.A., Morgan, M.G.: Atmospheric whistlers. Proc. Inst. Radio Engineers **47**, 200–210 (1959)

Hill, K.G.: Carrier frequency as a factor in phonotactic behaviour of female crickets (*Teleogryllus commodus*). J. comp. Physiol. **93**, 7–18 (1974)

Hinde, R.A.: Animal behaviour. A synthesis of ethology and comparative psychology (2nd ed.). New York: McGraw-Hill Book Co. 1970

Hodgkin, A.L., Huxley, A.F.: A quantitative description of membrane current and its application to conduction and excitation in nerve. J. Physiol. (Lond.) **117**, 500–544 (1952)

Hopkins, C.D.: Sex differences in electric signaling in an electric fish. Science **176**, 1035–1037 (1972)

Hopkins, C.D.: Lightning as background noise for communication among electric fish. Nature (Lond.) **242**, 268–270 (1973)

Hopkins, C.D.: Electric communication in fish. Amer. Sci. **62**, 426–437 (1974a)

Hopkins, C.D.: Electric communication: functions in the social behaviour of *Eigenmannia virescens*. Behaviour **50**, 270–305 (1974b)

Hopkins, C.D.: Electric communication in the reproductive behavior of *Sternopygus macrurus*. Z. Tierpsychol. **35**, 518–535 (1974c)

Horch, K.W., Salmon, M.: Production, perception and reception of acoustic stimuli by semiterrestrial crabs (Genus *Ocypode* and *Uca*, family Ocypodidae). Forma et Functio **1**, 1–25 (1969)

Huber, F.: Neuronal background of species-specific acoustical communication in orthopteran insects (Gryllidae). In: The biology of brains (ed. W.B. Broughton), pp. 61–88. New York: John Wiley & Sons 1974

Kalmijn, A.J.: The detection of electric fields from inanimate and animate sources other than electric organs. In: Handbook of sensory physiology, Vol. III/3, (ed. A. Fessard), pp. 147–200. New York: Springer 1974

Katsuki, Y., Suga, N.: Neural mechanisms of hearing in insects. J. exp. Biol. **37**, 279–290 (1960)

Kiang, N.Y.-S., Watanabe, T., Thomas, E.C., Clark, L.S.: Discharge patterns of single fibres in the cat's auditory nerve. Cambridge: M.I.T. Press 1965

Knudsen, E.I.: Behavioral thresholds to electric signals in high frequency electric fish. J. comp. Physiol. **91**, 333–353 (1974)

Lissmann, H.W., Machin, K.E.: The mechanism of object location in *Gymnarchus niloticus* and similar fish. J. exp. Biol. **35**, 451–486 (1958)

Lissmann, H.W., Mullinger, A.M.: Organization of ampullary electric receptors in Gymnotidae (Pisces). Proc. roy. Soc. B **169**, 345–358 (1968)

Maler, L., Finger, T., Karten, H.: Differential projections of ordinary lateral line receptors and electroreceptors in the gymnotid fish, *Apteronotus (Sternarchus) albifrons*. J. comp. Neurol. **158**, 363–382 (1974)

Marler, P.: The filtering of external stimuli during instinctive behavior. In: Current problems in animal behavior (eds. W.H. Thorpe, O.L. Zangwill), pp. 150–166. Cambridge, England: Cambridge Univ. Press 1961

Mauro, A., Conti, F., Dodge, F., Schor, R.: Subthreshold behavior and phenomenological impedance of the squid giant axon. J. gen. Physiol. **55**, 497–523 (1970)

Mudry, K., Constantine-Paton, M., Capranica, R.: An integrative center for the detection of the mating call in anurans? 5th Ann. Mtg. Soc., Neuroscience Abstracts, p. 555. New York 1975

Nocke, H.: Physiological aspects of sound communication in crickets (*Gryllus campestris* L.). J. comp. Physiol. **80**, 141–162 (1972)

Roth, A., Szabo, T.: The receptor potential and its functional relationship to the nerve impulse analyzed in a sense organ by means of thermal and electric stimuli. J. comp. Physiol. **80**, 285–308 (1972)

Roth, L.M.: A study of mosquito behavior. Amer. Midl. Nat. **40**, 265–352 (1948)

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

Sabah, N.H., Leibovic, K.N.: Subthreshold oscillatory responses of the Hodgkin-Huxley cable model for the squid giant axon. Biophys. J. **9**, p. 1206 (1969)

Scheich, H.: Neuronal analysis of waveform in the time domain: midbrain units in an electric fish during social behavior. Science **185**, 365–367 (1974)

Scheich, H., Bullock, T.H.: The detection of electric fields from electric organs. In: Electroreceptors and other specialized receptors in lower vertebrates. Handbook of sensory physiology, Vol. III/3 (A. Fessard, ed.). N.Y.: Springer 1974

Scheich, H., Bullock, T.H., Hamstra, R.H., Jr.: Coding properties of two classes of afferent nerve fibers: high frequency electroreceptors in the electric fish, *Eigenmannia*. J. Neurophysiol. **36**, 39–60 (1973)

Schneider, D.: The sex-attractant receptor of moths. Sci. Amer. **231**, 28–35 (1974)

Srivastava, C.B.L.: Morphological evidence for electrical synapse of "gap" junction type in another vertebrate receptor. Experientia (Basel) **28**, 1029–1030 (1972)

Stagge, J., Schief, A.: The detection of signals in electric fish (*Gnathonemus petersii*) in the presence of noise. Cybernetic problems in Bionics. (eds. H.C. Oestreicher, D. Moore). New York: Gordon Breach Science Publishers 1966

Steinbach, A.B.: Diurnal movements and discharge characteristics of electric gymnotid fishes of the Rio Negro, Brazil. Biol. Bull. **138**, 200–210 (1970)

Suga, N.: Electrosensitivity of specialized and ordinary lateral line organs of the electric fish, *Gymnotus carapo*. In: Lateral line detectors (ed. P. Cahn), pp. 395–409. Bloomington: Indiana Univ. Press 1967

Szabo, T.: The activity of cutaneous sensory organs in *Gymnarchus niloticus*. Life Sci. **7**, 285–286 (1962)

Szabo, T.: Sense organs of the lateral line system in some electric fish of the Gymnotidae, Mormyridae and Gymnarchidae. J. Morph. **117**, 229–250 (1965)

Szabo, T.: Anatomy of the specialized lateral line organs of electroreception. In: Handbook of sensory physiology, Vol. III/3 (ed. A. Fessard), pp. 13–56. New York: Springer 1974

Szamier, R.B., Wachtel, A.W.: Special cutaneous receptor organs of fish. VI. Ampullary and tuberous organs of *Hypopomus*. J. Ultrastruct. Res. **30**, 450–471 (1970)

Wachtel, A.W., Szamier, R.B.: Special cutaneous receptor organs of fish: The tuberous organs of *Eigenmannia*. J. Morph. **119**, 51–80 (1966)

Waxman, S.G., Pappas, G.D., Bennett, M.V.L.: Morphological correlates of functional differentiation of nodes of Ranvier along single fibers in the neurogenic electric organ of the knife fish *Sternarchus*. J. Cell Biol. **53**, 210–224 (1972)