J Comp Physiol A (2001) 187: 45–52
DOI 10.1007/s003590000176

ORIGINAL PAPER

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Plasticity of the electric organ discharge waveform of male *Brachyhypopomus pinnicaudatus*. II. Social effects

Accepted: 24 November 2000 /

Abstract Many electric fish produce sexually dimorphic electric organ discharges. Although electric organ discharges are comprised of action potentials, those of the Gymnotiform family Hypopomidae show significant plasticity in response to stress and time of day. We show here that male *Brachyhypopomus pinnicaudatus* (Hopkins 1991), adjusts the degree of sexual dimorphism in its electric organ discharge depending on immediate social conditions. Three to five days of isolation resulted in gradual decrease of two sexually dimorphic waveform characters: duration and amplitude. Introduction of a second fish to the experimental tank restored electric organ discharge duration and amplitude. Duration recovered quicker than amplitude, and both recovered faster in the presence of males than females. In studies of other electric fish species, treatment with steroid sex hormones have taken several days to increase sexual dimorphism in the electric organ discharge. The socially induced changes seen in this study are initiated too quickly to involve classic steroid action of genomic transcription and thus may depend on another mechanism. Socially induced regulation of the male's electric organ discharge waveform is consistent with the compromises in signaling strategy shown by other taxa with costly sexual advertisement signals.

Key words Electric fish · Electrogenesis · Gymnotiformes · Hypopomidae · Communication

Introduction

The electric organ discharges (EODs) of electric fish are model systems for exploring the regulation of action potentials (Bass 1986; Bennett 1961; Zakon 1998). Some authors have stressed the temporal stability of the EOD, either for its function in electrolocation (Bullock 1970; Moortgat et al. 1998; Rasnow et al. 1993; Rose and Heiligenberg 1985) or for its role as an indicator of individual identity (Crawford 1992; Friedman and Hopkins 1996; McGregor and Westby 1992). Other researchers have focused on plasticity in the EOD, both as a means of exploring regulation of action potentials and for its role in regulating communication signals in the context of reproduction (reviewed by Zakon et al. 1999).

In contrast to the temporal stability that characterizes EOD waveforms of most electric fish, EODs of the neotropical pintailed knifefishes (genus *Brachyhypopomus*; Hypopomidae, Gymnotiformes) can change very quickly. Waveform changes on the time-course of hours have been documented from the sexually dimorphic EOD waveforms of males of two species of *Brachyhypopomus*. In one study, competition for resting sites produced overnight changes in the EOD of male *B. occidentalis*, in which the loser's EOD duration was typically reduced more than that of the winner (Hagedorn and Zelick 1989). Male *B. pinnicaudatus* have been shown to reduce the duration and amplitude of their EODs within minutes of capture and social isolation (Franchina and Stoddard 1998). Several studies found spontaneous day-night oscillation in the duration and amplitude of the EODs of males of *B. occidentalis* and *B. pinnicaudatus* in ways that enhance the sexual dimorphism in the early evening when most spawning occurs (Franchina and Stoddard 1998; Hagedorn 1995; Silva et al. 1999).

The EODs of most *Brachyhypopomus* species are biphasic, with pronounced sexual dimorphism in the second phase (Hagedorn and Carr 1985; Hopkins et al. 1990; Kawasaki and Heiligenberg 1989; Sullivan 1997; Westby 1988). Females of our focal species, *B. pinnicaudatus* (Hopkins 1991), produce 1.1-ms-long, biphasic electric signals, symmetric around 0 V; males produce asymmetric EODs with a longer second phase (Hopkins et al. 1990). Males normally have greater EOD ampli-

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tudes, at least in part because mature males are longer than females and length is correlated with amplitude. At night, males increase EOD duration by 37 ± 12% and amplitude by 24 ± 9% (Fig. 1), (Franchina and Stoddard 1998). In our captive population of *B. pinnicaudatus*, only males show spontaneous day-night changes in the EOD waveform, changes that enhance sex differences in the waveform during the early evening night (Fig. 1). Sexual dimorphism in the day-night change in EOD duration and amplitude is consistent with the proposed role of the EOD in social communication (Hagedorn 1988; Hopkins et al. 1990).

In this study, we explored the effects of isolation and social stimulation on the EOD waveform of male *B. pinnicaudatus*. We show here that males increase the magnitude of sexually dimorphic EOD characters in response to a change in social conditions, and some of these electric changes occur within minutes of experimental manipulations.

