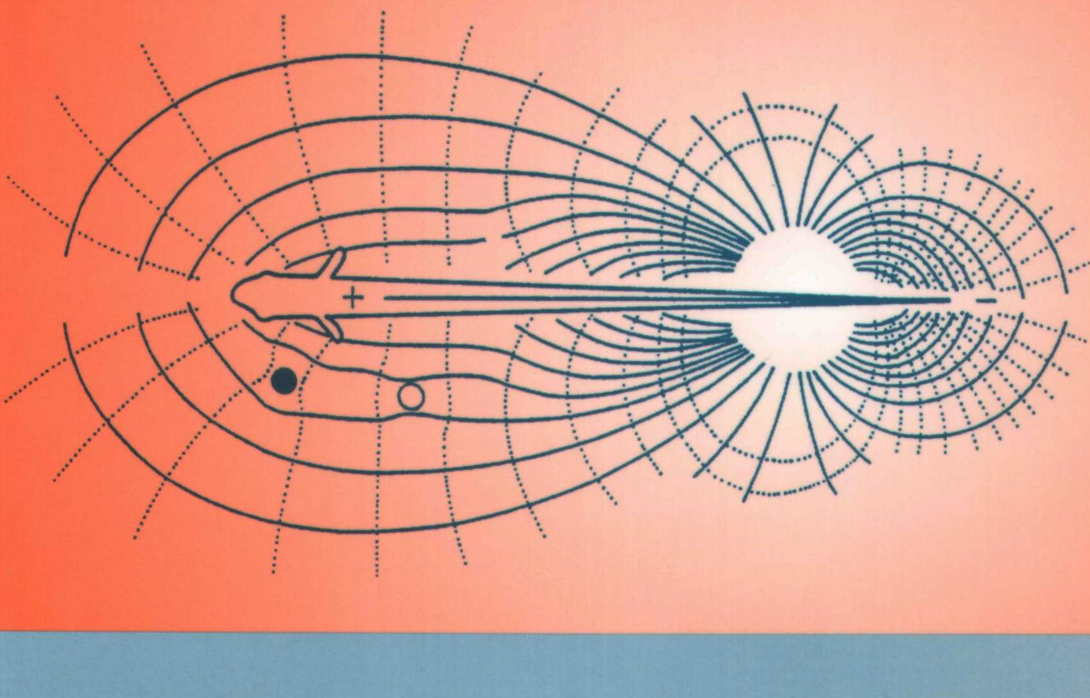
Bernd Kramer

Electroreception and Communication in Fishes

Progress in Zoology Volume 42



GUSTAV FISCHER

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Bernd Kramer

57 Figures and 1 Table

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To the memory of
Thomas Szabo
eminent pioneer in the field of electroreception
gentleman und friend

Abbreviations

Abbreviations in italics refer to "pulse fishes" only, not to "wave fishes". (Pulse fishes discharge their electric organs in a discontinuous, pulse-like fashion; wave fishes in a continuous manner, similar to a sine wave; see Chap. 5, Fig. 2.6)

EOD	electric organ discharge
HD	high discharge rate
IDI	refers to the *inter-discharge interval* code of communication in elephantfish
JAR	jamming avoidance response
MUR	medium uniform (discharge) rate
PLR	preferred latency response
PLA	preferred latency avoidance
PSP	postsynaptic potential
RAL	regularly alternating discharge rate pattern
SD	standard deviation
SDI	sequence of inter-discharge intervals
SE	standard error
SI	sharp increase in discharge rate
SID	sharp increase in discharge rate followed by a decrease to the resting level
SI-HD	sharp increase in discharge rate followed by a steady-state high discharge rate
ΔF	the frequency difference between two wave signals such as a wave
EOD	and a sine wave. In this case, $\Delta F = F_{Fish} - F_{Stim}$

Electroreceptor organ types

ampullary	common, original vertebrate electroreceptor. Sensitive in the very low frequency range or even D.C. A few teleost taxa have an "ampullary" receptor of different origin.	
tuberous	only found in a few teleost taxa; specialized for detecting electric organ discharges. Sensitive to relatively high frequencies (depending on the species and its electric organ discharge).	
P	probability coder	in wave-discharging gymnotiforms
T	time or phase coder	
B	burst duration coder	in pulse-discharging gymnotiforms
M	pulse marker	
D	mormyromast	in the Mormyridae
K	Knollenorgan	

Contents

Preface

This is a review of electrocommunication in fishes, that is, an account of how lower aquatic vertebrates gain information by electrical signals. Because scientists and students specialized in other fields of biology often find the access difficult, the present review also includes brief introductions into electroreceptors, electric organs, sensory functions and some evolutionary issues that are essential for an understanding of the topics more central to this review.

The review aims to give a concise report of recent progress in the functional analysis of the behaviour of electrocommunication and its behavioural physiology. It differs from existing, relatively recent reviews by its taxonomically broader scope, not being restricted to certain teleost fishes (Hopkins 1986, 1988; Kramer 1990a, 1994), or by its emphasis on all forms of communication behaviour in lower aquatic vertebrates rather than the neural organization of the jamming avoidance response in *Eigenmannia* (Heiligenberg 1991). Strategies of localization and orientation by electric fields have been treated in detail by Kalmijn (1988) and Hopkins (1993); these topics are only briefly discussed in the present review. The same holds true for the equally fascinating field of active electrolocation in weakly electric teleosts which is more completely dealt with in Bastian (1986, 1990).

For their support and collaboration I thank many colleagues and students who have joined our laboratory for some time. I am especially indebted to R. Wehner for his critical encouragement over the whole preparation period of this text. R.C. Peters and W. Rathmayer gave most valuable critical comments on the manuscript which was also edited by the latter. I wish to thank them both for their generous support.

Note added in proof:

After completion of the manuscript another detailed review has appeared:

Moller P (1995) Electric fishes: history and behavior. Chapman & Hall, London.

According to J. Crawford (pers. comm.; based on Bigome 1990) most studies on the mormyrid *Pollimyrus isidori* mentioned in this review, probably have used *P. adspersus* rather than *P. isidori*.

1 Electroreceptive Fishes

Although all organisms respond to electric shocks if sufficiently strong, only some aquatic vertebrates use feeble electric currents routinely for orientation, object location, or communication. Only the latter organisms are called electroreceptive. We know electroreception from *all* classes of lower, aquatic vertebrates (fishes and some amphibians), but not invertebrates. Electroreception is equally not present in terrestrial vertebrates nor their aquatic descendants; that is, reptiles, birds, and mammals, with a recently discovered exception among the primitive, egg-laying monotremes of Australia which are not dealt with in this book (Scheich et al. 1986; Gregory et al. 1987; Griffiths 1988; Andres and von Düring 1988, 1993; Andres et al. 1991; Proske et al. 1993; see Appendix). A recent claim for electroreception in a placental mammal living amphibiously in fresh water is virtually taken back in the same paper (Gould et al. 1993); another report specifically excludes electroreception in a similar placental mammal (Schlegel and Richard 1992).

Electroreceptive lower vertebrates have in common: (1) specific sensory organs with electroreceptor cells of the common, the ampullary, kind embedded in the skin; (2) afferent nerve fibres connecting to (3) specialized brain ganglia, nuclei or laminae, and specific fibre tracts to higher brain areas. Some teleosts have an additional, the tuberous, kind of electroreceptor (see Chap. 2.2).

Electroreceptor organs of lower vertebrates form part of the lateral line system that also carries mechanoreceptors; it is innervated by cranial nerves, only (nos. 7, 9 and 10) (see, for example, Starck 1978; Hildebrand 1995). The lateral line system and the internal ear are so closely related by structure, function and ontogeny that together they are called octavo-lateralis (or acousticolateralis) system. (The internal ear is also innervated by a cranial nerve, the statoacoustic, or 8th, nerve.)

Electroreception is now regarded as a primitive vertebrate trait, present already in some jawless fishes, the lampreys, which are among the few living representatives of the most primitive vertebrates, the Agnatha (Bodznick and Northcutt 1981). The cartilaginous fishes (Chondrichthyes) such as sharks, skates, rays and chimaeras (or ratfishes) are all electroreceptive (review, Bodznick and Boord 1986). Their sister group, the huge class of bony fishes (Osteichthyes), also possess the ampullary type of electroreceptor, very likely by common descent (Fig. 1.1); with the exception of one taxon, the neopterygians, the ancestors of which have lost electroreception (Northcutt 1986).

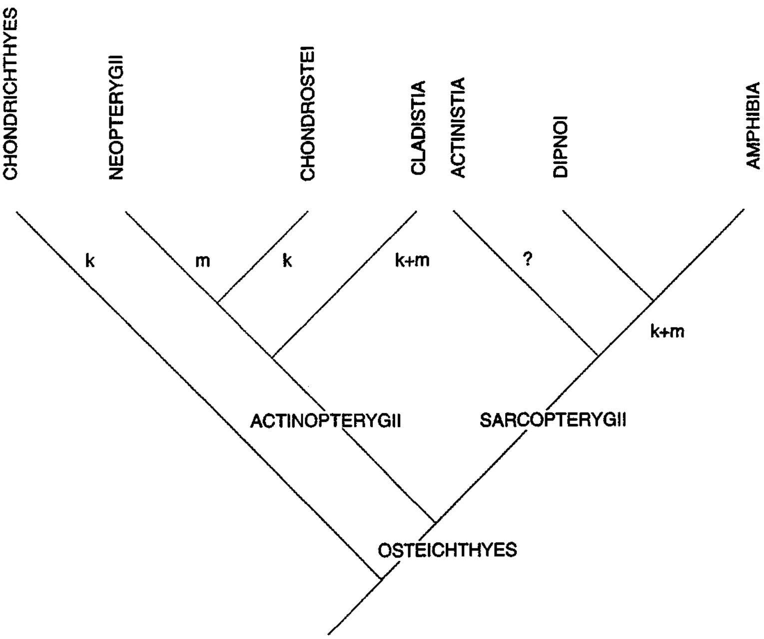


Fig. 1.1: Phylogeny of jawed fishes (Pisces) and their descendants in relation to electroreception. The apical surface of ampullary electroreceptor cells bear kinocilia *(k)* or microvilli *(m)*, or both *(k+m)*; *?* indicates uncertain status. The Neopterygii (which include the teleosts) are not electroreceptive except the catfishes, the gymnotiforms, and the mormyriforms. Their secondarily acquired ampullary electroreceptor cells differ from those of all other groups by their lack of kinocilia although they do possess microvilli. (Modified from Northcutt 1986)

One of the two radiations of the Osteichthyes, the lobe-finned fishes (Sarcopterygii), are probably all electroreceptive (Northcutt 1986); this has been shown in the few surviving lungfishes (Dipnoi) and is very likely true also in the relict *Latimeria* (Actinistia; Bemis and Hetherington 1982; Forey 1990). Extinct relatives of *Latimeria,* the rhipidistians, had an extensive pore-channel system in their dermal bone covering head and scales that probably accommodated electroreceptor organs and their innervation. It is the rhipidistians that, according to most authors, gave rise to the modern amphibians (Carroll 1988, 1993). Of the three living orders of amphibians, the salamanders (Urodela) are electroreceptive; this is probably also true for a second order, the caecilians (Gymnophiona), while frogs and toads (Anura) are not electroreceptive (review, Fritzsch and Münz 1986; Roth and Schlegel 1988).

