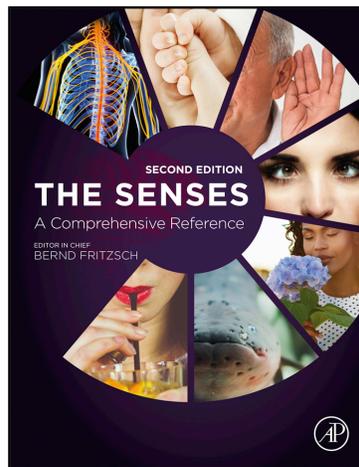


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From Kramer, B., 2020. Communication and Waveform Analysis in Weakly Electric Fishes With Special Emphasis on Mormyrids. In: Fritzsche, B. (Ed.) and Bleckmann, H. (Volume Editor), *The Senses: A Comprehensive Reference*, vol. 7. Elsevier, Academic Press, pp. 255–280.

ISBN: 9780128054086

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7.15 Communication and Waveform Analysis in Weakly Electric Fishes With Special Emphasis on Mormyrids

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Abbreviations

AP	Action potential
EOD	Electric organ discharge
FM code	Frequency code modulation
HD	High discharge rate display (steady state)
IDI code	Inter-discharge interval code
JAR	Jamming avoidance response
PLA	Preferred latency avoidance
PLR	Preferred latency response
SI	Sharp frequency increase
SI-HD	Sharp frequency increase followed by a steady-state, high discharge rate display

7.15.1 Abstract

The electric sense in fishes was discovered in the 1950s. African snoutfish (Mormyridae) and South American knifefishes (Gymnotiformes) generate electric fields for testing their environment by Active Electrolocation, and for communication. These fishes' electric organ discharges (EODs) are species-specific (or -characteristic) pulses or continuous waves, and vary widely in waveform, duration (frequency) and strength. In mormyrids the sequence (or pattern) of pulse intervals carries motivational and species-specific information. In a natural hybrid species complex, choosy females of the parent species block a speciation reversal by their preference for conspecific EOD waveforms, and rejection of the hybrid form. Electrosensory discrimination thresholds appear adapted to the fine detail of the EOD pulse waveforms on a μs -scale, with spectral cues not required in *Pollimyrus adspersus*. In some mormyrid species, breeding males add a strong D.C. component to their EOD, which attracts females but also

low-frequency sensitive catfish predators. In several species, specific EOD patterns, as well as loud vocalizing, accompany courtship and spawning. The larvae's early EODs of long pulse duration and initially low rate is replaced by an adult short EOD in young juveniles; parental care is present in *Pollimyrus* species. Three syntopic species gave examples of conflictual and cooperative electrocommunication in a semi-natural environment. *Eigenmannia*, a wave gymnotiform fish, is highly phase sensitive to stimuli of 0 Hz frequency difference, which evoke a Jamming Avoidance Response (which is a frequency shift away from the stimulus). The strength of the JAR depends on the phase difference stimulus to EOD. At a sufficient frequency difference, trained, food-rewarded *Eigenmannia* discriminate waveforms by a temporal mechanism that does not require spectral cues. *Eigenmannia* is incapable of discriminating stimuli that are phase-locked at maintained frequency identity.

7.15.2 Lissmann's Discovery

The young zoologist Hans W. Lissmann (1909–95) obtained his doctorate of Hamburg University in 1932. He had studied the behavior of Siamese fighting fishes in the Institut für Umweltforschung directed by Jacob von Uexküll, and was desperately looking for a job outside Nazi Germany (Alexander, 1996). At the University of Cambridge, he became aware of the weak electric signals generated by a specimen of the tropical African freshwater fish *Gymnarchus niloticus*. He wondered what the function of the signals might be (Lissmann, 1951). The signals were continuous sinusoidal waves of constant amplitude and frequency (300 Hz), and clearly too weak for stunning prey or warding off predators, two functions known for the strong-electric South American electric eel, *Electrophorus electricus*, that can emit volleys of powerful electric shocks. Both species are big and dangerous freshwater predators in tropical rivers and lakes. The reports of European explorers, such as Alexander von Humboldt, had made the electric eel famous since the 18th century.

Through his studies of *Gymnarchus*, Lissmann discovered the electric sense of fishes, and in 1954 he was elected a Fellow of the Royal Society. With ingenious experiments, Lissmann demonstrated the sensory function of *G. niloticus*' weak electric discharges in a new sensory feat for an aquatic vertebrate, Active Electrolocation, even before the sensory organs, electroreceptors, were known. By Active Electrolocation, *G. niloticus* detects live organisms or dead matter as impedance inhomogeneities of its self-generated electric field according to an object's conductivity, even at night, or in muddy water, and with the prey not even noticing (Lissmann, 1958).

This discovery entailed light on the biology of *G. niloticus*. *G. niloticus* has three kinds of electroreceptor organs with exceedingly high absolute or relative sensitivity. The organs detect the self-generated electric field. *G. niloticus*' brain is of enormous size, capable of integrating the electrosensory input of its lateral line nerves. These discoveries were soon shown to hold also for the other weakly electric fishes of Africa, the related Mormyridae (snoutfishes or elephant fishes), and, by an astounding case of convergent evolution, the only distantly related South American gymnotiform knifefishes (Fig. 1).

Lissmann's discoveries acted like a starting shot for the study of the structure and function of the electric sensory and motor system of African (osteoglossiform) and South American (gymnotiform) electric fishes, as well as for the many non-electrogenic, but electroreceptive fishes (see reviews by Bennett, 1971a,b; Szabo, 1974; Szabo and Fessard, 1974; Grundfest, 1957; Murray, 1974; Bullock, 1982; Bullock and Heiligenberg, 1986; Scheich and Bullock, 1974; and others). These studies focused mainly on the anatomy and physiology of the electric system, but scientists also began to take note of the species diversity of mormyrids and gymnotiforms. Both fish groups are among the most speciose endemic taxa of their respective continents.

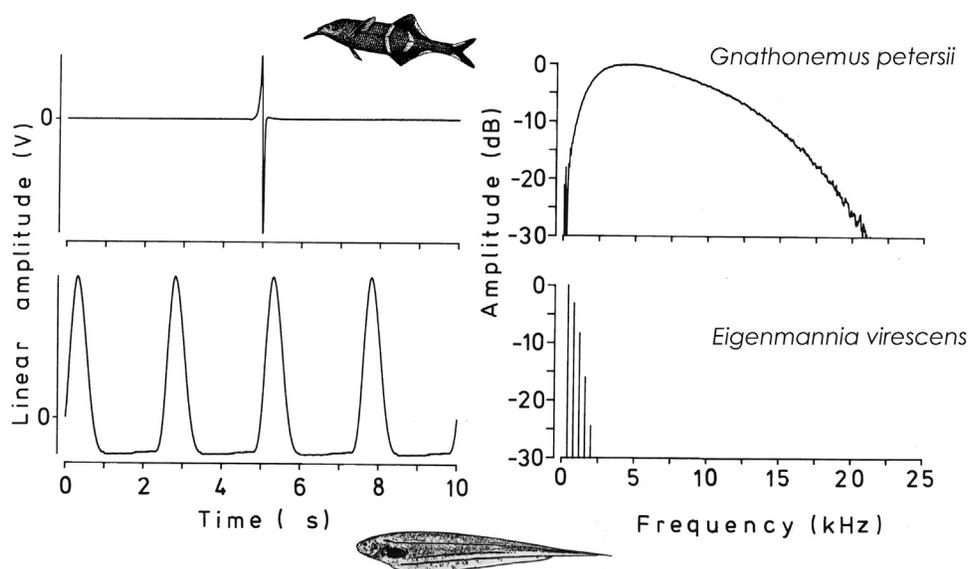


Figure 1 Electric organ discharges (EODs) recorded from an African mormyrid (top) and a South American gymnotiform electric fish (below). All African mormyrids generate EODs in pulse form, most gymnotiforms in wave form. The unique African *Gymnarchus niloticus* generates a wave EOD. Left diagrams are oscillograms (amplitude over time), right diagrams, amplitude over frequency in kHz. In these Fourier amplitude spectra, amplitudes are expressed as dB attenuation relative to the strongest spectral component of each waveform. Note pulse EODs occupy little space in the time domain (left) compared to the frequency domain (right), and vice versa for wave EODs. From Kramer, B., 1990. *Electrocommunication in Teleost Fishes: Behavior and Experiments*. Springer-Verlag, Berlin, modified.

From the beginning, Lissmann wondered about the possibility of electric communication in *G. niloticus* and mormyrids. Accidental observations such as Szabo's first permanent recording of electrical interaction in a captive, heterospecific pair of the mormyrid genus *Mormyrops* strengthened the communication hypothesis (Szabo in Lissmann, 1961). However, the question was how to prove this hypothesis? In a time when equipment such as computers, videorecorders, instrument tape recorders and digital storage oscilloscopes were either not available or not affordable. In addition, leading authorities of the humanities were skeptical of true communication in animals that – in their opinion – demands a cognitive level only present in the human. Even the ethologist Niko Tinbergen shied away from using the word communication in his famous textbook 'The study of instinct' that set the tone for years to come, and saw many reprints (Tinbergen, 1951). Therefore, the first tentative studies discussing communication in electric fish usually put the word 'communication' in quotation marks, to show that the author was aware of the critical discussion. 'The question of animal awareness', the title of Donald Griffin's groundbreaking book published 1976, helped to open minds regarding cognition in animals. The discoverer of echolocation in bats was a respected representative of the exact sciences and not known to publish unwarranted coffee-table talk.

7.15.3 The Question of Electro-Communication

The first dedicated experiment clearly supporting 'communication' showed electric organ discharge (EOD) rate changes when the experimenter slowly moved one snoutfish, sitting in a horizontally movable porous pot at one end of a long aquarium, toward a stationary specimen at the other end. By this method, the authors determined response distance (Moller and Bauer, 1973), and, in an improved design, assumed detection distance, by the EOD rate changes (startle responses) one or both fish displayed (Squire and Moller, 1982; Szabo and Moller, 1984). The experimental design aimed to exclude all stimuli except electrosensory ones, such as visual (the presence of widespread vocalizations among mormyrids had not yet been discovered). The title of the paper kept the quotation marks around the word 'communication', probably because the experiment gave no hint about what – or if at all – the two fish had been chatting; hence, whether communication as we understand it had occurred.

Freely ranging mormyrids in aquaria gave Sharp Increases in discharge rate (SI), usually followed either by a Decrease to the resting level (SID), or by a steady-state High Discharge (HD) rate display (in combination, an SI-HD), that accompanied intense aggressive and Lateral Display (LD) behaviors. The observation of intricate EOD latency-coupling behaviors on the millisecond-level among pairs of mormyrids further supported a communication function of the EOD (Bauer and Kramer, 1974; Bell et al., 1974; Kramer, 1974; Lücker and Kramer, 1981). The EOD has a social cohesion function in a group-living mormyrid (with possible vocalizations not excluded; Moller, 1976). Also in the gymnotiforms observations and recordings suggesting electrical communication were made (Black-Cleworth, 1970; Hopkins, 1972, 1974a,b,c; Westby, 1974, 1975a,b,c) (Fig. 2).

In order to exclude all but electrosensory stimuli, and so to firmly establish electrocommunication, playback experiments were called for. They aimed to shed light on the potential signal value of a display. Prerecorded high discharge rate sequences, when played back to a resident *Gnathonemus petersii* via an electric dipole decoy, proved highly efficient in evoking full threat, attack and lateral display behaviors aimed at the decoy. The decoy was a short plastic rod fitted with silver ball electrodes to generate an electric field geometry similar to that of a conspecific. In spite of the decoy bearing no physical resemblance to a fish, the experimental subject responded to it as if it were a conspecific (even in daylight, and only when the decoy was electrically active).

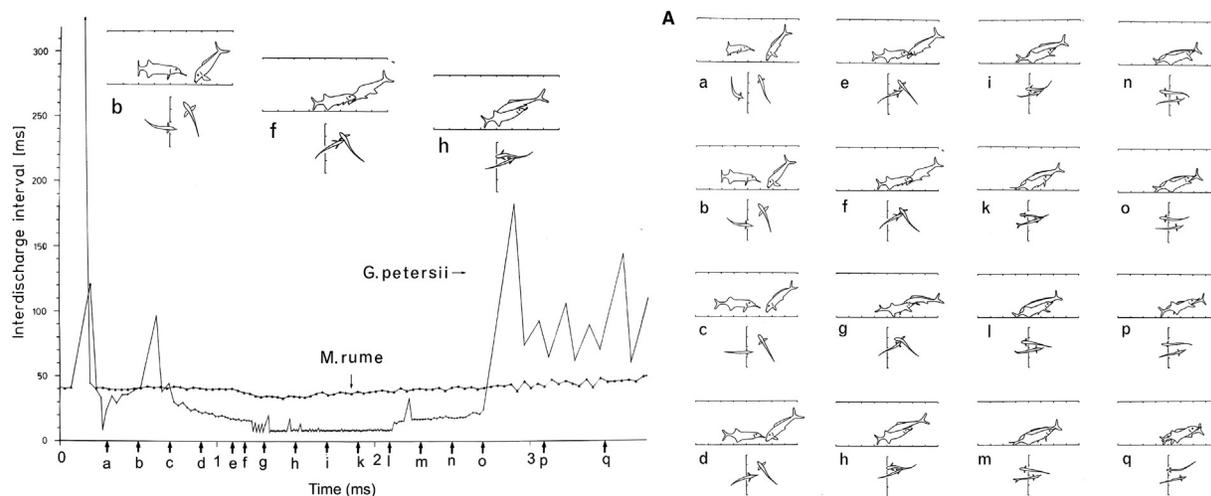


Figure 2 Aggression and stereotyped, concurrent EOD activity in a resident *Gnathonemus petersii* (with barble, left in inset image b) directed at an intruding *Mormyrus rume* (both mormyrids). Inset images drawn from a video film, with the scene seen from the side and from below. Abscissa, time in seconds, ordinate, inter-discharge interval (IDI) in milliseconds. Each dot is one interval, connected by lines to show trends. Note a Sharp Increase in EOD rate (SI) between letters c and f, which is the moment of head butt, followed by a steady-state, high discharge rate at two levels (HD, ending at letter o). Tick marks on scale of inset images, 5 cm. Highest discharge rate (also for the species) is about 125 Hz, corresponding to inter - EOD intervals of 8 ms. Fully documented in Kramer and Bauer (1976).

Playback of a discharge sequence recorded from a solitary, resting specimen evoked much weaker responses, such as repeated 'intention movements' to leave its daytime shelter, accompanied by brief and moderate discharge rate increases followed by a decrease to the resting level (SIDs, Kramer, 1979) (Fig. 3).

So far, these studies had documented discharge rate displays accompanying diverse overt behaviors, and their effectiveness to evoke behavioral responses when played back to a receiver fish in the absence of all other stimuli: visual, mechanical, auditory, olfactory. Hence, the existence of an electrical communication channel using discharge rates (or inter-discharge interval patterns, IDI) in so-called pulse fish was real. Further study showed that certain IDI patterns observed in several mormyrid species mediated threat and aggression, species recognition, courtship and spawning behaviors (e.g., Bratton and Kramer, 1989; Kramer and Lückner, 1990; Kramer and Kuhn, 1994; Werneyer and Kramer, 2005; Baier and Kramer, 2007). In so-called wave gymnotiforms, the communication signals consisted of frequency modulations, discharge arrests, and sometimes discharging in a form of synchrony, phase-coupling (e.g., Langner and Scheich, 1978). These general conclusions also held for the EOD interactions observed during threat and aggression, courtship and spawning in several gymnotiform species.