Materials and methods

Environmental conditions

Laboratory-raised *B. pinnicaudatus* lived in mixed-sex groups of 10–30 adults in communal outdoor pools (~1 m × 2 m, 30 cm deep), which were covered with water hyacinths (*Eichornia crassipes*). We adjust the sex ratio in the outdoor breeding pools so females outnumber males about four to one. Water conductivity in the pools was maintained at about 100 μS cm^{-1} (10 kΩ cm^{-1}), though it dropped after heavy rainfall. pH was neutral or slightly acidic. The natural rainy season in Miami, Florida stimulated breeding throughout the experiments; all subjects were in reproductive condition. We identified sex based on morphology of the caudal filament (Fig. 1; Hopkins et al. 1990). The original stock came from Argentina and the experimental animals were sixth generation captive bred.

EOD recordings and experiments took place in two identical tanks (120 cm × 44 cm × 44 cm; 232 l) within an indoor light-tight chamber. Water conductivity, temperature, and light cycles were kept constant throughout all indoor tanks and were set to mimic outdoor conditions. Recirculated water falling on the surface (artificial rain) was sufficient to induce spawning indoors, so we kept conductivity constant during each experiment (102 ± 2 μS cm^{-1}; 9.8 kΩ cm^{-1}). Six 40-W fluorescent bulbs above each tank were on from 0600 hours to 2000 hours (14 h), causing the temperature to rise during the day from 27.5 °C to 29.0 °C, on average; a tank heater kept the temperature above 27 °C at night. The faintest visible light suppressed nocturnal activity in this species, so an array of infrared LEDs (OP293A, Newark Electronics) backlit the tank at night for infrared-sensitive CCD video cameras (Cohu 6410; Javelin JE7862). Oligochaete "blackworms" were available ad libitum as food. The experimental tanks contained water hyacinths for cover.

EOD recording

In gymnotiforms, the recorded EOD waveform and amplitude are affected greatly by the orientation and distance of the fish relative to the recording electrodes (Hopkins 1986). Therefore, repeated measurements of the EOD may be compared only if the position of the fish is constant with respect to the electrodes. However, restraining the fish prevents normal behavior and may increase stress. We took advantage of the natural tendency of *B. pinnicaudatus* to seek dark, confined spaces during the day to limit the position of the test fish without restraining it.

Plastic mesh partitions divided the tank into three compartments, with the sides joined by a 22-cm-long, narrow mesh tube (Fig. 2). A grid on the back of the tank indicated the lengthwise position of a fish in the tube to the nearest centimeter. During the day, test fish preferred to rest in the tube, which was narrow and shaded by surface plants. Therefore the test fish was approximately centered between two carbon recording electrodes located on the far ends of the tank (120 cm apart). This geometry proved the least sensitive to movement (Franchina 1997). Fish could move lengthwise ± 15 cm from the center position without affecting EOD amplitude or duration. A High-8 VCR (Sony EVO-9500A) recorded both the video camera image of the tank and the amplified electric signal (Charles Ward Electronics amplifier BMA-200) on one digital audio channel, 16 bits at 48 k samples/s. A timer flashed an LED and created a brief click on the second audio channel every 2 s for synchronization of the visual and EOD records. At night, we videotaped as the test fish swam through the tube, then used frame-by-frame analysis of the videotape to select the EOD produced when the fish was centered.

At ~0800 hours of the first 24-h period, we transferred an experimental male into one end of the experimental tank, then waited 30–60 min for him to settle in the mesh tube. Every 2 h during the day (0600–2000 hours) and night we recorded the experimental male's position while he was centered in the tank (resting in or swimming through the mesh tube). Fish serving as social stimuli stayed in the center compartment, allowing electric, visual, and olfactory communication, but limited physical contact.

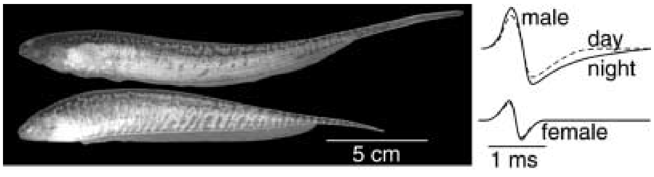

Fig. 1 *Brachyhypopomus pinnicaudatus* have sexually dimorphic caudal filaments (tails) and produce sexually dimorphic electric organ discharges (EODs). The male's EOD becomes increasingly larger and longer at night during the normal hours of spawning

