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## **Temporal Structure of Non-Propagated Electric Communication Signals**

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**Abstract.** Acoustic and electric communication differ in one important respect: while acoustic communication signals propagate through air or water as a wave, electric signals do not propagate, but exist instead as electrostatic fields. As a result of propagation, acoustic signals are distorted during transmission in a largely unpredictable way. Sound receivers, therefore, may not be able to recognize fine details in the waveform of an acoustic signal, but may have to rely instead upon time intervals between repetitions of a waveform, on the frequency of a signal, or on frequency modulations. By contrast, non-propagating electric communication signals are immune to many sources of signal distortion that affect sounds. Consequently, electric signal receivers may reliably use waveform cues to recognize a sender's identity and discriminate between signals. As examples, mormyrid electric fish encode species and sex differences in the fine structure of the electric organ discharge waveform and sense the differences using temporal cues. Gymnotiform pulse-discharging electric fish may employ scan-sampling for waveform analysis: a specialized mechanism analogous to a digital sampling oscilloscope for slowly scanning a repetitive waveform.

### **Introduction**

Electric communication signals from electric fish differ from either terrestrial or aquatic acoustic communication signals in one very important way: during transmission, sound signals propagate away from the signaler as a wave phenomenon while, in contrast, electric signals do not

propagate at all. They exist solely as locally restricted electrostatic fields. This paper will address this important distinction, and its implications for animal communication.

Since the early 1970's a number of studies of sound communication in animals have examined acoustic properties of different environments and their effects on

sound transmission. Because virtually all of the effects that have been studied to date: the role of atmospheric absorption, the effect of the ground, the importance of turbulence, temperature and humidity stratification, and the influence of different types of vegetation and plant architecture, are explained in terms of the wave nature of acoustic signals, they are not applicable to electric communication. Most of these studies have emphasized the importance of sonic transmission over long distances, and as such have been mainly interested in sound attenuation. One common question is whether or not an animal's call or song is adapted to long-distance propagation through the natural environment in which it is living. More recent studies have explored how sounds become garbled by different environmental conditions. Although there is still much to learn, there is now an interesting literature on the relationship between environmental acoustics and adaptive strategies for sound production.

By contrast, we know comparatively little about the effects of different environments on the transmission of electric signals from electric fish. While electrostatic theory can be applied to signal transmission from electric fish, empirical data are lacking for special environmental conditions too complex to be modeled theoretically. My goal here is to outline a series of contrasting adaptations for signaling and receiving with sound waves versus electric currents.

Some of the early studies on the ecology of sound by Morton [1970, 1975] and Chappuis [1971] investigated the rate of sound attenuation as a function of frequency in tropical and temperate forests

and grasslands. Liskens et al. [1976], Waser and Waser [1977], Marten and Marler [1977], and Marten et al. [1977] have pursued a similar line of research [see reviews in Wiley and Richards, 1978; Michelsen, 1978, 1983]. Several of these authors have identified 'transmission windows' in the spectrum of excess attenuation where sounds are expected to penetrate most easily through a forest environment. Embleton [1963] and Eyrings [1946] attempt to relate these findings to the acoustic-resonance properties of vegetation. Even in the absence of vegetation, sound propagation is affected by atmospheric absorption, an effect which is particularly important at high frequencies, especially in high-humidity environments [Griffin, 1971]. All of these studies have attempted to characterize different environments as frequency-selective filters for sound.

Other studies have examined more complex acoustic properties of natural environments caused by stratifications in atmospheric temperature [Ingard, 1951; Officer, 1958; Pridmore-Brown and Ingard, 1955; Rudnick, 1941]. As sounds are propagated through a stratified or layered (non-homogeneous) medium, where the velocity of sound is continuously changing, the sound wavefronts will be refracted. Under some environmental conditions, this may effectively produce a transmission wave-guide which will facilitate transmission in certain directions, but produce shadow zones in others. Wind may similarly produce refraction of sound and introduce shadow zones near the ground where there is a gradient of wind velocity [see Wiley and Richards, 1978]. Similar effects have been noted for sound

propagation in water [Officer, 1958; Payne and Webb, 1971].

Sound reflections introduce additional complications. Sound reflections from the ground set up interference patterns that may affect some frequencies but not others [Marten et al. 1977; Marten and Marler, 1977], but these effects are dependent upon the surface texture and the composition of the ground [Michelsen and Larsen, 1983] and are therefore difficult to predict.

Reflections from non-moving objects in the environment (stationary spatial heterogeneities) will introduce echoes and reverberations into the received sound. Moving spatial heterogeneities and atmospheric turbulence will introduce time-varying echoes that will produce amplitude modulations in signals of long duration. Sound propagating in aquatic environments will experience multi-path transmission echoes that will degrade a received signal [Officer, 1958; Hawkins and Myrberg, 1983]. All of these effects, absorption, refraction, and reflection, are wave-propagation phenomena which are not expected to occur in the electric modality where signals do not propagate.

Although I emphasize the difference between electric and acoustic signal transmission, there are still many similarities between the two modalities that make the comparison a natural one: the anatomy, physiology, and pharmacology of the sensory receptor cells; the mechanisms of frequency-based tuning by receptors; the organization and physiology of the central nervous system for these two sensory systems; and the importance attached to the function, communication, for the two types of sense organs.

### **Propagated versus Non-Propagated Signals**

Sounds propagate, electric-fish signals do not. Sound is initiated by the vibration of an object in a compressible elastic fluid. As the object vibrates, it sets the particles of the fluid medium into motion, and this motion produces a change in the pressure of the medium. The change in pressure causes the particles in the adjacent medium to move and the medium to undergo a pressure change of its own. This chain of events leads to the propagation of the disturbance away from the vibrating source as a longitudinal acoustic wave. The velocity at which the wave propagates is determined by square root of the ratio of pressure to density changes in the medium, a ratio which is different for different types of media. Most textbooks on acoustics derive a general formula for sound propagation velocity [Kinsler and Frey, 1962]. In air, we know that the velocity of sound is about 343 m/s (at 20 °C); and in fresh water, it is about 1,481 m/s.