Among the sister group of the lobe-finned fishes, the by far larger group of ray-finned fishes (Actinopterygii), we find electroreception in two out of three taxa; namely, the Cladistia (bichirs or polypteriform fishes), and the Chondrostei (sturgeons and paddlefishes). It is only the ancestors of the remaining ray-finned fishes, the neopterygians which include the huge group of teleosts, which must have lost electroreception (review, Northcutt 1986), and whose descendants stand therefore apart from all other lower aquatic vertebrates (Fig. 1.1).

The neopterygians are represented by three taxa, two of which are rather primitive and have but a few surviving members: these are the gars (Ginglymodi, e.g. *Lepisosteus)* and the bowfin (Halecomorphi, *Amia*). The third group are the modern teleosts which represent about half of all vertebrate species (more than 20 000). All these neopterygian fishes, with the exception of a few teleosts among the Osteoglossomorpha and the Ostariophysi, are *not* electroreceptive.

The ancestors of the few teleosts that are electroreceptive must have reacquired the electric sense (in a distinctly modified form), while the large majority of teleosts is completely unresponsive to feeble electric currents. The few electroreceptive teleosts possess a new type of ampullary electroreceptor; some taxa even have in addition other kinds of electroreceptor, none of which resemble the original ampullary receptor type (Northcutt 1986).

Electroreception within the teleosts (Lissmann 1958) must have reevolved at least twice (perhaps three times), and only in fresh water: within the African tribe of primitive bony-tongued fishes (Osteoglossomorpha), and within a subgroup of the modern Ostariophysi (Fig. 1.2), fishes with a Weberian ossicles connection from the swim bladder to the ear, affording them good hearing (Lauder and Liem 1983; Finger et al. 1986). The osteoglossomorphs that are electroreceptive comprise the Mormyroidei (elephantfishes or snoutfishes; Lissmann 1958), and their relatives, the Xenomystinae (members of the African knifefishes or featherbacks; review, Braford, Jr. 1986), which are only very distantly related to the South American knifefishes. The electroreceptive ostariophysans are the South American knifefishes (Gymnotiformes; Lissmann 1958) and the ubiquitous catfishes (Siluriformes; Parker and van Heusen 1917; Roth 1968; Peters and Bretschneider 1972). All of these electroreceptive teleosts are primary freshwater fishes, only a few catfishes have adapted to marine life. The Siluriformes are the only electroreceptive freshwater teleosts of world-wide distribution (Fig. 1.2).

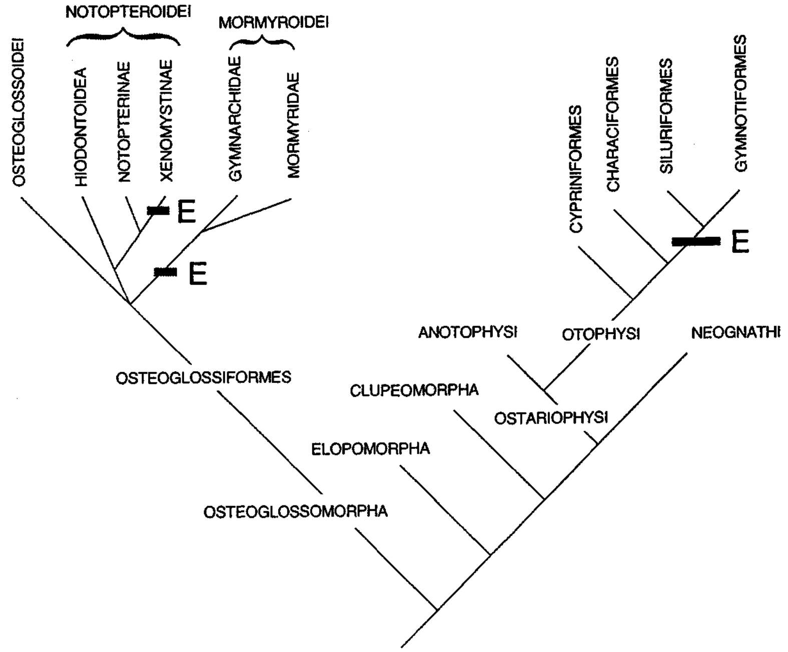


Fig. 1.2: Phylogeny of electroreceptive freshwater teleosts (including a few catfishes that have adapted to marine life). Electroreception in teleosts must have evolved at least twice (*E*): in some Osteoglossomorpha and in the siluriform/gymnotiform lineage of the Ostariophysi. There may be a third instance among the Notopteroidei because the Xenomystinae, or African featherbacks, but not the Notopterinae, are electroreceptive (as indicated). In addition to their ampullary electroreceptors common to all these fishes, the South-American Gymnotiformes and the African Mormyroidei have independently evolved tuberous electroreceptors tuned to the spectral frequency content of these fishes' electric organs. (Modified from Finger et al. 1986, which was adapted from Lauder and Liem 1983, following Nelson 1984 for the Osteoglossomorpha.)

2 Electroreceptors Are Voltmeters

Electroreceptive sensory cells are hair cells, forming part of the octavo-lateral sensory system. In fishes, this comprises mechanoreceptive sensory systems for hearing, the maintenance of equilibrium, the detection of gravity and rotation, and of water currents along the body. Electroreceptive sensory cells are similar to mechanoreceptive sensory cells of vertebrates; in fact, the ampullae of Lorenzini have long been regarded as mechanoreceptors (Bullock 1974). Electroreceptors as well as mechanoreceptors are contacted by cranial sensory nerves only; unlike their mechanoreceptive counterparts, electroreceptors do not have an efferent innervation.

2.1 Ampullary Electroreceptors

Ampullary electroreceptors are exceedingly sensitive to weak electric field gradients: about 5 nV/cm in marine fishes, 1-5 µV/cm in freshwater fishes (reviews, Kalmijn 1988; Zakon 1986, 1988; Bretschneider and Peters 1992); they respond to D.C. or low-frequency stimuli, only. For weak stimuli, primitive ampullary receptors, such as those found in cartilaginous fishes, nonteleost bony fishes and amphibians, respond best to an externally negative stimulus, underlining their common origin. This is in contrast to the few teleost taxa which possess ampullary receptors responding best to (weak) stimuli of opposite polarity (positive outside; review, Zakon 1988). There is also a morphological difference (Fig. 2.1): ampullary electroreceptor cells of nonteleosts always bear a kinocilium at their apical (lumenal) face, sometimes in addition to microvilli. Teleost ampullary receptor cells, however, bear microvilli, but no kinocilium (Szabo 1974).

Ampullary electroreceptor cells and their supporting cells form the sensory epithelium lining an ampulla found at the end of a transepidermal canal which is open to the outside (Fig. 2.2). Marine fishes usually have long canals, while freshwater fishes have short canals, with the receptor opening directly above the ampulla. The canal is filled with jelly of a low resistivity (25-31 Ω·cm) similar to that of sea water (Murray 1974; Zakon 1986; Kalmijn 1988).

The ampullary organs of elasmobranchs have long been known as "ampullae of Lorenzini" (since 1687; see Zakon 1988). These sensory organs and also their teleost counterparts are well-adapted to an electrosensory function for a number of reasons: The ampullary canal is lined with several layers of flattened cells of high resistance connected by tight junctions (6 $M\Omega\cdot cm^2$, 0.4 $\mu F\cdot cm^2$; Waltman 1966; review, Kalmijn 1988). The skin of freshwater teleosts (and also of the only freshwater

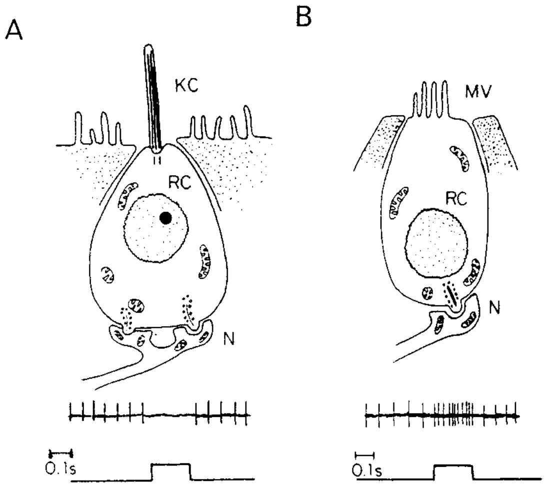


Fig. 2.1: Ampullary electroreceptor cells *(RC)* of nonteleosts (**A**) bear an apical kinocilium *(KC)*, sometimes in addition to microvilli *(MV)*, while electroreceptive teleosts (**B**) have only microvilli and no kinocilium. The spontaneously active, afferent nerve *(N)* fibres increase their firing rate when the electrical stimulus (in this case a square-wave pulse of 200 ms) is positive outside the ampulla in teleosts, while in all nonteleosts a negative stimulus is required for a similar response. (From Bullock and Heiligenberg 1986, modified).

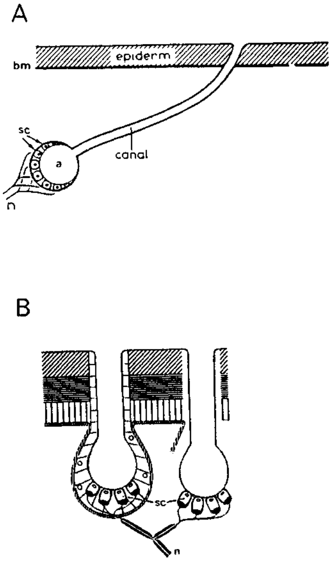


Fig. 2.2: Ampullary electroreceptor organ consisting of a layer of receptor cells (*sc*) lining an ampulla which is connected to the outside by a canal, which is long in marine fishes (**A**) and short in freshwater fish (**B**). The organ is lined by the basement membrane (*bm*), hence, represents an entirely epidermal structure invaginating into the underlying corium. The sensory cells are contacted by only one kind of afferent nerve fibre (*n*) in both teleosts and nonteleosts. (From Szabo 1974)

elasmobranch studied) is of high resistance (up to 50 $\text{k}\Omega\cdot\text{cm}^2$ in mormyrids; Bennett 1971b) because of the requirements of osmoregulation (it is waterproof and relatively impermeable to ions in connection with the salt and water balance of the body fluids); compared to fresh water, the body fluids are relatively good conductors (5000 μS/cm; Kalmijn 1974). In marine elasmobranchs (which maintain isotonicity with sea water by urea) the skin is of low resistance; their tissues are less conductive than the surrounding sea water. When placed in an electric field the optimal positions for an electroreceptor differ for freshwater and sea-water fishes: the inside of a freshwater fish is relatively isopotential (Bennett 1965; Bennett 1971b); therefore, the largest voltage drop is across the skin at the two points widest apart along the field gradient, and a short canal will do (Murray 1974) (Fig. 2.3). A similar arrangement has even been found in the river stingray *Potamotrygon* which is a descendant from marine ancestors (Szabo et al. 1972).

In sea water, however, the voltage gradient extends throughout the body, and a receptor with a long canal (in the direction of the field gradient) will "see" a greater potential difference between the receptor opening and the position of the ampulla than a receptor with a shorter canal. The potential difference is faithfully measured because the canal walls are isolated so well. Under these conditions, long canals radiating in all directions would be advantageous; this is actually found in marine elasmobranchs. Long canals, originally (but inadequately) also termed "ampullae of Lorenzini", have been found in the marine catfish *Plotosus* which is a descendant from freshwater teleosts (reviews, Szabo 1974; Kalmijn 1988).