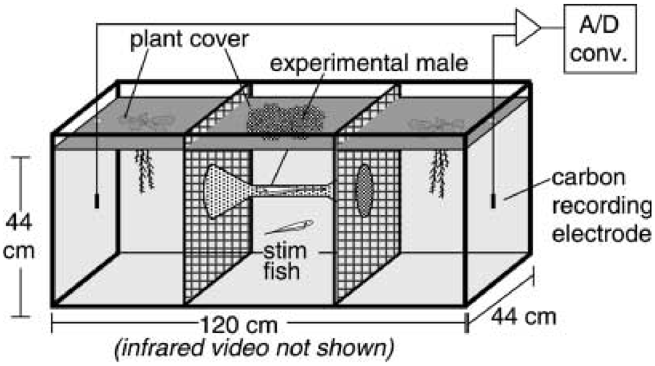

Fig. 2 The experimental tank used for measuring change in EOD duration and amplitude. Both fish were completely unrestrained. The experimental male could cross the middle compartment through a mesh tube, but the stimulus fish was confined to the middle by electrically transparent mesh panels. EODs are recorded across carbon dipole electrodes at either end of the tank. This geometry and tank size (120 cm × 44 cm × 44 cm; 232 l) creates a zone in which the fish can move lengthwise ± 15 cm from tank center without affecting EOD measurements. EOD electric field magnitudes are referenced to a calibrated 5 cm dipole, 10 cm away (Franchina and Stoddard 1998)

In the first experiment, we recorded the EODs of 13 experimental males every 2 h for 24 h after 3–5 days of isolation in 80-l tanks. Isolation tanks were similar to the experimental tanks in all respects except size (i.e., similar artificial rain, water conditions, ad libitum food, water hyacinths). We recorded EODs of 4 of the 13 at the beginning of isolation as well. We compared their EODs to those of 18 control males transferred directly from a breeding pool along with a male or female stimulus fish. Mean total length of all males was 20.7 ± 2.6 cm.

In the second experiment, we compared the restorative effect of a male and a female stimulus on the EODs of 14 males (mean total length 21.2 ± 1.9 cm) isolated for 1 week before each treatment. We recorded the test males' EODs every 2 h for three 24-h periods; at midnight (2400 hours) of the second period, we added a stimulus fish to the center compartment. For 2–3 h after introducing a stimulus fish, we recorded EODs approximately every 15 min, as the fish's movements allowed. Stimulus males were matched to within 2 cm of the experimental male's total length; stimulus females were 16.3 ± 1.5 cm in total length. Because isolated males reach maximum EOD duration and amplitude by 2300 hours in the diel cycle (Franchina and Stoddard 1998), we assumed any increase in the experimental male's EOD was caused by the stimulus. Pilot studies indicated that the response to a female might require several days (Franchina 1997), so we extended the female treatment by housing the experimental male with two females for 7 days in a 120-l breeding tank. On day 10, we returned the male and one female to the experimental tank and recorded the male's EOD for 24 h. The order of stimulus presentation (male first versus female first) was balanced and did not affect results (MANOVA; $P > 0.3$).

We selected and measured EODs as described previously (Franchina and Stoddard 1998), extracting from each digitized EOD the peak-to-peak amplitude and the duration at 10% of peak amplitude, interpolating to increase accuracy. We focused our analyses on maximum EOD durations and amplitudes for each fish during each 24-h period. To evaluate the effect of isolation on the EOD, we performed unpaired *t*-tests comparing EOD maxima between EODs of males isolated 3–5 days ($n = 13$) and control males ($n = 18$). To evaluate the effect of social stimulation on the EOD, we determined two EOD maxima for the second 24-h measurement period in the experimental tank: one before adding the stimulus fish and a second after. We used paired *t*-tests to contrast the response to male and female stimuli within subjects ($n = 14$). *P*-values are 1-tailed unless otherwise stated, the direction based on pilot data (Franchina 1997). To gauge the completeness of EOD recovery with the social stimuli, we use Fisher's PLSD post-hoc tests to compare EODs of control fish taken directly from the communal outdoor pools (first experiment) with EODs of the males in the second experiment who were isolated for a week then exposed to males or females as described above (results in Table 2).

