

Plasticity of the Electric Organ Discharge Waveform: Contexts, Mechanisms, and Implications for Electrocommunication

Philip K. Stoddard

Department of Biological Sciences, Florida International University, SW 8th St., Miami, Florida 33199 USA. E-mail: Stoddard@fiu.edu

ABSTRACT

Electric signals are made up of action potentials. Through most of the previous century, action potentials were thought to be fixed by the physiology of the excitable membranes and thus immutable. As this view has changed, so has our understanding of electric signal production. Electric fish readily change the shapes of their electric waveforms and the underlying action potentials. The information transmitted by changes in waveform is not well understood, but the contexts of these changes provide clues that may guide us in exploring the roles of EOD waveform in communication. This chapter explores the dynamic changes in the EOD waveforms of gymnotiforms and what is known of their control and context.

Key Words: Gymnotiformes; *Brachyhypopomus pinnicaudatus*; Modulation; Plasticity; Development; Hormone, Melanocortin, ACTH; Serotonin; Androgen; Communication; Predation.

1. INTRODUCTION

Students of the natural world can observe the signals of weakly electric fish by slipping two wires into the water connected to an audio amplifier or oscilloscope. If the fish are mormyrids from Africa, the discharge rate varies

considerably, with strings of pulses interspersed among longer intervals of silence. But if the fish are gymnotiforms from the Neotropics, the signals continue without a break. The interpulse intervals are longer in 'pulse fish' than in 'wave fish', but the fish never seems to turn off. After watching this endless train for the first time I asked my advisor, 'How do you tell when the fish is communicating?' The master stared in silence at the screen of the oscilloscope, then laughed 'Good question.'

The problem is not a trivial one, for most of the time, day or night, the gymnotiform fish buzzes or hums along, producing virtually identical electric organ discharges (EODs) at a steady rate. These nocturnal fish continue to electrolocate by day when they are resting as an early warning system to detect approaching predators (do fish sleep?). But patient observation and recording reveals that these EOD waveforms change in rate and shape, and do so on a variety of time scales, from weeks to milliseconds. The information transmitted by these changes is not well understood, but the social contexts of the changes provide clues that may guide us in exploring the roles of EOD waveform in communication. Other texts have reviewed the modulation of discharge rate (Heiligenberg, 1991; Stoddard, 2002; Zakon, 2003). This chapter focuses on the dynamic changes in the EOD waveforms of gymnotiforms and what is known of their control and context. Parallel work on the mormyrid electric fish has been reviewed elsewhere (Landsman, 1995).

2. RESULTS

2.1 Why Change the Waveform?

By altering the timing of EODs, an electric fish is able to communicate exclusively in the time domain. Certainly, time codes can convey huge amounts of information, as they do in modern-day digital transmission systems. Most sensory systems, however, have particular frequency biases, and many resolve multiple frequency bands. Thus, the structure of sensory systems predisposes animals to shape their signals in ways that pass information in the frequency domain as well as the time domain. EODs of larval gymnotiforms are always simple monophasic pulses resembling a single period cosine function. Such a pulse has a very broad spectrum; essentially flat from 0 Hz up to the frequency that equals the reciprocal of the period of an equivalent cosine pulse (Fig. 22.1). Thus, to use the frequency domain for communication, the fish must reshape the spectrum in some meaningful way. Hostile eavesdropping poses another reason for changing the spectrum of the larval EOD. Ampullary electroreceptors, found on catfish and gymnotiforms, as well as most pre-teleost lineages of fish, are acutely sensitive to low frequencies, from 0 Hz (DC) up to around 100 Hz (Peters and Buwalda, 1972; Dunning, 1973) (Gymnotiforms also possess less sensitive tuberous electroreceptors that are tuned to higher

frequencies, e.g. Hopkins, 1976; Shumway and Zelick, 1988). Much of the spectrum of the larval EOD resides in the low frequency band of the ampullary electroreceptors. With catfish and gymnotiforms so well represented in the big river systems of the Neotropics, the larval EOD probably functions as an 'eat me' signal to a large fraction of the piscine biomass. Evidence for the conspicuousness of these waveforms comes entirely from lab studies (Hanika and Kramer, 1999, 2000; Stoddard, 1999) and experimental field studies would be most valuable.

Consistent with the predation risk, most gymnotiform electric fish modify those larval EODs in ways that eliminate or regulate the amount of energy available for detection by other fish bearing ampullary electroreceptors. They change their waveforms by modifying the electrocytes over the course of development. Later, by dynamically controlling the waveforms as adults, gymnotiforms can transiently reintroduce this energy into their signals for use in courtship or territorial behavior.

2.2 Waveform Changes in Early Development

In most gymnotiform species, the EOD changes as the fish grows and matures. Three strategies are common in the gymnotiforms, typified by the pulse fish and two different families of wave fish.

In all gymnotiforms, larval electrocytes are formed by the fusing of myocytes, the loss of contractile proteins, and the increased expression of voltage-gated ion channels. In all cases, the new electrocytes produce monophasic EODs. The three families of gymnotiform pulse fish (Gymnotidae, Hypopomidae, and Rhamphichthyidae) modify their electrocytes to produce biphasic action potentials as adults (Bennett, 1961, 1971; Franchina, 1997b). The cells form strong cytoplasmic and extracellular structures and change from their original fusiform shape into rostro-caudally compressed disks or cubes (Fig. 22.1). Voltage-gated sodium channels are redistributed on both posterior (innervated) and anterior (non-innervated) surfaces (Fig. 22.2), allowing the cell to fire two action potentials in rapid succession. Both action potentials produce inward currents, but those currents are in opposing directions with respect to the fish's body (Bennett, 1961, 1971). The first action potential produces a headward current, the second produces tailward current; temporal offset of the two currents results in a biphasic extracellular potential. Summation of many such action potentials produce a biphasic EOD outside the fish.

Most pulse fish have evolved further tricks to add phases to the EOD. Many pulse fish develop complex electric organs that produce different waveforms in different places on the body surface (Watson and Bastian, 1979; Stoddard et al., 1999). Some Hypopomidae and perhaps all Rhamphichthyidae develop accessory electric organs on their heads that produce additional EOD phases (Bennett, 1971). Most Gymnotidae develop a subpopulation of

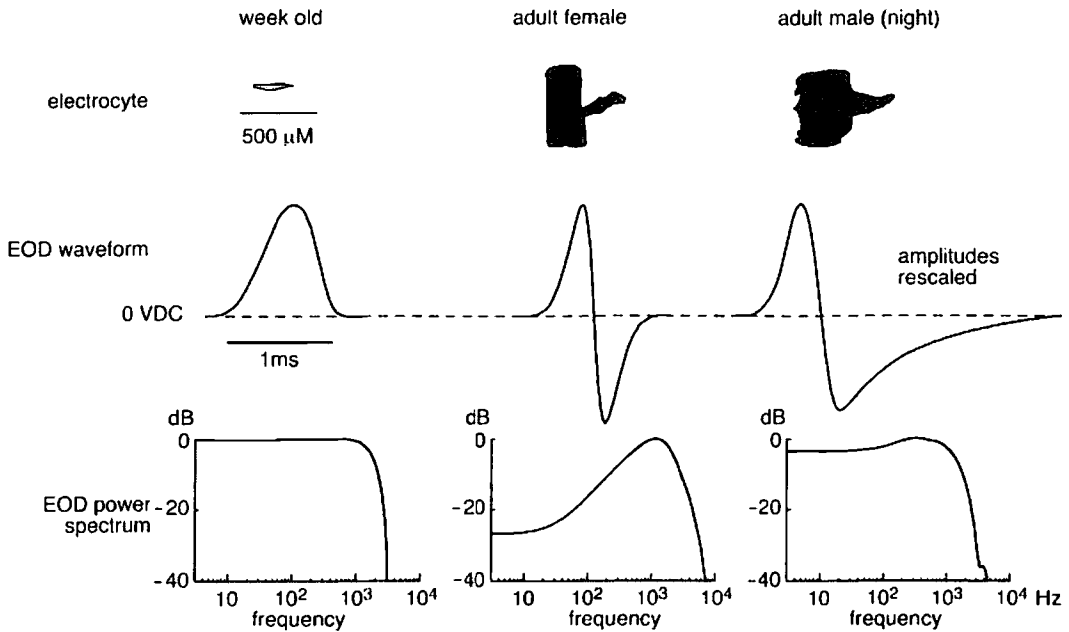


Fig. 22.1: Electrocytes, EOD waveforms, and EOD spectrograms of *Brachyhyppopomus pinnicaudatus* (the 'pinni'). Electrocytes were traced from cut sections (Franchina, 1997b; Hopkins, et al., 1990). EODs were recorded several body lengths from the fish. As electrocytes change shape, they become capable of firing two action potentials—one from each face—which produces a biphasic EOD. Ampullary electroreceptors are sensitive to energy below 100 Hz. Monophasic pulsed EODs, as made by larvae and small juveniles, have a flat spectrum, whereas adult females and older juveniles show a strong depression in the low frequencies detectable by ampullary electroreceptors, thought to be an adaptation to reduce risk of predation by electroreceptive predators. Adult males lengthen the second phase of their waveform, particularly at night, thereby restoring some energy in the spectral range of the ampullary electroreceptors. If the cumulative area of the EOD waveform lying above and below 0 VDC (horizontal dashed line) is equal, the low frequencies are generally depressed. Significant asymmetry with respect to 0 VDC diverts energy to the lowest spectral frequencies. EODs recorded by the author.

electrocytes innervated on both active faces, and so can fire multiple phases (Szabo, 1961 in Bennett, 1971; Trujillo-Cenóz et al., 1984).