7.15.4 Is Electro sensory Discrimination Good Enough for Communication?

How well do fish discriminate pulse rates, or IDI patterns? The discrimination limen of trained, food-rewarded *P. adspersus* for constant pulse rates of around $20 \times s^{-1}$ was 2%, even when pulse trains were presented separately (well spaced in succession,

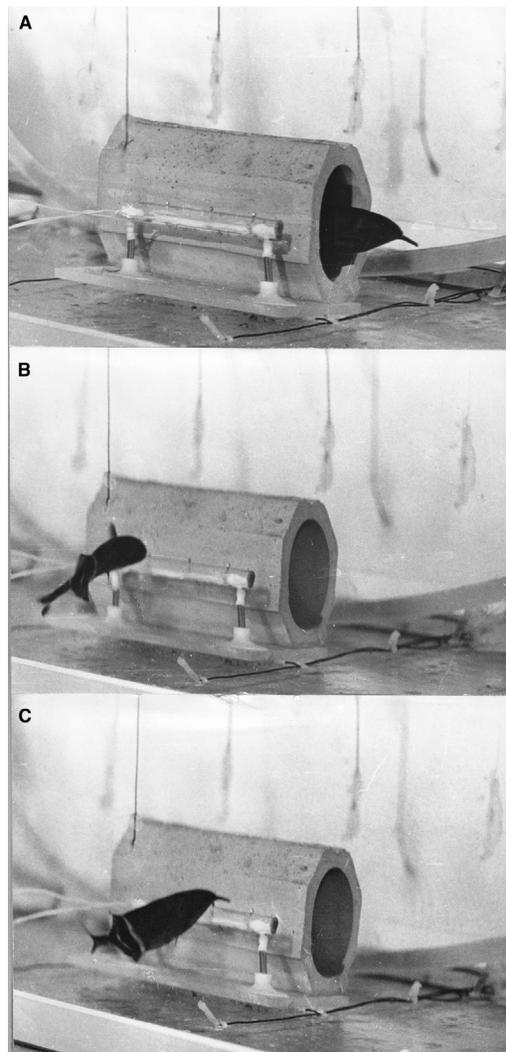


Figure 3 Motor responses of *G. petersii* on play-backs of social signals via a dipole. A dipole with three silver ball electrodes mounted on a Plexiglas rod generated an electric field slightly head-tail asymmetric similar to that of a conspecific. (A) Startle responses were observed significantly more often during stimulation with an attack pattern (one of these shown in Fig. 2) compared with a rest pattern. A startle response was a rapid forward and backward movement during which the fish never totally left its porous-pot hiding-place (B) Attack responses on the dipole model were observed significantly more often during stimulation with the attack pattern. (C) In many instances a Lateral Display accompanied by a high discharge rate followed the attack responses in the same manner as observed during social behavior. Photos, Kramer, B., 1979. Electric and motor responses of the weakly electric fish, *Gnathonemus petersii* (Mormyridae), to play-back of social signals. *Behav. Ecol. Sociobiol.* 6, 67–79.

akin to a test for perfect pitch). This is in the best range for humans when acoustic clicks are played to selected individuals in their twenties (Kramer and Heinrich, 1990). The frequency discrimination limen for *Eigenmannia*, a wave gymnotiform, was only 0.2% for sine wave stimuli of up to four times its own EOD frequency, when tested with alternating frequency bursts. This value is similar to the best ones reported in the human for auditory stimuli, presented in a similar way. These data show that the sensitivity for stimuli following either an IDI code (mormyrids) or an FM code (gymnotiform wave fish) is exceedingly high. The resting EOD frequency of wave gymnotiforms is so stable (standard deviation, 0.01% over 1000 EOD cycles, or even lower) that even small frequency changes stand clearly out (Bullock, 1969; Bullock et al., 1975; Kramer, 1987). With these conclusions confirmed, did we know all that was to know about the mechanisms of electrocommunication in these fish? No, we certainly did not.

There is also the great waveform diversity of the EOD pulse itself, especially in mormyrids, and of continuous wave signals in apteronotid gymnotiforms (Kramer et al., 1981; Albert and Crampton, 2005; Hopkins, 1981; Kramer, 2019). Already early students of electric fish, such as Bennett (1971a), had observed and documented some of the great species diversity of EOD pulse waveforms in mormyrids and gymnotiforms, as well as of waveforms in certain wave gymnotiforms. This diversity was astounding and became the object of much interest, both proximate (mechanism) and ultimate (function) (Fig. 4).

The basic mechanism of EOD pulse generation is the same for all pulse and many wave species, the action potential (AP) of a skeletal muscle cell (exception: apteronotids). Bennett (1971a) elucidated the mechanisms of how the electric organ (mormyrid and gymnotiform) may generate different, often species-specific or -characteristic, pulse waveforms. An electric organ whose non-innervated, opposite electrocyte faces are not electrically excitable generates a monopolar, usually head-positive EOD pulse of a waveform similar to an AP (such as found in all strong-electric fishes like *Electrophorus*, but also in some mormyrids such as *Hippopotamyrus szaboi*, *Mormyrus tenuirostris*). In the organs of other weakly electric fish the neurochemically evoked AP of the innervated electrocyte face triggers electrically an AP of the opposite cell face, which is of reversed polarity and occurs at a short delay, resulting in a bipolar EOD resembling a single-cycle sinusoid. Consequently, this mechanism reduces both EOD peak amplitude and spectral low-frequency content (for example, *G. petersii*). Still other mormyrids, such as *P. adspersus*, generate a triphasic EOD where the electrically evoked AP of the opposite electrocyte face not only is delayed relative to the AP of the innervated face, but also much shorter and stronger, and (of course) opposite polarity. In still other mormyrids the stalks of the electrocytes (that are contacted by the motoneurons; Bennett, 1971a) contribute notably to the EOD waveform by additional, small potentials, as, for example, seen in the pentaphasic EOD waveform of *Pollimyrus castelnaui*. These stalks vary in an amazing degree of complexity among species (Bass, 1986). In gymnotiform pulse species, small additional electric organs at various locations in the body modify the externally measured EOD waveform as generated by the long main organ, such as in *Gymnotus carapo* (for review, see Bass, 1986) or *Brachyhyppopomus beebei* (see Stoddard and Markham, 2008 for possible functions in the near field).

Gymnotiform wave species are either monotonous in waveform, varying just in species-characteristic frequency ranges and harmonic distortion, whereas the phase relationships among harmonics remain the same throughout the sternopygids (as far as they are known). The EOD waveforms of apteronotids, however, vary so much among species they appear to be free from constraints. In addition to varying in frequency range and harmonic distortion, apteronotid waveforms are of almost any conceivable shape within physiological limits. Their secret lies in an ontogenetic difference compared to sternopygids: the myogenic larval

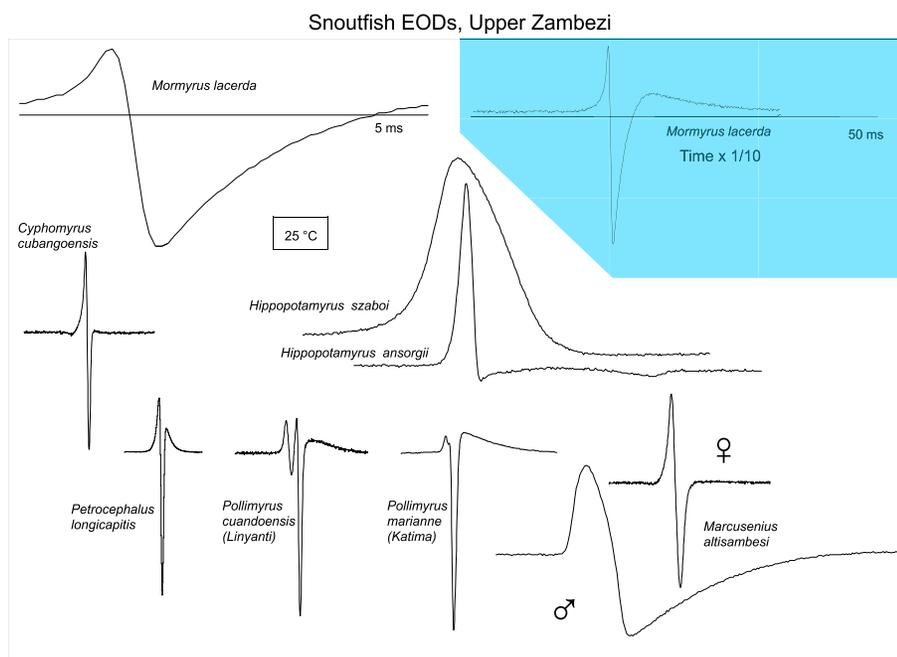


Figure 4 Several mormyrid species' EODs from the Upper Zambezi – Linyanti River community of mormyrid fishes, drawn to scale. Background in color: to show the extra-long EOD of *Mormyrus lacerda* at a time scale compressed by a factor of 10. The EOD of *Marcusenius altisambesi* is sexually dimorphic in local summer, when males develop a long discharge that recedes to the female discharge in winter. Head-positivity is upwards, zero lines = time bars. Kramer, B., 1996. *Electroreception and Communication in Fishes*. Gustav Fischer Verlag, Stuttgart, Jena, Lübeck, Ulm, updated.

electric organ (Kirschbaum, 1983) of apteronotids soon degenerates and is replaced by a neurogenic organ that persists in adulthood (de Oliveira-Castro, 1955; Bennett, 1971a). The neurogenic organ affords the Apterontidae waveforms of a higher frequency, of greater harmonic distortion, and great flexibility regarding the phase relationships among the constituent harmonics, resulting in a multitude of EOD waveforms (Kramer, 2019). The comparison of waveform diversity in mormyrids and apteronotids, and how it is achieved, shows that evolution can find similar solutions - species-specific EOD waveform diversity - by totally different means. It also shows once again that the convergent evolution of weakly electric African and South American fish was quite independent.

What are the selection pressures that underlie the evolution of all this complication? Do fish sense these fast EOD potential changes and elaborate waveforms that are often much shorter than an AP (for the pulse EODs) in the first place? For a stable waveform display of EODs, the human needs a triggerable oscilloscope, which was not available before about 1943, just in time for Hans Lissmann to observe the discharges of *G. niloticus* in his Cambridge laboratory in 1949. Do fish possess the equivalent of an oscilloscope?

Expecting failure, we trained several *P. adspersus* to discriminate between playbacks of a short, triphasic EOD, pre-recorded from a conspecific, and the somewhat longer, biphasic EOD of *G. petersii*. One stimulus was food-rewarded, the other not (we also used the two species with reversed roles). To our surprise, the experimental subjects of both species showed us this task was easy. We therefore tested whether the *P. adspersus* discriminated among different conspecific EODs, pre-recorded from different individuals, and presented pairwise. The experimental subjects mastered even this more difficult task, in spite of the similarity of conspecific EODs. This result supports the assumption of individual recognition by EOD pulse waveform, which appears adaptive given the long nocturnal courtship and fractional spawning behavior of *P. adspersus*. Pair partners join and separate dozens of time over many hours in a spawning night, and the highly aggressive male looks out for egg and larvae eaters, such as other females. He collects the eggs from the last visit of the female or (if present) straying larvae in his mouth and transports them to his nest (Kirschbaum, 1987; Bratton and Kramer, 1989; Baier et al., 2006).

In these experiments, successful EOD pulse discrimination was independent of stimulus amplitude, which supports categorical discrimination (Graff and Kramer, 1992). We did not yet know, however, whether the fish discriminated the stimuli by their differences in spectral composition (a short pulse is higher pitched than a long one) or by waveform (such as displayed on an oscilloscope). Natural *P. adspersus* EODs resemble each other, but are not identical and vary in several variables simultaneously. Therefore, we decided to use synthetic EODs the characteristics of which we could control.

Two superimposed Gaussians are sufficient to model mathematically the intraspecific variation of *P. adspersus*' triphasic EOD waveform by varying three variables (Westby, 1984). One Gaussian mimicks the neurochemically evoked summed APs of the innervated posterior electrocyte faces, giving rise to a head-positive potential P (of 150–250 μ s duration in our *P. adspersus* laboratory population). The other Gaussian represents the electrically evoked APs of the opposite, non-innervated cell faces that give rise to the strong and short N phase of opposite polarity, and less than 50 μ s duration. In the mathematical model, the standard deviations of the Gaussians are wide for the former and narrow for the latter, which is also of threefold strength and subtracted from the former. When both Gaussian peaks coincide in time, the two head-positive P peaks of the EOD, P1 and P2, are of equal strength. The P1/P2 amplitude ratio is one in this case; it decreases by advancing the N phase and increases by delaying the N phase. The natural variation of the P1/P2 ratio was 0.04 (weak P1, strong P2) to 3.33 (strong P1, weak P2; $N = 24$) in our sample of *P. adspersus*. We used Westby's mathematical model to generate synthetic EODs for playback experiments, with variables adjusted to meet the center of the natural variation. Data points of the discrete functions were separated by 2 μ s as required by the programmable D/A converter (Kramer and Weymann, 1987) (Fig. 5).

We trained seven *P. adspersus* to leave their daytime shelter to receive a food reward at the opposite side of the aquarium, whenever an electric fish decoy, a dipole, played back the S+ (rewarded stimulus), a symmetrical synthetic waveform termed signal0. The zero indicates temporal coincidence of the two Gaussian peaks. A fish aiming for a reward when the alternative waveform, S- (unrewarded stimulus), was played back, was discouraged to continue approaching the reward station by a few air bubbles injected in its path. Initially, for an S- we chose a great difference from signal0 to facilitate the learning of the two stimulus types, only one of which - signal0 - was rewarded. In these S- stimuli, the N phase was advanced or delayed by 30 μ s. All experimental subjects learned to discriminate between the S+ and the S- by this method of conditioned discrimination. Stepwise, we made the S- more similar to the S+ by reducing the temporal displacement of its N-Gaussian peak from its P-Gaussian peak. The trained fish still detected an advance or delay of the N phase in the S- by 2 μ s ($N = 2$), 6 μ s ($N = 1$), and 10 μ s ($N = 2$). The two most sensitive fish with the best values were unable to detect a 1 μ s shift of the N phase, however (Paintner and Kramer, 2003).

Even the most similar stimulus pair that were still discriminated by two of our fish, signal0 and signal-2, differed in their spectral amplitude distributions, that is, in perceived pitch (however little). Therefore, the question whether fish discriminate different waveforms based on a spectral or rather temporal sensory mechanism was still open at this point. We tested three experimental subjects whether they discriminated among stimuli of identical amplitude spectra but different waveforms (hence, different phase spectra). We used signal+10 as an S+ and signal-10 as an S-. All fish discriminated between these stimuli after only short training. In an additional test series, we contrasted signal+8 to signal-8 and obtained the same result. Therefore, we conclude that *P. adspersus* use a temporal sensory mechanism of discrimination, one that can detect waveform differences even when spectral cues are not available. We have not yet discovered the fishes' 'oscilloscope' (Paintner and Kramer, 2003).