In contrast, an electric fish produces a signal in water which does not propagate away from the source as an electromagnetic wave, but exists, instead, as an electrostatic field. This statement requires a brief explanation. Obviously, any alternating current source will produce an electric and a magnetic field, which will interact to produce an electromagnetic wave which propagates at close to the speed of light. Wavelengths will be extremely long for the source frequencies below 20 kHz characteristic of electric fish, and the fish, being very small by comparison, will be poor at radiating electromagnetic waves. Furthermore, electromagnetic waves are

absorbed rapidly in water and they will be attenuated in a small fraction of a wavelength. We can effectively neglect the magnetic field and consider only the electric field as an electrostatic field near to the source [Bacher, 1983]. This near-electric field behaves much like a DC voltage source connected to passive resistive (ohmic) elements. The amplitude of an electric field varies spatially, as can be predicted from electrostatic theory; temporal variations in the electric field at different recording sites are synchronized with the temporal variations at the source, hence there is no time-dependent propagation of the signal away from the source. All this assumes that the source of the electric field is stationary, i.e., not itself moving. If the source moves, like a nerve impulse along an axon, then the waveform of the electric field sensed at a distance in the volume conductor will change from place to place, as demonstrated by Lorente de N6 [1947]. Some electric fish have apparently evolved a variety of mechanisms to prevent this by synchronizing their electric organs, through the use of compensatory delays in electromotor-nerve conduction velocity, delays in synaptic transmission at the electric organ or the spinal electromotor neuron, or delays in the spike propagation within the stalk of the electrocyte [see Bennett, 1970, p. 498, for review]. Mormyrid electric fishes from Africa similarly produce a synchronous electric discharge in their electric organs. Both types have signals originating from a single, non-moving source. Some of the pulse gymnotiform fishes of South America, with their electric organs extending from the tip of the tail to the end of the pectoral fin, are somewhat less perfectly synchron-

ized, and as a consequence, their discharge waveforms do vary from place to place, especially at close range [Bennett, 1961].

The shape of an electric field in water may be predicted from elementary electrostatic theory (see any general textbook on electrostatics). Even the complex fields generated by an electric fish can be quite effectively modeled by generating a numerical solution to the Laplace equation for electrostatics. Heiligenberg [1975], Bacher [1983], and Hoshimiya et al. [1980] have solved the Laplace equation for the complex field geometry around an electric fish by setting up equivalent circuits composed of a matrix of resistive elements laid out to simulate the water, the shape of a fish, the aquarium walls and objects in the aquarium. These authors found good agreement between fields predicted for an electrostatic dipole and empirical measurements. The amplitude of the voltage (= potential, a scalar) recorded from a monopolar electrode referenced to a very distant electrode, decreases according to the inverse square of the distance from a fish. The magnitude of the electric field (a vector) is proportional to the inverse cube of distance from the source. Both potential and electric field vary according to the cosine of the angle between the dipole source axis and the position of the recording electrode(s) in space. Knudsen [1975] has shown a very close resemblance between an electric fish's electric field, and that from a simple dipole source, at least for distances greater than 10 cm where there is a minimal influence from the fish's own body which is a conductor. We expect that electric signal transmission in natural environments will be similar to that in aquaria, except that the effect of distance

on signal attenuation may be influenced by the depth of the water.

What are the important differences between a propagated signal, like sound, and a nonpropagated signal, like an electric discharge? A complete answer to this question would take us into a lengthy discussion of the biophysics of wave propagation, which is beyond the scope of the present paper. I hope only to highlight a few important points here.