Typical of wave fish, members of the family Sternopygidae discharge their electric organs with intervals no longer than the EOD waveform itself, producing a continuous wave. Continuous production of EODs narrows the spectrum greatly. Further, sternopygids produce an active head-negative DC current that offsets the EOD's baseline so that the wavetrain is re-centered around zero volts. Centering the EOD around zero volts nulls the net DC offset, eliminating the remaining 0 Hz component. For a good explanation of spectral shifting by waveform manipulation, see Bradbury and Vehrencamp (1998). The mechanism for this DC offsetting is unknown, but probably involves the ion-exchange pump restoring the Na⁺ balance after an EOD. Cessation of the EOD gradually eliminates the DC offset over a minute's time (Bennett, 1971). Note: by convention, EOD waveforms are always represented in the head-

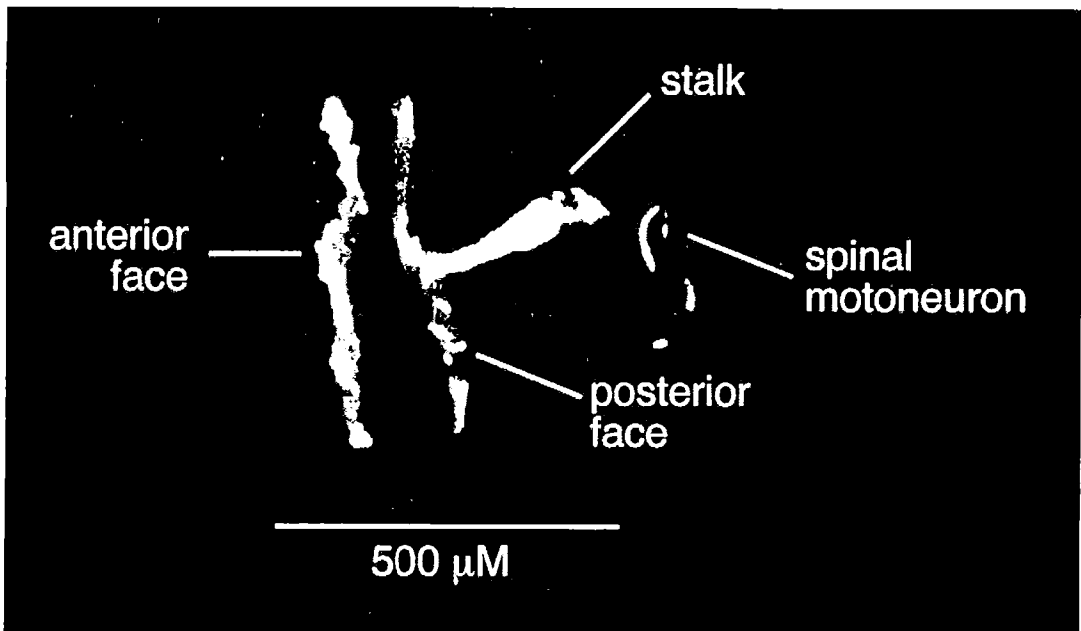


Fig. 22.2: This electrocyte of a female *Brachyhyppopomus pinnicaudatus* reacted with an antibody for the voltage-gated sodium channel provided by S.R. Levinson. Secondary fluorescent label is the light colored area, which shows sodium channel to be localized to the two active faces of the electrocyte, the stalk, and the spinal nerve that innervates the electrocyte. Photo courtesy of V.J. Hodge.

minus-tail orientation, in such a manner that a headward sodium current within the electric organ is measured as a positive potential near the fish's head, and represented as an upward deflection of the voltage trace measured outside the body.

Like the other gymnotiforms, apteronotids begin independence with a larval electric organ of myogenic origin that produces a monophasic EOD. Over the next few weeks, apteronotids gradually replace this larval electric organ with a neurogenic organ derived from spinal motoneurons that grow to form a loop. Action potentials propagating (1) down then (2) back up the loop produce a biphasic waveform (Bennett, 1971). In genera such as *Apteronotus*, the adult EOD waveform has nearly equal area above and below 0 VDC, thus produces almost no DC energy. But in other genera such as *Adontosternarchus*, the EOD is imbalanced, showing an area in the head-negative rather than head-positive directions. This DC asymmetry may play a role in communication, as will be explained later.

2.3 Changes in the EOD with Sexual Maturity

As gymnotiforms mature sexually, some taxa develop sexual dimorphism in the EOD waveforms. Sexual differentiation of waveforms is the rule among the wave fish, though it appears selectively among pulse fish. Such changes emerge over the course of weeks to months.

As wave fish mature sexually, the spectral peak of the EOD increases or decreases. The spectral peak is determined by two features, the EOD pulse duration and the discharge rate. EOD pulse duration changes as though the EOD is stretched or compressed. Compared to juveniles, EODs of mature males are typically lengthened and those of females are typically shortened, though in certain apteronotids this pattern is reversed. These changes in the animal's entire waveform have been shown to correspond to changes in the action potentials measured in individual electrocytes (Bass and Volman, 1987; Mills and Zakon, 1991; Markham and Stoddard, 2005), and have been traced to sex differences in sodium and potassium currents (Dunlap et al., 1997; McAnelly and Zakon, 2000). Corresponding to this change in EOD pulse duration, the interval between EODs changes in the same way, lengthening for fish that extend pulse duration, and shortening for those that reduce pulse duration. Thus, the ratio of EOD to silence (the duty cycle) remains unchanged, which allows the frequency spectrum to shift up or down without broadening. The result is a twofold difference in the spectral peaks of males' and females' EODs (Hopkins, 1974).

Pulse fish of the genus *Brachyhypopomus* (family Hypopomidae) develop characteristic sexual dimorphisms in the EOD waveform. As males mature, their tails grow longer and thicker, their EOD amplitudes increase, and the large, head-negative phase of their EODs (the 2nd phase in biphasic species) increase in duration (Hagedorn, 1988; Hopkins et al., 1990). The lengthening of the 2nd phase is due to an increase in repolarization time of this phase, easily characterized by a single parameter, the time constant τ_{p2} . τ_{p2} is the exponent of an inverse exponential function fitted to the decay of the 2nd phase of the biphasic EOD (Fig. 22.3). Increase in τ_{p2} changes the EOD spectrum in two ways and opens the door for a third mechanism that will be discussed in the section on rate changes. First, increases in τ_{p2} lower the spectral peak producing consistent sex differences in the peak power frequency of male and female EODs. Second, extending the second phase of the EOD without altering the first phase produces asymmetry with respect to 0VDC, with more energy now lying below 0 V than above (Fig. 22.1). This change restores some of the low frequency energy that was lost when the juvenile developed a symmetric biphasic EOD from the larval monophasic EOD.

Data from the Hypopomidae (*Brachyhypopomus occidentalis* from Panama and *B. pinnicaudatus* from tropical and subtropical South America) reveal dynamic regulation of the EOD waveform (Hagedorn and Zelick, 1989; Hagedorn, 1995; Franchina and Stoddard, 1998; Silva et al., 1999). These patterns and mechanisms of plasticity will probably be found to apply to other gymnotiforms and perhaps mormyrids as well (Carlson et al., 2000; Terleph and Moller, 2003).