A communication signal that encodes individual identity (as in *P. adspersus*' EOD) is useful depending on its reach. We tested *P. adspersus*' discrimination faculty for its reach in an aquarium of 2.4 m length, using signal+8 as an S+ and signal-8 as an S-. Starting at a stimulus-fish distance of 30 cm that we increased by 5-cm steps, we found that the spatial discrimination limit is at about 130 cm (at 4.9 μ V/cm field strength and 100 μ S/cm water conductivity). This reach is similar to the detection threshold determined by a spontaneous EOD rate increase (SI), a startle response, in another somewhat larger mormyrid, *Brienomyrus niger* (Squire and Moller, 1982; Moller et al., 1989). *P. adspersus*, as tested here, not only detects the presence of an approaching intruder but also

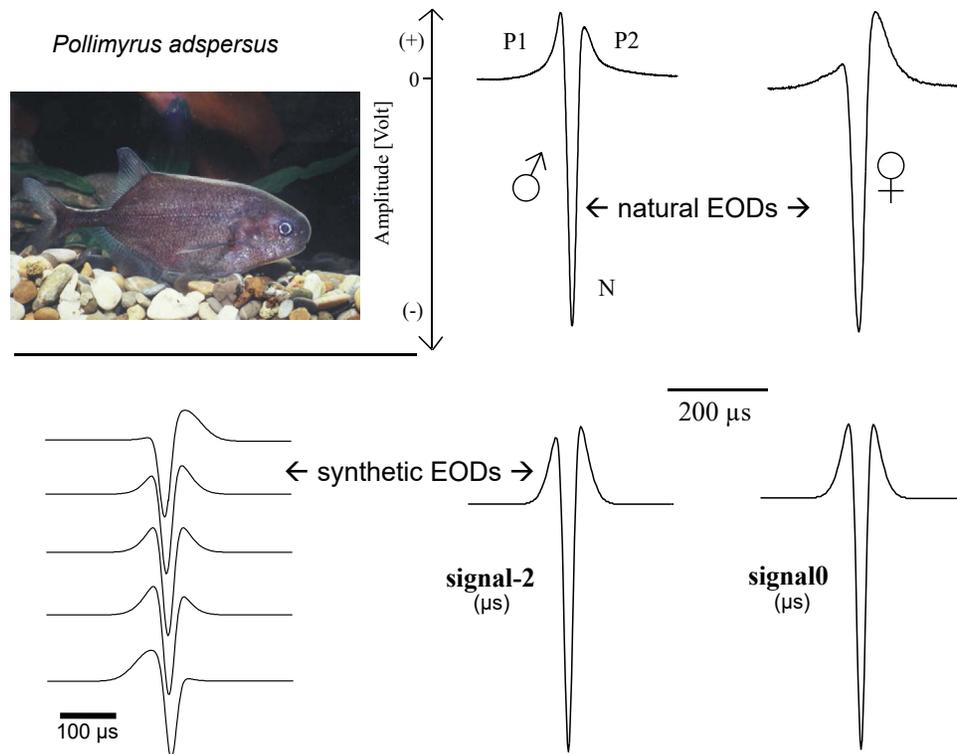


Figure 5 EOD waveform discrimination in *Pollimyrus adspersus*. Top panel, natural EODs showing a tendency for a sex difference, which are examples for broadly overlapping distributions. Note time bar of 200 μ s. Lower panels, left: 'synthetic' EOD waveforms, calculated by subtracting a narrow, strong Gaussian from a broader positive one, at different displacement times between the Gaussian peaks (from -30 to $+30$ μ s, zero being coincidence). Lower right panel, the two most similar stimulus waveforms between which two experimental subjects still discriminated in a conditioned choice test. The waveforms differ by a 2 μ s shift of the inverted Gaussian relative to the positive one. Paintner, S., Kramer, B., 2003. Electroreceptive basis for individual recognition in a weakly electric, mormyrid fish, *Pollimyrus adspersus* (Günther, 1866). *Behav. Ecol. Sociobiol.* 55, 197–208, modified.

its identity at a distance. We conclude it is the Knollenorgane rather than the Mormyromast organs that mediate this sensory feat, because of the great difference in sensitivity between the two receptor systems. We proposed a mechanism of differential neural coding of *P. adspersus* EODs based on the rate of voltage change and the known response properties of Knollenorgane (Bell, 1989; Bell and Grant, 1989; Hopkins and Bass, 1981). We have not been able to test it (Paintner and Kramer, 2003; see also Hopkins and Bass, 1981 for a similar suggestion for another EOD waveform).

The EOD waveforms of *P. adspersus* males and females differ significantly in P1/P2 ratio, suggesting its usefulness to identify sex partners in courtship and spawning (Westby and Kirschbaum, 1982). However, in males the average P1/P2 was < 1 , in females P1/P2 > 1 ($N = 10$ for males, $N = 14$ for females; Bratton and Kramer, 1988), there was extensive overlapping of statistical distributions. We concluded Westby and Kirschbaum's (1982) method of sexing their *P. adspersus* was unreliable. Sex partners have successfully spawned in our lab, in spite of a female's EODs showing the 'wrong' type of P1/P2 ratio. We therefore believe the variation of P1/P2 ratio supports individual identification rather than sex recognition. The sex difference in P1/P2 may be due to the anabolic effect of androgens such as testosterone, yielding a stronger electric organ in males (cf. Bass et al., 1986). The stronger P phase current in a male organ would trigger the N phase earlier in relation to the P peak than in females. A female ready to spawn recognizes a male by his loud advertising vocalizations and his conspicuous, highly aggressive patrolling behavior around his nest area. In addition, there is a sex difference in EOD echoing, or phase-coupling, behavior: males exhibit a PLR (Preferred Latency Response), females a PLA (Preferred Latency Avoidance; Kramer, 1978; Lückner and Kramer, 1981). Therefore, the individual variation in *P. adspersus*' EOD waveform may not result from sexual selection, in spite of its statistical significance. In some other species, examples of sexually selected sex differences in EOD waveform do exist (see further below).

7.15.5 Evolution of EOD Waveform in a Hybrid Species Complex

The sibling species complex of three dwarf stonebasher species of the Okavango-Zambezi system in Namibia and Botswana, which are so similar that they are hard to tell apart, gives an instructive example for the evolution of these fishes' electric communication system. The dwarf stonebasher, *P. castelnaui*, inhabits the Okavango, has a pentaphasic EOD waveform, usually 12 scales around the caudal peduncle and represents – according to the cytochrome *b* gene tree – the basal clade. Both the Zambezi dwarf stonebasher, *Pollimyrus marianne*, and the Kwando dwarf stonebasher, *Pollimyrus cuandoensis*, are derived from *P. castelnaui* (Kramer et al. 2003, 2014). *P. marianne* exhibits a triphasic EOD waveform and usually 16 scales around the caudal peduncle, whereas *P. cuandoensis* is

intermediate, both with its usually 14 scales and an EOD waveform combining elements of both other species at great variability. *P. cuandoensis* inhabits the smaller Kwando River that runs in parallel to and in-between both major rivers at equal distance, the Okavango in the west and the Zambezi in the east. The Kwando is a tributary to the Zambezi by the connecting Chobe but has tenuous links also to the Okavango (Fig. 6).

Whereas in *P. adspersus* the stalks piercing the electrocytes do not electrically contribute (less than 1/500th, Westby, 1984; Teugels and Hopkins, 1998), this is obviously different in *P. castelnaui* and *P. cuandoensis*. Markowski et al. (2008) generated *P. castelnaui*'s pentaphasic EOD waveform mathematically by adding a third electrical activity (as a Gaussian) to Westby's (1984) mathematical model for *P. adspersus*' EOD waveform. The extended model was capable of generating all individually varying *P. castelnaui* EODs tested at a near-perfect fit, by adjusting amplitudes, duration and relative delay times for the three successive electrical excitations. It was also capable of generating the triphasic Zambezi waveform of *P. marianne* by small parameter changes, including individual Zambezi stonebasher waveforms with small dents or slope changes in its P phase.

Both Okavango (2 out of 8) and Zambezi (4 out of 4) dwarf stonebasher showed significant spontaneous preference for their own species' playback EODs in a T maze test without reward nor punishment. Not a single specimen showed the opposite preference (Markowski et al., 2008). The common ancestor of both dwarf stonebasher species in the two main rivers may already have had a pentaphasic EOD that was simplified to a triphasic one when the Zambezi dwarf stonebasher differentiated from the Okavango dwarf stonebasher. In both species' larvae the emerging adult EOD waveforms are identical until about day 40, when only in Okavango larvae an additional electrical excitation, corresponding to the third Gaussian in the model, emerges (Baier et al., 2006).

Based on the maternal cytochrome *b* evidence, *P. cuandoensis* was recognized as a hybrid species with unidirectional origin and an intermediate phenotype, and *P. marianne* as the 'mother' species and *P. castelnaui* the 'father' species (following the terminology of Wirtz, 1999). The three species form a monophyletic clade, with *P. castelnaui* sister to the other two species (Kramer et al. 2003, 2014). Why does this three-sibling complex not collapse back again to a single species, a reversal of speciation? Conditions for such a scenario seem to be met: there is a hybrid species (*P. cuandoensis*) in a contact zone with occasional access to both parent species, by the Zambezi's seasonal flooding the terminal sections of the Kwando River (Chobe) from the east, and the Selinda (Magwegqana) spillway from the Okavango in the west. The choosy females of the two parent species block a speciation reversal, as suggested by spontaneous preference choice tests in the laboratory. Both parent species' females (*P. castelnaui*, N = 4 out of 5; *P. marianne*, N = 5 out of 5) discriminated against the EODs of *P. cuandoensis* males (N = 6), apparently because of their 'shaggy', EOD waveforms that combine features of both parent species' EODs in a way to resemble neither, at great variability among individuals. The single

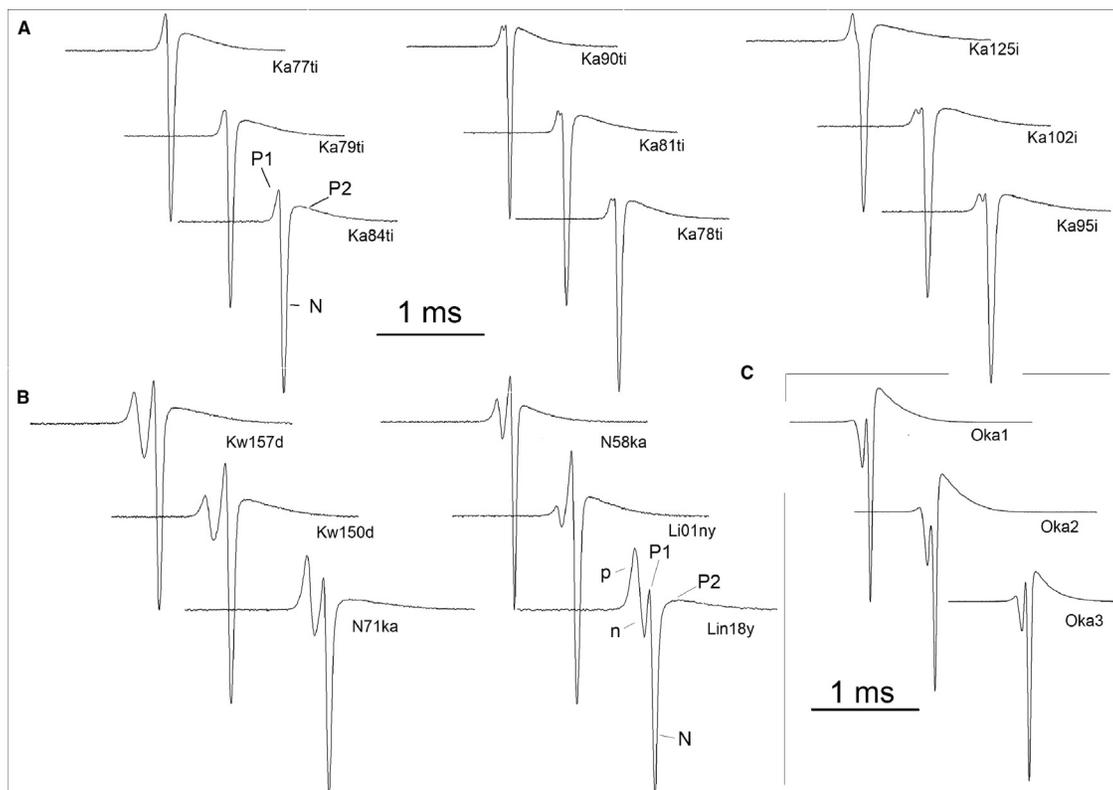


Figure 6 Three species of dwarf stonebasher from Namibia/Botswana, field-recorded. (A) *Pollimyrus marianne*, inhabiting the Upper Zambezi River. (B) *P. cuandoensis*, inhabiting the Kwando River. (C) *P. castelnaui*, inhabiting the Okavango River and delta. *P. cuandoensis* is a hybrid form of the two other species. The EOD of *P. cuandoensis* combines elements of the two parent species' EODs at great variability, in a way found in neither. Kramer, B., Van der Bank, H., Flint, N., Sauer-Gürth, H., Wink, M., 2003. Evidence for parapatric speciation in the mormyrid fish, *Pollimyrus castelnaui* (Boulenger, 1911), from the Okavango - upper Zambezi River systems: *P. marianne* sp. nov., defined by electric organ discharges, morphology and genetics. *Environ. Biol. Fish.* 67, 47–70, modified.

P. cuandoensis female available for the test preferred a Zambezi dwarf stonebasher's EOD to all other EODs presented, including those of her own species ($N = 6$; Schmid and Kramer, 2014). We have not found evidence for clear sex differences in EOD waveform in the dwarf stonebasher species, except for a very minor one in *P. castelnaui*'s pentaphasic waveform (Markowski et al., 2008). Similar to *P. adspersus*, only the male dwarf stonebasher (of all three species) vocalize during courtship, defend a nest, patrol the area around the nest, collect and transport the eggs to the nest and tend to the larvae (Baier and Kramer, 2007; Baier et al., 2006).

7.15.6 Species Recognition by IDI Pattern in Mormyrids?

The EOD waveform clearly signals the species identity of an individual dwarf stonebasher, whereas IDI patterns signal its behavioral state that may change at any moment. We studied the question of species specificity of IDI patterns in this sibling species complex; in other words, do they speak the same language? We found great similarity in equivalent IDI patterns between *P. castelnaui* and *P. marianne*; not in any one of the behaviors we studied did we find differentiation in associated IDI patterns (Baier and Kramer, 2007). This includes EOD activity during diurnal resting, nocturnal swimming, and territorial agonistic encounters. Not even during courtship and spawning could we find species-specific IDI activity (three pairs of *P. marianne*, five pairs of *P. castelnaui*). In contrast, the male's vocal advertising that precedes courtship and spawning did show acoustic species differences among the three dwarf stonebasher species (Lamml and Kramer, 2006). Apparently, the EOD waveform tells a female whether a male is conspecific or not, but the acoustic advertising (in combination with an appropriate IDI activity) appears to be instrumental in a female dwarf stonebasher's choice of a male. In three closely related bulldog species, formerly considered *M. macolepidotus*, allopatric differentiation in sound production during social interaction and reproduction, was also found (Lamml and Kramer, 2007).

Campylomormyrus tamandua and *C. rhynchophorus* displayed quite similar EOD waveforms but differed clearly in their nighttime swimming IDI patterns in our laboratory. One of four *C. rhynchophorus*, apparently a male, generated an EOD lasting 3.3 ms, about 20 times longer than that of its conspecifics. Given a choice, the *C. rhynchophorus* significantly preferred associating with a fish decoy playing back conspecific IDI patterns rather than a *C. tamandua* pattern. The *C. tamandua*, however, did not show any preference for neither pattern, perhaps because they were juveniles that join mixed species schools in the wild more easily than the adult *C. rhynchophorus* we used (Kramer and Kuhn, 1994). The genus *Campylomormyrus* is of Central African distribution with *C. tamandua* also widely occurring in West Africa. Our specimens were imported by a tropical fish dealer direct from Kinshasa (Zaire), and originate from an affluent of the Stanley Pool, 150 km off Kinshasa. The two species are easily distinguished by external morphology, size and coloration, and do not seem to be nearly so closely related as the *P. castelnaui* sibling trio. Another small mormyrid, *Petrocephalus bovei*, clearly preferred conspecific IDI playback patterns to those of *Pollimyrus isidori* or *B. niger*. These three species' nighttime swimming patterns were not significantly different in terms of histograms and mean discharge rates, but differed in terms of the sequence of pulse intervals, as revealed to the human eye and by autocorrelation (Lücker, 1982; Kramer and Lücker, 1990). These results support the notion that with increasing phylogenetic distance (in the latter case, involving three genera), IDI patterns differentiate to become species-specific in addition to situation-specific (Fig. 7).

Why do mormyrids discharge during the diurnal inactivity period in the first place? One reason that is probably valid for most species is group cohesion (Moller, 1976). In daytime, most mormyrids display a variable IDI pattern of low and 'irregular' pulse rate that is, of a wide range of IDIs, and associated histograms with two or three peaks. In *Marcusenius altisambesi*, a novel resting IDI pattern serves the male to advertise to females even during the diurnal inactivity period. Male *M. altisambesi* residing in the center compartment of a large tank usually generate their species' version of the variable resting activity of 4–12 Hz, characterized by a wide range of IDIs (about 15–500 ms), and a broad histogram with two or three peaks. However, when a female replaced a male neighbor, experimental males ($N = 4$) switched to a regularized IDI pattern (16–28 Hz, IDI range 11–100 ms, and a single histogram peak). The regularized IDI pattern vanished when – back again – a male replaced the female. The regularized pattern attracted females, as shown by playback preference tests. Six experimental females (in the center compartment of a large tank) had a choice between a dipole generating a variable and a dipole generating a regularized male IDI pattern, at equal distances on either side. Five (of six) females preferred to stay close to the dipole generating the regularized IDI pattern, whereas one female showed the opposite preference (Machnik and Kramer, 2011). How fish (both sexes) knew the sex of their neighbors is unknown. It could not be EOD duration because the laboratory-kept males displayed short EODs as in 'local winter' in the wild, and the dipoles generated short EODs. In this species, both sexes vocalize during courtship (Lamml and Kramer (2007), but this was not monitored in the study. Apart from an advertising function, the males' regularized IDI pattern could help advance gonadal recrudescence in the females (see Lehman, 1963 for ring doves).