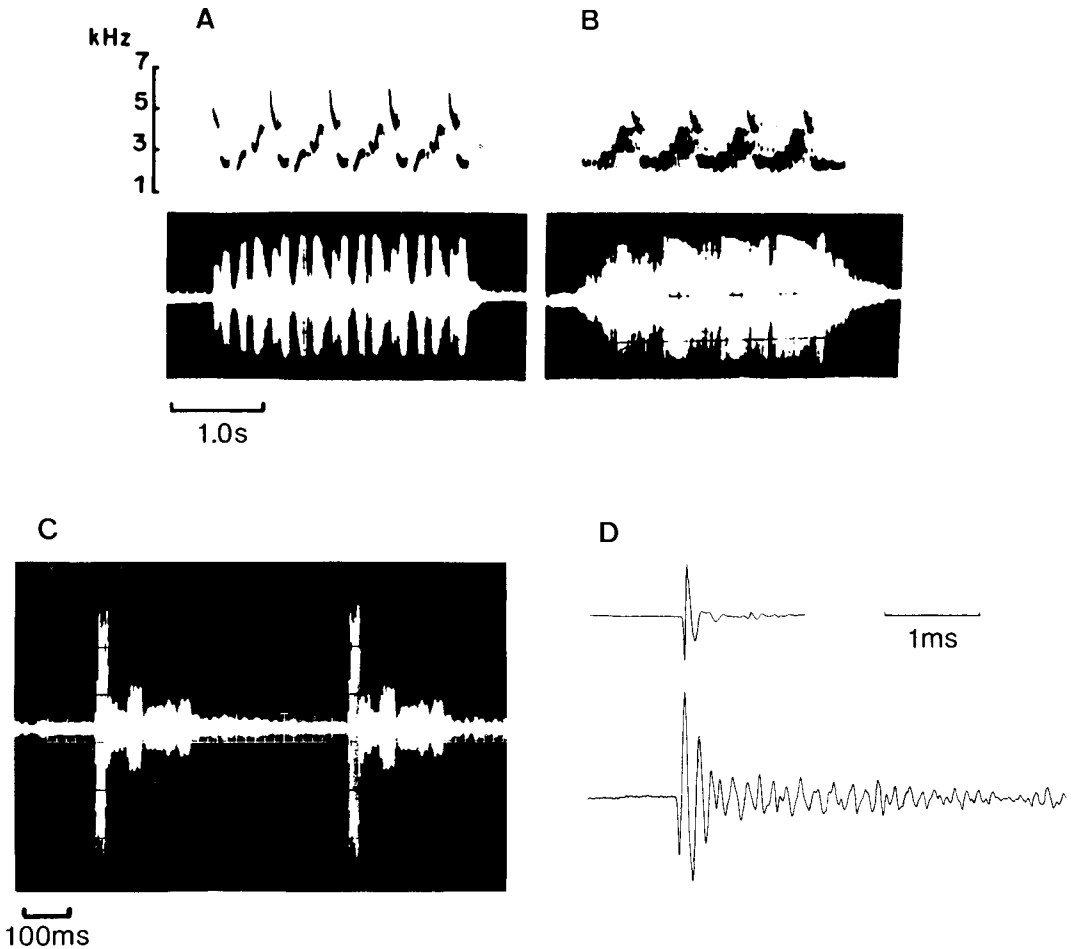
### Effects of Signal Propagation

Because sound propagates at a finite velocity, there will be perceptible delays in the time of arrival of sounds at different points in space. In air, these delays will amount to about  $29 \mu\text{s}/\text{cm}$  of straight-line travel; in water, they will be about  $6.7 \mu\text{s}/\text{cm}$ . While these times are short, there is now abundant evidence, elegantly described in this volume by Carr and by Sullivan, of their importance for azimuthal sound localization by birds, and for target range estimation by echolocating bats. No such delays are available to electric fish as cues for signal source azimuth since arrival times will be simultaneous.

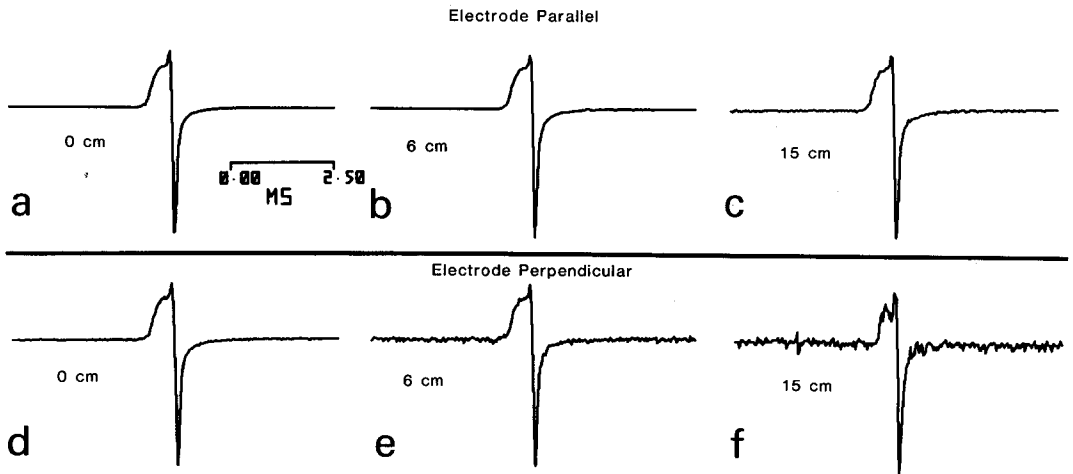
Another important consequence of sound propagation is the production of echoes. Sound waves are reflected off any object that has an acoustic impedance different from that of the medium, so long as the object is large compared to the wavelength of the sound in the medium. The reflection of a sound wave is much the same as the reflection of a light wave, and Fermat's principle of minimum travel time applies to sound as well as light. The most important effects of reflections are

the production of distinct echoes, the production of multiple echoes due to multipath propagation off several surfaces (in water, the surface and the bottom), the production of interference patterns from reflections off the ground or other large surfaces, the establishment of standing waves in response to continuous sounds, scattering by small objects in the environment, and the production of reverberations by a multiplicity of objects in the environment. Acoustic engineers have stressed the importance of multiple echoes from walls and ceilings of rooms both in terms of the intensity of propagated sound, and the intelligibility of human speech [Kinsler and Frey, 1962; Cremer and Müller, 1982], but it is only recently that biologists have been concerned with the effects of reverberation times in natural habitats [Wiley and Richards, 1978; Richards and Wiley, 1980; Michelsen and Larsen, 1983]. Richards and Wiley [1980] illustrate the effects on birdsong of transmission through 50 m of forest (fig. 1). Each syllable or note in figure 1 can be seen to have a persistent echo or reverberation both in the time-domain oscillogram and in the sound spectrogram. Pure tone bursts of sinewaves produce characteristic patterns of reverberation after passage through 25 m of forest which persist for 200 ms (fig. 1). High-resolution oscillographs of reverberations were recorded by Michelsen and Larsen [1983] while playing acoustic clicks from a loudspeaker through 1 m of vegetation (fig. 1).