Hagedorn and Zelick (1989) paired male *Brachyhypopomus occidentalis* in contests for hiding tubes. The next morning, the loser had raised the spectral

peak of his EOD more than the winner. As explained above, such a change would result from an alteration of the 2nd phase duration, in this case the loser shortened his 2nd phase more than the winner. Subsequent studies of *Brachyhypopomus* have shown that the EODs change dramatically between day and night (Hagedorn, 1995; Franchina and Stoddard, 1998; Silva et al., 1999), with more rapid social and stress-mediated effects superimposed on the day-night oscillations (Franchina et al., 2001; Stoddard et al., 2003). These effects will be explained in greater detail and will include preliminary data from studies currently in progress in my laboratory.

Dynamic changes in the EODs of *Brachyhypopomus* change the EOD between more feminine and masculine forms. We refer to the increase in amplitude and 2nd phase duration as 'enhancement', rather than masculinization, because these changes are common to both sexes, though greater and more prevalent in males (Silva et al., 1999).

2.4 Circadian Rhythms

Limited data suggested the day-night changes in EOD were true circadian rhythms, characterized by free-running oscillations under constant photic conditions (Hagedorn, 1995; Franchina, 1997a; Stoddard et al., 2003). Ongoing studies show that EOD amplitude, EOD 2nd phase duration, and discharge rate continue to oscillate on ~24 period for at least a week under constant darkness or constant light. The EOD waveform characters tend to run down over the course of several days, whereas the rate oscillations attenuate less over a period of time. In spite of some run down, the persistence of these oscillations under constant photic conditions qualifies them as true circadian rhythms (Fig. 22.3). Interestingly, EOD amplitude and τ -p2 can either vary together or not. The rise in EOD amplitude typically begins in the early afternoon, peaking 2–3 hours after dark. τ -p2 usually begins to increase 30 min before dark, yet peaks around the same time as amplitude. Amplitude most often has fallen to its 24-hour low by late morning, whereas τ -p2 often continues to fall through the afternoon. Oscillations of EOD amplitude are much reduced in winter, whereas those of τ -p2 are more persistent.

2.5 Socially Mediated Changes

In social isolation, males lose their circadian oscillations. Addition of male or female tank mates causes a rapid enhancement of the EOD, visible within minutes. Maintenance of social conditions fully restores the circadian oscillation of τ -p2 in a single day, and amplitude over the course of 3–9 days. Recovery is fastest in the presence of a male slightly smaller than the focal male (Franchina et al., 2001).

If we place two fish in the same shelter tube and track the EOD changes minute-to-minute, both fish undergo rapid EOD enhancement, with the first

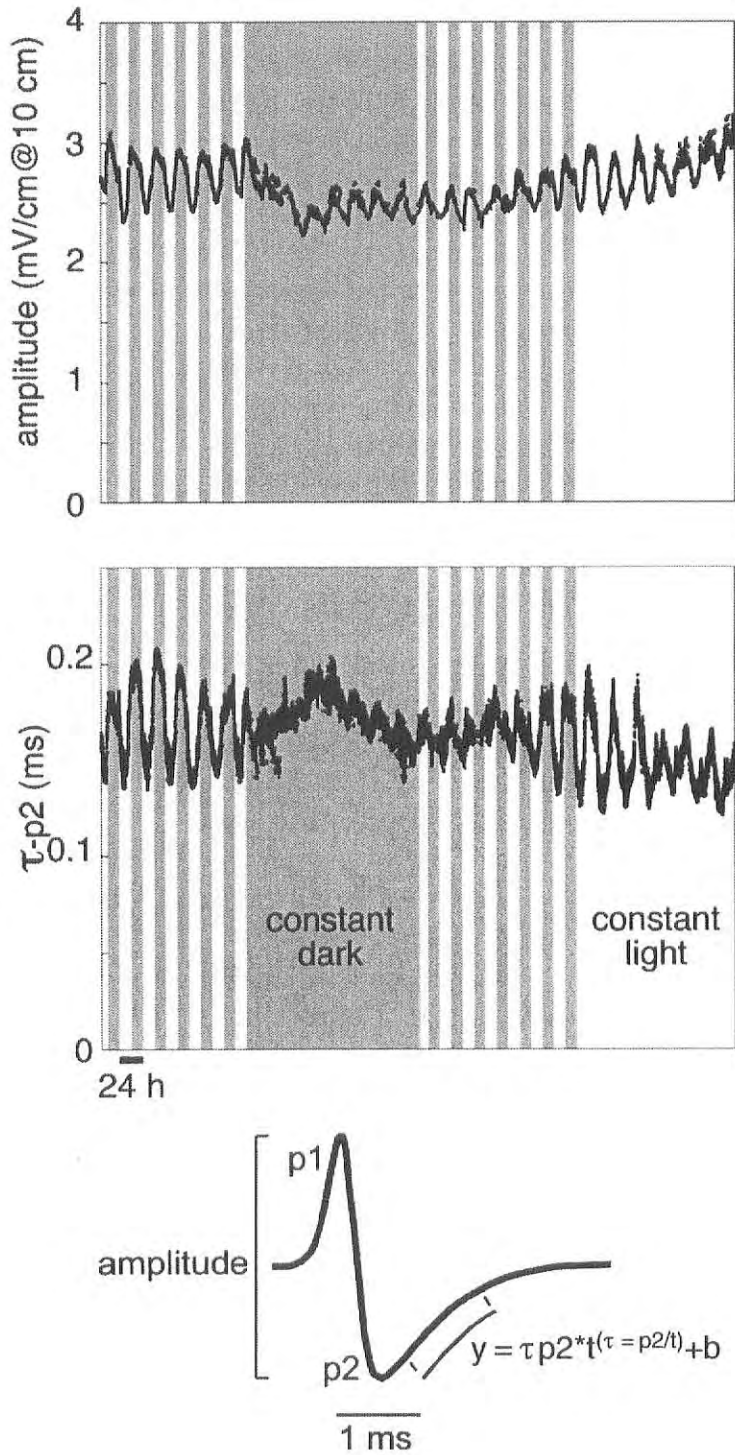


Fig. 22.3: EODs of captive male *Brachyhyopomus pinnicaudatus* show strong circadian rhythms in amplitude and duration. These EOD rhythms are apparent under 12:12 LD conditions and continue to free run under constant darkness and constant light. The fish are fed at random times to avoid food-entrainment and temperature is held constant. EOD amplitude is measured peak-to-peak and EOD duration is measured by the time constant τ -p2 of the decay of the second phase. Data from the author's lab.

changes visible in six minutes, peaking in 30 to 90 minutes (Fig. 22.4). When we return the fish to their original tanks, the EODs return to their former shape equally fast. EOD enhancements in such forced encounters are expressed both in males and females. If we place fish in the same tank but separate shelter tubes, they will not interact until nightfall. Before dark, the only obvious change is the circadian rhythm. After dark, however, the EODs may undergo further enhancements in ways that depend on the social relations of the individuals (Fig. 22.5). Pilot data by Vielka Salazar in my lab suggest that a fish enhances his EOD if it is already greater in amplitude than that of a male tank mate. Thus, a male will enhance his EOD in the presence of a smaller male or a