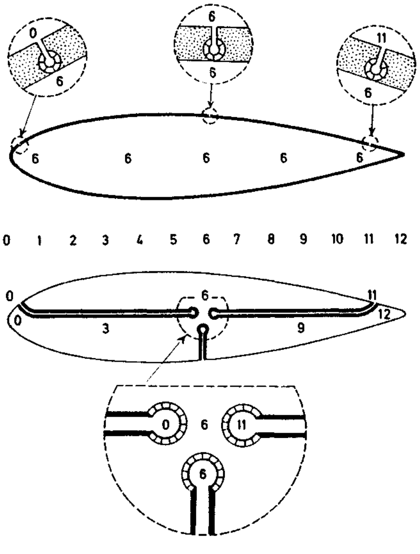


Fig. 2.3: Diagrammatic representation of the physical effect of an electrical field extending over the length of a freshwater teleost (*top*) and a marine elasmobranch (*below*). Numbers are potentials (in arbitrary units) as referred to a distant point. Thick lines represent high resistance boundaries, that is, the epidermis in teleosts, and the ampullary canal walls in elasmobranchs. Note that in teleosts very short ampullary canals (length = epidermis thickness) are sufficient to sample the maximum potential difference, while in elasmobranchs very long canals are necessary. (From Murray 1974)

In elasmobranchs the ampullae proper are grouped together in a few subcutaneous capsules the walls of which have, like the skin, "intermediate" resistance relative to the jelly-filled ampullary canal and the sea water of low resistance, and the wall of the ampullary canal of very high resistance. The resistance of the stroma within the capsule is low. This ingenious arrangement makes possible differential operation and cancelling of any fluctuating potentials common for the ampullae in the capsule (Montgomery 1984; Kalmijn 1988) (Fig. 2.4). Common mode rejection by differential operation should explain how it is possible that elasmobranch fishes can detect nanovolt field gradients in the external medium in the presence of much stronger fields due to the animal's own physiology.

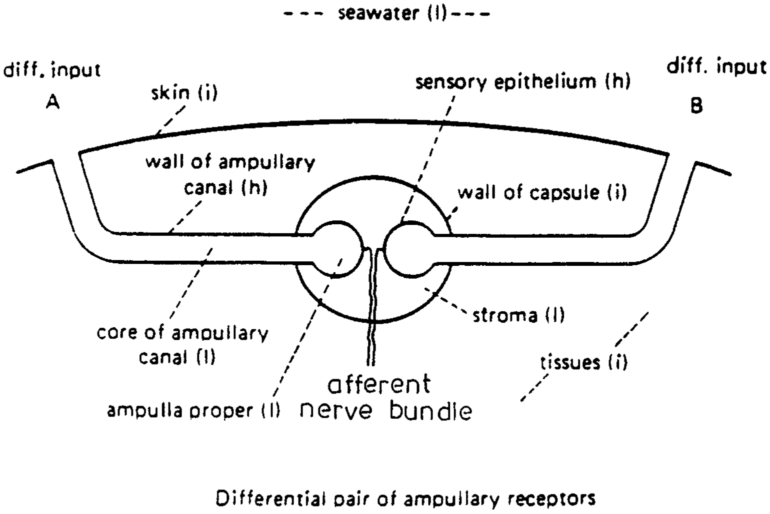


Fig. 2.4: Differential operation of elasmobranch ampullary receptor system in sea water. The individual ampullae measure the potential difference between their openings (*A*,*B*) and the capsule. Common-mode potentials of the capsule are suppressed by subtracting the potentials received from different ampulla populations. For this system to work a high (*h*) resistance of the ampulla canal walls is necessary, while the skin and other tissues are of intermediate (*i*) resistance, except the stroma of the capsules, the jelly within the ampullae, and the sea water which are all of low (*l*) resistance. (From Kalmijn 1988, modified)

Afferent fibres from ampullary receptors are spontaneously active; receptor stimulation results in either an increase or a decrease in action potential frequency, depending on the polarity of the stimulus. Following a response there is an adaptation back towards the resting frequency, with an opposite rebound at "off" (Fig. 2.5).

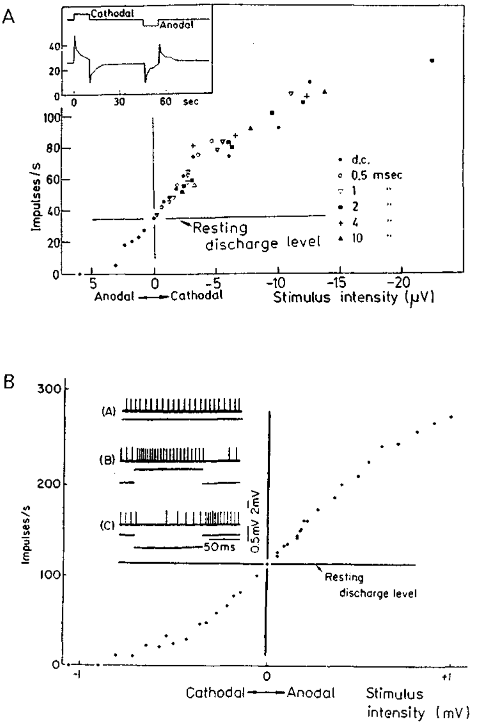


Fig. 2.5: Stimulus-response relationships in afferents from ampullary electroreceptors. **A** Marine elasmobranch *(Raja ocellata)*; **B** Freshwater teleost (the gymnotiform fish *Gymnotus carapo)*. Note that in **A** cathodal d.c. stimulation is excitatory, anodal stimulation of only a few µV inhibitory ("cathodal" means the negative electrode is at the opening of the canal, the positive electrode elsewhere on the fish). This is in contrast to **B** which is also less sensitive. *Inset* in **A**: time course of action potential rates in response to anodal and cathodal stimuli of 100 µV. (From Murray 1974 and Bennett 1971b, modified)

In teleosts, the basal face of the sensory cell has a smaller surface area and a higher resistance than the apical area. Therefore, it is the basal membrane that limits the current flow through this cell. The apical surface seems to play an active role in the regulation of sensitivity: the microvilli determine the effectiveness of a stimulus and, hence, sensitivity, apparently by a change in surface area and ion channel conductancy (Heijmen and Peters 1994).

A weak stimulus that is outside positive depolarizes this membrane area, causing it to secrete a chemical transmitter which leads to an increase of the rate of action potentials in the afferent fibre. In the catfish *Kryptopterus*, a compound similar to, but not identical with, glutamate has been proposed (review, Bennett and Obara 1986). Recent pharmacological, electrophysiological, immunohistochemical and ultrastructural studies have, however, confirmed L-glutamate as the most likely transmitter in ampullary receptor organs of the catfish *Ictalurus nebulosus*: it is only found in the sensory cells and their afferent nerve fibres (Heijmen et al. 1994), and it effectively increases the action potential frequency in these nerve fibres when applied to the organ (Andrianov et al. 1992). The L-glutamate receptor has been further characterized as being of the AMPA (D,L-α-amino-3-hydroxy-5-methylisoxazole-4-

propionic acid) subtype (Andrianov et al. 1994). Glutamate has also been found in electroreceptor cells of gymnotiforms (Denizot et al. 1990).

Ampullary receptor cells are voltage-to-chemical transducers; in catfish probably operating through non-voltage-sensitive or non-specific cation channels (Bretschneider and Peters 1992); see also Sugawara and Obara (1989) and Sugawara (1989a,b). In elasmobranchs there might be voltage-sensitive Ca-channels (open when activated; Bennett and Obara (1986). In teleosts it is believed that the physical stimulus itself, if greater than 10 μV, causes the change in transmitter release (through "high gain synapses"; review, Bretschneider and Peters 1992), while in the marine Chondrichthyes both receptor faces seem to interact in such a way as to amplify the physical stimulus, resulting in the incredibly high sensitivity of 5 nV/cm (measured behaviourally; Kalmijn 1988). The frequency range of highest sensitivity to sinusoidal stimulation is 6-8 Hz in elasmobranchs, and 10-30 Hz in teleosts (review, Kalmijn 1988).

2.2 Tuberous Electroreceptors

Tuberous electroreceptors are found in a few teleosts only: in the electrogenic Mormyroidei and Gymnotiformes (reviews, Bennett 1971b; Szabo 1974; Zakon 1986, 1988), and perhaps also Siluriformes, if an anatomical finding in just one South American species can be confirmed as to its presumed function (Andres et al. 1988). Tuberous electroreceptor organs are fired by electric organ discharges (EODs); they are of two functional (and, especially in mormyroids, also morphologically distinct) types: (1) time marker units of high sensitivity and short, fixed latency to a supra-threshold EOD; (2) amplitude coders that are relatively insensitive in absolute terms, encoding minute intensity changes of a fish's own EOD. The first type mainly supports electrocommunication, the second active object detection.

A common distinction from ampullary receptors is the higher frequency range tuberous receptors respond to whereas their low-frequency sensitivity is often reduced. Tuberous electroreceptor organs therefore tend to have bandpass characteristics; some show marked tuning to a certain "best" frequency (that is, the frequency of lowest threshold), others are more broadband. In most cases this is an adaptation to the spectral properties of these fishes' wave or pulse EODs (Fig. 2.6; discussed in more detail in Chap. 5).

Adequate stimuli for tuberous receptors are electric organ discharges. With the possible exception of the South American catfish mentioned above, tuberous receptors are known only from teleosts with electric organs. Just like teleost ampullary receptors, tuberous receptors must have evolved at least twice; they differ amazingly in anatomy, even within the Gymnotiforms or Mormyriforms.

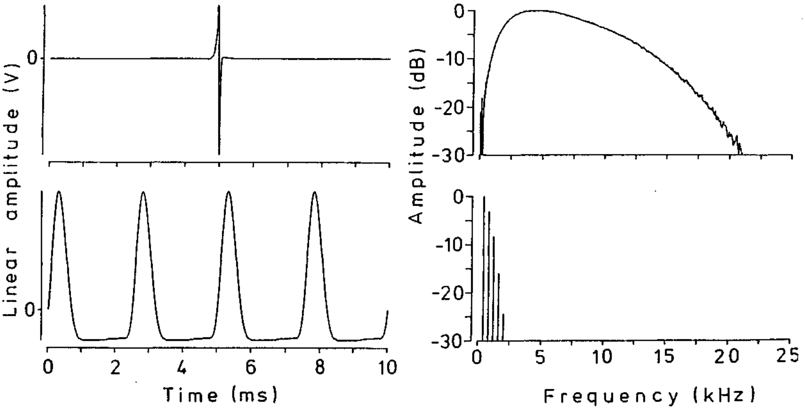


Fig. 2.6: Two electrical phenotypes, pulse (*top*) and wave EOD (*below*), are found in electrogenic fishes. *Left,* Oscillograms show the waveforms in the time domain; *right,* amplitude spectra show the broad-band frequency content for the pulse EOD and the harmonic spectral composition for the wave EOD in the frequency domain. Pulse-discharging fish, *Gnathonemus petersii* (Mormyridae); wave-discharging fish, *Eigenmannia lineata* (Gymnotiformes). (From Kramer 1990a)

Like ampullary receptors, tuberous receptors are located in an epidermal invagination into the corium. The name "tuberous" refers to the fact that these receptors are covered by the skin, usually without a canal opening to the skin surface. Because the space above a tuberous receptor is filled by loose plug cells, functionally there is a channel for the electric current flow across the skin also in tuberous receptors.