These illustrations again point to the importance of the vegetation in introducing echoes which persist for 3–4 ms after an original click. In Richards and Wiley's [1980] study, reverberation time and inten-



**Fig. 1.** Reverberations and echoes affect the temporal structure of a received sound transmitted through the atmosphere. **A, B** Spectrograms (above) and oscillograms (below) of recorded song from a Carolina wren (*Thryothorus ludovicianus*) recorded at 10 m (**A**) and 50 m (**B**) from a singing bird in a forest demonstrate the effects of reverberation. Note that the basic temporal pattern of frequency is preserved at 50 m, but the details of the amplitude envelope are completely lost. **C** Oscillogram of a 25 ms tone burst of 1 kHz sinewaves recorded 25 m from a loudspeaker in forest, 0.5 m from the ground. The reverberations introduced by the atmosphere, ground, and vegetation are highly repeatable from one tone burst to the next. Echoes persist for approximately 200 ms at this carrier frequency. **D** Illustration of the distortion of a short acoustic impulse by vegetation. The sound impulse recorded in a free field at 1 m (above) and after having traveled through 2 m of vegetation at 20 cm from the ground (below). The gain of the lower trace has been increased by a factor of 10 compared to the upper trace. **A, B, C** Adapted, with permission, from Richards and Wiley [1980]. **D** From Michelsen and Larsen [1983].



**Fig. 2.** EOD waveform recorded from a mormyrid using bipolar electrodes oriented parallel to (above) and perpendicular to (below) the long body axis of a fish at varying distances (0, 6, 15 cm). The amplitude of each EOD has been scaled to the same peak-to-peak amplitude. Although the signal-to-noise ratio decreases with distance, especially when perpendicular to the body axis, the overall waveform remains constant [from Bass and Hopkins, 1985].

sity were found to be greatest in forests with foliage present compared to forests without foliage or grassland, which had the lowest reverberation index. Michelsen and Larsen [1983] record multiple echoes from a click stimulus played in an open habitat, and ascribe the effect to echoes from the ground.

Bass and Hopkins [1985] illustrate a similar experiment for an electric organ discharge (EOD) from a mormyrid fish (fig. 2). Although the recording distances are shorter than those for sound propagation, we see no apparent temporal distortion in the shape of the EOD at different distances or directions around the source. We do observe a change in the signal-to-noise ratio as the signal becomes weaker for certain expected directions. Field recordings from a variety of species of tethered mormyrids at known distances and

angles from the signaler, show no waveform variations except for expected amplitude and polarity changes. Recordings from free-ranging mormyrids always have constant waveforms [Hopkins, 1980, 1983]. Similarly, the waveform of a pulse gymnotiform's EODs recorded at different distances and directions away from the source are relatively constant (fig. 3). One typically observes a variation in the relative amplitudes of peaks in a multiphasic waveform at different locations around a pulse gymnotiform. These variations are minor compared to the large and significant changes in the EOD waveform close to the fish's skin. When electrodes measure the EOD at very close range [i.e., within 1–2 mm from the skin; Watson and Bastian, 1979] they pick up highly variable EODs for various reasons: first, in some gymnotiforms, like *Gymnotus carapo*, a

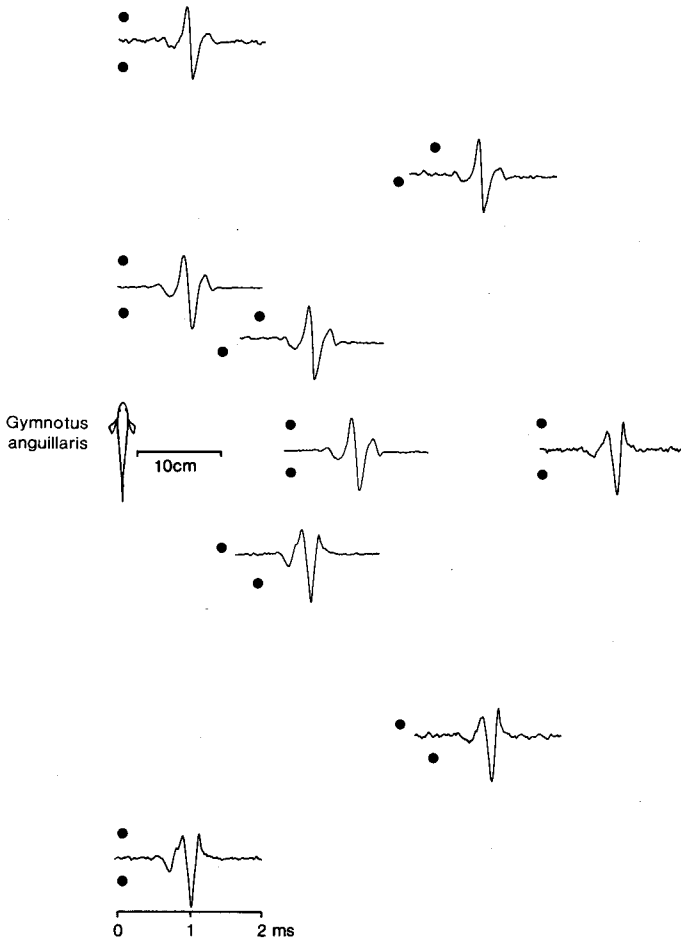


Fig. 3. The waveform of the EOD from the pulse gymnotiform fish, *Gymnotus carapo*, has 4 peaks, starting initially head negative. The EOD shows slight variation in waveform depending on the recording position. Bipolar recording electrodes are indicated by filled circles at different recording orientations and positions around the captive specimen; and the average of 5 recorded EODs is shown as the trace between the two electrodes. The electrodes and fish, seen from above, are drawn to scale. The recordings were made in a 16 cm deep stream in Surinam (width > 3 m) by Hopkins and Heiligenberg [unpublished]. The time axis shows 2 ms. All EODs are scaled to the same peak-to-peak amplitude.

specialized group of electrocytes in the anterior electric organ [Bennett, 1971] appears to contribute to a change in the EOD waveshape close to the head; and second, the electric organ may not be completely synchronized in its firing, and this will lead to a propagated dipole field which may cause subtle spatial changes in waveform in the far field. There has been no systematic study of either of these effects which will undoubtedly vary between species.