Results

Social isolation caused a significant decline in nightly maximum EOD duration and amplitude (Figs. 3, 4A). Males isolated for 3–5 days produced EODs with shorter maximum durations (77% ± 16%; mean ± SD) and smaller maximum amplitudes (66 ± 28%) than control males housed socially (2-sample *t*-test; 29 *df*; $P < 0.0003$ for both). However, isolated and control males showed statistically insignificant differences in the relative amount of day-night EOD change (duration: isolated 31 ± 10% versus control 36 ± 10%, $P = 0.07$; amplitude: isolated 22% ± 7% versus control 23 ± 10%, $P = 0.3$). EOD amplitude and duration declined in isolated males regardless of tank size (480 l for Fig. 4A and others in pilot study; 80 l for experimental subjects in this study).

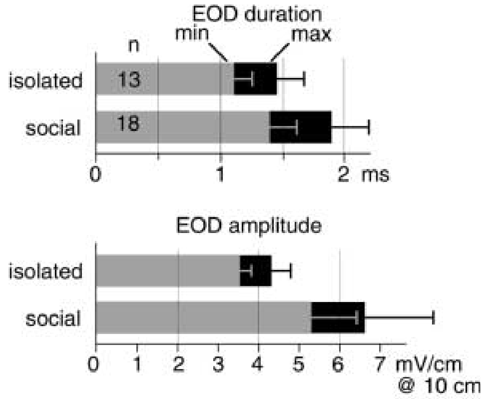

Fig. 3 Mean EOD duration and amplitude declined after 3–5 days of isolation compared with control males kept with another male or female (error bars = 1 SD). Both minimum and maximum daily EOD duration and amplitude declined in isolated males (unpaired *t*-test; $P < 0.0003$). The relative amount of day-night change was unchanged after isolation

After a week of isolation, the EODs continued to change between day and night, but the nightly maxima had reached a stable low. Maximum EOD duration and amplitude did not differ between the two nightly peaks prior to addition of a conspecific, (paired *t*-tests; 13 *df*; 2-tailed; $P > 0.2$–0.5). Further, male EOD values showed no systematic difference in maximum EOD characters immediately before the two social treatments (stimulus male or female: paired *t*-test; 13 *df*; 2-tailed, $P < 0.8$ for both; summary Fig. 5, examples in Fig. 4B, C), nor did the order of treatment have any residual effect after re-isolation (ANOVA; 1 *df*; $p < 0.6$ duration, $p < 0.3$ amplitude).

Previously isolated males increased their EOD duration and amplitude significantly after either a conspecific male or female was added to the experimental tank (Fig. 5, Table 1). At midnight when the stimulus fish was added to the tank, EOD duration and amplitude had already peaked for the night and begun to decline. After addition of a conspecific, EOD duration and amplitude increased again and reached new nightly maxima within 1.85 ± 1.11 h (mean ± SD; e.g., Fig. 4B). Timing of duration and amplitude maxima did not differ significantly that night, nor did the sex of stimulus fish affect timing of the new maxima. In each record examined, EODs of experimental males could be seen to change within 15 min (the first data point) after addition of the stimulus fish. In one instance, we recorded continuously to catch every pass the subject fish made through the measurement tube before and after addition of a stimulus male: increases in EOD duration and amplitude were discernible within 12 min (Fig. 6). Our future studies will focus in greater detail on the initiation of the EOD change.

Both sexes of stimulus fish elicited a significant increase in EOD duration within 2 h (Table 1, Fig. 5), stimulus males producing a larger increase than stimulus females. In fact, 2 h of a male stimulus caused sufficient