7.15.7 Marcusenius: Sexually Dimorphic EODs

Male EODs in most of the southern African *Marcusenius* species are longer and more variable than female EODs. For example, the Upper Zambezi bulldog, *M. altisambesi* that occurs also in the Okavango River, exhibits a seasonal sexual dimorphism in EOD waveform (see Fig. 4). Females and juveniles generate short EODs throughout the year ($386.9 \pm 9.2 \mu\text{s}$, $N = 47$ summer females; $340 \pm 3.57 \mu\text{s}$, $N = 22$ winter females), males, however, long EODs – that are long only in summer ($2980 \pm 330.3 \mu\text{s}$, $N = 15$ summer males; $334.1 \mu\text{s} \pm 7.55$ $N = 8$, winter males; all at 25°C). Males attaining sexual maturity increase the duration of their EOD up to $4779 \mu\text{s}$ in a steplike fashion, more than 10 times the female/juvenile average, at a time when the Zambezi and Okavango are in flood and bulldogs breed. Long male discharges occur in summer only (rainy season), not in local winter.

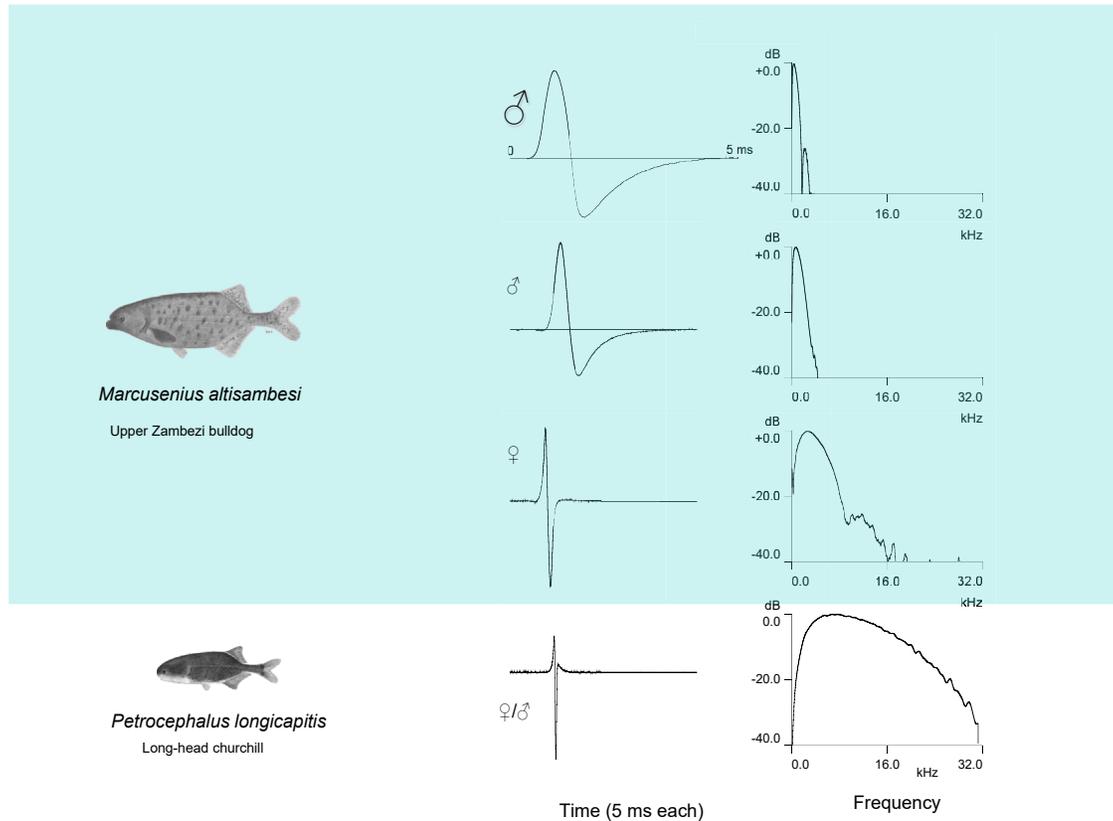


Figure 7 Fourier amplitude spectra (right panels, amplitude over frequency in kHz) of the EODs (left panels, amplitude over time) of two prey fish species for the sharptooth catfish, *C. gariepinus*. Male Upper Zambezi bulldogs, *M. altisambesi*, in breeding condition display EODs of up to 10 times the duration of female EODs and risk most to be taken out by catfish because of their low-frequency spectrum. Females, as well as churchills, *Petrocephalus longicapitis*, run a considerably lower risk because of their higher frequency EODs. Fish pictures from Skelton, P.H., 1993. A Complete Guide to the Freshwater Fishes of Southern Africa. Southern Book Publishers, Halfway House, South Africa.

Four of six female *M. altisambesi* gave stronger spontaneous responses to playbacks of the long EODs of field-recorded ‘summer males’ than to short EODs of ‘winter males’. The responses measured or counted were head butts, circling around the fish decoy used for playback, and association time close to the dipole decoy. None of these laboratory-kept females was in a clearly reproductive state, and still two-thirds responded to the EODs of breeding males recorded in their home river (Machnik et al., 2010). The observed behaviors were among those that occur in male-female pairs during courtship in this species (Lamml and Kramer, 2007), and were similar to those seen in *Marcusenius pongolensis* (Werneyer and Kramer, 2005). However, four of seven male experimental subjects (57%) responded in the opposite way to females: they avoided the long playback EODs and preferred to associate with the decoy playing short EODs (three individuals responded to neither signal; Machnik et al., 2010). This is evidence for sexual selection of the male long discharge by female choice (intersexual selection), whereas intrasexual selection by male competition seems to be absent in *M. altisambesi* (Machnik et al., 2010). *M. altisambesi* breeds on a floodplain of a reservoir river, the Upper Zambezi, where there is plenty of (flooded) grass and other vegetation, and spawning sites no limiting factor. *M. altisambesi* do not construct a nest.

7.15.8 Not Only Females are Listening

The question arises what initiated an evolutionary process that led to male pulse lengths that are more than 10 times the length of female/juvenile EODs? The amplitude spectrum of long male discharges is very low-frequency, and EODs were surely stimulating not only the females’ Knollenorgane, the communication receptors, but also their low-frequency sensitive ampullary organs of extremely low threshold. By comparison with short EODs, the effect of long EODs must be similar to a big thump from a subwoofer in a stereo system, stimulating the females much stronger than ordinary, short EODs. When accentuated male characters differ in strength, females tend to choose the stronger (Ryan and Keddy-Hector, 1992), as confirmed in *M. altisambesi* females stimulated with playback male EODs of varying length (Machnik et al., 2010). Therefore, *M. altisambesi* males generating the longest EODs likely have the greatest fitness. However, not only females are listening in the Zambezi and Okavango. Catfish, such as the sharptooth catfish, *Clarias gariepinus*, also detect long male EODs by their ampullary, low-frequency electroreceptor organs, whereas the short juvenile and female EODs were beyond detection threshold (Hanika and Kramer, 2000). Bulldogs, probably mainly males, made up 64% of the stomach contents of 363 dissected catfish in summer, at the time of the spectacular catfish runs in the Okavango (Merron, 1993). An equally common snoutfish, the churchill *Petrocephalus catostoma*, with a short EOD lacking low

frequencies (Kramer et al., 2012) represented only 26% of the catfishes' diet. (More likely than *P. catostoma* is the Okavango churchill *Petrocephalus okavangensis*, a new species, according to Bruton et al., 2018.) The median standard length of 456 bulldogs eaten was 12.5 cm (Merron, 1993), exactly the right size for full male maturity and the occurrence of the longest EODs (Kramer, 1997). Males just big enough to attain sexual maturity in their first year generated the longest EODs, whereas the biggest and oldest bulldog males did not display any of the very longest EODs (Figs. 8 and 9). 7).

Predatory pressure, most likely principally by catfish, on males with the longest EODs, the ones catfish detect best, keeps the maladaptive selection for still longer EODs by female choice in check. Predation pressure must have been so intense that long male EODs are limited to summer only, that is, to the time of reproduction. The seasonal sexual dimorphism in the EOD of Upper Zambezi bulldogs, *M. altisambesi*, seems to result from past runaway selection (Fisher, 1930) for long male EODs by female choice, which has eventually come to a stop by predator pressure (Hanika and Kramer 1999, 2000).

7.15.9 A Weaker Kind of EOD Sex Difference

Another bulldog species that had long been confused with *Marcusenius macrolepidotus* is *M. pongolensis*, reinstated by Kramer et al. (2007). We studied *M. pongolensis* specimens from sections of the Incomati and Sabie rivers inside or bordering the Kruger Park in South Africa. These rivers are rather short (compared with the Zambezi), and arise on a high plateau. The rivers carved deep valleys into the escarpment where steep sections and strong currents are common. Occasional torrential floods devastate the costal Lowveld before draining into the Indian Ocean. Accordingly, *M. pongolensis*' body is more fusiform and less deep than that of *M. altisambesi*, as suits a strong swimmer. The EODs from adult *M. pongolensis* bulldogs differ between the sexes, but in a way different from the Upper Zambezi bulldogs. Whereas *M. pongolensis* juveniles and females display similar EODs that remain constant for females, those from males start to increase in length at puberty in a linear, moderate way throughout their lives, with the biggest and oldest specimens generating the longest EODs (ranging from 329 to 975 μ s, field measured, '5% threshold criterion'). (Because of its asymptotic start and stop, an EOD started at an arbitrary 5% peak amplitude of the head-positive P phase and ended where the negative N phase crossed the -5% value.) Males therefore carry a status badge related to their size, fighting ability, and probably mating success (Kramer, 1997).

In a test for intrasexual selection, a male experimental subject in the central partition of a large tank was habituated to two 'familiar' male neighbors on either side for at least 1 week. The fish were in electrical and limited physical contact through plastic mesh screens. The test started when a dipole fish decoy replaced one 'familiar' neighbor, playing back a 'stranger' EOD waveform recorded from an individual the experimental subject had never seen. The attack rate of the experimental *M. pongolensis* males on the dipole model playing back the 'stranger' EODs (of 329 to 975 μ s length, field-recorded, '5% threshold criterion') increased with

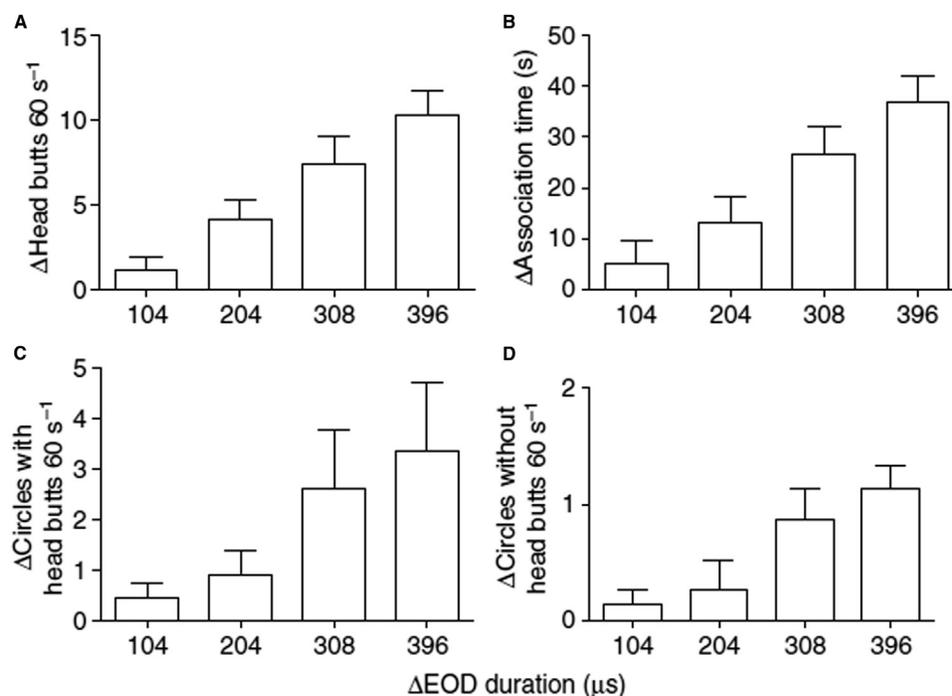


Figure 8 Ten *M. pongolensis* females' preference (pooled) of longer male EODs determined in double dipole playback tests. Behavioral scores shown as difference between scores for longer pulse minus scores for shortest pulse (of female duration, 320 μ s). Difference scores are shown as means + 1 s.e.m. For four behavioral variables the difference scores increased significantly with the difference in pulse pair duration (linear trend, significant). From Machnik, P., Kramer, B., 2008a. A male's playback signal turns female *Marcusenius pongolensis* receivers on or off depending on his behavioural state. *Commun. Integr. Biol.* 1, 128–131; Machnik, P., Kramer, B., 2008b. Female choice by electric pulse duration: attractiveness of the males' communication signal assessed by female bulldog fish, *Marcusenius pongolensis* (mormyridae, teleostei). *J. Exp. Biol.* 211, 1969–1977.

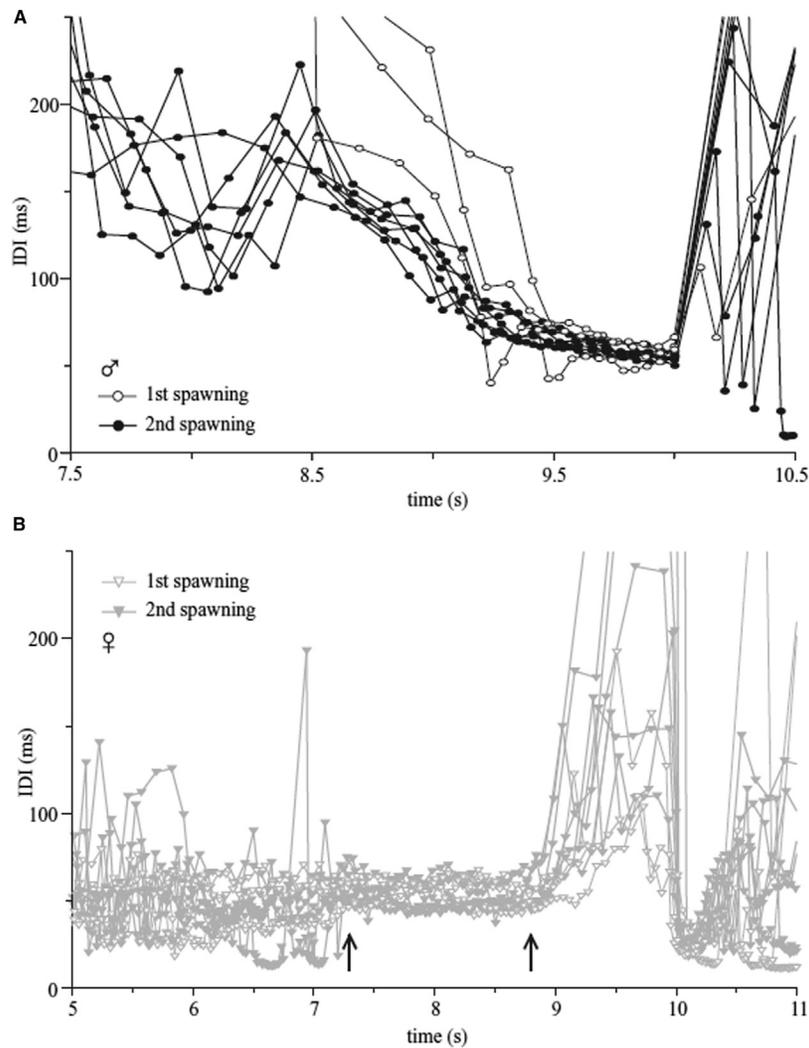


Figure 9 The simultaneous EOD patterns recorded from a spawning pair of *Marcusenius pongolensis* when both were in a parallel position, side by side. Data recorded from the same pair during two spawning nights. (A) Male EOD activity. Seven superimposed IDI patterns from the second spawning and three from the first spawning aligned such that the last EOD in a series of decreasing IDIs occurred at 10 s (when the spawning bout ended). Note the stereotyped IDI patterns from 8.5 s to 10 s. (B) Female EOD activity. Seven superimposed IDI patterns from the second spawning and three from the first spawning showing the simultaneous activity relative to (A). IDI, inter-discharge intervals. Each point is one interval. Mean female interval between arrows, 53.7 ± 5.1 ms. From Werneyer, M., Kramer, B., 2005. Electric signalling and reproductive behaviour in a mormyrid fish, the bulldog *Marcusenius macrolepidotus* (South African form). *J. Ethol.* 23, 113–125.

playback pulse duration. A familiar neighbor's EOD of a specified EOD duration evoked weaker responses than expected for a 'stranger' EOD of the same duration. The attack rate receded when a 'familiar' EOD pulse of the same duration, one of a previous tank neighbor, was played back (Hanika and Kramer, 2005). These results are compatible with the 'dear enemy' hypothesis (Fisher, 1958), and indicate sexual selection by male competition. When an unfamiliar male replaced a familiar tank mate, the experimental subject increased both its attack rate and EOD duration. Depending on the individual male, EOD duration increased from 28% to 5.7fold (from 356 μ s to an exceptional 2029 μ s). This effect was reversible and reproducible (Hanika and Kramer, 2008). A similar, short-lived increase of male EOD duration occurred just before and during courtship and spawning in two males in captivity (Werneyer and Kramer, 2005; Kramer et al., 2007). Therefore, in *M. pongolensis* sexual selection of two kinds must have shaped this species' reproductive behavior: intrasexual selection between male competitors, selecting for long EODs, and intersexual selection by females, also selecting for males with long EODs. Extra-long EODs, that is, the component that goes on top of the male 'status badge' in *M. pongolensis*, occur at a short time of actual reproduction only. The receding to the lower values before reproduction as soon as possible may have been selected for under predator pressure. *M. pongolensis* bulldogs do not form part of the catfishes' diet in their natural habitat (Bruton, 1979).