Refraction, diffraction and interference are other wave-propagation phenomena that are important in explaining the complexities of sound transmission; but all of these effects are irrelevant to electrostatic fields. Aylor [1972], Michelsen and Larsen [1983] and others [review in Michelsen, 1978] have found that reflections from the ground produce interference patterns which affect different frequencies of sound differently in transmission. Wiley and Richards [1978, 1982]



and Richards and Wiley [1980] have studied how long-duration continuous tones are modulated in amplitude by the effects of standing waves, turbulence, and scattering, all effects of wave propagation.

### **Temporal Properties of Sound and Electric Signals**

One obvious conclusion from the above comparison of sound and electric-signal transmission is that the temporal properties of received sounds will be altered by the environmental transmission, whereas those of electric signals will be minimally affected by transmission. A single sound click in air may be transformed into a slowly decaying reverberant sound lasting tens or hundreds of milliseconds, at least for certain environments where echoes are produced. A single electrical impulse, by contrast, will be received in much the same form as it was produced at the source. What are the consequences to the receiver of the presence or absence of introduced temporal smear in waveforms? What are the consequences in terms of adaptive strategies for encoding sounds versus electric signals into nerve impulses, and for recognition of these complex signals?

Temporal properties of signals and 'temporal coding' or 'temporal-pattern recognition' mean very different things to people working on different problems in acoustic and electric communication. To those interested in passerine bird song, temporal pattern may refer to the intervals between syllables [Marler and Isaac, 1960; Isaac and Marler, 1963] or to the microstructure of syllables [Marler and Pickert,

1984] or to the overall pattern of singing as a function of time. In cricket song, temporal patterning may refer to the time intervals measured in tens of milliseconds between pulses or chirps [Hoy et al., 1982; Pollack and Hoy, 1981]. For an auditory physiologist interested in the neural coding of complex sounds, temporal properties might refer to the zero-crossing times between cycles in the original waveform, events specified to a precision of milliseconds or tens of microseconds. It might be useful, therefore, when referring to temporal processing of complex sounds to specify the accuracy of temporal resolution of the system of interest. It may even be convenient to employ distinctive terms for referring to temporal analysis with a resolution of microseconds, milliseconds, hundreds of milliseconds or even seconds. The following three terms may prove useful.

#### *Ultrastructure Analysis*

This term can be used when the temporal resolution of interest is specified to an accuracy of 1–100  $\mu$ s. Less than the duration of a nerve impulse and of the jitter introduced into nerve firing patterns by synaptic transmission, an ultrastructural analysis of a sound or electric waveform represents a temporal hyperacuity for the nervous system, and evidently will require a degree of anatomical and physiological specialization for temporal analysis [Rose and Heiligenberg, 1985]. Sound localization in owls appears to depend upon a cue from the ongoing temporal disparity of the sound waveform at the two ears which can be as little as 10  $\mu$ s [Konishi et al., 1985; Moiseff and Konishi, 1981; Carr, this volume; Sullivan, this volume]. The jamming-avoidance response of electric

fish also depends upon a temporal analysis of zero crossings measured to a precision of about  $1 \mu\text{s}$  or less. Both are examples of temporal ultrastructural analysis.

#### *Waveform Analysis*

This term can be used when the temporal resolution is between  $100 \mu\text{s}$  and  $10 \text{ms}$  and where nerve impulses are phase-locked to the waveform of the stimulus. Mammalian and avian auditory-nerve fibers phase-lock to sinusoidal frequencies up to several kilohertz (time resolution of less than  $1 \text{ms}$ ). Single units cannot encode times with this resolution, cycle after cycle at these high frequencies, because of their refractory periods, but the analysis can be performed by a population of units firing probabilistically to the stimulus. Mormyrid electric fish appear to be analyzing time cues in EODs on the order of  $400\text{--}600 \mu\text{s}$  [Hopkins and Bass, 1981].

#### *Envelope Analysis*

The most common type of temporal analysis has a precision of  $10 \text{ms}$  to several hundred milliseconds, a temporal resolution which is suitable for following the overall envelope of a sound, but not its internal cycle by cycle structure. Amplitude modulations with frequencies between a fraction of  $1 \text{Hz}$  up to  $100 \text{Hz}$  fall into the domain of envelope analysis. Many vocal communication signals are known to be composed of amplitude modulations or of syllables repeated at  $10\text{--}100 \text{Hz}$ . The analysis of such signals may be accomplished by highly specialized neural circuits that are sensitive to the envelope of the waveform, not the carrier signal [Capranica and Rose, 1983; Rose and Capranica, 1983].

### **Waveform Analysis of Electric Communication Signals**

Let us now turn to two examples of temporal analysis of signals in the electric modality in order to demonstrate the importance of waveform analysis of electric signals. I will present two cases of waveform analysis: one from the mormyrid fishes of Africa and one from the other major group of freshwater electric fish, the Gymnotiformes of South America.

#### *Waveform Analysis of EODs in a Mormyrid*

Mormyrid fish produce electric discharges which have stereotyped, species-typical, and in some cases, sex-specific waveforms. Communities of electric fish from Africa show a remarkable diversity of waveforms spanning the range from 4-phase pulses lasting  $200 \mu\text{s}$  to biphasic pulses lasting  $8 \text{ms}$  [Hopkins, 1980, 1981]. A community of electric fish from Gabon, with associated waveforms, is shown in figure 4. Within this community of fish, there exist species with monophasic, biphasic, triphasic and tetraphasic discharges. Most EODs show the primary voltage transition as head-positive to head-negative, but occasionally we observe EODs that have a reverse polarity. EOD durations are highly divergent for different species; males typically have longer EODs than females whenever there is a sex difference. The existence of such an impressive overall diversity of EODs and the occurrence of sex differences in electric waveforms leads one to the suggestion that waveform analysis might be critical for species- and sex-recognition in mormyrids. Hopkins and Bass [1981]