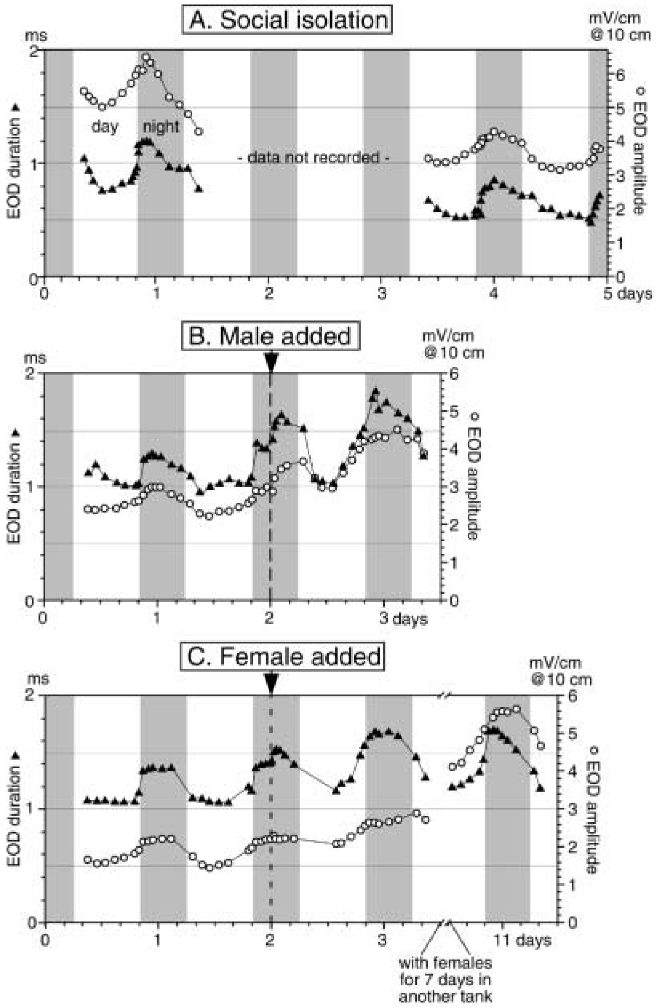

Fig. 4 Examples of a typical male's responses to **A** isolation, **B** addition of a male to the tank, and **C** addition of a female to the tank. **A** EOD duration (*triangles*) and amplitude (*circles*) cycle between day and night, but decline gradually over 5 days of isolation. **B** A different male has been isolated for 7 days. After his EOD duration and amplitude peaked for the night, a stimulus male was added to his tank. EOD duration and amplitude begin to increase within a few minutes and exceed the previous nightly maxima. The following night, EOD duration and amplitude increased further. **C** The same male was isolated for another 7 days, and a female was added to his tank after the nightly peak. EOD duration increased immediately that night, but amplitude did not. The following night, both maximum duration and amplitude increased. By day 11, amplitude more than doubled over its value during isolation

EOD durations to recover sufficiently that they were that were statistically indistinguishable from males taken directly from the communal outdoor pools (Table 2). On subsequent nights, duration maxima did not increase significantly beyond those recorded the first night the stimulus fish was added to the tank. Female stimuli probably elicited a further duration increase the next night, but high variability yielded a marginal P value of 0.08.

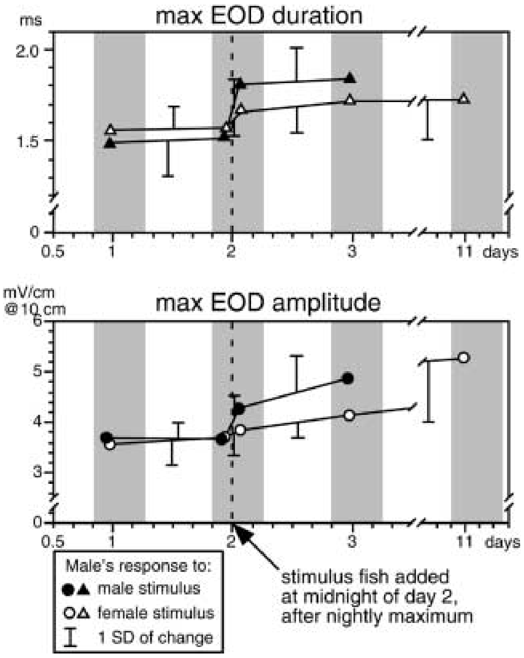

Fig. 5 Mean nightly EOD maxima of 14 isolated males in response to introduction of a male or female stimulus fish at midnight of day 2. *Error bars* are one SD of the *change* between successive maxima. Social stimuli of both sexes elicited immediate (10–120 min) increases in EOD duration. Male stimuli elicited immediate (10–120 min) and long-term (24 h) increases in EOD amplitude. Female stimuli elicited only long-term increases in EOD amplitude, more gradual than those produced by males. Within a week, males housed with females reached similar EOD amplitudes to males housed with males

Amplitude changes were more complex, showing profound differences in time-course and strong sensitivity to the sex of the stimulus fish. As seen with duration, EOD amplitude increased significantly within 2 h of the addition of a stimulus fish, but only for male stimulus fish. Females elicited no increase in EOD amplitude the night they were added to the focal males' tanks. EOD maxima increased significantly further the following night, this time in response to both stimulus sexes. By the second night with male stimuli, EOD amplitudes of focal males had recovered to about 75% the level of fish housed in communal pools, but amplitudes of focal males receiving female stimuli lagged at 64% of their communal counterparts (Table 2). We housed the female-stimulated males with two females for an additional week, by the end of which their EOD amplitudes had reached 80% the level of fish taken directly from the communal pools (Figs. 4C, 5, Table 2).