Mormyroidei and Gymnotiformes both have two types of tuberous electroreceptors which differ in response properties. The anatomical distinction is very clear-cut in Mormyroidei, but difficult, if at all possible, in Gymnotiformes (Fig. 2.7). Stated briefly, one type of tuberous receptor is a time marker for precisely reporting the occurrence of an EOD (a fish's own, that of another fish, or both), while the other tuberous receptor type reports on the amplitude of (especially) a fish's own EOD. Therefore, tuberous receptors enable some electrogenic teleosts, the Gymnotiformes and Mormyroidei, to detect, firstly, the presence of objects in their self-generated electric field (electrolocation), and secondly, the electric organ discharges generated by other individuals (within the context of electrocommunication).

The tuberous receptors of the large African family of Mormyridae are the Knollenorgane (K receptors) and the mormyromasts (D receptors); they represent the beginnings of two distinct sensory pathways in the brain (reviews, Bell 1986; Bell and Szabo 1986). The morphology of the Knollenorgane is fairly simple: with their basal parts, 1-35 receptor cells rest on a hillock of supporting cells, exposing 90% of their apical surface into individual perisensory spaces. The lumenal membrane of a

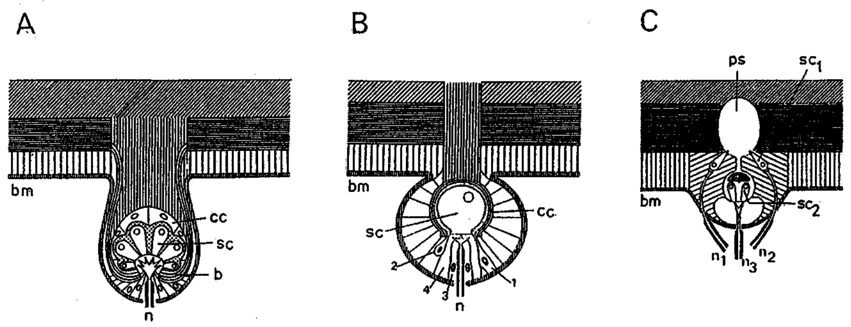


Fig. 2.7: Tuberous electroreceptors in electrogenic teleosts. **A** Gymnotiformes, **B** and **C** Mormyroidei. **A** The sensory cells (*sc*) in gymnotiforms share one common perisensory space; this is in contrast to the Knollenorgane of mormyriforms (**B**) where the sensory cells, if there are more than one, have individual perisensory spaces. **C** Mormyromasts possess two types of sensory cells, inner and outer, which are contacted by different nerve fibres. Note that each electroreceptor organ is electrically coupled to the external medium by loose "plug" cells forming a channel through the insulating epidermis of high resistance. (From Szabo 1974)

sensory cell is richly decorated with microvilli. Only one (branching) nerve fibre contacts all sensory cells of a Knollenorgan at their basal parts. The sensory cells are capable of generating action potentials; transmission to the postsynaptic afferent fibre is thought to be by electrical, fast synapses. Afferent fibres from Knollenorgane respond to an EOD by just a single action potential of fixed latency; the sensitivity of the receptor is high. Any variation of stimulus intensity is not reported by Knollenorgane (Fig. 2.8). Their tuning to the spectral properties of the EOD is only very broad, similar to that of mormyromasts.

Mormyromasts are the most complex electroreceptors (Fig. 2.7). They possess two types of sensory cell which are innervated separately; their apical membranes contact two different chambers of perisensory space, an inner and outer one, which are connected by a short canal and filled with a conducting, mucoid material. The 5-7 outer sensory cells differ from all other known electroreceptor cells by not having any apical specialization, neither microvilli nor kinocilium (the latter would be surprising in a teleost electroreceptor cell). The outer sensory cells have only "point contact" with the outer perisensory space, while the 3-5 inner sensory cells expose most of their microvilli-covered surface to their part of the perisensory space, the inner chamber. A mysterious mucoid ball rests on top of the inner sensory cells. The inner sensory cells are contacted by a single, branching nerve fibre, while there are two or three branching nerve fibres contacting the outer sensory cells. The nerve fibres from both sensory cell types project to different zones of the electrosensory lobe of the lateral line (ELL), the first input stage of the brain (Bell et al. 1989). Mormyromasts respond to an EOD in an intensity-graded fashion: stimuli of low intensity evoke just one action potential in the afferent fibre at long latency, stimuli of high intensity evoke a nerve impulse volley (up to nine impulses, depending on the fibre) with a dramatically reduced latency of the first action potential (for example, from 8 to 2 ms in a 6-impulse fibre; Fig. 2.8). The latency of the first action potential seems to carry all the information, with the significance of the following ones, if present, being unclear (Bell 1990).

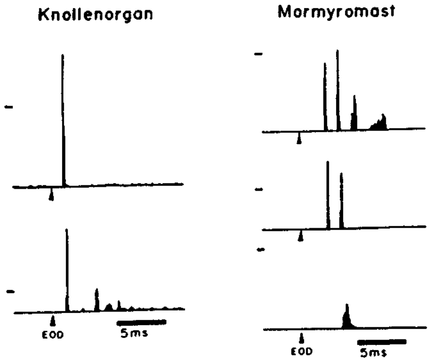


Fig. 2.8: Responses of mormyrid tuberous electroreceptors to electric organ discharge (EOD), shown as a peri-stimulus time histogram. Responses from two different Knollenorgane and three different mormyromasts are shown. *Ordinate* Occurrences (mark indicates 100); *abscissa* time. Note that afferents from Knollenorgane respond to a suprathreshold EOD by just one action potential of fixed latency, while mormyromast afferents may respond by several action potentials of varying latency, depending on the individual mormyromast and on stimulus intensity (not shown). (From Bell 1986)

The stimulus intensity/response curve is of sigmoid shape (similar to most receptors). Mormyromast sensitivity is rather low, 10-20 times less than that of Knollenorgane. The intensity of the fish's own EOD corresponds to the linear, centre part of the sigmoid curve. Thus minute changes of the fish's own EOD are represented by a sizable change in mormyromast response; therefore, mormyromast absolute sensitivity is low while differential sensitivity is high (in the steep part of the sigmoid curve). Recently, response differences from the two types of sensory cells were inferred from recordings of afferent nerve fibres near their (separate) central terminations (Bell 1990); these seem to encode differences in electrical impedance properties of electrolocation objects (von der Emde and Bleckmann 1992b; von der Emde and Bell 1994).

In the tuberous receptors of gymnotiforms 10-100 sensory cells share one perisensory cavity; there are no compartments like in the Knollenorgan (Fig. 2.7). The sensory cell surface is covered by microvilli.

In gymnotiforms with a pulse EOD, the two physiological receptor types are M and B units, while in gymnotiforms with a wave EOD, the two types are called P and T receptors (see below). M units mark the occurrence of a pulse EOD by a single action potential, similarly to Knollenorgane, with the latency barely affected by intensity changes. B units (burst duration coders) fire a variable number of action potentials in response to a pulse EOD (from 1 to 20). The latency of the first action potential as well as the number of the following ones, if present, changes with stimulus intensity (Fig. 2.9). Tuning to the spectral properties of a species' EOD varies widely: some units are well tuned to the frequency of spectral peak amplitude of an EOD, others are considerably "mistuned" in this regard, still others show broad, or very little, tuning.

In wave-discharging gymnotiforms, T (time or phase) units fire one action potential per discharge cycle. The phase relationship to the discharge cycle changes very little with stimulus intensity. P (probability) units increase their rate of firing with increasing stimulus amplitude; their responses do not show any phase relationship to the stimulus cycle. In general, P and especially T receptors are sharply tuned to an individual's EOD frequency (Fig. 2.9).

The complex subject of central electrosensory projections and information processing in the brain must be left out here for reasons of space limitation. For the weakly electric fishes, Mormyroidei and Gymnotiformes, a short introduction is given in Kramer (1990a) with pointers to the original literature. For a more detailed presentation see several reviews in the volume edited by Bullock and Heiligenberg (1986), containing also chapters on cyclostomes (Ronan 1986), chondrichthyes (Bodznick and Boord 1986), nonteleost bony fishes (Northcutt 1986), catfish (Finger 1986), African knifefishes (Braford, Jr. 1986), and amphibians (Fritzsch and Münz 1986). For the Mormyridae and the Gymnotiformes, see also the more recent reviews (Carr 1990; Heiligenberg 1991; Bell 1993; Meek 1993).

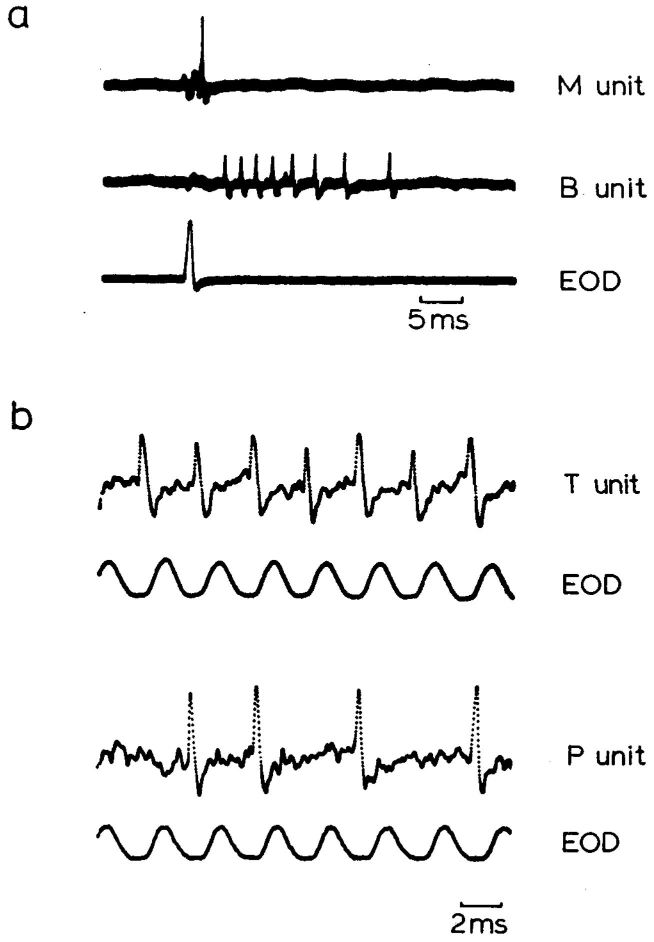


Fig. 2.9: Responses from tuberous electroreceptors to electric organ discharges (EOD) in gymnotiforms. **a** Afferent nerve responses in a species with a pulse EOD; **b** in a species with a wave EOD. Note that there are two kinds of receptors in both electrogenic phenotypes (species with a wave or pulse EOD), one marking the time of occurrence of an EOD (*M* and *T* unit), whereas the other is sensitive to intensity changes. For an intensity increase, this is a latency decrease together with an increase of the number of action potentials in *B* units, whereas *P* units respond by an increase of the firing rate with no fixed phase relationship to the EOD (not shown). (From Bastian in Heiligenberg 1977)

3 Electrogenic Fishes

Any living tissue generates electric fields associated with the regulation of its ionic balance; these radiate into the environment. In animals, electric fields also arise from normal nerve or muscle-cell activity, and, in most cases, are of low frequency and intensity: up to 0.5 mV relative to a distant electrode at close range in marine species (Kalmijn 1974); a few mV in freshwater teleosts (Peters and Bretschneider 1972; Roth 1972).