Direct evidence supports intersexual selection (female choice) in *M. pongolensis*: female ($N = 7$ of 8) attraction scores for playback male EODs of varying length increased with pulse length in linear fashion, from the female average pulse length of 320 μ s to 716 μ s (Machnik and Kramer, 2008a). However, long male pulses were attractive to females only when driven by an 'acceptable', nocturnally active (foraging), non-aggressive IDI pattern. The preference vanished when an IDI pattern of a diurnally resting or nocturnally aggressive male was used for playback (Machnik and Kramer, 2008b). (Fig. 8).

7.15.10 Courtship and Spawning

There are only very few records of electrocommunication during reproduction in mormyrids: for *P. adspersus* (Bratton and Kramer, 1989), for *Marcusenius senegalensis* (Scheffel and Kramer, 1997), for *M. pongolensis* (Wernerer and Kramer, 2005), for the *P. castelnaui*/*P. marianne* sibling species (Baier and Kramer, 2007), and for *Brienomyrus brachyistius* (Wong and Hopkins, 2007). To disentangle the EODs of unrestricted, freely moving fish of the same species, of constantly varying amplitude and polarity, is difficult and time-consuming. It is difficult to get most of these tropical or subtropical species to breed in the laboratory in the first place.

A brief description for *M. pongolensis* is given here. Overt reproductive behavior in *M. pongolensis* was much less elaborate than that observed in *P. adspersus* or the *P. castelnaui*/*P. marianne* pair of sibling species. Without 'superfluous' preliminaries such as courtship, the female joined the male's (aquarium) territory where the male had not constructed a nest, in contrast to the *Pollimyrus* species. Also in contrast to these, the bulldog male showed very little aggression toward the intruding female. The female spawned repeatedly in short bouts, as did the other mormyrid species (up to three spawning bouts per minute, fractional spawning). She spawned near the male's hiding place with the male in parallel position to her, and before leaving the site after each bout, scattered the eggs by vigorous tail flips that also displaced the male laterally. When she returned to the male's hiding place only moments later, she produced the next couple of eggs (about 25–60 eggs per bout). Both fish generated specific IDI patterns during spawning bouts. The female marked its sudden escape after each spawning bout by a sharp increase in discharge rate. The spawning ended after 45 min. Neither parent provided parental care; on the contrary, the female ate the eggs as occurs often in captive fish (Wernerer and Kramer, 2005) (Fig. 10).9.

Acoustic sound production and vocal communication are an integral component of social interactions and spawning behaviors, and present in every mormyrid species so far tested. It was found in *G. petersii* (Rigley and Marshall, 1973), *P. isidori* and *P. adspersus* (Crawford et al., 1986; Bratton and Kramer, 1989). The fishes of the Upper Zambezi, Okavango and eastern South Africa were not

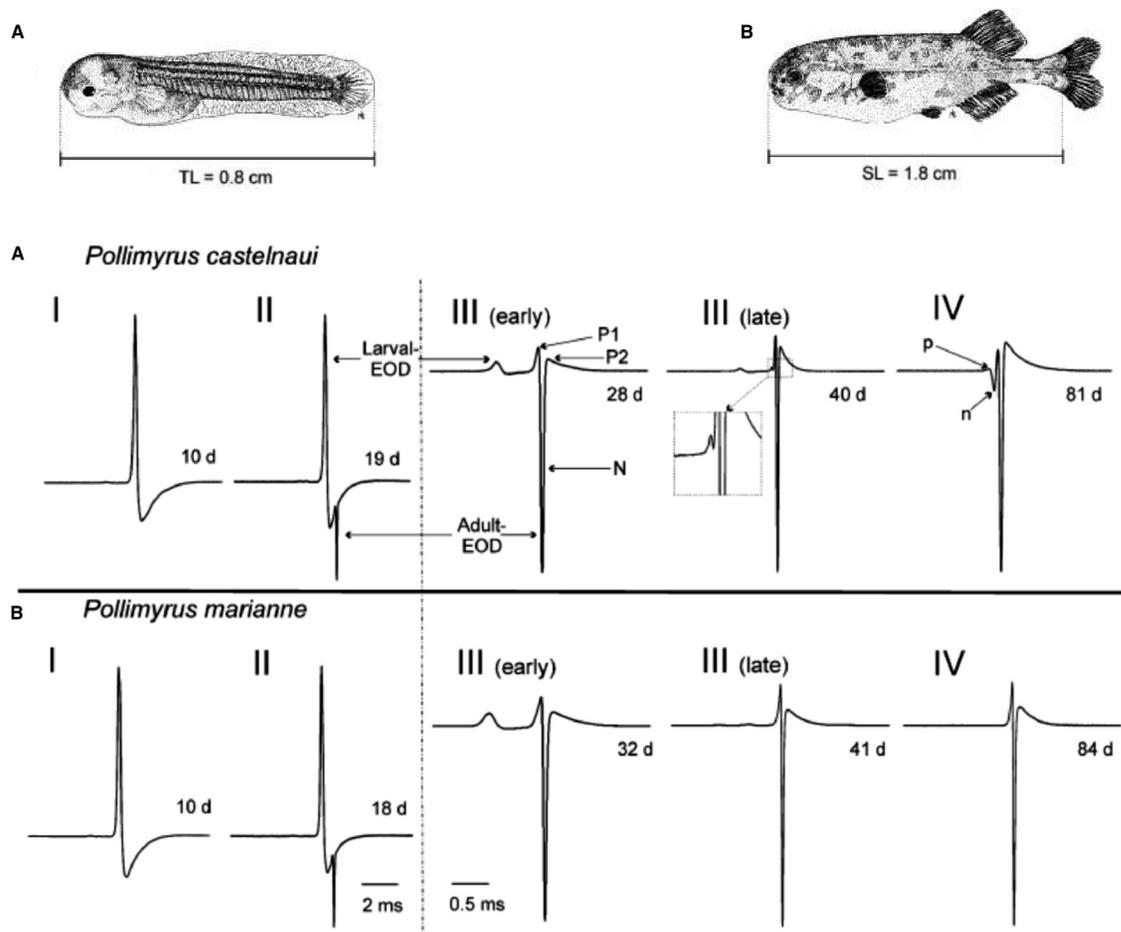


Figure 10 Ontogeny in *Pollimyrus castelnaui*. **Top panel**, Larvae 10 days and 3 months old, respectively. (A) EOD recordings for *P. castelnaui*. (B) for *P. marianne*. Note that through developmental stages I – III the two species' EODs are virtually identical, except for early in stage III, an additional excitation in the P1 phase of *P. castelnaui* emerges, precursor of what distinguishes its future adult EOD from that of *P. marianne*'s EOD. The resulting adult EODs differ between the two species in the amplitude of the positive peaks: P1 high and P2 low in *P. marianne*, vice versa for *P. castelnaui*. From Baier, B., Lamml, M., Kramer, B., 2006. Ontogeny of the electric organ discharge in two parapatric species of the dwarf stonebasher, *Pollimyrus castelnaui* and *P. marianne* (mormyridae, teleostei). *Acta Zool. (Stockh.)* 87, 209–214, modified.

less 'weakly electric and strongly acoustic (Crawford et al., 1997)', such as the *Pollimyrus castelnaui/marianne* trio (Lamml and Kramer, 2005, 2006), *Petrocephalus longicapitis* (Lamml and Kramer, 2008) and *M. macrolepidotus*, *M. altisambesi* and *M. pongolensis* (Lamml and Kramer, 2007).

7.15.11 Larval EOD Development

M. pongolensis eggs from another spawning event were allowed to develop into adults. The very early development of *M. pongolensis* larvae was similar to that described for *P. adspersus* (Kirschbaum, 1975; Kirschbaum and Westby, 1975; Postner and Kramer, 1995), and for *P. castelnaui/marianne* (Baier et al., 2006). Larvae hatch on day 4 (depending on temperature) and display a larval EOD similar to that of *P. adspersus* on day 8. Another three days later, the larval discharge has stabilized to the form that is seen throughout its existence for about 60 days (Westby and Kirschbaum, 1977). The larval EOD is a monopolar, head-positive pulse of 330 μ s duration, followed by a very weak and long negative potential. The total duration of the EOD is about 1.9 ms. Beginning at around day 43, a miniature, three-phasic adult EOD emerges which is locked to the larval EOD at a delay of about 0.7 ms (not so in *M. pongolensis*, see below). As the adult EOD increases in strength each day, the larval EOD weakens and finally vanishes after 20 days of existence of the double discharge. This scenario is identical to the one seen in *P. castelnaui* and *P. marianne* who followed a similar EOD development (Baier et al., 2006). In *P. adspersus*, a large and bulky larval organ located in the trunk generates the larval discharge, and degenerates when the adult electric organ located in the caudal peduncle develops and eventually takes over with its adult EOD (Denizot et al., 1978, 1982). A similar ontogeny with a sequence of two serially arranged electric organs is, therefore, assumed for *P. castelnaui/P. marianne/P. cuandoensis*.

As reported above, the EODs of *P. castelnaui* are pentaphasic, of *P. marianne* triphasic. This comes about because only in *P. castelnaui*'s adult EOD, which emerged already at around day 20 in both species, a third excitation developed at around day 40 (Baier et al., 2006). The third excitation, when modeled as a Gaussian, gave a near-perfect fit of the pentaphasic adult waveform of *P. castelnaui*. In certain individuals of *P. marianne*'s EOD, that remained essentially triphasic throughout life, small indentations or slope changes in the P phase were also modeled successfully using the third excitation (or Gaussian; Markowski et al., 2008). These small deviations from an ideally triphasic waveform are seen as historical remnants, reflecting the phylogeny of *P. marianne* as derived from *P. castelnaui*. (Fig. 10).

Whereas the earliest larval EOD development in *M. pongolensis* corresponded to that described in the *Pollimyrus* species, the subsequent development to the adult EOD was different in *M. pongolensis* where there was no double discharge. The primordial monopolar, long larval discharge developed into the much shorter, bipolar adult discharge by gradual transformation in *M. pongolensis*. Beginning at around day 40 and 17 mm length, the larval head-negative after-potential began to shorten and continually increase in (negative) strength, until the adult EOD waveform was reached at around 60 days of age and 30 mm length (Werneker and Kramer, 2006). Because in *M. pongolensis*' larval development there was no double pulse, there is no evidence for two separate, serially arranged electric organs as in the larvae of the *Pollimyrus* species. In the *Pollimyrus* species, paternal care seems to stop with the advent of the adult EOD, when the larvae are aggressively chased away). In *M. pongolensis* there was no parental care. The southern African members of the genera *Pollimyrus* and *Marcusenius* appear to be only distantly related within the Mormyridae (suggested by mtDNA comparison, Kramer and Wink, 2013). v (Fig. 11).

7.15.12 Larval Electro-Sensory and -Motor Development

P. adspersus larvae 8–10 days old discharged at a very low rate of 2.4/s which gradually rose to an adult resting value of 8/s between days 21–25. From the beginning, the statistical distribution, or histogram, of IDIs was broad and had three peaks or 'preferred' IDIs, and was fairly similar to the adult one (Kramer and Postner, 1997; for adult data, see Kramer, 1978). From about day 40 on, the three peaks were more distinct and the agreement among the larvae as to their position similar to that found in adults. Already from day 11 on, SIDs accompanied swimming bouts like in adults. Starting around days 35–40, similar EOD activity accompanied bouts of hovering. From day 11 on, larvae responded to electrical stimuli by Preferred Latency Responses of a mean 19–20 ms, which shortened to a mean 12 ms on day 31, hence, were within the range for adults (see Kramer, 1978; Lücker and Kramer, 1981). The motor system of the larvae appeared mature from day 40 on, that is, before the onset of the adult EOD.

We determined electrosensory thresholds by using trains of 10 pulses at 5/s that evoked spontaneous EOD-stop responses. The stimulus pulses varied in pulse duration, intensity and waveform, and were generated by a function generator: a bipolar single-cycle sine wave pulse (0°–360°), a monopolar, single-cycle sine wave pulse (90°–450°), and a monopolar square wave pulse. Larvae 10–15 days old showed V- or U-shaped tuning curves to the two sine wave pulses, and no tuning to the square wave pulse. The monopolar sine wave pulse was the most effective stimulus, with a V-shaped tuning curve and a lowest threshold value of 10.9 μ V_{p-p}/cm at 1 ms pulse duration. This pulse corresponded closely to the larval EOD which also had its spectral peak close to 1 kHz. The larval receptor system was well tuned to the larval EOD, and not to the adult EOD the spectral peaks of which were between 8 and 25 kHz. In addition to conventional spectral tuning, the electrosensory system of the larvae was tuned to a waveform similar to its own larval pulse.

Larvae 54–60 days old proved more sensitive than the younger larvae by at least 10 dB, with a broad U-shaped tuning curve. Monopolar, not bipolar, single-cycle sine wave pulses were (again) the most effective stimuli also in these older larvae, with pulse durations between 0.1 and 1 ms. These older larvae were well adapted to receive adult EODs even though they still had a larval EOD (that is, before the advent of the miniature adult EOD). Therefore, the increase in sensitivity and broader tuning was not brought

about by entrainment. The system remained tuned to a monopolar waveform, albeit to a negative one, as the adult EOD of *P. adspersus* is a mainly head-negative pulse (Kramer and Postner, 1997).

7.15.13 Sympatric Specializations in Ecology and Behavior

Next to nothing was known on questions such as: are sympatric species specialized among each other regarding their ecological niches; is there evidence for interspecific communication, for competition, for dominance hierarchies and/or cooperation? Because of numerous technical difficulties in the wild, not least working in the dark, such studies need to be done in large aquaria where the fish can range freely and the operator create conditions conducive to the study of their behavior. 'Freely ranging' means a specimen's EODs, as seen by the fixed aquarium electrodes, will constantly change in amplitude and polarity, hence, are difficult to track. The present study managed to separate the EODs of up to five specimens discharging simultaneously; very likely, a world record.