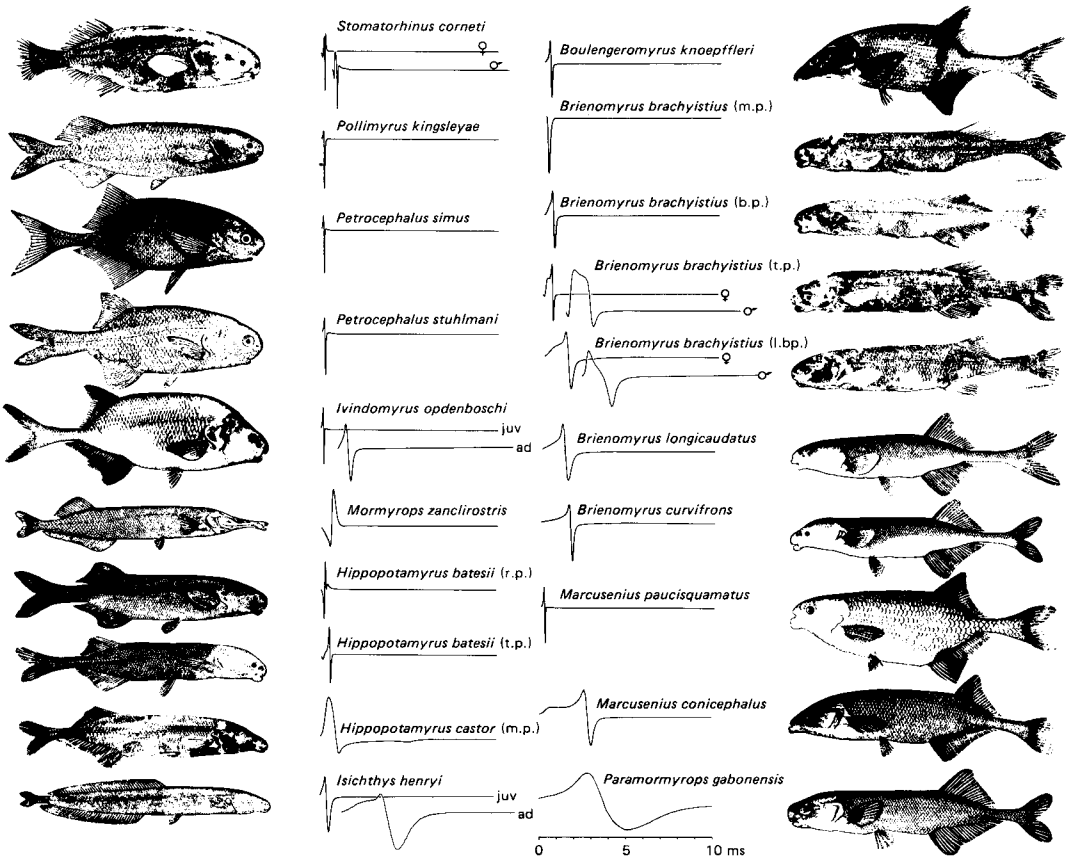
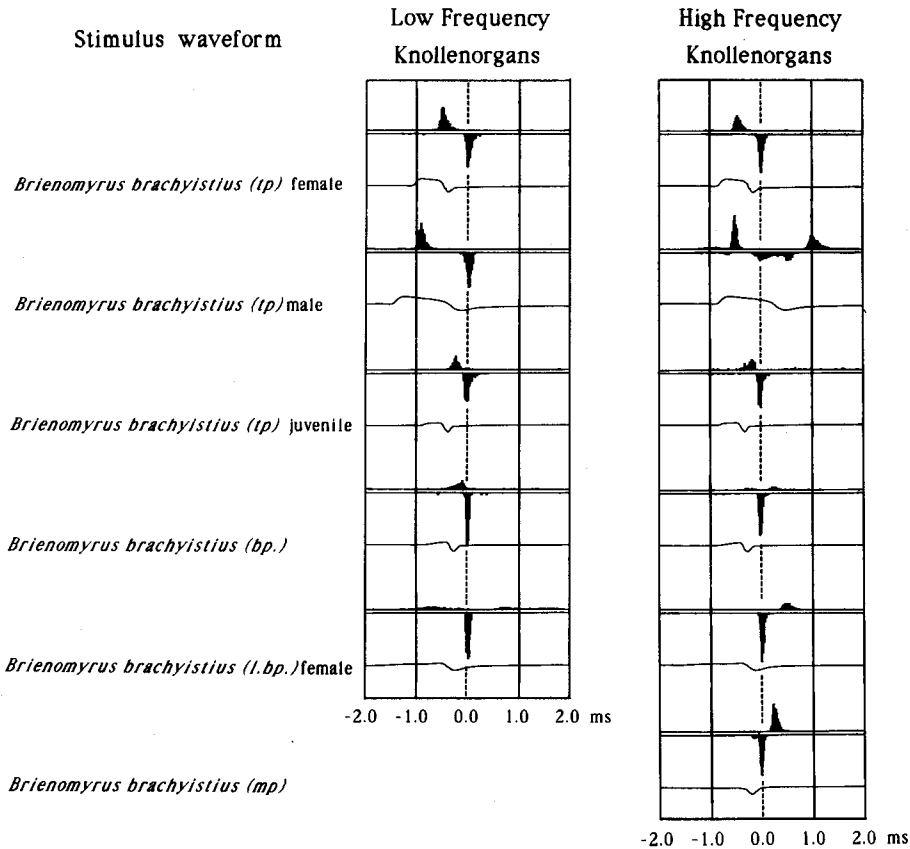


Fig. 4. EOD waveforms of mormyrid fishes from the Ivindo River district of Gabon, West Africa, plotted on the same time axis. Head negativity is plotted upward in each trace [from Hopkins, 1983]. juv = Juvenile; ad = adult; m.p. = monophasic; b.p. = biphasic; t.p. = triphasic; l.bp. = long biphasic.

tested the hypothesis directly by demonstrating that one mormyrid, *Brienemyrus brachyistius* (triphasic) was capable of discriminating EODs differing in waveform. The behavioral assay used in these experiments was the electrical 'rasp' response of the territorial male, an electrical courtship display given in response to the approach of a female or an electric female mimic. They showed that this species could discriminate EODs having identical power-

spectral characteristics on the basis of differences in waveform. They also showed that simple stimuli, like rectangle waves were confused with natural female EODs whenever key features of the EOD waveform, such as times of transitions between voltage levels, were imitated in the rectangular waveform.