In certain fishes, however, we find electric organs, consisting of closely packed, orderly arranged groups of cells whose only known function is the production of an electric field outside the body (reviews, Bennett 1971a; Bass 1986). In most cases, these cells are modified muscle cells; in one taxon it is the endings of spinal motor nerves which take over that function. These electric organs are under the exclusive control of the brain. The electric fields range from very weak (in the order of magnitude given above for incidental stray fields) to very strong (500 Volts or more; Bennett 1971a). These fishes are said to be electrogenic.

The terms "strongly" and "weakly electric fishes" often do not correspond to systematic categories; there are even species which are both strongly and weakly electric (like the South American electric eel, *Electrophorus electricus*). In the whole animal kingdom, it is only among two classes of jawed aquatic vertebrates (Pisces) that we find electrogenic members: these are the cartilaginous fishes (Chondrichthyes) and the bony fishes (Osteichthyes; Fig. 1.1; Appendix).

Within the cartilaginous fishes, only some Batidoidimorpha (rays) have electric organs (the predominantly marine, weakly electric Rajidae or skates, comprising 14 genera with about 190 species; and the strongly electric, marine Torpedinidae or electric rays, 10 genera with about 38 species). Among the Osteichthyes (bony fishes) it is only in 4 among the many orders or suborders of teleosts that we find electrogenic species, all of them, except the stargazers (see Chap. 5.5), living in fresh water. These 4 orders are the Mormyroidei (elephantfishes; probably all of about 200 species), very few Siluriformes (catfishes; at least 2 electrogenic species), the Gymnotiformes (South American knifefishes; probably all of at least 108 species), and the Perciformes (three electrogenic species among the marine stargazers). Electric organs must have evolved at least six times independently; two times among the rays, and four times among the teleosts (Pickens and McFarland 1964; Bennett 1971a; Bass 1986; Pietsch 1989).

Independently, in the Mormyroidei and the Gymnotiformes electric organs are almost certainly a derived group character, that is, present in all members of each group, but not in their respective sister groups (a synapomorphy). Perhaps a similar situation applies for the Rajidae and the Torpedinidae. This is in contrast to the large taxa Siluriformes and Perciformes only very few members of which are known to possess electric organs.

We might expect all these electric fishes to be more sensitive to electric currents than ordinary teleosts; that is, we expect them to possess electroreceptors of some kind (see Chap. 2). This turned out to be true for all electrogenic fishes but one taxon: even the few stargazers that are electrogenic (genus *Astroscopus*), lack electroreceptors (like Perciformes in general).

The classification of an electric fish as either weakly or strongly electric is sometimes arbitrary; there are intermediate cases (for example, the stargazers). Organs that are discharged for brief periods only during prey attack, or during defence, usually are "strong" organs; their discharges cause discomfort or pain to a human handling the fish. A particularly strong discharge is that of a disturbed or an attacking electric eel which is, according to historical reports from natives (Ellis 1913), able to "knock a man down" in its natural environment (South American fresh water bodies). Also according to natives, the "puraqué" (local name for electric eel) is said to harvest palm fruit which it has been observed to eat, by electroshocking the base of a tree (B. Kramer, pers. report from Manaus, Amazonas).

Continuously discharging electric organs are all weak, although that of *Mormyrus hasselquistii* a pulse species, is so strong that it can cause discomfort to the human hand placed near a fish in its original water (pers. field obs.).

3.1 Electric Organs

Electric organs usually consist of modified muscle cells, or electrocytes, which are unable to contract but still capable of generating action potentials which are often unusually large (reviews, Bennett 1971a; Zimmermann 1985; Bass 1986). In different species, electric organs are derived from the most diverse muscles and thus can be found almost anywhere in a fish's body (Fig. 3.1). For example, in the weakly electric skates electric organs are located in the long, extremely slender tail, while in the strongly electric rays electric organs are part of the head region of their flattened, disc-shaped body. These head organs are derived from branchial muscle; the electric ray *Narcine* has an additional weak organ (as seem to have many torpedinids, although it may degenerate early in life).

In the weakly electric elephantfishes (Mormyroidei) we find two possible locations of electric organs: (1) In larval mormyrids (Denizot et al. 1978) and in the adult *Gymnarchus niloticus* (Srivastava and Szabo 1972, 1973) of the monotypic family Gymnarchidae, the electric organ is rather long and arises from several columns of axial muscle (up to about a third of a fish's length); (2) The adult organ of mormyrids, which functionally replaces the larval organ at about 60-80 days of age

(Kirschbaum and Westby 1975; Westby and Kirschbaum 1977, 1978), is short and compact, and located in the caudal peduncle of the tail fin (Szabo 1958, 1961; Bruns 1971).

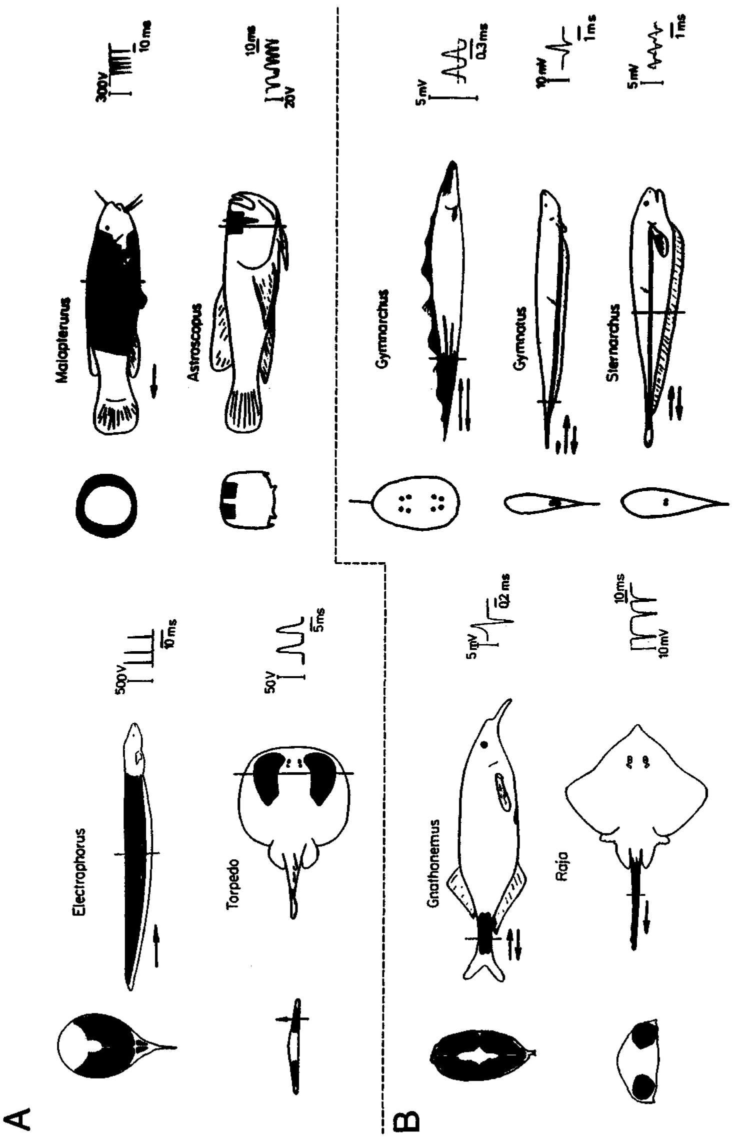
In the strongly electric catfish, the electric organ is formed by peripheral muscle cells (apparently from pectoral muscles; reviewed in Schikorski et al. 1992) such that the catfish's body is enclosed by a tight jacket. In another group of smaller catfishes, the squeakers (Mochokidae), a few of which have recently been discovered to generate very weak electricity, the organ appears to be derived from sonic muscle dorsal to the swim bladder (Hagedorn et al. 1990).

In most South American knifefishes (Gymnotiformes, except the Apteronotidae), the electric organ resembles that described for *Gymnarchus*, except that gymnotiform electric organs tend to be very long, running from almost the tip of the tail to somewhere near the pectoral fins. Some gymnotiforms have accessory electric organs the function of which is unclear. In one gymnotiform family, the Apteronotidae, the electric organ is formed from the presynaptic endings of spinal motor nerves. Apteronotids, like their fellow gymnotiform family sternopygids, have a temporal larval organ of myogenic origin (Kirschbaum 1983). The electric eel has three organs: the weak organ of Sachs, the strong Main organ, and Hunter's organ which seems to contribute to both the strong and weak discharge. The stargazer has part of its eye muscles transformed to an electric organ (for review, see Bennett 1971a; Bass 1986).

The dipole fields generated by electric organs usually are horizontally oriented, in a fish's long axis; so is the orientation of the electric organ. In a few cases, however, the field vector (that is, current flow) is vertically oriented; the same holds true for these fishes' electric organs. In the strongly electric rays and the stargazer this is in accordance with these fishes' vertically directed prey capture behaviour (see Chaps. 5.1, 5.5).

Strongly electric fishes all have a monopolar pulse discharge which seems to lead to most effective shocking of the prey or predator (especially if repeated at high frequency). Polarity is a fixed species character but does not seem to be functionally critical, as examples for both polarities exist (either head-positive or head-negative in horizontally attacking fish, or else either dorsal-positive or dorsal-negative in vertically attacking fish). Weakly electric fishes often have bipolar or even more complex discharge waveforms. The polarity of the first phase of a pulse, if there is more than one, is positive or negative, depending on the species..

A typical electric organ of myogenic origin consists of several stacks of orderly arranged, flattened cells with each cell innervated separately by a spinal electromotor neuron (Fig. 3.2). Because the whole organ is enclosed by a tight jacket of connective tissue, there are only little shunt currents, and the voltage differences generated by the individual electrocytes add up. The electric current generated by the organ is


A
Electrophorus
500V
10ms
Torpedo
50V
5ms
Malapterurus
300V
10ms
Astroscopus
10ms
20V
B
Gnathonemus
5mV
0.2ms
Raja
10ms
10mV
Gymnarchus
5mV
0.3ms
Gymnotus
10mV
1ms
Sternarchus
5mV
1ms

channelled such that it must leave the body in order to return to the opposite pole of source (this is important in freshwater fishes with water conductivity, usually below 100 μS/cm in the tropics, being considerably lower than that of the body fluids which is about 5000 μS/cm).

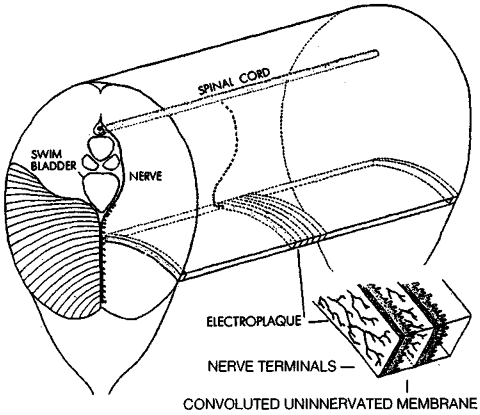


Fig. 3.2: Main organ of the electric eel (*Electrophorus electricus*) in a schematical representation. Note serial arrangement of electrocytes or plaques. Electromotor nerves dotted. The enlarged detail of two neighbouring electroplaques shows branched nerve terminals and convoluted membranes of the uninnervated face. (From Grundfest 1960)

In strongly electric fishes, impedance matching to the surrounding water is especially obvious, both on a gross morphological level and also regarding membrane physiology. In freshwater fish, such as the South American strongly electric eel, we only find about 70 columns in parallel consisting of about 6000 electrocytes each. Therefore, in this fish it is the voltage that is maximized (up to at least 500 V). In a marine environment this would not be possible; here it is the current that should be maximized. Accordingly, in the strongly electric ray there are many relatively short columns in parallel, yielding a low voltage-strong current output. The number of columns is 500-1000, the number of electrocytes per column about 1000 in *Torpedo*. The discharge amplitude is only 50 V in air, corresponding to a massive power output of greater than 1 kW at the peak of the pulse. For an unknown reason marine electric fish generate (unusually large) postsynaptic potentials (PSPs) instead of muscle action potentials.