The experimental males exhibited normal social behavior. At night, test males and stimulus males showed aggression towards one another through lateral displays, serpentining, and rapid EOD rate changes (e.g., Westby 1975). All but one male expressed interest in the stimulus female by producing courtship "chirps" (e.g., Stoddard et al. 1996). At least 9 of 14 test males held with females for a week between measurement sessions induced those females to spawn.

Table 1 Maximum nightly electric organ discharge (EOD) duration (dur) and amplitude (ampl) increases from isolation levels (mean ± SD) following addition of a stimulus fish ($n = 14$). Non-significant P values are listed in parentheses. All other EOD duration and amplitude increases are statistically significant (paired t-test; 13 *df*; $P < 0.01$, 1-tailed). M > F contrasts indicate test periods in which EOD increase in response to male stimuli significantly exceeded those in response to female stimuli. Percentage increases for the first 2 h are referenced to maximum values measured night 2, an hour or so before the stimulus fish was added, not the to EOD values immediately before the stimulus fish was added. Male stimulus fish produced a significantly larger increases in duration and amplitude than females the night they were added to the tank, but the difference in effect between the two sexes diminished by the next night. EOD duration increased only the night the stimulus fish was added to the tank, but EOD amplitude continued to increase the next day (and week, for female stimuli). Stimulus males elicited a larger increase in EOD duration than females the first night only, but no significant difference in EOD amplitude that night or any other. Order of stimulus treatment (m, f versus f, m) had no effect (MANOVA; $P > 0.3$)

Stimulus fish's sex	EOD	Time-course of EOD increase			Total
		First 2 h	Next 24 h	Next week	
Male	dur	15 ± 15%	2 ± 19% ($P = 0.3$)	–	17 ± 18%
Female	dur	5 ± 9%	4 ± 14% ($P = 0.08$)	1 ± 21% ($P = 0.4$)	10 ± 22%
Male	ampl	14 ± 43%	16 ± 71%	–	32 ± 72%
Female	ampl	1 ± 41% ($P = 0.9$)	9 ± 30%	24 ± 18%	37 ± 10%
Contrasts	dur	$P = .002$	($P = 0.3$)	–	($P = 0.1$)
M > F	ampl	$P = .01$	$P = .07$	–	$P = 0.2$

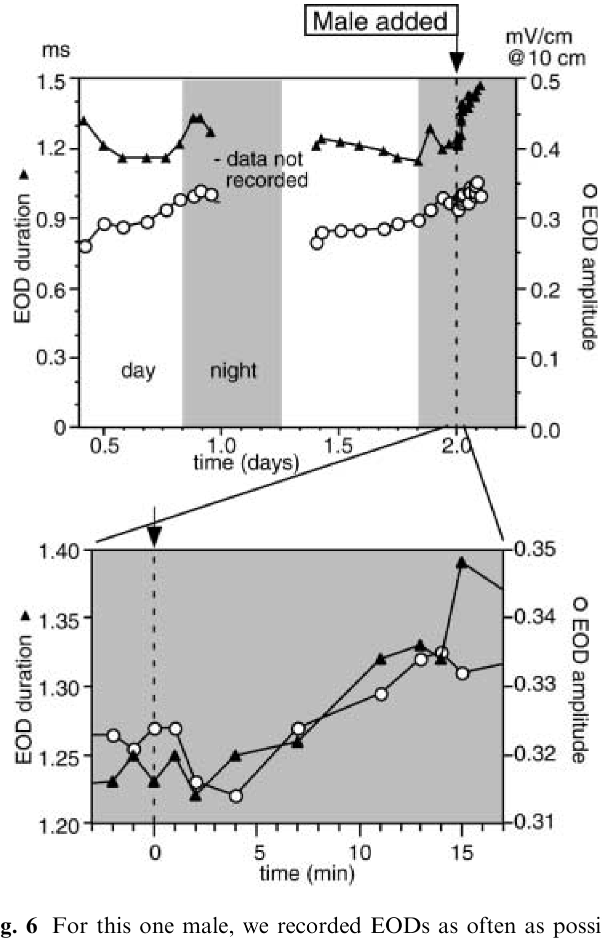

Fig. 6 For this one male, we recorded EODs as often as possible around the introduction of a stimulus male to the tank. His EOD duration had already peaked and fallen for the night, and his EOD amplitude was still dropping. Within 12 min after the stimulus male was added, EOD duration and amplitude increased discernibly. The lower graph is a close-up of the data in the upper graph (note the change in axis values)

Discussion

We found that isolation caused a slow decline of EOD duration and amplitude, while social stimuli restored sexual dimorphism in these characters. Neither the function nor mechanism of these changes has been shown conclusively, but the data and some related studies give us helpful leads.