This section is based on fish of three sympatric species that were caught on August 9, 1994 from the same location on the Upper Zambezi River at Katima Mulilo, East Caprivi, Namibia. We rushed twelve specimens of long-head churchill (*P. longicapitis*), seven specimens of Cubango stonebasher (*Cyphomyrus cubangoensis*) and seven Szabo's stonebasher (*Hippoptamyrus szaboi*) to our laboratory within 2 days. Various combinations of specimens of all three species shared three large tanks, which were equipped with many hiding places in the form of rocks, crevices and caves, drift wood, the submerged 'jungle' of roots of live plants (*Philodendron*), sand banks, a water fall and programmed rain. The main aquarium had a capacity of 3000 L ($3 \times 1 \times 1 \text{ m}^3$), the others 700 L. Water temperature and conductivity were $25 \pm 0.5^\circ\text{C}$ and 100–200 $\mu\text{S}/\text{cm}$, respectively. Water was partially exchanged once every other week. The L:D cycle was 12:12 h. In an attempt to simulate the Namibian summer season, an L:D cycle of 14:10 h was also used. We aimed to create conditions as similar as possible to the fishes' home river.

The largest tank held eight churchills, two Cubango stonebasher and one Szabo's stonebasher. We observed and filmed the fishes' nighttime behavior in total darkness under infrared illumination and recorded the electrical activity by a multi-electrode arrangement devised to capture every single EOD. A semi-automated computer system helped to analyze the reams of data collected (Scheffel, 1998; Scheffel and Kramer, 2000, 2006). The three species' EOD waveforms were characteristically different.

The Szabo's stonebasher were intolerant of each other and had to be kept separately (one per tank). Szabo's stonebasher was the dominant fish in each aquarium. On its nocturnal foraging tours, it was never attacked by any other fish and could go anywhere it liked.

Next in hierarchy were the churchills that avoided Szabo's stonebasher whenever it came near. The churchills held permanent individual hiding places and mosaic-like territories with fixed boundaries they defended against conspecifics in the first place. Trespassing conspecifics employed a stealth tactic: switching off their discharge. No sooner had the territory owner detected the perpetrator it charged viciously. In its own territory a churchill was dominant over all other churchills. The churchills were less nocturnal than Szabo's stonebasher and were sometimes quite active during daylight. When there was little food they sometimes formed groups or schools that moved together with little aggression (Fig. 11). 12).

The shiest, strictly nocturnal fish were the Cubango stonebasher. Even the LED light of an electronic apparatus (facing away from the tank) made them immediately return and seek cover. They always moved in a group, with one individual leading and emitting a regularized, almost steady state IDI pattern with short IDIs that were slowly rising in length but shortening again at the next turn. In a pair of two, the following individual generated a variable pattern of low rate with many 'Preferred Latencies' of ca. 12 ms to the EODs of the leading fish; an observation that had never before been seen in this species and may shed light on the function of this mysterious behavior. (Fig. 13).

Cubango stonebasher were subdominant to the two other species with a remarkable difference. The churchills chased them away from almost everywhere; Szabo's stonebasher, however, either ignored them, that is, tolerated their presence even when close, or mixed and moved along with them. It was not always possible to decide whether Szabo's stonebasher was leading or following the group of Cubango stonebasher. The high degree of aggression the Cubango stonebasher received from the churchills apparently made them seek the company of Szabo's stonebasher on its foraging sprees. Sometimes, when circling around Szabo's stonebasher it appeared they were 'inviting' him to mix with them. Therefore, we believe we did not only see conflict and competition among the three species but also instances of cooperation.

7.15.14 Some Notes on Mormyrid Taxonomy as Relevant to the Present Studies

7.15.14.1 Marcusenius Gill, 1862

With about 47 species, *Marcusenius* is the largest genus in the mormyrid family, and apparently still growing. For example, *M. macrolepidotus* of southern Africa, the 'bulldog fish', so-called because of its prominent lower chin appendage, was recognized to represent eleven allopatric species differing in anatomy, genetics and behavior. The type locality of *M. macrolepidotus* is Tete on the Lower Zambezi. The bulldog fish thus defined, traditionally ranged in southern, West, Central and East Africa – an enormous area including many different, transcontinental catchments. The comparison of allopatric populations in South Africa, Namibia, Botswana and further to the north, east and west resulted in two resurrected species, and eight new species (Kramer et al., 2007; Maake et al., 2014). All members so far studied in southern, West, Central and East Africa generate similar, bipolar EOD waveforms. The EODs differ quantitatively in waveform variables and in the degree the male EOD resembles (or does not resemble) the female and juvenile waveform (Kramer, 1997). For example, in *M. ussheri* (Côte d'Ivoire, West Africa) and *M. altisambesi* (Upper Zambezi

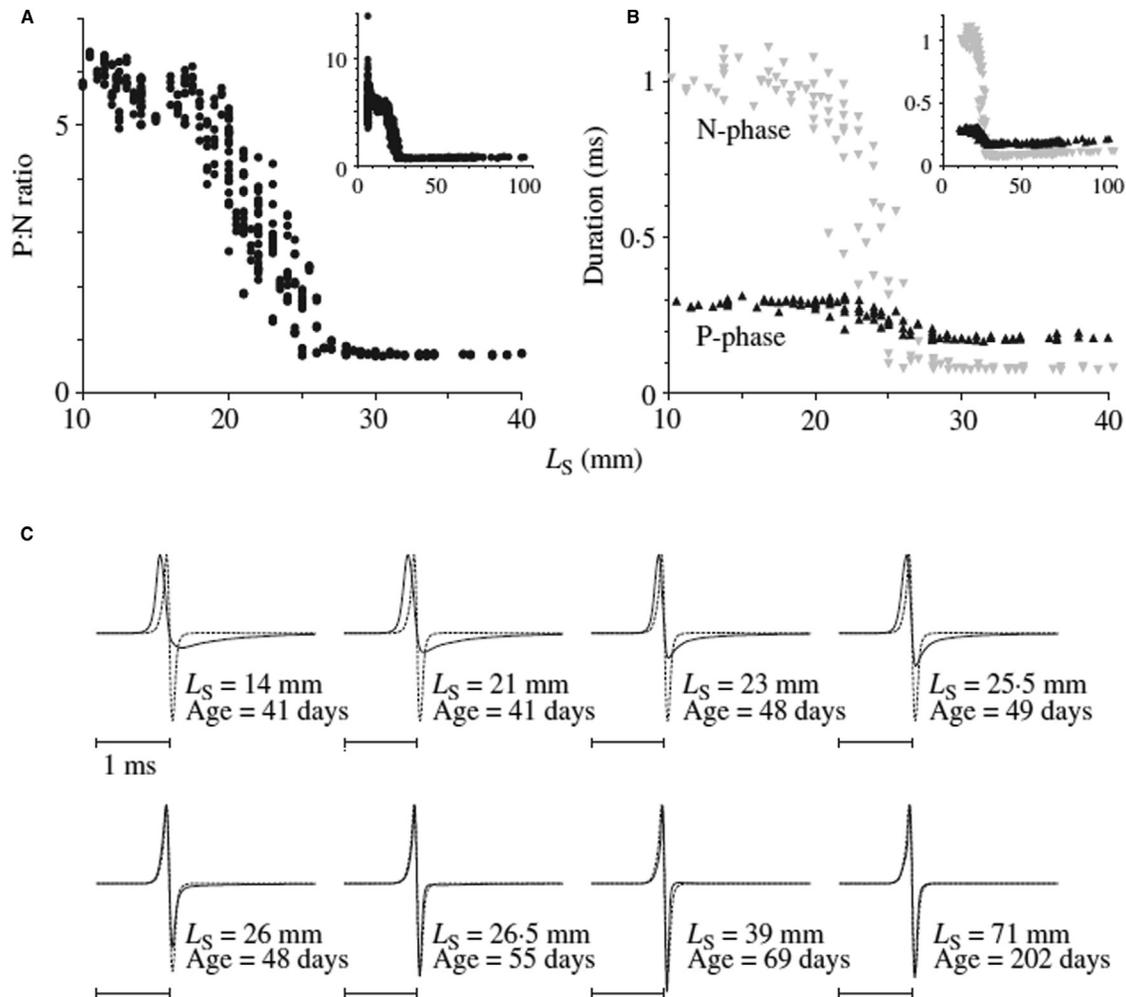


Figure 11 Development of EOD in *Marcusenius pongolensis*. (A) Development of the P:N amplitude ratio with growth. (B) Development of P duration and N duration with growth (water temperature 24°C). The insets show all data, whereas the main figures show the period of strongest change (from 17 to 27 mm L_S , standard length). (C) Examples of waveforms to illustrate the gradual transition from larval to adult EOD. Individual larval EODs are normalized to same P amplitude. The *dotted line* is a superimposed adult female EOD. From Wernerer, M., Kramer, B., 2006. Ontogenetic development of electric organ discharges in a mormyrid fish, the bulldog *Marcusenius macrolepidotus* (South African form). *J. Fish. Biol.* 69, 1–12.

and Okavango) the male EOD is about 10 times the length of female EODs, at least in the reproductive season. In contrast, there does not seem to be any sex difference in, for example, the Ivorian *M. furcidens* (Kramer, 2013a,b,c). This conclusion may be incorrect with better knowledge of the life history of the species involved. Besides *M. ussheri* and *M. furcidens*, two more *Marcusenius* species inhabit the Côte d'Ivoire: *M. senegalensis* and *M. gracilis*.

The presence of four *Marcusenius* species in Côte d'Ivoire (Kramer, 2013a,b,c) and three in South Africa (*M. pongolensis*, *M. caudisquamatus* and *M. krameri*), all with only minor differences in a similar EOD waveform (Kramer et al., 2016a,b), asks for an explanation. An understanding of the species packing in Côte d'Ivoire and South Africa depends on a better knowledge of river evolution. Furthermore, the last major revision of the Mormyridae by Taverne (1971, 1972) has left untouched the definition of *Marcusenius*. It is so wide that it may include some members of other genera (John P. Sullivan, personal communication).

7.15.14.2 *Hippopotamyrus* Pappenheim, 1906

This genus includes species with both small and drastic EOD waveform differences among some of its members. Their EOD waveforms include head-positive, monopolar ones that are differentiated by pulse duration and weak head-negative after-potentials of long duration and various waveforms (such as *H. szaboi*), and a pentaphasic one in *H. longilateralis* from the Cunene river on the Namibian/Angolan border (Kramer and Swartz, 2010) (Fig. 12–14).

The lack of a precise type locality precludes a revision of the *Hippopotamyrus ansorgii* species complex. Its type locality is given as 'Angola. Between Benguella and Bihé'. This area the size of Ireland is the catchment area of at least three large Angolan rivers, the Cunene, Cuanza and Okavango. The Cunene is perhaps less likely since the discovery of *H. longilateralis* in this river.

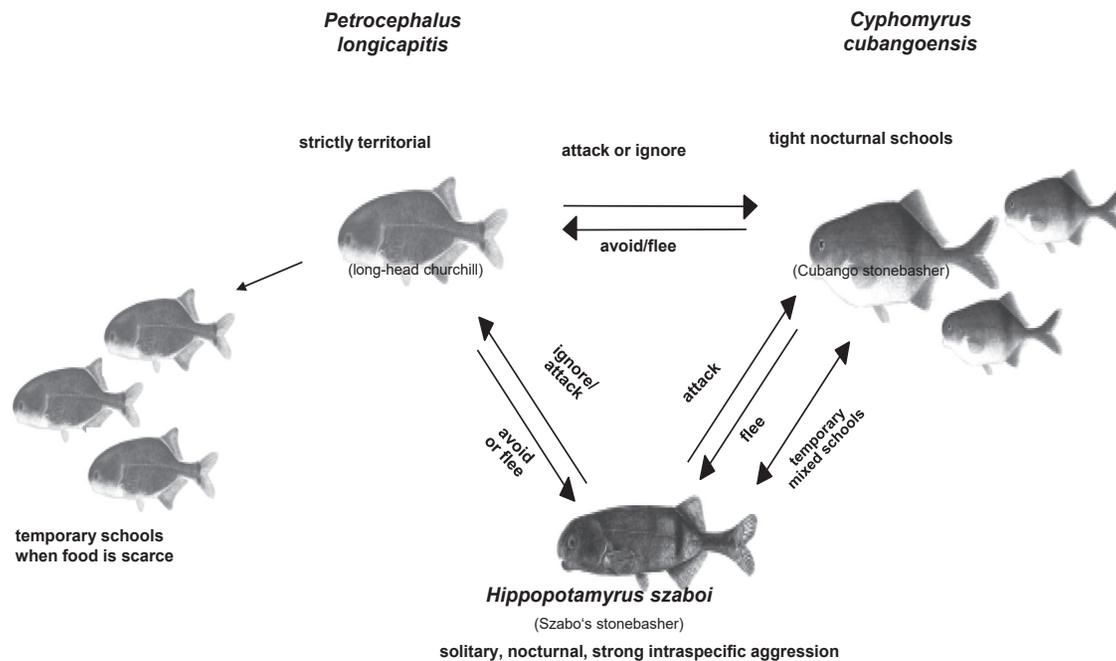


Figure 12 Dominance hierarchy among three syntopic mormyrids from the Upper Zambezi River. Szabo's stonebasher, *Hippopotamyrus szaboi*, is highest in hierarchy, and generates a monopolar D.C. pulse. Then follow the long-head churchill, *Petrocephalus longicapitis*, which is dominant over the Cubango stonebasher, *Cyphomyrus cubangoensis*. Both display EODs in the high frequency spectral range with very little, or no, D.C. From Scheffel, A., Kramer, B., 2000. Electric signals in the social behaviour of sympatric elephantfish (mormyridae, teleostei) from the upper Zambezi river. *Naturwissenschaften* 87, 142–147, modified. Fish pictures from Skelton, P.H., 1993. *A Complete Guide to the Freshwater Fishes of Southern Africa*. Southern Book Publishers, Halfway House (South Africa).

7.15.14.3 *Mormyrus* Linnaeus, 1758

Mormyrus species are big and solitary fish, they are never caught in a group. A baited trap was often effective. As far as is known, *Mormyrus* species have a characteristic bipolar, long discharge, usually of strong amplitude and long N phase duration across most of tropical and subtropical Africa, that may be felt as mild discomfort when handling the fish (for example, *Mormyrus rume*). This property may have earned a form of *Mormyrus*, which was present in the lower reaches of the Nile, divine status in ancient Egypt where it was represented on ancient murals and as a small figurine with a crown. *Mormyrus hasselquistii*, a massive fish of the Comoé River in Côte d'Ivoire, has no trumpet snout like most *Mormyrus* species. It generated a discharge so strong that it was recorded in neighboring aquaria several meters away, and caused pain when handled. As a surprise, *Mormyrus tenuirostris* from Kenya's Tana River had a purely monophasic, head-positive DC discharge of very short duration (less than 400 μ s, compared to the biphasic, longest EOD of almost 7000 μ s generated by *Mormyrus lacerda* of Upper Zambezi-Okavango-Cunene distribution in southern Africa. The EODs of male *M. rume* were almost twice as long as those of females. The Côte d'Ivoire alone holds three *Mormyrus* species in its Bandama and Comoé rivers (Kramer, 2013a,b,c).

7.15.14.4 *Mormyrops* Müller, 1843

Certain *Mormyrops* species attain a length of up to 1.5 m. *Mormyrops anguilloides* is widespread in Africa, but not present in the southern and western Upper Zambezi, Okavango and Cunene rivers. We studied specimens from Côte d'Ivoire and the Middle and Lower Zambezi. The EODs of *M. anguilloides* were biphasic (Comoé River) or tetraphasic (Bandama River, Middle and Lower Zambezi River). Specimens from the Comoé and Bandama rivers in Côte d'Ivoire were differentiated both morphologically and in EOD waveform and duration, but a revision based on the comparison of allopatric populations is precluded by the loss of Linné's holotype, a type locality no more specific than 'habitat in Nilo' (lives in the Nile), and by the absence of a neotype. *M. breviceps* generates EODs of long duration that start with an unusual head-negative potential (Kramer, 2013c). Males generated longer EODs than females in both species. *M. anguilloides* is a piscivorous predator reported to hunt in groups (Arnegard and Carlson, 2005).