Fig. 3.1: Some electric fishes and their organs. **A** strongly electric, **B** weakly electric. Electric organs are black. A cross-section through the organ is shown, as taken from the level of the *vertical bar* (in Gnathonemus, the whole cross-section between vertebral column and skin is electric organ). *Arrows* indicate the direction of current flow (monopolar in all strong-electric fishes and in *Raja*); their relative length indicates amplitude of phases if there are more than one. *Torpedo* and *Raja* are cartilaginous fishes, all others are teleosts. *Astroscopus*, a stargazer (Perciformes); *Malapterurus*, the electric catfish (Siluriformes); *Gymnarchus* and *Gnathonemus*, Mormyroidei; the remaining are Gymnotiformes. (Adapted from Bennett 1971a; Libouban et al. 1981; Bratton and Ayers 1987; Lissmann 1963; Denizot et al. 1982; Scheich 1982; Bass 1986)

An electrocyte generates an extracellularly measurable potential difference, that is, becomes a dipole current source, by neurally evoked depolarization of its innervated membrane (Fig. 3.3; Altamirano et al. 1953). Like in any vertebrate motor endplate (or neuromuscular synapse) for which electric organs continue to be preferred study objects, this is achieved by the secretion of acetylcholine. The uninnervated face may be inactive (as in all strongly electric fish), yielding monopolar EODs (Fig. 3.3).

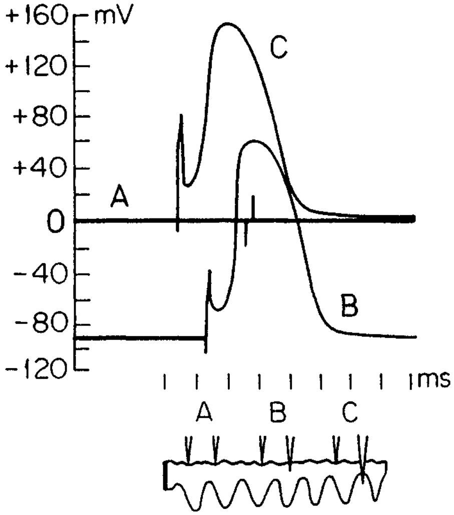


Fig. 3.3: Recordings from an electrocyte of the electric eel; electrode pair arrangement indicated below. **A** With both electrodes extracellularly close to the same face of an electrocyte, no potential difference is recorded. A large resting potential of -90 mV is seen when one electrode is advanced into the cell (**B**) which disappears on leaving the cell on its opposite face (**C**). An action potential evoked by a brief electrical stimulus (note diphasic artifact) is seen both in electrode arrangements **B** and **C**, that is, not only in intra- but also in an extracellular recording (**C**), of undiminished amplitude. In the electric eel the extracellularly recorded potential is very large by its substantial overshoot. (From Bennett 1971a)

Each electrocyte is excited separately by a motor nerve because the excitation of one electrocyte tends to prevent its neighbour cell from firing (the innervated face of the next cell in series with an electrocyte is hyperpolarized by the current of the active cell). In order to be effective, a neural command signal has to reach each cell synchronously. In fishes with long organs, conduction time is kept constant by certain mechanisms, such as nerves running in loops or by the variation of nerve fibre diameter, ensuring synchronous firing of all cells (Bennett 1971a).

In many weakly electric fishes the uninnervated face of an electrocyte is excited electrically by the current generated by the opposite cell face. The result is a biphasic pulse, because the action potential of the uninnervated face is of opposite polarity and delayed by a fraction of a ms (Fig. 3.4). There is little or no net current associated with these discharges.

A basically biphasic pulse waveform may be modified by the consequences of morphological or physiological complexities. For example, some fishes have additional smaller organs that are fired in a certain phase relationship to the main organ, sometimes of opposite polarity; or electrocyte stalks may turn around and penetrate the cell so that it contacts the motor nerve on the opposite (uninnervated)

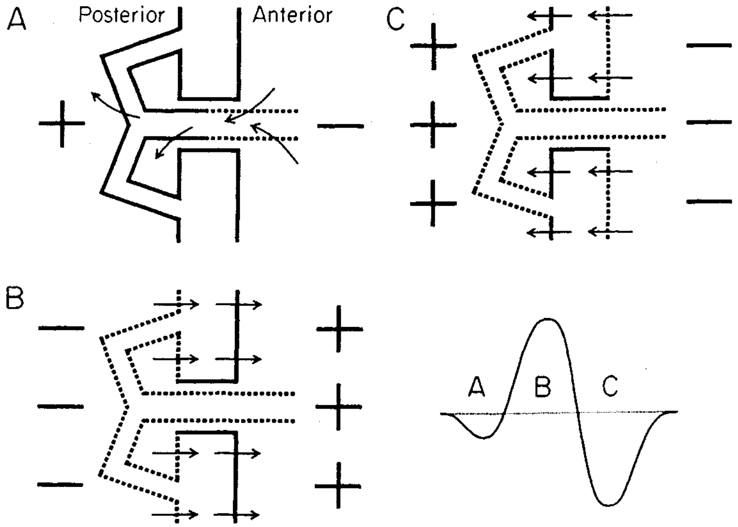


Fig. 3.4: Schematic explanation of a biphasic electric organ discharge (EOD) of a mormyrid, which in certain species is preceded by a smaller prepotential (*A* in EOD diagram, lower right). *Arrows* show direction of current flow; active membranes are indicated by dotted outlines in order to show which stage in the excitation sequence (**A**,**B**,**C**) corresponds to which phase in the EOD waveform. A head-negative prepotential *(A)* is present whenever the posterior, innervated faces of electrocytes possess stalks that penetrate the electrocyte and contact their motor nerve fibre from the "wrong", anterior face (such as here). Species with regular, nonpenetrating stalks contact their motor nerve fibre from the "correct", caudal face of the cell, and do not show a prepotential. The stalk potential invades the caudal face of the electrocyte, giving rise to the head-positive main phase of an EOD (*B*). The associated current flow through the electrocyte (**B**) triggers an action potential of the opposite, uninnervated face of the cell (**C**), giving rise to the head-negative main phase of an EOD (*C*). (From Bennett 1971a)

side. These stalks may be simple or complex, and they may, in certain species, penetrate an electrocyte even twice (by turning back again), so that the motor nerve contacts the stalks on the "correct" side of the electrocyte. These and other modifications of the basic pattern usually lead to additional phases in an EOD, very often making it characteristic for a species (Fig. 3.4).

An especially great diversity of EOD waveforms is found in the South American Apteronotidae (Kramer 1990a). During ontogeny, their "neurogenic" electric organs develop from nerve cells. Although the larvae of these fishes possess "myogenic" organs arising from muscle tissue (Kirschbaum 1983), their adult organs consist of spinal electromotor fibres (Bennett 1971a). Apteronotids generally discharge at very high frequencies, often beyond those of other electric fishes, or nerve and muscle cells in general (depending on the species, apteronotids discharge at about 500-1800

Hz; Fig. 3.5). But certain members of their sister group, the Sternopygidae, that all possess myogenic electric organs also discharge at very high frequencies (greater than 800 Hz; Kramer et al. 1981).

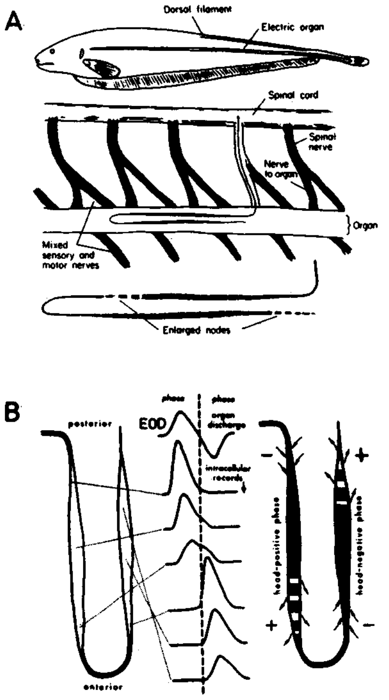


Fig. 3.5: **A** Anatomy of the neurogenic electric organ of an apteronotid (teleosts, Gymnotiformes). The electric organ lies just beneath the spinal cord. A spinal nerve fibre enters the organ, runs headward for several segments and returns to about the point where it entered the organ. The fibre is myelinated and shows a characteristic pattern of nodes and of fibre diameter change. **B** Physiology of neurogenic electrocyte of an apteronotid. *Arrows* Direction of current flow. The upper potential tracing represents a differentially recorded EOD between head and tail; its genesis from two electrocyte potentials of opposite polarities, resulting from the successive excitation of the proximal and the distal, recurrent parts of the electrocyte, is explained in the traces below. The second, delayed potential is evoked by the first one. In these intracellular recordings all potentials are shown as being of the same polarity; however, recorded differentially and extracellularly in rostro-caudal direction, the two potentials from the two parts of the electrocyte have opposite polarities. (From Bennett 1971a)

For a brief introduction into the neural control of electric organs which cannot be dealt with here for limitation of space, see the review by Kramer (1990a). For more detailed reviews see Bennett (1971a); Dye and Meyer (1986); Carr and Maler (1986); Bell and Szabo (1986); Grant (1993). For the electric catfish *Malapterurus electricus*, see Schikorski et al. (1992).

4 The Detection of Weak Electric Fields

The three possible functions of electroreception in fishes are: The detection of prey and other objects, orientation, and electrocommunication. The great usefulness of the electric sense for an aquatic organism is brought home by the fact that among primitively aquatic classes of vertebrates, all major radiations, including even some Amphibia, are electroreceptive; the only exceptions being the enigmatic Myxini, and the Neopterygii among the Osteichthyes (the Myxini are not considered vertebrates by some authors; Blieck 1992; review, Carroll 1993). But even among the neopterygians the electric sense has reevolved in some teleosts (see Chap. 1; Appendix).

Being electroreceptive enables a fish to lead a secret, nocturnal life, undetected by diurnal predators. As no living organism is able to prevent weak electric currents leaking from its body it is of great selective advantage to detect these signals from a distance, even when the potential prey is buried under sand. Also, orientation by environmental electric fields should afford a nocturnal fish to travel considerable distances, thus enhancing its chances of success of finding food, a mate, or a place to rear its young. For a nocturnal fish electric organ discharges are advantageous for signalling during reproductive behaviour, as the spread of chemical signals (pheromones) is difficult to control in the water, and mating calls may attract predators (however, the small mormyrid *Pollimyrus isidori* attracts females to its territory by mating calls; see Chap. 5.2.4.). In addition, electric organ discharges are a means to actively explore the physical properties of a fish's environment, that is, the presence and electrical properties of objects.