Behavioral significance of the EOD change

No study has shown directly the function of sexual dimorphism in EOD duration or amplitude. The two options are communication and electrolocation. Electrolocation seems an unlikely basis for sexual dimorphism the signal of *Brachyhypopomus*, especially considering that the electric waveform of this fish is similar between the sexes at the head (Stoddard et al. 1999) where most electroreceptors are located (Szabo and Fessard 1974; Yager and Hopkins 1993). It is hard to imagine how a male would improve electrolocation by increasing duration of the second phase of the EOD or why he would reduce EOD duration and amplitude as soon as spawning time ended if that reduced his ability to electrolocate. We have initiated a study to determine whether modulation of EOD duration and amplitude affects electrolocation. Increasing EOD duration slightly lowers the EOD spectral peak (Hagedorn and Zelick 1989; Hopkins et al. 1990) and increasing EOD amplitude increases the distance the EOD can be detected by other fish (Brenowitz 1986). Both changes are consistent with a putative role of the EOD in reproduction or territorial behavior.

We cannot say why males have a stronger effect than females on EODs of males, or whether differences in response to the two sexes has any adaptive significance. Our experiment included no systematic control for non-

Table 2 To gauge the completeness of EOD recovery with the social stimuli, we compare EODs of social control males taken directly from the communal outdoor pools containing 10–30 other fish (first experiment) with EODs of the males in the second experiment who were isolated for a week, then exposed to males or females. Duration recovered more rapidly than amplitude, and male tankmates elicited a quicker recovery than females. Males in the social control category were different individuals from those in the other columns; $n = 18$ for social controls, $n = 14$ for all others. *P* values are shown from Fisher's PLSD post-hoc tests comparing EODs of the social control males with the experimentals; small *P* values indicate significant differences. Bonferroni's inequality requires a *P* value below 0.009 to set the cumulative probability of type I error below 0.05

	Social control	Isolated 1 week	2 h with 1 male	24 h with 1 male	2 h with 1 female	24 h with 1 female	Week with 2 females
EOD duration							
Mean (ms)	1.89	1.56	1.79	1.82	1.66	1.72	1.73
SD	0.30	0.28	0.33	0.26	0.26	0.28	0.27
% of full social	100%	82%	95%	96%	88%	91%	92%
P value	–	0.01	0.34	0.50	0.03	0.10	0.13
EOD amplitude							
Mean (mV cm^{-1})	6.56	3.63	4.21	4.87	3.84	4.20	5.22
SD	1.75	1.10	1.28	1.49	1.32	1.40	1.05
% of full social	100%	56%	64%	74%	59%	64%	80%
P value	–	0.0001	0.0001	0.001	0.0001	0.0001	0.009

specific stimulation (e.g., a fish or electric signal other than a potential mate or rival), so we cannot state with certainty that the EOD increase males show in the presence of females is specific to females. Perhaps response is proportional to the degree of social interaction and not to the sex of the stimulus fish per se. Stimulus and experimental males frequently challenged one another through the mesh dividers. Female *B. pinnicaudatus* normally approach males only when they are ready to spawn. In the outdoor pools, males are exposed chronically to both sexes, but in the field the possibility exists that males may encounter one sex more frequently than another. In a pilot study ($n = 2$) males did not modulate their EOD in response to steady playback of the male waveform (Franchina 1997), so non-interactive electric signals do not appear to be sufficient stimulation. Below we speculate on possible adaptive significance of the EOD changes.

One possible adaptive reason for stronger responsiveness to male stimuli is that the EOD is important in a male's ability to deter other males from potential oviposition sites (males attract females into floating plant cover for courtship and spawning; C.R. Franchina et al., unpublished observations). A similar pattern of social signal modification occurs in the cricket frog (Wagner 1989, 1992). Although body size in cricket frogs is correlated with dominant calling frequency for physical reasons, males lower their frequency in response to another male with a frequency lower than their own. The frequency decrease correlates with willingness to fight. Male *B. pinnicaudatus* do seem to use their signal in an aggressive context. When we observe two males under infrared light, males often approach one another tail first, sticking their tail in the other male's face (C.R. Franchina, unpublished observations).