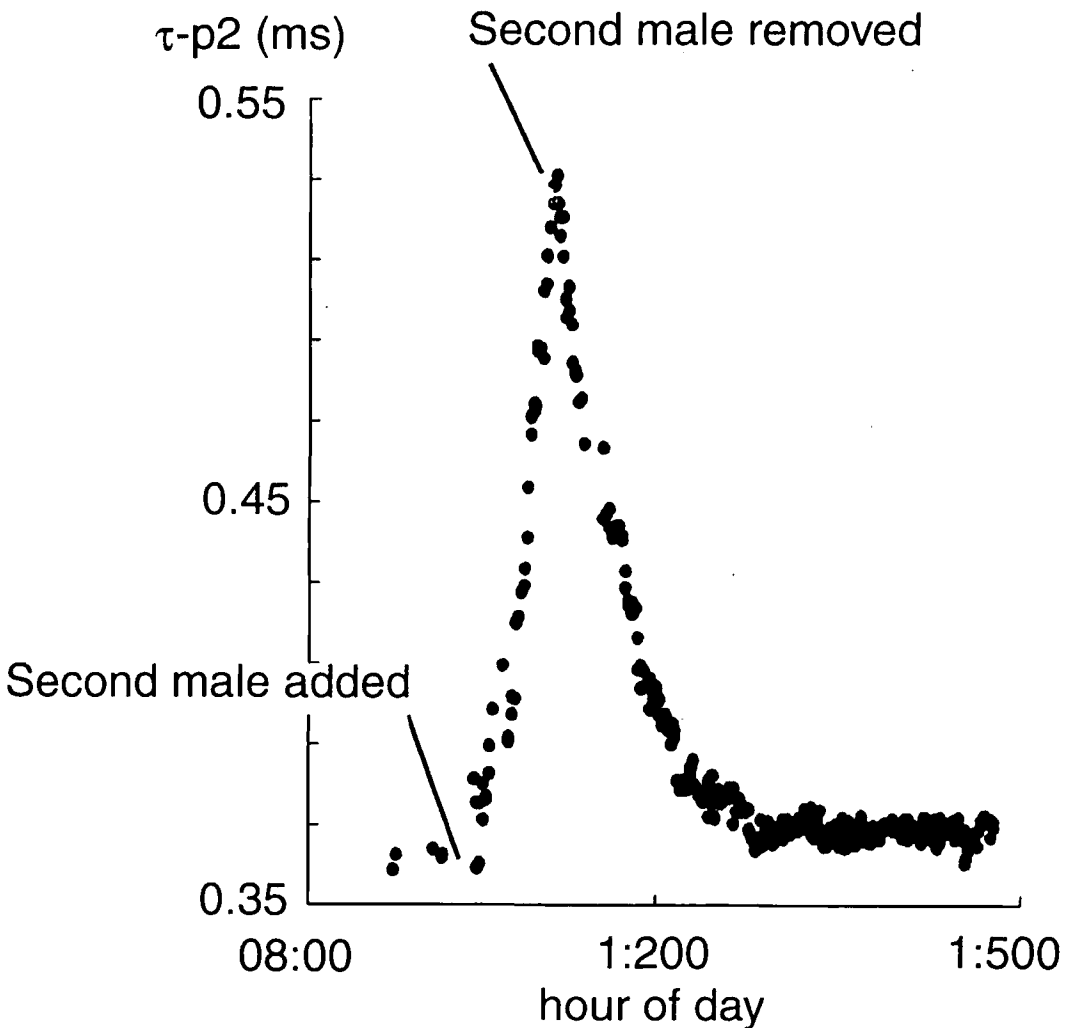


Fig. 22.4: When a second fish of the same sex is added to the shelter tube of a resting *Brachyhyopomus pinnicaudatus*, the EOD is quickly enhanced. When the second fish is removed, the EOD returns to its previous shape. Shown here is a male's change in τ -p2. EOD amplitude may increase under such conditions as well, but not as reliably. Data from the author's lab.

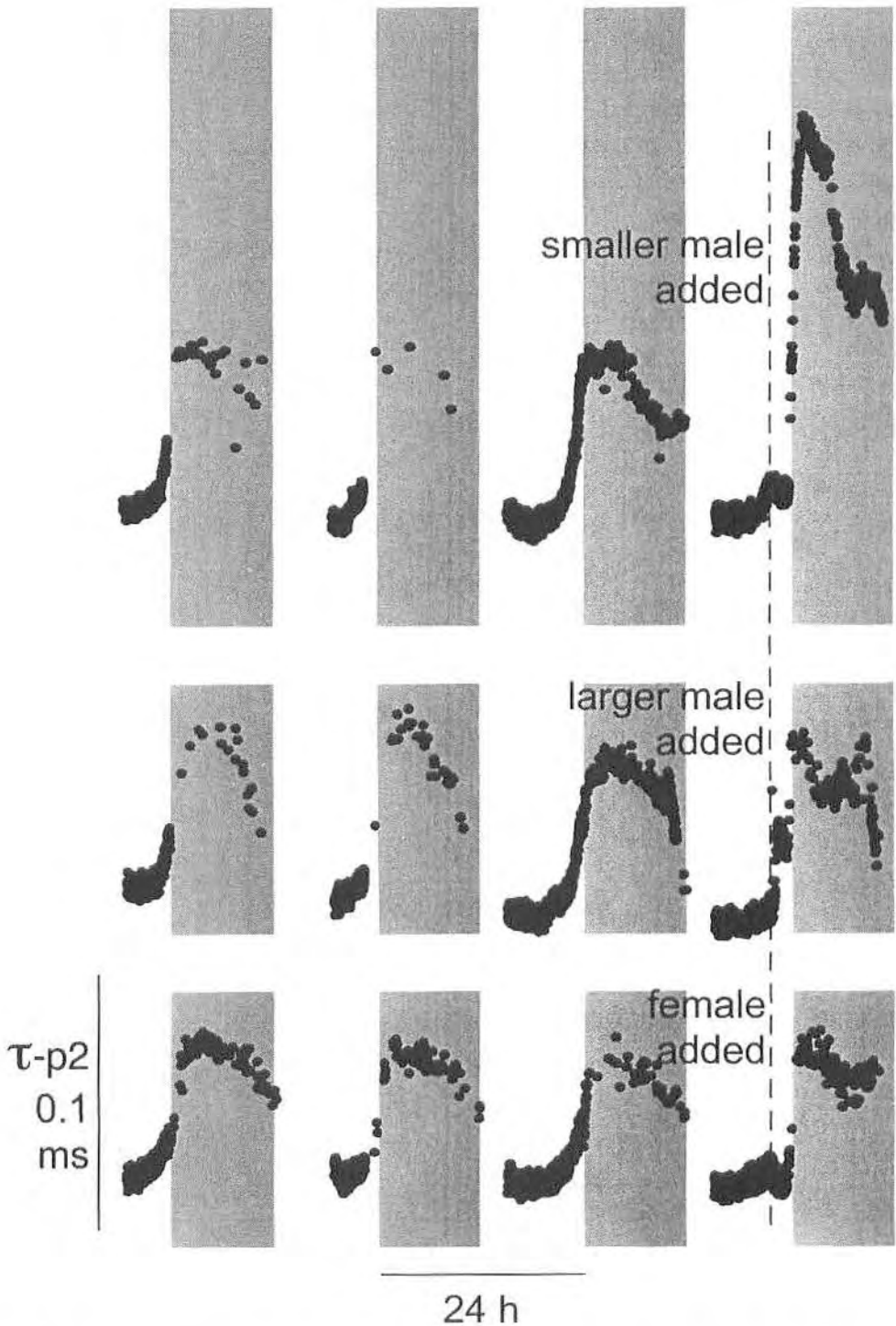


Fig. 22.5: Addition of a second fish to a tank containing a single male *Brachyhyppopomus pinnicaudatus* alters his EOD waveform at night when the two fish begin to interact. In this experiment, the two fish in each tank were separated by plastic screening and could not contact each other. Addition of a smaller male produced the largest rise in $\tau\text{-P}2$. Males increased their EODs less in the presence of females and larger (perhaps intimidating) males, but did add a second peak late in the night. Data courtesy of V. Salazar.

larger male with a smaller EOD, but not in the presence of a male with a larger EOD or a female.

2.6 Stress-mediated Changes

When hypopomids are captured in the field, the EOD diminishes and circadian oscillations are greatly attenuated. The worst possible conditions for maintaining normal EOD conditions (if such truly exist) would appear to be a crowded, sunlit bucket, with no shelter, in other words, exactly the conditions that usually prevail when we collect wild fish. Loss of previous EOD enhancements can be mitigated if one moves the fish quickly to a naturalistic setting with similar social density, water temperature, food, and aquatic vegetation (Franchina et al., 2001; Quintana et al., 2004). Unless all the conditions are right, the EOD will probably not regain the degree of enhancement seen at night in the wild.