Electroreceptive fishes seem to have a "competitive edge" over aquatic invertebrates and the non-electroreceptive fishes (that is, the majority of teleosts), as they have a "private" communication channel. The functions of electroreception are best understood in relation to the sensors: ampullary electroreceptors on the one hand, tuberous on the other. This is because functional criteria, like "passive" *versus* "active" electroreception, or the sensitivity for certain frequency ranges, overlap for both receptor types, although a segregation of function in those fishes which have both is clearly detectable.

4.1 Functions of Ampullary Electroreceptors

Electroreceptors may operate in the "active" or "passive" mode (Kalmijn 1988). "Passive" would be the detection of fields of extraneous origin while "actively" operating electroreceptors detect the fields generated by the fish itself, either by its electric organ discharge (in the case of an electric fish), or by its motion through the earth's magnetic field (in the case of a marine elasmobranch, and perhaps some other fishes; see below).

4.1.1 Passive Mode

Ampullary electroreceptors detect weak electric fields of extraneous origin in the passive mode (for example, Peters and Bretschneider 1972; Peters and Meek 1973; Pals et al. 1982; review, Kalmijn 1988). Geochemical and electromagnetic fields of sufficient strength are found in natural waters; bioelectric fields emanate from prey organisms. The spectral frequency content of these fields is low (or even D.C.). Famous examples are the sharks which detect the bioelectric fields generated by their prey using their electroreceptors, the ampullae of Lorenzini (review, Kalmijn 1988).

4.1.1.1 Prey Detection

Bioelectric D.C. and low-frequency fields have been measured from all living marine and freshwater organisms that have been studied (see Chap. 3.); especially strong fields are generated by wounded organisms (review, Kalmijn 1974). Electrically evoked feeding responses have been observed not only in sharks (Kalmijn 1974) and stingrays (Blonder and Alevizon 1988) but also in freshwater teleosts, such as catfish or weakly electric fish (review, Kalmijn 1988) and salamanders (Himstedt et al. 1982; Fritzsch and Münz 1986) which all have ampullary, low-frequency electroreceptors.

The dogfish *Scyliorhinus canicula* and the skate *Raja clavata* proved to be most sensitive to D.C. fields, and almost nearly as sensitive at 1, 2, and 4 Hz (Peters and Evers 1985; Kalmijn 1988). At 8 Hz the threshold had increased by a factor of two. By an attacking fish's motion relative to an electric dipole source, a pure D.C. field is transformed to a low-frequency field (in the frame of reference of the fish's electroreceptors), depending on the distance from the dipole and on swimming speed. The frequency band to which the teleosts responded extended to somewhat higher values compared to the cartilaginous fishes tested (sharks, rays and skates; review, Kalmijn 1988). The observed threshold sensitivities and attack distances were 5 nV/cm and 40 cm in marine sharks, and 5 µV/cm at 5 cm distance in freshwater teleosts.

4.1.1.2 Orientation by Environmental Fields

In the oceans electric fields are generated by the flow of water through the vertical component of the earth's magnetic field, while in freshwater bodies fields of electrochemical, rather than electromagnetic, origin prevail (review, Blakemore 1991). These environmental fields are potential orientational cues as indicated by the behaviour of trained animals (Roth 1969; review, Kalmijn 1988).

In the sea motional-electrical fields from less than 5 nV/cm to up to over 500 nV/cm have been measured. These field strengths are well in the range of sensitivity of sharks, rays and skates (Fig. 4.1) and may inform elasmobranch fishes about their drift with the water, or provide them with orientational cues during their movements in familiar territory.

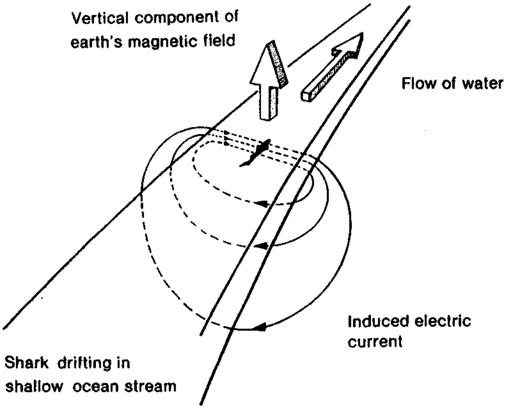


Fig. 4.1: Motional-electrical field of shallow ocean current through magnetic field of the earth. The associated voltage gradients are within the sensitivity of sharks and may be used for orientation by these animals. (From Kalmijn 1988)

Fields of presumably electrochemical origin as observed in freshwater bodies tend to be stronger than the motional-electric fields in the sea. Captive catfish were successfully trained to use a uniform electric field of a minimum of 1 µV/cm for finding home (Peters and van Wijland 1974). A similar result was obtained with weakly electric fishes (review, Kalmijn 1988). Therefore, facts and experiments support the view that electroreceptive fishes may use ambient electric fields for orientation. The fields are of predominantly electromagnetic nature in the ocean, of electrochemical nature in fresh water.

4.1.1.3 The Detection of Communication Signals

Ampullary electroreceptors clearly have a function in intra- and interspecific electric communication. Weakly electric, marine skates communicate by electric organ discharges which are monopolar and hence have a high D.C. component to their amplitude spectrum. The ampullary receptors are sensitive to these low-frequency components; there are no other receptors which could mediate these skates' sensitivity for their electric organ discharges (Bratton and Ayers 1987; Baron et al. 1982).

Also the ampullary electroreceptors of weakly electric, teleost fishes may respond to these fishes' electric organ discharges (Bell and Russell 1978; Bell 1989). Some species' pulse EODs are monopolar; hence, have a high D.C. component like those of skates. But also the biphasic, triphasic, etc., pulse EODs of many mormyrid and gymnotiform weakly electric fishes have low-frequency components of sufficient strength to stimulate these fishes' ampullary receptors, although the amplitude spectra of these EODs peak at high frequencies. As ampullary receptors have a lower threshold to weak electric fields than tuberous electroreceptors, their sensory input should not be neglected. In the mormyrid *Gnathonemus petersii* a fish's reafference from ampullary receptors (which is evoked by its own EOD) is cancelled by an adaptable, central nervous "expectation" mechanism (Bell 1986, 1989, 1993; Bell and Russell 1978).

The wave fish *Eigenmannia*, the EOD of which does not have a D.C. or low-frequency component, may detect the low-frequency amplitude modulation arising from the superimposition of its own electric field by that of a conspecific (Bullock et al. 1972b; see also Kramer 1987, 1990a). This has been shown in the wave fish *Apteronotus leptorhynchus* (Bastian 1987a,b). Also, the spectral low-frequency component associated with social "chirping" (brief offs of the EOD) is detected by ampullary receptors and transmitted to the brain (Metzner and Heiligenberg 1991, 1993). The behavioural significance of this afferent input in fishes with tuberous receptors that are specialised for detecting EODs is not yet clear.

4.1.2 Active Mode

There are two possible instances of active operation of ampullary electroreceptors: when they respond to the electric fields induced by a (marine) fish's swimming through the earth's magnetic field (Chap. 4.1.2.1.), and when receptors respond to an electrogenic fish's own electric organ discharges (Chap. 4.1.2.1.). Both types of sensory responses depend on a fish's own action, and should or do increase with the strength of that action (everything else being equal).

4.1.2.1 A Magnetic Field Compass

There are presently two sensory mechanisms by which organisms may orient in the earth's magnetic field which have experimental support: The first is coupling of permanently magnetic material within or outside the body of organisms to the geomagnetic field. This has been demonstrated in magnetotactic bacteria, and is highly likely in at least some other organisms (Blakemore 1975, 1981, 1991). The second involves electro-orientation through the Faraday effect (Kalmijn 1971, 1981, 1988; Blakemore 1991).

In the putative "active mode" of the ampullary electroreceptors in a marine shark, the strength of the field at a receptor depends on the swimming speed and swimming direction relative to the horizontal component of the earth's magnetic field. The electromotive force which is induced through the Faraday effect is oriented perpendicularly to both the swimming direction and the magnetic field (Fig. 4.2), and is believed to be the basis for the magnetic sense of elasmobranchs. This sensory capacity would offer the fish complete compass data.

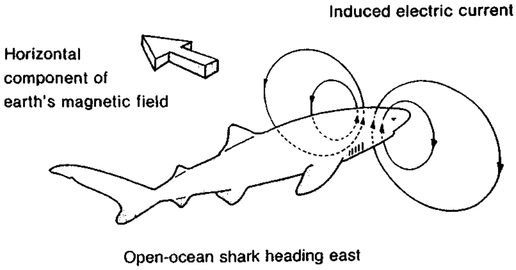


Fig. 4.2: Motional-electrical field of shark swimming through earth's magnetic field in easterly direction. The induced electric current leads to dorso-ventral potential differences which may inform the fish about its compass heading. (From Kalmijn 1988)

Because sea water has a much higher conductivity than the body fluids, the voltage U induced by the fish's movement depends on the speed v and the strength of the horizontal component of the earth's magnetic field B_h:

$$U = \int_{canal} (\vec{v} \times \vec{B_h}) \cdot \vec{ds},$$

s being the length of the ampullary canal (of dorsoventral orientation in a normally swimming shark). For an unambiguous interpretation of the induced electric potentials the animal must probe the magnetic field in different directions (Kalmijn 1988).

By crossing the vertical component of the earth's magnetic field the fish also receives a horizontally oriented, transverse potential. This differs from the predominantly horizontally-oriented field induced by ocean currents by being independent of swimming direction. The field induced by the shark's motion points to the left of the fish in the northern hemisphere and to its right in the southern hemisphere. Together, the transverse and the dorsoventral potentials may give the animal its magnetic latitude. This would enable the fish to navigate in the ocean (Kalmijn 1981).

Training experiments using the stingray *Urolophus halleri* in a circular tank showed that it could discriminate two identical enclosures, one in the magnetic east, the other in the magnetic west. When the earth's magnetic field (horizontal component) was reversed by the aid of Helmholtz coils the ray chose the other enclosure in most cases (Fig. 4.3) (Kalmijn 1981).

The experiments also showed that the stingray could, in strictly horizontal magnetic fields as found on the equator, detect the polarity of the field. Birds are believed to be unable to detect the sense of the magnetic field in equatorial regions, and it is not known how they solve the 180° ambiguity during their transequatorial migrations (for review, see Berthold 1994).

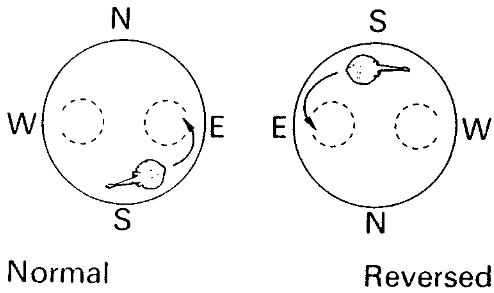


Fig. 4.3: A stingray's discrimination of two similar enclosures, one in the magnetic east and the other in the magnetic west. In the magnetic east the fish received a reward, and a punishment in the west. The magnetic field was reversed from trial to trial in random order, and the stingray changed its preference of enclosure accordingly. The experiments were done in a circular fibreglass tank of 1.8 m diameter. (From Kalmijn 1981)

In electroreceptive freshwater fishes this electromagnetic compass mechanism probably does not apply (Kalmijn 1988; Blakemore 1991): firstly, freshwater catfishes and weakly electric fishes are at least two orders of magnitude less sensitive to low-frequency electric fields than are marine elasmobranchs; secondly, the induced electric fields are weaker in fresh water than in sea water (by about 30%).