Another possibility for EOD change in the presence of males is that his EOD is critical for attracting females, but the sexual dimorphism carries an extra energetic cost or a predation risk. Males might only amplify the sexual dimorphism in the presence of competing males. A similar phenomenon is reported for Túngara frogs (*Physalaemus pustulosus*; Ryan 1985). Males calling singly give only the first part of the two-part call. The second part of the call, given in the company of other males, attracts both females and predatory bats. Males may compete directly for females by giving better signals than the nearby males. Thus, a competing male may be a stronger stimulus for enhancement of a risky courtship signal than the presence of the female it is meant to attract.

Female *B. pinnicaudatus* prefer larger males with more sexually dimorphic EODs (Curtis 1999), though experiments have not yet shown whether the EOD waveform is the chosen trait. Contests over resources among male fish generally favor those of larger size, because size so frequently determines the outcome of a direct physical competition (Andersson 1994). Among males recently removed from social pools (first 24 h), both nightly peak amplitude and the day-night change in amplitude correlated positively with total length (Franchina and Stoddard 1998). However, EOD amplitude and total body length in this study were not correlated after introduction of male stimuli to pre-isolated males. Maximum EOD amplitude may be indicative of some combination of male body condition and size, but whether EOD amplitude indicates total body length or capacity for energetic expenditure cannot be stated at this time. Studies are underway in our laboratory to measure the energetic costs of electrogenesis in this species and the function of electric signal characters in mate choice.

Mechanisms for EOD change

EODs are composites of action potentials from arrays of electrocytes. In the mormyrid electric fish where the electric organ is short and restricted to the caudal peduncle, sexual dimorphism in the EOD has been attributed solely to sex differences in the individual electrocytes (Bass and Volman 1987; Bass et al. 1986). Sex differences in the biphasic EODs of the gymnotiform

Brachyhypopomus species have been attributed to sexual dimorphism in the morphology and action potentials of individual electrocytes and in the gross morphology of the caudal filament (Hagedorn and Carr 1985; Hopkins et al. 1990). As described in the companion study (Franchina and Stoddard 1998) steroidal regulation of ionic currents in the electrocytes is a probable mechanism for gradual changes in EOD duration and amplitude seen in other taxa (reviews by Landsman 1995; Zakon 1996). Social initiation of EOD waveform change in reported here occurs too quickly for classic genomic steroid action involving DNA transcription but is consistent with the time-course associated with non-genomic steroid effects (reviews by Moore and Evans 1999; Wehling 1997). The gradual increases in EOD amplitude across several days is consistent with a genomic steroid mechanism. Because electric organs of gymnotiform electric fish extend through most of the body length, spinal conduction plays a significant role in electrocyte synchrony and thus EOD shape (Caputi et al. 1993; Lorenzo et al. 1990). We need to determine whether the spinal cord contributes to the changes seen in the EOD waveform in *B. pinnicaudatus*.

An interesting pattern in our data concerns the differences in male EOD change elicited by exposure to males and females. Both sexes elicited a rapid rise in the male's EOD duration, but response to males was faster and larger. Only male stimuli elicited a significant rapid rise in EOD amplitude. Male and female stimuli may produce different time courses in EOD recovery by eliciting release of different hormones or different quantities of the same hormone, or by eliciting differential regulation of hormone receptor affinities or secondary mechanisms. The physiology underlying the socially mediated changes in EOD structure shown here awaits further investigation. The ability to induce rapid changes in the EOD of *B. pinnicaudatus* makes this fish a promising model for investigation of rapid social modification of signals and excitable membranes.

Acknowledgements C.R.F. and P.K.S. designed the study, C.R.F., V.L.S., and C.H.V. collected data, all authors analyzed the data, and C.R.F. and P.K.S. wrote the paper. C. Curtis contributed significantly to upkeep of the fish colony, M. Kilburn built the darkroom for behavioral observation and A. Moinudden helped with pilot data collection. We thank members of H. Zakon's laboratory for a critique of the manuscript. Support and equipment were provided by NIH grant GM08205 to PKS. Pilot experiments were supported by E. Adkins-Regan, the Field of Neurobiology and Behavior at Cornell University, the FIU Foundation, and a grant from the President's Council for Cornell Women to CRF. Experiments complied with the "Principles of Animal Care" publication No. 86-23, revised 1985, of the National Institute of Health.

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