When we inject a male *B. pinnicaudatus* with anything (e.g., saline) and place it back in the measurement tank (the 'EOD Machine'), we often witness that the EOD has dropped in amplitude by 40–60%. Within two to five minutes, the EOD has fully recovered (Fig. 22.6). Lowering the EOD amplitude at the

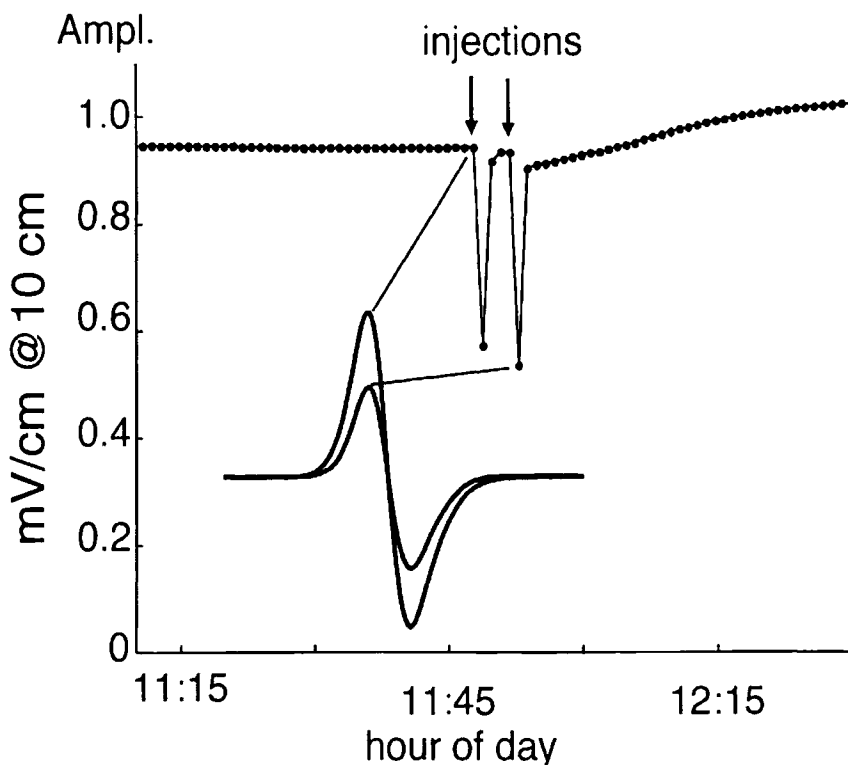


Fig. 22.6: Intramuscular injection of anything into *Brachyhypopomus pinnicaudatus* frequently results in an immediate drop in EOD amplitude with no change in EOD duration. The EOD recovers in a few minutes. Shown here is a male's response to two injections, one of saline, the second of serotonin. A similar drop can be seen in Fig. 22.8 following an androgen implant. Data from the author's lab.

tail end would not affect the electric field at the head (Stoddard et al., 1999), and thus should not affect the fish's ability to navigate, but it would reduce the ability of an electroreceptive predator to track the fish as it flees. We suspect the sudden amplitude drop is an adaptive response to a perceived predation attempt.

2.7 Instantaneous Alteration during Complex Social Signals

Gymnotiform electric fish emit complex signals during courtship and aggression. Two types of complex signals given by *B. pinnicaudatus* can alter the EOD waveform and the EOD spectrum. During aggression and courtship, male *B. pinnicaudatus* produce rapid accelerations of the EOD rate lasting tens to hundreds of milliseconds (Fig. 22.7). These accelerations may lower the

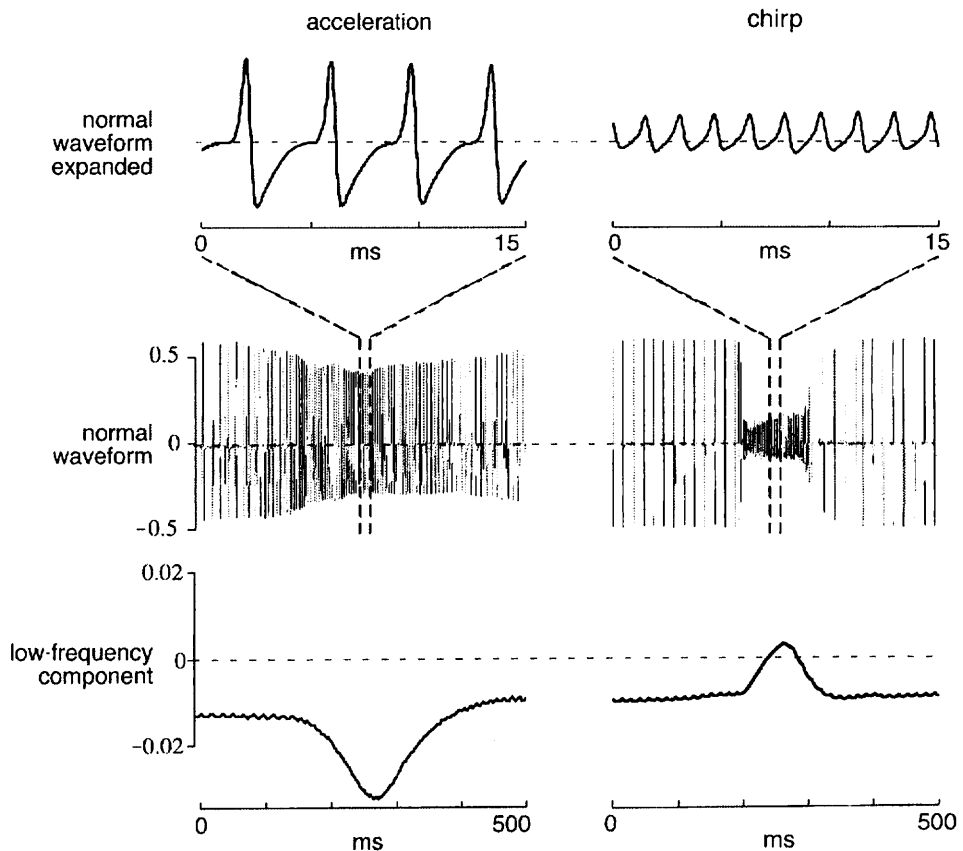


Fig. 22.7: Acceleration and chirp signals given by male *Brachyhyppopomus pinnicaudatus* during courtship and spawning, respectively. In the acceleration signal the discharge rate increases and decreases smoothly, with little change in the EOD waveform. During the chirp, the large modulations in discharge rate are abrupt. During the chirp, electrocytes cannot recover fully between action potentials, resulting in diminished amplitude. Because the male's EOD is asymmetric with respect to 0 volts DC, these changes cause a change in ratios of net area above and below 0 VDC. These changes are reflected in the low-frequency component, shown at the bottom of the figure. Low-frequency components are revealed here lowpass filtering the signal (eight pole Butterworth, 10 Hz corner frequency). The amplitude scale is in relative units. Data from the author (P.K. Stoddard, 2002).

EOD amplitude a few percent but do not change the second phase. One must remember from the discussion above that the extended second phase of the male EOD means that more energy lies below the 0 V baseline than above. When the fish accelerates its EOD, the mean wavetrain has more negative energy than before. This produces a negative DC blip that will be detectable by the ampullary electroreceptors of nearby receivers.

In *Brachyhypopomus*, if the courtship progresses to spawning, accelerations cease and the male gives a different complex signal, variously called a “chirp” (Kawasaki and Heiligenberg, 1989) or ‘decrement burst’ (Hagedorn, 1988; Shumway and Zelick, 1988). Chirps comprise EODs given in such rapid succession that the electrocytes cannot recover fully between them and the action potentials diminished in size until the chirp stops (Fig. 22.7). Like accelerations, chirps last 10s to 100s of milliseconds, the duration seeming to vary with the social context. Female *Brachyhypopomus* have been noted to give short chirps (Hagedorn and Zelick, 1989) but their social meaning is not clear—they may be agonistic. Because EOD amplitude drops sharply during the male’s chirp, the average negative energy is likewise reduced, causing the mean DC component to rise towards 0 V. When the chirp ends, the EOD recovers, the negative energy is restored, and the mean DC component drops away from 0 V. A string of chirps (~3/s) during spawning thus produces a rising and falling wave in the low-frequency spectrum.

Just as every gymnotiform family has a mechanism to cancel low frequency energy in the EOD, each seems to have exploited this mechanism in reverse to resynthesize low-frequency energy during courtship (Stoddard, 2002). Males of the wave genus *Eigenmannia* introduce low-frequency energy into its chirp by ceasing the EOD for an equivalent period. Since *Eigenmannia*’s electrocytes produce a steady head-negative DC current, a brief silencing of the EOD results in a brief drop to the negative baseline. Restoration of the EOD train restores the net voltage to 0 V. So, just as the chirp train of *B. pinnicaudatus* creates a series of head-positive low-frequency pulses, *Eigenmannia*’s chirp train produces a series of even larger head-negative low-frequency pulses. This low frequency signal is thought to induce females to spawn (Hagedorn and Heiligenberg, 1985).

2.8 Neuroendocrine, Biochemical, and Ionic Mechanisms of EOD Change

The EOD changes described thus far are brought about through action at different loci in the electromotor system.