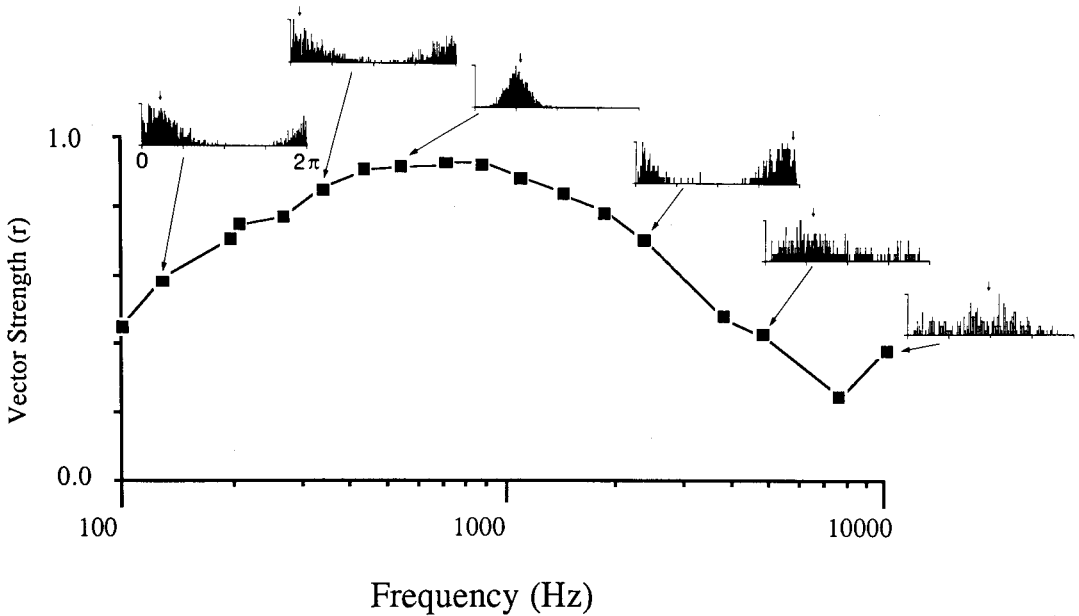
Hopkins and Bass [1981] also demonstrated that EODs are encoded by the putative communication sensor in mormy-



**Fig. 5.** Compound post-stimulus time histograms of spike activity from two single knollenorgan electroreceptors from *B. brachyistius* (triphasic) in response to different EOD waveforms. Each waveform is presented in the normal polarity to generate the upward-directed histograms, and then in the inverse polarity at the same magnitude to generate the downward directed histogram. The stimulus waveforms are indicated under each histogram. Stimuli are 10 dB or more above threshold for eliciting a single spike. Responses typical for low-frequency tuned (characteristic frequency  $\approx 500$  Hz) electroreceptors are shown in the left column and those for high-frequency tuned receptors ( $\approx 1,500$  Hz) are shown in the right column.

rids, the knollenorgan electroreceptor, has 1–3 nerve spikes which are phase-locked to the outside-positive-going voltage transitions in the stimulus waveform. By playing digitized EODs to single knollenorgans, they were able to devise artificial (square-wave) stimuli that could imitate the correct temporal pattern of spikes in

the afferent nerve. These synthetic stimuli, when used in playback experiments, were effective in eliciting a species-specific response from a territorial and courting male. By playing a variety of EOD waveforms to single knollenorgan receptors, Hopkins and Bass were able to compare the responses to the species-specific EODs



**Fig. 6.** The degree of synchronization, measured as the vector strength ( $r$ ) plotted against stimulus frequency for one knollenorgan electroreceptor. Period histograms (insets) are used to measure the degree of phase-locking. Representative period histograms are shown for indicated data points. Period histograms show spike density vs. stimulus phase, from 0 to  $2\pi$ . The  $r$ -value is a circular statistical measure for the mean vector length and ranges between 0 (random phase) and 1.0 (all spikes at same phase of stimulus). Phase-locking is best at frequencies near the characteristic frequency determined from a tuning curve (1011 Hz). Phase locking up to 10 kHz is unusual for vertebrate auditory receptors [from Arnesen and Hopkins, 1985].

with those obtained for all other species living in the same general habitat and geographical area. Patterns of receptor spike activity are shown in figure 5. The temporal patterns exhibited by these compound spike histograms demonstrate the high degree of phase-locking of knollenorgans to these fast EOD waveforms.

The degree of phase-locking of the knollenorgan receptor can be measured by generating a period histogram of the receptor spike responses to pure sinusoidal stimuli. Period histograms are plots of spike density as a function of stimulus phase, for all frequencies within the

threshold range of the receptor. Phase preferences can be estimated by measuring the vector strength of a response using circular statistics. Arnesen and Hopkins [1985] found significant phase-locking to frequencies as high as 10 kHz in knollenorgans where the mean characteristic frequency is 2.3 kHz. Period histograms and vector strengths as a function of frequency are shown in figure 6. What is impressive about the knollenorgan receptor is the degree of phase-locking at high frequencies. Undoubtedly this is essential to the temporal coding of waveforms seen in species- and sex-recognition behavior.