7.15.14.5 *Petrocephalus* Marcusen, 1854

The type locality of *P. catostoma* is the Rovuma River that arises east of Lake Malawi, and discharges into the Indian Ocean. By several synonymizations in the second half of the 20th century, *P. catostoma* ranged from Lake Victoria in Uganda to the Pongola River in

South Africa, and from the Congo and Cunene rivers discharging into the Atlantic to the Indian Ocean. For some of these synonymizations no reasons were given. Similar to the situation in '*M. macrolepidotus*', a comparison of allopatric populations revealed that '*P. catostoma*' was a catch-all species term that contained not only six nominal species or subspecies that had to be reinstated or elevated to species rank. It also contained seven unrecognized new species (Kramer and Van der Bank, 2000; Kramer et al., 2012). The field-recorded EODs of the southern African species all resembled each other in their triphasic waveform; however, most proved differentiated when waveform variables were compared quantitatively. Morphological, electrical and genetic data all contributed to the taxonomic decisions.

7.15.14.6 *Pollimyrus Taverne, 1971*

P. castelnaui (Boulenger, 1911) used to be the only *Pollimyrus* species present in whole southern Africa, whereas there are 16 valid species in West, Central and Eastern Africa listed in Eschmeyer's Catalog of fishes (2020). A comparison of allopatric *P. castelnaui* populations from the Okavango, Zambezi and Kwando rivers revealed differentiation on the species level. *P. castelnaui* inhabits the Okavango, *P. marianne* the Upper Zambezi, and *P. cuandoensis* the Kwando River (Kramer et al. 2003, 2014). Pending more comparisons of allopatric populations, *P. castelnaui*'s distribution is still given as a huge 'southern Africa' in the Catalog. Crawford (personal communication, 1996, based on Bigorne, 1990) in his early studies misidentified some of his *P. adpersus* specimens, obtained through the aquarium trade, as the very similar *P. isidoridi*. We believe the same is also true for our own early '*P. isidoridi*' studies.

7.15.14.7 *Cyphomyrus Myers, 1960*

Based on osteological characters, Taverne (1971) synonymized *Cyphomyrus* with *Hippopotamyrus* Pappenheim, 1906 by priority. We suggested reinstating *Cyphomyrus* based on morphological and molecular-genetic comparisons (Van der Bank and Kramer, 1996; Kramer and Van der Bank, 2011), a suggestion supported by further studies involving more species (Kramer et al., 2004; Kramer and Swartz, 2010). *Cyphomyrus* includes *Cyphomyrus discorhynchus* of Lower and Middle Zambezi distribution, with Tete as the type locality. Over the length of the Lower and Middle Zambezi, *C. discorhynchus* showed a marked degree of subspecific, geographical differentiation in anatomy in form of a cline. There was a more pronounced degree of differentiation, including EODs, in specimens caught in the Zambezi upstream of the Victoria Falls, in the Chobe, Kwando and Okavango. We therefore reinstated *C. cubangoensis* that had erroneously been synonymized with *C. discorhynchus* (Kramer and Van der Bank, 2011). The type locality of *C. cubangoensis* is near Kuvango on the upper Cubango River in Angola, and its distribution is the Upper Zambezi in its Namibian part (former Caprivi) down to the Victoria Falls, the Chobe, Kwando and Okavango including the delta.

Cyphomyrus includes four more species in Central Africa, the Nile system and North-East Africa.

7.15.15 Signal Waveform Analysis in a Wave Gymnotiform

Gymnarchus niloticus is the only electric fish among the Osteoglossiformes endemic to Africa that generates a wave EOD, a continuous signal of constant frequency, whereas all Mormyridae generate pulse EODs, which are short compared to longer and widely variable intervals. This is in contrast to the South American Gymnotiformes or electric knifefishes, the majority of which generate wave EODs of great frequency stability. For these fish, their wave EOD (compared to a pulse EOD) presents a problem for electrocommunication: masking by their own strong EOD. Since a wave EOD is on all the time, time-sharing as seen in pulse fish is not possible. None withstanding, wave fish are as sensitive regarding frequency and intensity discrimination as pulse fish (Kramer and Kaunzinger, 1991). The absolute threshold for an external threshold is similar to that of pulse fish (for a review, see Kramer, 1996). Paradoxically, a *Sternopygus macrurus*, after having been electrically silenced by surgery, experienced a drastic sensitivity loss by 30 dB (Fleishman et al., 1992). Even though in this fish, *Sternopygus*' own strong EOD no longer masked a weak external signal, the fish was 'electrically hard of hearing'. Stimulating an intact, non-operated *Sternopygus* or *Eigenmannia virescens* with a sine wave of exactly EOD frequency yielded a similar sensitivity loss; for *Eigenmannia*, also any one of the higher harmonics of the fundamental frequency had the same effect (Fleishman et al., 1992; Kaunzinger and Kramer, 1995). This shows the fish need a minimum frequency difference between signal and EOD in order to assess the stimulus, a condition known as beating. A fish does not sense the external signal as it occurs (as pulse fish do), but the signal riding on a fish's own strong wave EOD. Without one's own EOD there is no sensing of what the neighbor says.

Eigenmannia males, females and juveniles differ in EOD waveform. In the EOD of each, the fundamental frequency f_1 is strongest, and a few higher harmonics decline rapidly in intensity. Male EODs are strongest in harmonic content, juvenile EODs weakest, that is, closest to a sine wave (Kramer, 1985). Trained food-rewarded experimental specimens discriminated playback female from male EODs, also sine waves from sawtooth waves (the latter are particularly rich in harmonics; Kramer and Zupanc, 1986). Naïve, untrained specimens of both sexes preferred to associate with dipole decoys generating female rather than male EODs (Kramer and Otto, 1988) (Fig. 13-15).

We studied the question of whether the fish discriminated the signals by spectral analysis of the harmonic distortion (that is, the overtone content which defines the timbre of an acoustic signal), rather than by temporal waveform analysis of the beating signal.

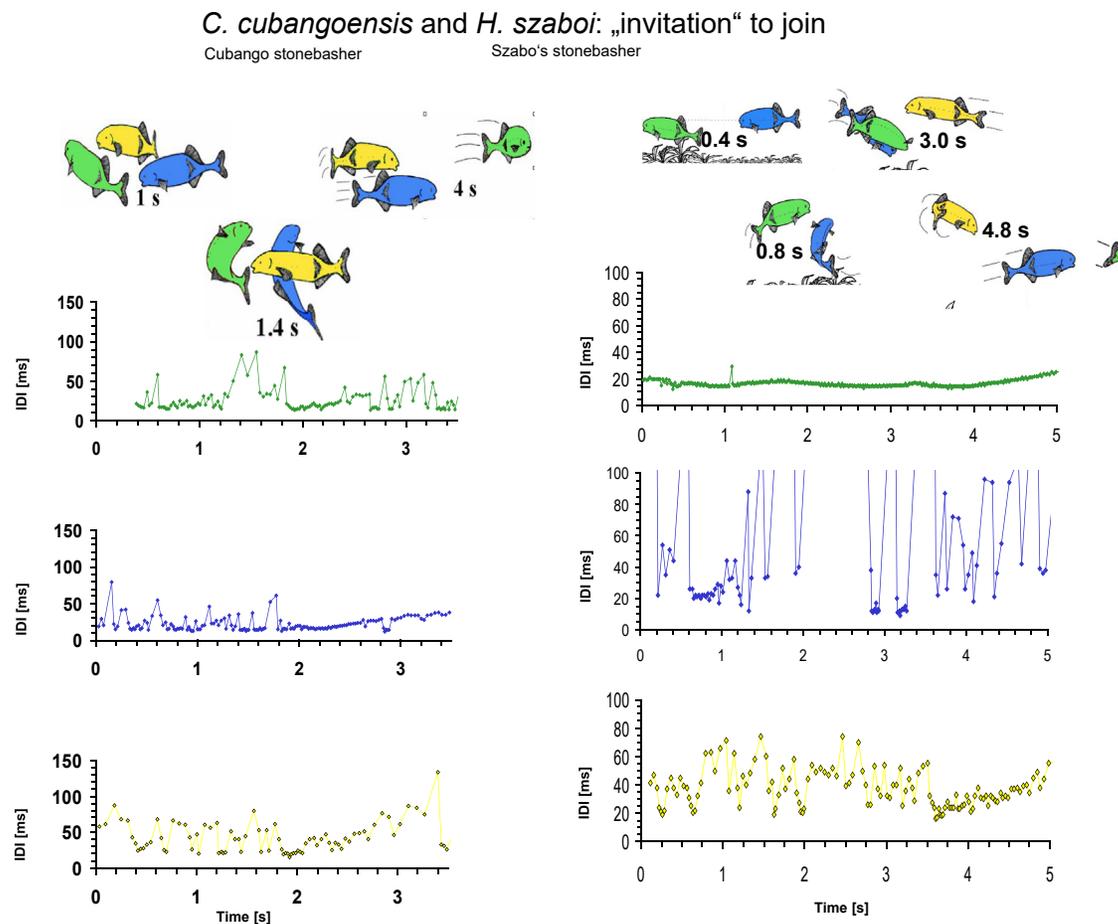


Figure 13 Nighttime interaction between two Cubango stonebasher, *Cyphomyrus cubangoensis*, and a dominant Szabo's stonebasher, *Hippopotamyrus szaboi*. Diagrams represent inter-discharge intervals (IDI) over time, separately for each fish. *Left panels*, episode where a pair of Cubango's stonebasher (blue and green) circled around the Szabo's stonebasher (yellow), as if inviting him to join. Then the Cubango stonebasher resumed swimming further on with the Szabo's stonebasher following. This was initiated with the Cubango's stonebasher displaying an IDI pattern else only seen intraspecifically in leading fish, of an almost constant discharge rate that rose only slowly (left panels, around 2 s). *Right panel*, similar episode, with the green Cubango's stonebasher leading, and both its conspecific and (last) Szabo's stonebasher following. Both following fish displayed an irregular EOD pattern of low rate. These peaceful interactions contrasted markedly from those in which the long-head churchill, *Petrocephalus longicapitis*, was involved. From Scheffel, A., Kramer, B., 2006. Intra- and interspecific electrocommunication among sympatric mormyrids in the upper Zambezi river. In: Ladich, F., Collin, S.P., Moller, P., Kapoor, B.G. (Eds.), *Communication in Fishes*. Science Publishers Inc., Enfield, New Hampshire, USA, pp. 733–751, modified.

To tackle this question, we generated signals consisting of a fundamental sine wave f_1 and added its first harmonic, f_2 (of two times the frequency of f_1 , and at -3 dB relative to f_1 , like in an *Eigenmannia* male EOD). One stimulus, termed signal ϕ_0 , had the positive peaks coinciding, and was arbitrarily termed '0° phase difference'. The S—, termed signal ϕ_{90} , had its f_2 a quarter of a cycle (90°) delayed with respect to f_1 . Both stimuli were identical in terms of Fourier amplitude spectra, but different in waveform. A human fails to distinguish the two signals played by a loudspeaker (Fig. 14): 16).

None of the trained, food-rewarded experimental subjects failed to discriminate the two stimuli played back by dipole decoys (Kramer and Otto, 1991). These experiments were made at frequency differences fish-EOD of 50 or 30 Hz; consequently, the fish analyzed beats of these frequencies, and the mechanism was a temporal one. The temporal properties of beats and the sensory coding, central nervous and motor responses have been studied extensively by Szabo (1967), Bullock et al. (1972a,b), Scheich and Bullock (1974), Scheich (1977a,b), Heiligenberg (1991) and others. However, how exactly the fish analyze beats has remained a matter of controversy. Our own results regarding how fish detect frequency and intensity (Kauzinger and Kramer, 1996) are summarized in a sensory model based on time-marking T-electroreceptor afferences (Kramer & Kauzinger in Kramer, 1996, for a review see Kramer, 1999a). The sensory mechanism we propose is compatible with the above results in trained and naive fish, and the sensory physiology as established by Scheich, Bullock, Szabo and others (for a review, see Zakon, 1988).

Our sensory model predicts that, for successful waveform detection as demonstrated above, a minimum frequency difference is required between the stimulus and the EOD. At a difference that is too small, a fish should show a Jamming Avoidance Response

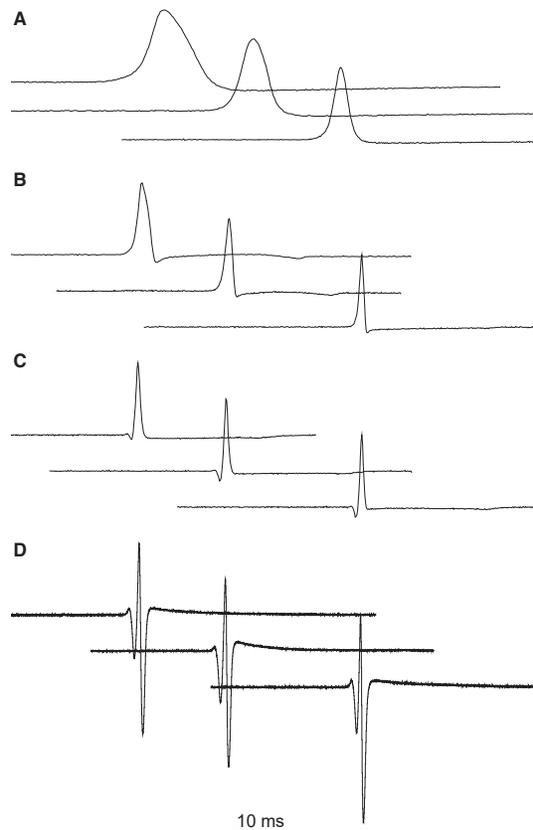


Figure 14 EODs of members of the *Hippoptamyrus ansorgii* species complex. (A) *H. szaboi* (Upper Zambezi River); (D) *H. longilateralis* (Kunene River); (B) one form of *H. ansorgii* (Upper Zambezi River); (C) another form of *H. ansorgii* (Kwando River). All of these were '*H. ansorgii*' until recently, or still are. Two of these four forms were recognized as new species on morphological grounds, but the other two, and surely other allopatric forms as well, cannot be identified because of the poorly described type locality of *H. ansorgii*. The three EODs per form or species show the longest, the shortest, and a pulse of middle length, recorded in the field (Kramer and Swartz, 2010).

(JAR, Watanabe and Takeda, 1963). A JAR is a frequency shift away from the stimulus, and is only expected at small frequency differences, except for a frequency difference of 0 Hz according to most authors at the time (including Heiligenberg et al., 1978; Heiligenberg, 1991, 1993, not confirmed by Kramer, 1987 and subsequent studies).

We frequency-clamped and phase-locked the stimuli (signal ϕ 0 and signal ϕ 90) to the EOD of the fish, that is, it was stimulated at 0 Hz frequency difference and a specific phase locked to the EOD. The electronic apparatus held both frequency difference and phase value (stimulus-fish) cycle per cycle dynamically constant, so that the fish could not escape the stimulus. As predicted, the fish were unable to discriminate under these circumstances. They did discriminate once the electronic feedback loop was opened. A strong JAR preceded the decision to 'go and get a food reward' by a few seconds; 'strong' by comparison with the usual laboratory JAR-test situation with no behavioral consequences (Kramer, 1999b) (Fig. 15-17).

We concluded the fish analyzed the temporal properties of the beat signal. Since the JAR is evoked already at threshold stimulus strength (in the 1 μ V/cm range), we hypothesized that the time-marking T electroreceptors, not the amplitude-coding, relatively insensitive P receptors, were involved. Thresholds for phase-locked stimuli of 0 Hz difference in trained, food-rewarded specimens depended significantly on the phase difference between EOD and stimulus. Phases that advanced or delayed the zero-crossings of the superimposed signal (stimulus plus EOD) had significantly lower thresholds than stimuli at other phases. For suprathreshold stimuli of constant strength, the strength of the spontaneous, non-conditioned JAR as a function of phase difference was an (inverted) mirror image of the threshold curves. The JAR responses were significantly stronger at phase values where sensitivity (or zero-crossings delay or advance) was high and vice versa, albeit at a somewhat greater inter-individual variability, as is common in non-conditioned responses (Kaunzinger and Kramer, 1996; Kramer, 1996) (Fig. 16-18).