Changes in the tonic discharge rate are mediated by changes in the intrinsic oscillation rates of pacemaker neurons in the medulla and the spinal motoneurons they drive (Schaefer and Zakon, 1996; Smith, 1999; Smith and Zakon, 2000). In cases where the tonic discharge rate is sexually dimorphic, the sex differences have been correlated with circulating levels of the teleost

androgen 11-keto-testosterone (11-KT) (Zakon et al., 1990, 1991; Dunlap et al., 1998). Experimental administration of androgens masculinizes the waveform, alters the pacemaker and spinal motoneuron oscillation frequency and, conveniently, alters the tuning of some of the fish's own tuberous electroreceptors to track the altered discharge spectrum. Experimental application of estrogen has the opposite effect, feminizing these traits (Schaefer and Zakon, 1996; Dunlap et al., 1997).

Changes in the duration and amplitude of the EOD waveform occur on multiple time scales. The slowest changes—those associated with development and sex differentiation—are mediated by sex steroids, both in Gymnotiformes (reviews: Zakon, 1993, 1996, 1998) and mormyrids (reviews: Landsman, 1995; Herfeld and Moller, 1998). The masculine forms (e.g., longer pulse duration in most taxa), are correlated with 11-KT levels, and may be induced in females or undifferentiated juveniles with sustained-release androgen implants. Effects of androgen implants are slow, appearing over the course of days (Fig. 22.8), and attenuating after the steroid is expended. Sex differences in EOD duration can be traced down to the level of voltage gated ion channels. Longer-duration EODs are associated with longer-duration action potentials (Mills and Zakon, 1991), slower-inactivating sodium currents (Ferrari et al., 1995), and slower-activating delayed rectifier potassium currents (McAnelly and Zakon, 2000). Sex differences in EOD amplitude are not as well understood because few labs have been able to obtain calibrated EOD amplitudes. Electric organs are larger in male *Brachyhyopomus* and electrocytes are thicker with more convoluted active membrane surfaces (Hopkins et al., 1990). Application of androgens brings about the same effect on females (Hagedorn and Carr, 1985).

More rapid effects, such as the circadian and social effects described above, are not brought on by injection of androgens. Instead, the pituitary melanocortin peptides adrenocorticotrophic hormone (ACTH) and melanocyte-stimulating hormone (α -MSH), appear to be the circulating regulators of EOD shape. In the pulse fish *B. pinnicaudatus*, injection of either melanocortin peptide brings about a rapid enhancement EOD amplitude and τ -p2 and direct application of either peptide to electrocytes in a dish increases these same parameters in the extracellular action potential (Fig. 22.9) (Markham and Stoddard, 2003, 2005). In the wave fish *Sternopygus*, however, only EOD amplitude changes quickly following melanocortin administration (Markham, McAnelly and Zakon, unpubl.). Melanocortin peptides bind to membrane melanocortin receptors, upregulating adenylyl cyclase, and activating intracellular cAMP. Cyclic AMP, in turn, activates protein kinase A (PKA), which phosphorylates serine and threonine residues to alter protein function. Application of membrane permeable 8-Br-cAMP has been shown to enhance the action potentials and increase the inactivation time of sodium currents (McAnelly and Zakon, 1996). Likewise, the application of a PKA inhibitor blocks the EOD-enhancing effects of ACTH and cAMP.

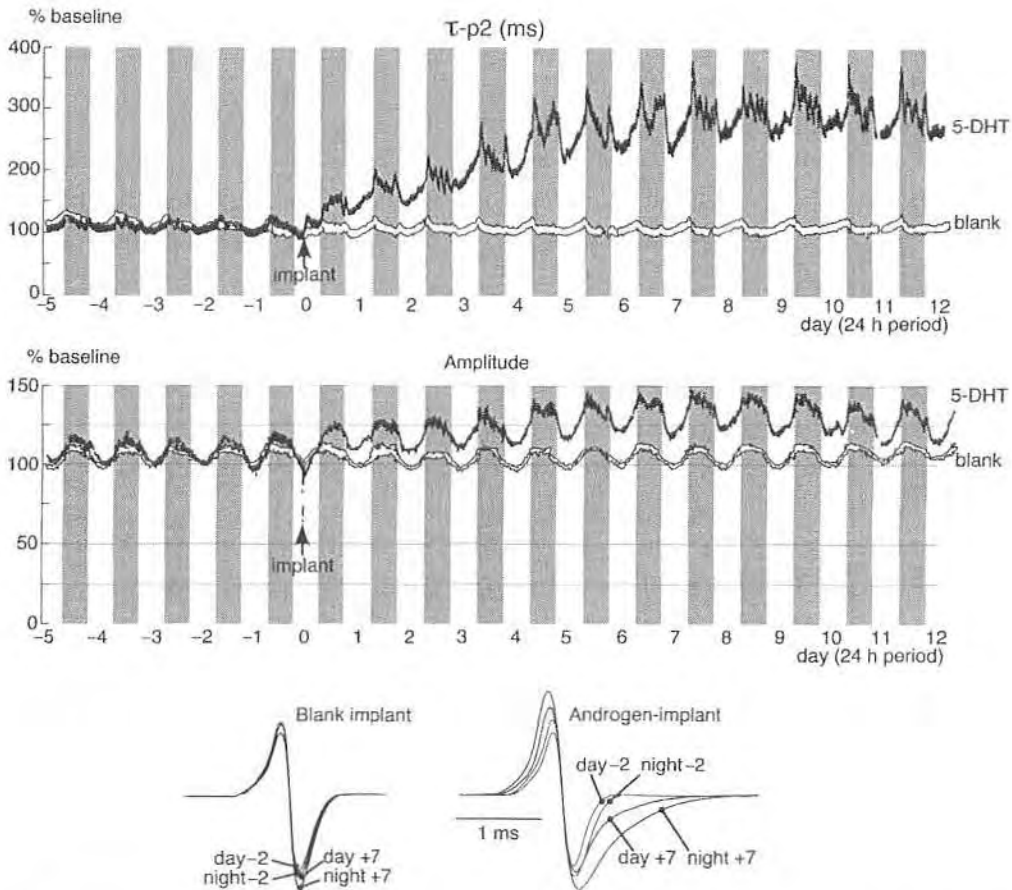


Fig. 22.8: Response of female *Brachyhypopomus pinnicaudatus* EOD duration and amplitude to implants of the non-aromatizable androgen 5-dihydrotestosterone. Another female with a blank implant is shown for comparison. EOD duration and amplitude increase over a week, coming to resemble a male's EOD. Furthermore, the circadian cyclicity is also enhanced in ways that resemble the male. Duration changes are more robust than amplitude changes. Data from S. Allee and the author.

Melanocortin release is regulated by several hypothalamic peptides including CRF, urocortin, and urotensin. These hormones, in turn, are released by myriad neurohormones. Serotonin (5-HT) injected into the periphery quickly enhances the EOD, but has no effect applied to electrocytes *in vivo* (Stoddard, 2003; Markham et al., 2004). Thus far, we have found that serotonin 1A and 2A receptors are involved in different aspects of EOD waveform regulation in *B. pinnicaudatus*, though which behavioral effects they control is as yet unknown (Salazar et al., 2002a). Serotonin, injected intramuscularly, enhances the EOD in minutes and blockage of the 5HT2A receptor with ketanserin significantly attenuates the action of 5-HT injection (Fig. 22.10). Ketanserin by itself has no effect. Blockage of the 5HT1A receptor with the antagonist WAY-100635 enhances the EOD, whereas activation of the 5HT1A receptor with 8-OH-DPAT causes the EOD to diminish over the next 5 hours