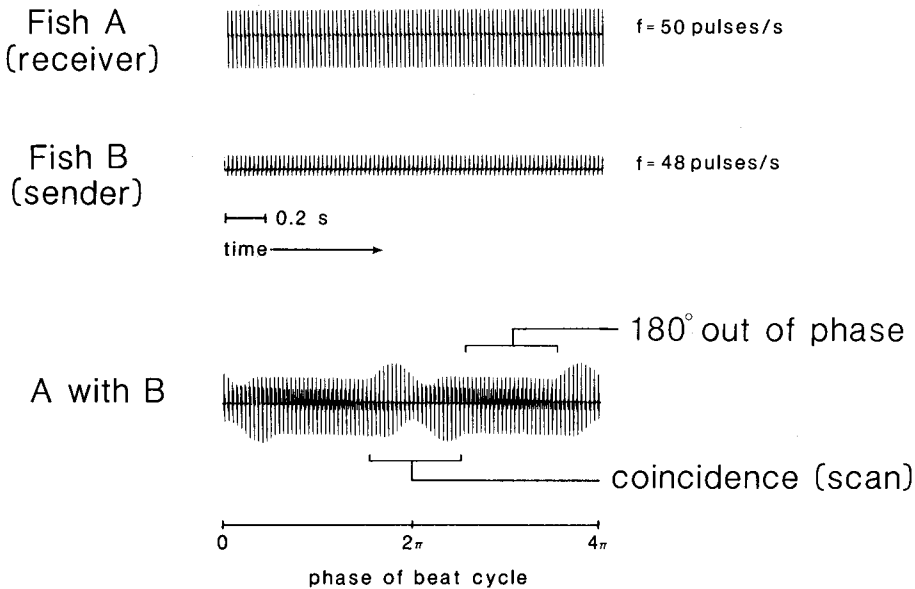


Fig. 7. Scan sampling is a hypothetical mechanism for increasing temporal acuity to fast EOD waveforms that may be used by pulse gymnotiform electric fish with regularly repeating electric discharges. The hypothesis is illustrated here for two fish with regular pulse trains: one sender and one receiver. Both sender and receiver have free-running discharges at different frequencies. A beat cycle of coincidences and alternations is established with a period equal to the inverse of the difference frequency. During the coincidence phase of the modulation cycle, the receiver may detect the signaler's EOD riding on top of its own. The receiver 'samples' the sender's EOD waveform as an amplitude modulation of its own EOD as its pulses scan past the sender's through the beat cycle. This process improves temporal acuity by spreading the samples out in time over several successive pulse repetitions [from Hopkins and Westby, 1986].

#### *Scan Sampling - A Mechanism for Fine Temporal Resolution Applicable to Pulse Gymnotiform Fish*

Quite a different mechanism for precise temporal analysis of EOD waveforms has recently been proposed by Hopkins and Westby [in press] for gymnotiform fishes with pulse discharges. Called 'scan sampling', Hopkins and Westby suggest that gymnotiform fishes glean information about the pulse waveform from a signaler by analysis of the beat pattern set up between its own and the signaler's pulse trains. Since pulse gymnotiforms produce

highly regular trains of EODs, a receiver should detect a sender's regular pulse train (which is not synchronized to its own) as a series of coincidences, in which the sender's pulses ride up on top of its own (fig. 7). The frequency of coincidences is simply the beat (or difference) frequency between the two pulse trains; the number of coincidences per beat cycle is proportional to the sum of the durations of the two pulses, and to the product of the two fish's discharge frequencies, but inversely proportional to the difference frequency [Hopkins and Westby, in press]. During

each coincidence, the receiver might be able to sample the waveform of the sender. With successive samples, scanned through the waveform at different phases of the signaler's EOD, the receiver might build a picture of the entire waveform, or some transformation of it. Scan sampling is thus analogous to the operation of a digital oscilloscope which samples repetitive waveforms at varying phases on successive sweeps to build up a complete waveform. The temporal slow-down of the original waveform is dramatic. For example, if the receiver discharges at 50 pulses/s and is close enough in discharge frequency to produce EOD overlap with the sender for 10 successive cycles, this would allow the sender's pulses to ride on top of its own, thereby producing a modulation cycle lasting for 200 ms, which is about 150 times longer the duration of most gymnotiform pulses.

The scan-sampling hypothesis has received some support from laboratory experiments with *Hypopomus beebei*, a gymnotiform with a pulse discharge. These fish were able to discriminate computer-synthesized electric signals which differ in polarity or phase-spectrum characteristics, but not in amplitude spectrum. Furthermore, the discrimination between pulse waveforms was easily observed when the computer stimulator was free-running, thereby permitting scan-sampling, but it was not observed when the stimulus was clamped to a fixed latency from the receiver's pulses. To date, there is no good experimental evidence that EOD pulse waveforms are used and recognized by pulse gymnotiforms in communication and sex or species recognition. The diversity of EOD waveforms, however, and the

occurrence, now noted in 3 species of pulse gymnotiforms, of sex differences in EODs strongly suggests that these waveforms are important for recognition, but scan sampling is but one of a number of possible waveform analysis mechanisms.

### Conclusion

For both the gymnotiform fishes and the mormyrid fishes, waveform analysis may be extremely important in signal recognition especially at the level of individual EOD waveforms. The mormyrids appear to encode EOD waveforms by precise phase-locking of spikes to the EOD waveform; gymnotiforms may employ scan sampling as an alternative mechanism. Neither of these mechanisms would ever be useful as a recognition mechanism in the acoustic modality where the predictability of a signal waveform is low because of distortions introduced during signal transmission by echoes and reverberations. In order for an animal to produce an unambiguous sound signal for species, sex, or individual identification, it may have to produce a longer-duration signal which will have characteristics such as tone frequency, that are resistant to environmental degradation. The comparison of electric and acoustic modalities provides an interesting insight into the divergent evolution of signals.

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