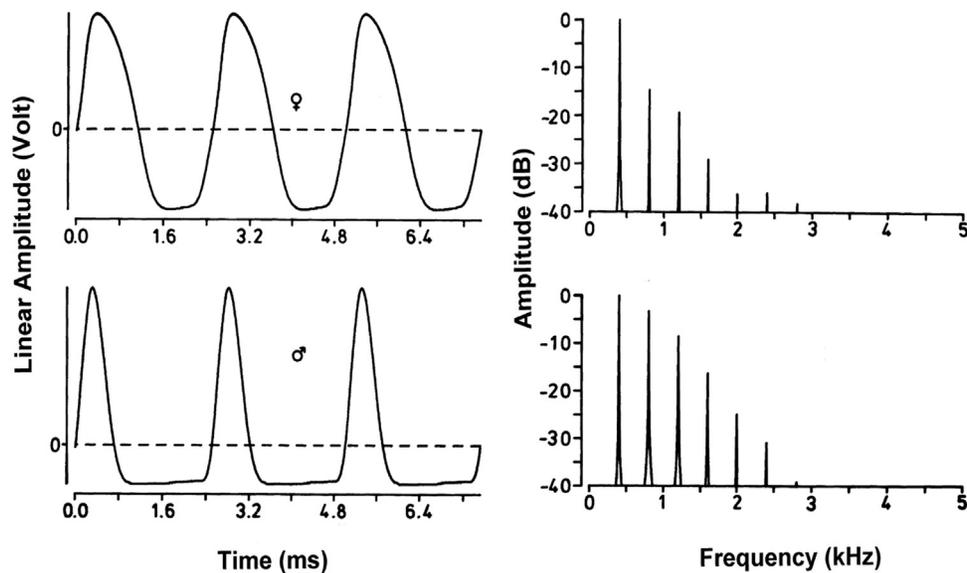


Figure 15 The EOD of the gymnotiform *Eigenmannia vireescens* differs between the sexes in waveform (left) and Fourier amplitude spectrum (right). The female EOD (top panels) is of a sinusoidal waveform, with higher harmonics of lower intensity than the male EOD (lower panels). Zero dB is defined as the intensity of the strongest harmonic, which is the fundamental frequency, or f_1 , in both (Kramer, 1985).

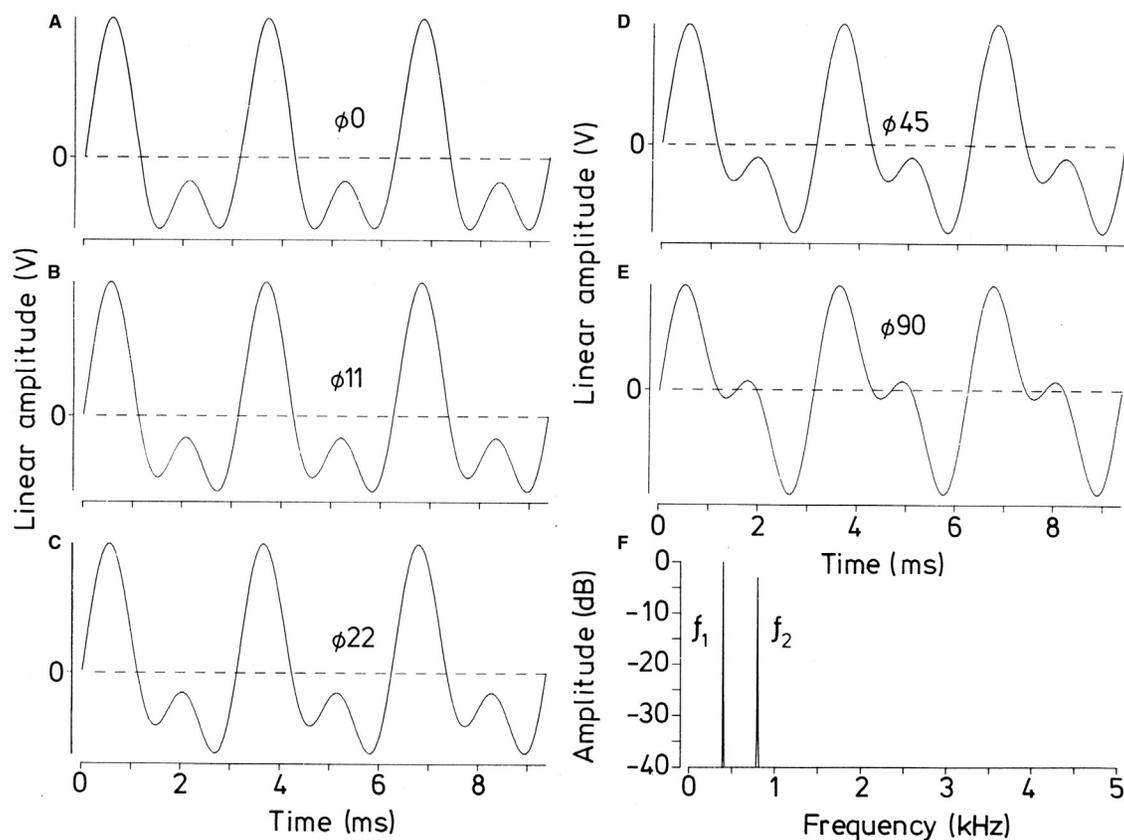


Figure 16 A 'family' of waveforms used for stimulation, which are identical in spectral composition (F) but differ in waveform (A-E). To a sine wave of frequency f_1 , its harmonic of twice that frequency, f_2 , and of -3 dB intensity re f_1 was added. The same intensity relationship holds for an *Eigenmannia vireescens* male EOD (disregarding still higher harmonics). In the waveform designated ϕ_0 (A) the positive peaks of f_1 and f_2 coincide, whereas there is a displacement between 11° and 90° in the other waveforms (B-E), as indicated. Trained, food-rewarded *Eigenmannia* discriminated all other waveforms from ϕ_0 , except ϕ_{11} which were apparently too similar to each other. Therefore, the discrimination threshold for *Eigenmannia* is assumed between ϕ_{22} and ϕ_{11} (Kramer and Teubl, 1993).

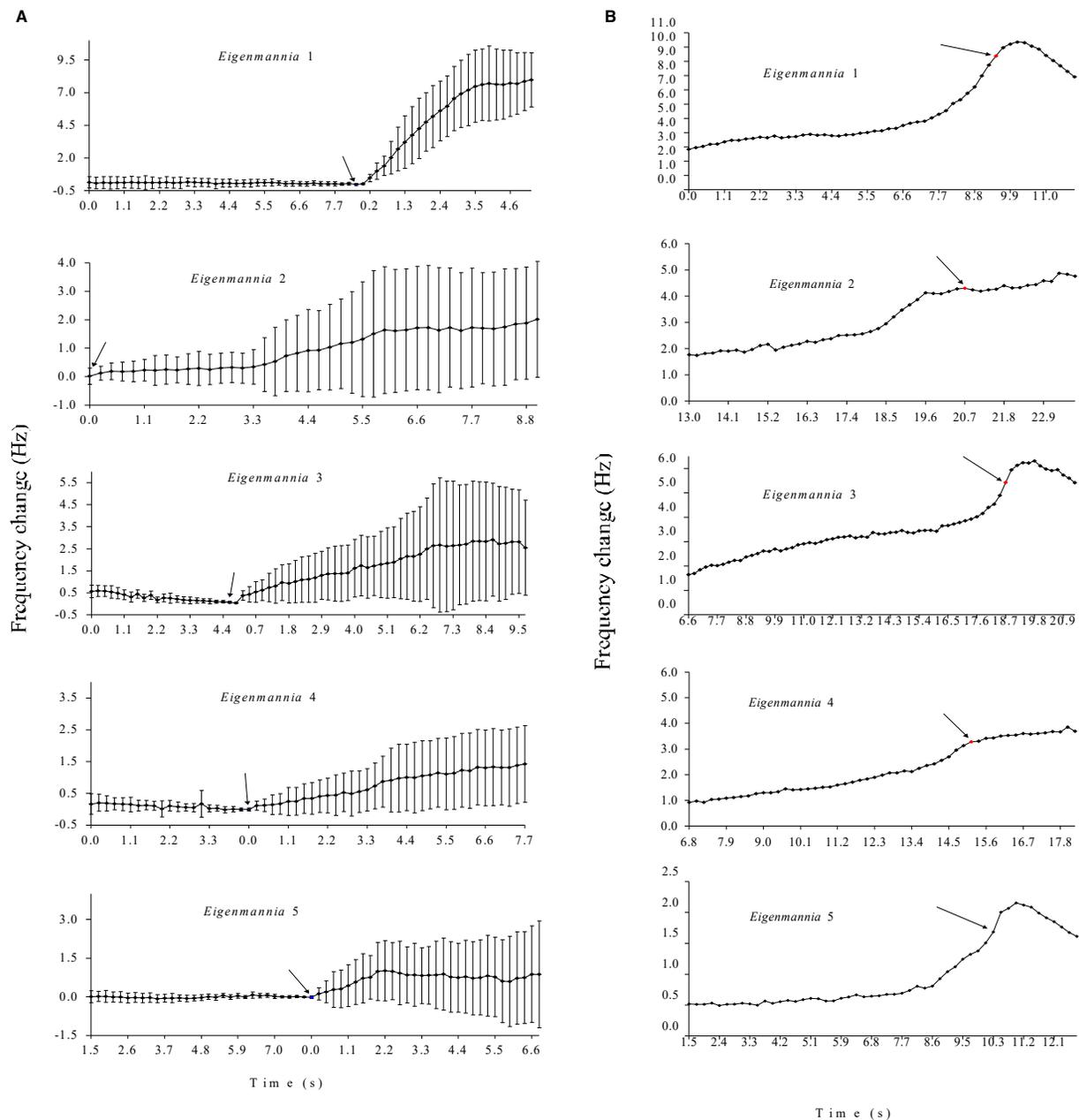


Figure 17 (A) Averaged jamming avoidance responses ($N \geq 9$) of five *Eigenmannia*, trained to receive a food reward 42 cm away from their hiding place, provided they showed a correct 'go' response to the rewarded stimulus S_{+zero} , and not to S_{-zero} . S_{+zero} and S_{-zero} were the waveforms A and E shown in Fig. 18, respectively. They were presented at a frequency difference of 0 Hz and a phase difference to the fish's EOD of 35° , that is, a sensation level of 29 dB (or $165 \mu\text{V} \cdot \text{cm}^{-1}$ peak-to-peak, corresponding to 49 dB for frequencies close, but not identical, to the EOD frequency). Shown are JARs as evoked by S_{+zero} stimuli (of constant frequency and an initial $Df = 0$ Hz, note arrows where time was set back to zero; maximum frequency error $+0.08$ Hz with respect to the fish's EOD). Ordinate, frequency change of EOD with respect to EOD frequency at stimulus onset (arrows). Each point represents the mean of 20 EOD cycles sampled within a time window of 220 ms, using a 10 MHz clock. For each fish, between 9 and 17 individual curves were aligned such that the times of stimulus onset coincided, and averaged (values are means \pm S.D.). (B) Averaged frequency change for the same five trained *Eigenmannia*, as evoked by S_{+zero} stimuli. As in (A), but individual frequency curves ($N = 9-17$) were aligned such that the times of 'go' for a food reward coincided (arrows), and averaged. From Kramer, B., 1999b. Waveform discrimination, phase sensitivity and jamming avoidance in a wave-type electric fish. *J. Exp. Biol.* 202, 1387–1398.

The JAR was useful for the fish to discriminate the rewarded signal in our discrimination task, or, surely more generally, to identify the EODs of other fish in a social context, whenever an external signal is close to a fish's own EOD frequency (Kramer, 1999b). The JAR subserves a waveform discrimination function that would enable *Eigenmannia* sp. also to detect, for example, approaching apteronotid predators (that are reported to bite off *Eigenmannia* tails, or worse; Lundberg et al., 1996) by their characteristic EOD waveforms (Kramer, 1990, 2019).

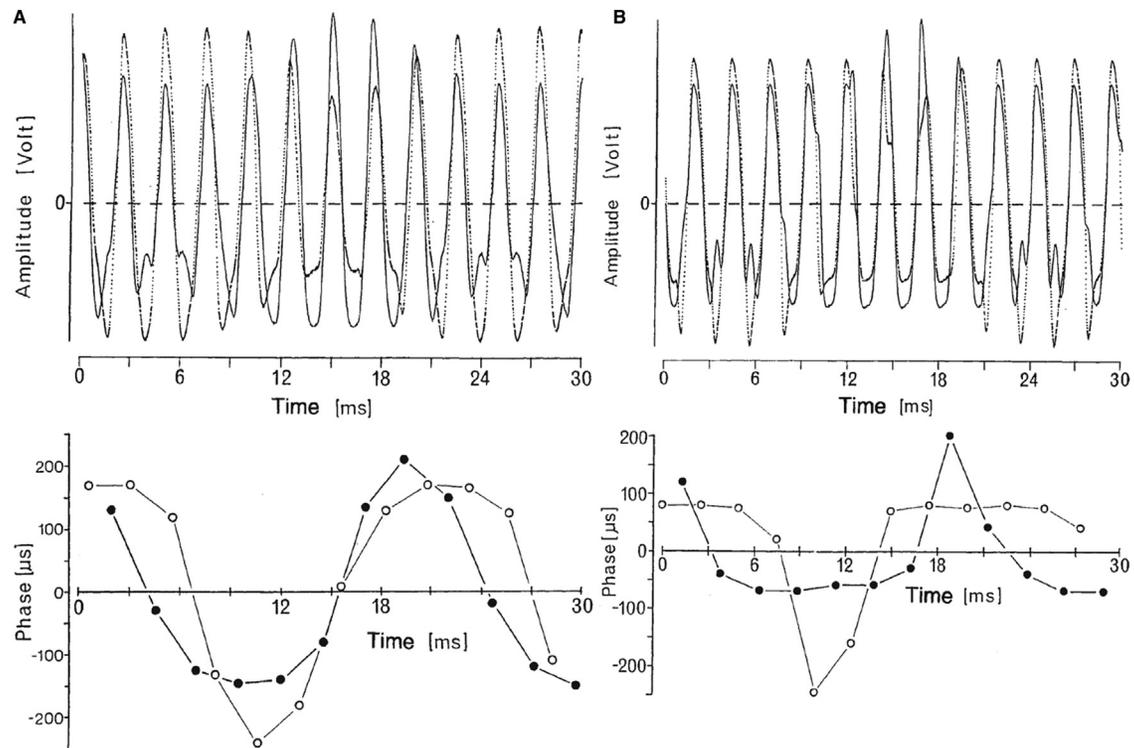


Figure 18 Waveform detection by beat analysis in *Eigenmannia*. **Top** (A, B) A female *Eigenmannia*'s EOD of 400 Hz is superimposed by another fish's EOD of 30% amplitude and 450 Hz, that is, it is modulated in both amplitude and times of zero-crossings at a beat frequency of 50 Hz, corresponding to a beat cycle of 20 ms (centered). (A) The other fish's EOD is a female, (B) male waveform. *Full line* The superimposition of EODs is additive, *dotted line* subtractive (as seen by the electroreceptors of the right and left body sides). **Below** (A, B) The modulation of zero-crossings, expressed as the difference between both superimposed signals (that is, right versus left body sides) is shown over time. This phase modulation follows the time course of the modulating EOD waveform: female for the *left* (A), male for the *right* (B) diagram. *Full dots* for positive-going zero-crossings, *empty dots* for negative-going zero-crossings. Note that with a more realistic frequency difference between both fishes' signals (for example, 4 Hz) the waveform sampling or scanning would be less crude (100 EOD cycles for a beat cycle instead of only 8 as shown here). From Kramer, B., Otto, B., 1991. Waveform discrimination in the electric fish *Eigenmannia*: sensitivity for the phase differences between the spectral components of a stimulus wave. *J. Exp. Biol.* 159, 1–22.

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