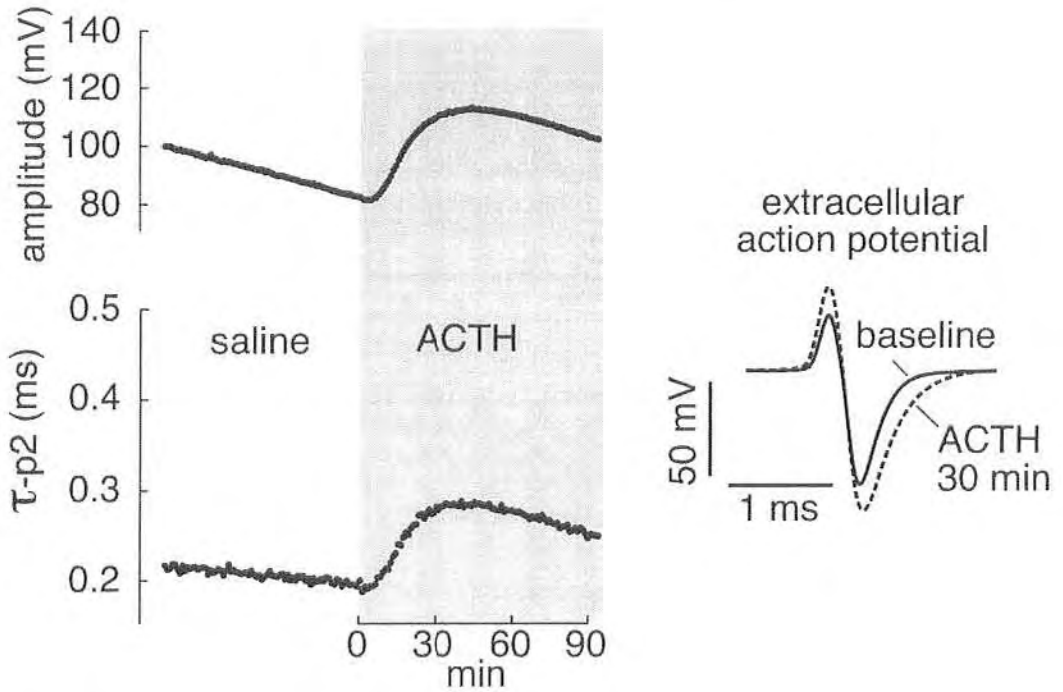


Fig. 22.9: The melanocortin peptide hormone ACTH (adrenocorticotrophic hormone) enhances both amplitude and duration of the extracellular action potential when applied *in vitro* to single electrocytes of *Brachyhypopomus pinnicaudatus* (Markham and Stoddard, 2003, 2005). Prior to ACTH application, the baselines probably decline because the electrocytes have been removed from the fish and the endogenous circulating melanocortins.

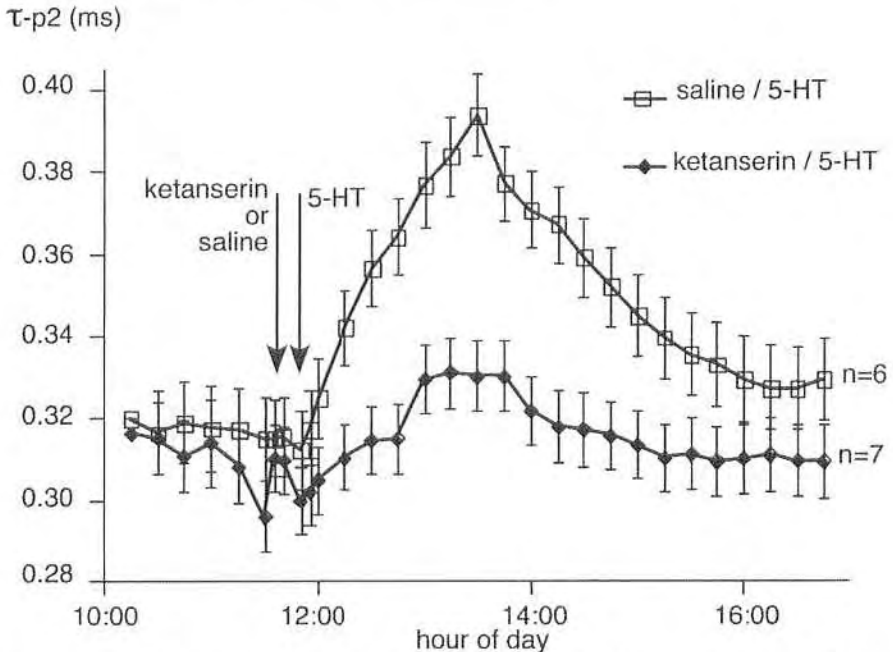


Fig. 22.10: Pre-treatment with the serotonin receptor agonist ketanserin significantly attenuated the response of the EOD waveform to injection with serotonin 30 min later. These data in combination with other pharmacology implicate a 5HT_{2A}-like receptor in the rapid increases of the EOD waveform in response to intramuscular injection of serotonin (Salazar et al., 2002b).

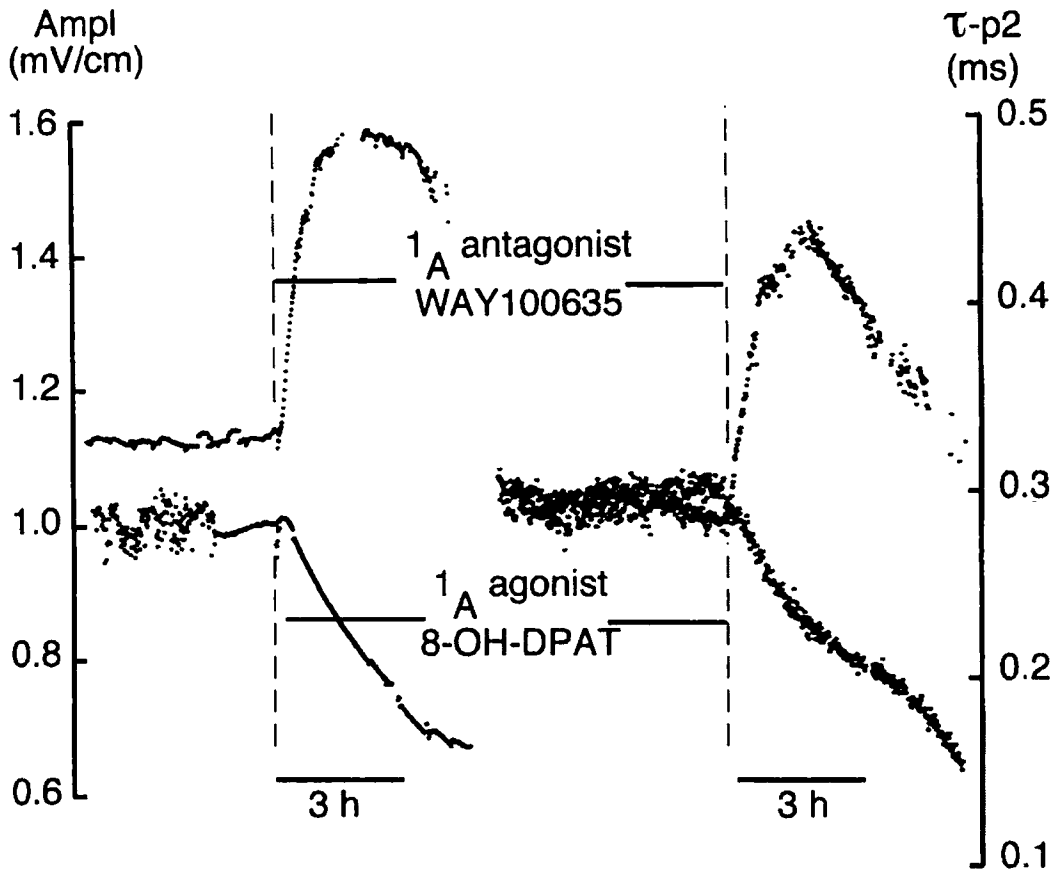


Fig. 22.11: Intramuscular injections of male *Brachyhypopomus pinnicaudatus* with agents highly selective for the 5HT_{1A} receptor show that a receptor of this pharmacological profile is constitutively active and regulates the EOD. Circadian rhythms were subtracted in order to isolate drug effects. Data from the author's lab.

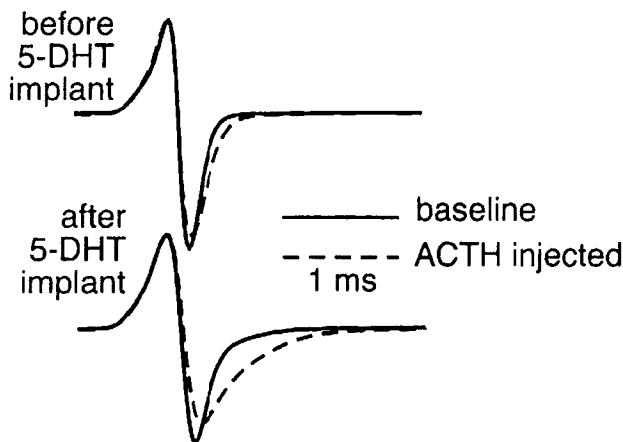


Fig. 22.12: Implants of the non-aromatizable androgen 5-dihydrotestosterone not only masculinize the EOD of female *Brachyhypopomus pinnicaudatus*, but also increase the responsiveness of her EOD to injections of melanocortin peptides. EOD amplitudes are rescaled to equate the first phase (p1). Changes in EOD duration appear more robust than changes in EOD amplitude. S. Allee and P. Stoddard, unpubl. data.

(Fig. 22.11). Thus, the 5HT1A receptor seems to be involved in a central pathway that regulates the baselines for EOD amplitude and τ -p2 (e.g., in the hypothalamus), whereas the 5HT2A receptor appears to be involved in a separate enhancement pathway accessible from the circulatory periphery (e.g., the intermediate lobe of the pituitary).

While androgens do not induce rapid change in the EOD waveform, they do seem to potentiate those changes. Implanting female *B. pinnicaudatus* with the non-aromatizable androgen 5-DHT facilitates the EOD enhancing effects of ACTH several fold (Fig. 22.12). Androgens could potentiate responsiveness to melanocortins via any number of mechanisms. They might either alter the makeup of the voltage gated ion channel populations in the electrocyte membranes, upregulate melanocortin receptors in the electrocyte membranes, or they may even upregulate some part of the intracellular second messenger machinery that works between the melanocortin receptors and the ion channels.

In contrast to the circadian oscillations and social responses, the instantaneous drop in EOD amplitude seen in response to injection is probably not the result of a humoral modulator. The rapid drop is most pronounced following a serotonin injection, but may be elicited by saline injection as well. Injection of adrenalin or noradrenalin has no sustained effect on the EOD. On occasion, we have observed the rapid drop in a restrained male. After injecting, it appears that electrocytes in the tail went silent while those in the trunk remained active. The spatial pattern of recovery suggested the tail electrocytes were returning to activation in a steady progression from anterior to posterior as though connected by a zipper. Since the cells in the pacemaker nucleus are tightly coupled (Spiro, 1997), the site of gating must lie downstream, probably in the spinal cord.

Instantaneous control of EODs given during social signaling is mediated by the prepacemaker nuclei in the diencephalon. Different clusters of prepacemaker neurons project onto the pacemaker and relay neurons in the medullary pacemaker nucleus. Differential activation of the prepacemaker subnuclei can elicit accelerations or chirps (Kawasaki and Heiligenberg, 1989, 1990; Spiro, 1997). The reduction of waveform during a chirp is a combined result of pacemaker drive and electrocyte biophysics.

2.9 Behavioral Contexts of EOD Modulation

In an odd inversion of knowledge, we currently understand more about the physiological control of electric signaling behavior than its social function. Our understanding of the meaning of electric waveform modulation is largely circumstantial and equally unsatisfactory.

We do know that males of many taxa have different waveforms than females and juveniles, and we are aware that males exercise more dynamic control of their waveforms. Based on observed sexual dimorphism in the EOD

waveforms and sex-specific responses, people have speculated that EODs might be involved in mate attraction (e.g., Hopkins and Bass, 1981; Shumway and Zelik, 1988; Hopkins et al., 1990; Triefenbach and Zakon, 2003) but we still lack direct experimental proof. Consistent with this speculation, anecdotal observations indicated that male *Brachyhypopomus brevirostris* enhance the sexual dimorphism of the EOD on nights of successful spawning (Kawasaki and Heiligenberg, 1989). We know that sexually receptive female *B. pinnicaudatus* will select larger over smaller males through a screen divider and that the chosen larger males had larger waveforms with longer second phases (Curtis and Stoddard, 2003). While we did find that the presence of females gradually restores the EOD of a socially isolated male, we also found that another male is a more potent stimulus (Franchina et al., 2001). Males readily enhance their waveforms in the presence of other males provided those males have smaller EODs (Fig. 22.5). The overall picture suggests that males are intimidated by other males with larger EODs, that they use their EOD to dominate smaller males, and that their EOD enhancements are involved in attraction and courtship of females at some level.

If the EOD serves as a badge of social status, we can understand why different males might have different degrees of signal enhancement. But this does not explain why males reduce their signals on a circadian rhythm, and why male signals lose most of their sexual dimorphism under social isolation. We have two hypotheses, both of which have some support. First, the increased duration of the EODs of *Brachyhypopomus pinnicaudatus* increases fivefold the amount of energy detectable by the ampullary receptors of conspecifics and predators alike (Stoddard, 2002). This low-frequency energy may be attractive to females, but it would behoove a male to minimize that part of his emission spectrum when females are not prospecting for mates. Second, we have recently found that the EOD is an expensive signal for males, constituting one-fifth of their daily energy budget, whereas the smaller signals of females use only 2–4% of their daily budget (Salazar and Stoddard, in prep.). This finding suggests that males may be limited in their ability to sustain signals of enhanced amplitude and duration. Some of our lab data supports this hypothesis. When males were carefully fed, the body length correlated with EOD amplitude at night (Franchina and Stoddard, 1998; Curtis and Stoddard, 2003). However, when body condition varied, the fattest males had the largest EOD amplitudes, and body length ceased to predict EOD amplitude (Salazar, 2003).

3. DISCUSSION

Waveform plasticity differs in some key ways between wave and pulse gymnotiforms. Changes to the EOD pulse duration changes the spectrum, which has a significant sensory consequence in wave fish because the sensory

spectra of their tuberous receptors so closely track their EOD discharge spectrum (Hopkins, 1976). If a wave fish were to modulate its pulse duration quickly, its discharge spectrum would not match its sensory spectrum. Thus, unlike in the pulse fish *Brachyhyppomus*, the wave fish *Sternopygus* shows only rapid modulation of EOD amplitude and not duration (McAnelly and Zakon, 1996; Zakon et al., 1999; McAnelly et al., 2003). Changes in EOD duration are slow, and matched by changes in tuning of electroreceptors (Keller et al., 1986; Mills and Zakon, 1987, 1991; Ferrari and Zakon, 1989).

Several studies have explored the possibility of individual recognition among neighboring electric fish (McGregor and Westby, 1992; Scudamore and McGregor, 1993; Friedman and Hopkins, 1996). Individual recognition requires waveforms to remain individually distinctive over a period of time. Presumably rapid plasticity, as seen in the genus *Brachyhyppomus*, works against individual recognition. Extremely territorial species similar to those found in the genus *Gymnotus* may have more stable EODs.

4. OUTSTANDING QUESTIONS

Predation: We know that electroreceptive predators are more sensitive to EODs with energy in the spectrum of the ampullary electroreceptors, but we don't have any field data on the role of EODs in predation. Such information would be welcomed.

Sexual selection: The prevalence of sexual dimorphism in the EODs of gymnotiforms and mormyrids implicates sexual selection as a shaping force in the evolution of electric signals, but we have little convincing data on the roles of EODs in male–male competition or mate choice by females (Shumway and Zelick, 1988; Curtis and Stoddard, 2003; Triefenbach and Zakon, 2003). What does the modulation of a particular EOD parameter mean to a receiver? High energetic costs of male EODs suggest that a high-amplitude EOD informs a receiver of either sex that the signaler has amassed significant energy stores. Indeed, a recent study in my lab found a tight correlation between male body mass and EOD amplitude, irrespective of body length (Salazar, 2003). Changes in EOD duration have less effect on energetic costs, and may be related to historic female preferences. If enhancement of the low-frequency spectrum attracts predators—as lab studies indicate it should—then this signal trait could serve as a handicap trait (Zahavi, 1975, 1977).

Channel regulation: Just as EODs display a huge range of variation and modulation, so must the voltage-gated ion channels in their electrocytes be uniquely adapted for particular waveforms and for the ability to undergo both slow and rapid modulation. The central role of ion channel conduction in neural and cardiac disease warrants exploration of animals that produce action potentials with such precise variation and well-defined modulation capabilities.

Social modulation of circadian rhythms: The social environment controls the EOD waveform in a very detailed manner. Through what structures and pathways are changes in social environment carried to the EOD? The social environment can produce both chronic and acute changes in the release of many hormones and neurotransmitters. We now know that androgens effect slow changes in the EODs of gymnotiform and mormyrid electric fish, and we also know that melanocortins work directly on electrocytes of gymnotiforms. Do melanocortins also modulate EODs of mormyrids? How do androgens regulate the ability of electrocytes to be modulated by the rapid modulators? How do gymnotiforms reduce the EOD masculinizing effects of melanocortins when they are stressed (or do they)? We have a lot still to learn.

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