In teleost fishes lacking electroreception, especially in migratory species such as eels, salmon, tuna, and trout, a keen geomagnetic responsiveness has also been established (Tesch 1974; Rommel, Jr. and McCleave 1972, 1973; Quinn 1982; Walker 1984; Chew and Brown 1989; and others). Blakemore (1991) considers a sensory mechanism incorporating biogenic magnetite the most likely explanation for these fishes' long-distance orientation.

4.1.2.2 The Detection of Object Location and Communication Signals

An electrogenic fish's ampullary electroreceptors may detect its own electric organ discharges (reafference). This is certainly true in the extremely sensitive receptors of marine skates and rays (weakly and strongly electric, respectively), although we do not yet know for sure the significance of this sensory input. It could be, similar to tuberous electroreceptor reafference in weakly electric teleosts, active object detection, as suggested by Baron et al. (1985); there is, however, no evidence in support of this hypothesis. Alternatively, ampullary sensory input evoked by a skate's or a ray's own EOD might serve as a reafference, thus enabling the fish to discriminate its own EODs from those of neighbours.

Active object detection in a nonelectric catfish (*Ictalurus nebulosus*) sounds impossible but has recently been demonstrated (Peters and van Wijland 1993). The fish uses the bioelectric D.C.-field associated with the regulation of its ionic balance in order to detect conductivity anomalies close to its ventral region.

The significance of reafferent ampullary information is unknown for weakly electric teleosts; perhaps it is simply unavoidable. In the mormyrid *Gnathonemus petersii* the reafferent input from the ampullary receptors, responding to the low-frequency content of a fish's own discharge, is blanked by an adaptable, central nervous "expectation" mechanism (Bell and Russell 1978; Bell 1989, 1993); this blanking is unknown for other fishes' EODs and does not seem to occur in Gymnotiformes.

The ampullary receptors of wave gymnotiforms probably detect the sudden amplitude change of their wave EOD caused by the introduction of an impedance inhomogeneity in the water next to a fish. In the high-frequency fish *Apteronotus* ampullary electroreceptors contribute to active electrolocation, although only in a minor way (Bastian 1987a). The interaction of *Eigenmannia*'s wave EOD with that of a conspecific produces beats the low-frequency component of which might be detected by ampullary receptors. Because of the particular physiology of *Eigenmannia*'s electric organ (Bennett 1971a), a D.C. current is generated for a short time whenever the fish turns off its discharge. Brief "offs" commonly occur during social signalling; the associated D.C. signals can be detected by ampullary receptors (Metzner and Heiligenberg 1991, 1993).

4.2 Functions of Tuberous Electroreceptors

Tuberous electroreceptors are the specific receptors weakly electric teleosts, the Mormyroidei and the Gymnotiformes, have evolved to detect their own electric organ discharges, or those generated by their conspecifics and members of other species of electrogenic fishes (see Chap. 2.2). Accordingly, tuberous receptors are usually tuned to much higher frequencies than ampullary receptors, although some are in addition sensitive in the low-frequency range (reviews, Zakon 1986, 1988). The functions of tuberous receptors are: (1) active object detection (electrolocation; Chap. 4.2.1); (2) probably to support the location strategy by which other electric fishes may be found from a distance (see Chap. 4.2.2); (3) the transmission (encoding) of electric organ discharge displays, as received from other electric fishes (Chap. 4.2.3).

Tuberous receptors form part of an active sensory system which also functions passively. There are two types of tuberous electroreceptor in weakly electric fish (Mormyroidei and Gymnotiformes), one operating primarily in the active, the other primarily in the passive mode (see Chap. 4.1). However, both can - and normally do - also operate in the other mode; for example, when tuberous electroreceptors analyse the interaction pattern of a fish's wave discharge superimposed by that of a conspecific, a situation that defies any classification along the active/passive scheme.

4.2.1 Active Object Detection by Electric Organ Discharges

Active object detection or electrolocation dependent on electric organ discharges is an evolutionary feat only found in the teleost fishes Mormyroidei and Gymnotiformes from tropical freshwater bodies (Lissmann 1958, 1963; Lissmann and Machin 1958; recent reviews, Bastian 1986, 1990, 1994). Electrolocation is based on a complex sensorimotor system comprising the electric organ that generates a test signal, tuberous electroreceptors that are coadapted to the spectral properties of the fish's own organ discharge, and huge brain regions specialized to perform complex computations on the signal (the electric organ discharge), as received from and modified by the environment (reviews, Bennett 1971b; Szabo 1974; Szabo and Fessard 1974; Bullock 1982). In its function and complexity, this system is comparable to the echolocation, or SONAR, system of bats (for example, Neuweiler 1984, 1993; Pollak and Casseday 1989; Suga 1990), although in electric fishes the range of the system is severely limited by physical constraints (Knudsen 1975; Bastian 1994).

In addition to the different forms of physical energy used for the test signal in both systems, the two differ in many regards, however. Thus fishes not only detect the presence of an object, if sufficiently close, but also its insulating or conducting properties relative to water (which would obviously not be possible in air, nor using acoustic signals). The impedance of an object may be due to ohmic or capacitative properties (Scheich and Bullock 1974) which are detected and discriminated by the fish (Meyer 1982; von der Emde 1990; von der Emde and Ringer 1992; von der Emde and Ronacher 1994). Live organisms have considerable capacitative properties (Schwan 1963).

Fish also detect the movement of an object. While relative movement between a bat and its target results in a Doppler frequency shift of the echolocation calls (which the bat uses to compute relative velocity; Schnitzler 1968, 1972), there is no such frequency shift due to movement in electric signals as received from the aqueous environment. However, the spectral properties of an organ discharge, as seen by a local electroreceptor in the fish's skin, may be changed by a sufficiently close object with high capacitance, depending on the spectral properties of the organ discharge (von der Emde 1990).

The field distortions caused by objects of a conductivity different from that of the surrounding water are detected by the fish as a change of the transepidermal voltage gradient in the area of the skin next to the object (in the direction of the voltage

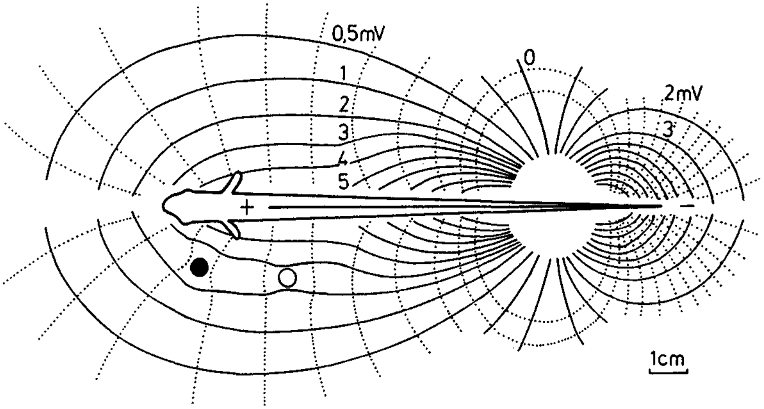


Fig. 4.4: Active electrolocation in a weakly electric fish. Horizontal section through the electric field generated by a fish's organ (indicated by central *line* in the fish's body and tail). The dipole field is shown as the lines of equal current density, or lines of force (*dotted*) which are normal to the isopotential lines (with mV numbers), following their gradient. The EOD waveform as a function of time is also shown (*top*). Note that an insulator (*white circle*) and a conductor (*black circle*) distort the fish's field in opposite ways. The adequate stimulus for local electroreceptors in the fish's skin, which are found by following the dotted current lines, are an increase in current intensity as caused by a conductor, whereas a decrease is caused by an insulator (if sufficiently close). The current intensity is proportional to the voltage gradient across the skin which can easily be measured. (Modified from Scheich 1982)

gradient). Good conductors increase the transepidermal voltage gradient for local electroreceptors while insulators have a decreasing effect (Fig. 4.4).

The effect of an object on the transepidermal voltage difference decreases as the negative second power of the distance of the object from the skin, severely limiting the range of active electrolocation. Doubling of the object's distance results in a reduction of the useful signal, the change in transepidermal voltage at a local electroreceptor, to one-quarter. Consequently, the behavioural detection limit of plastic or glass rods of 2-4 mm in diameter was found to be only 2-4 cm in weakly electric fishes (Lissmann and Machin 1958). In precisely controlled experiments fish detected moving targets both by their mechanical and electrical cues, but earlier (that is, at slightly greater distances) electrically (Bastian 1987b). In contrast to mechanical cues, the electrical cues also provide information about the nature of the object.

In the Mormyridae the electroreceptors supporting active object location are the mormyromasts (with their two types of sensory cell), whereas the reafferent input from the Knollenorgane, the other type of tuberous electroreceptor, is blocked by a corollary discharge in the brain that is associated with the central-nervous organ command (see Chap. 3.2). The Knollenorgane are, therefore, not involved in active object location.

In gymnotiform wave fishes tuberous receptors are of the P and T type while in gymnotiform pulse fishes these are called B and M receptors (see Chap. 2.2). Like mormyromasts in mormyrids, P and B type receptors code for stimulus amplitude; therefore, they are definitely involved in active electrolocation. T and M type receptors are sensitive for small changes in the timing of electric organ discharges and thus probably mediate these fishes' sensitivity for capacitative shunts. Therefore, in gymnotiforms probably both types of tuberous receptor are involved in active object detection (Bastian 1987a).

4.2.2 Localizing an Electric Fish as a Dipole Source

How does an electric fish find another electric fish for their nocturnal courtship and mating to take place? At the beginning of a courtship night a male *Pollimyrus isidori* (Mormyridae) tries to attract females to its territory by mating calls of presumably long range compared to that of its EOD, of relatively weak amplitude (Crawford et al. 1986; Bratton and Kramer 1989). Acoustic signalling is, however, unknown in gymnotiforms, and even in *P. isidori* acoustic signalling begins to wane at the earliest convenience after establishment of contact with a female. For the rest of a spawning night (several hours), communication is based on the electric channel (Bratton and Kramer 1989) which is far more "private" than the acoustic channel (all predators can hear but only a few are electroreceptive).

From the dipole equations for a volume conductor (see general physics textbooks) it is clear that the signal generated by an electric organ discharge has a short range, only. The field potential V (relative to a distant point) falls off with the inverse square of the distance, while the field potential gradient E (a vector) decreases even more steeply, with the inverse cube of the distance. The communication range, or active space, is of elliptic shape (Fig. 4.5), and depends on a number of parameters; among the most important ones are the strength of the signal generated at the source (the dipole moment), and water conductivity (Knudsen 1974).

Within limits, a lower water conductivity extends the communication range (Knudsen 1974; Squire and Moller 1982). However, too high a water resistance may lead to EODs of abnormal, prolonged waveform, or to an incomplete organ discharge (Bell et al. 1976; Bratton and Kramer 1988; Kramer and Kuhn 1993). Electrogenic teleosts are adapted to tropical home waters of low conductivity, and 20 μS/cm (or 50 k$\Omega \cdot$ cm resistivity) does not seem to be too low for any species, some being able to cope with water of only 10 μS/cm (or 100 k$\Omega \cdot$ cm) without any impairment of their EOD (Kramer 1990a).

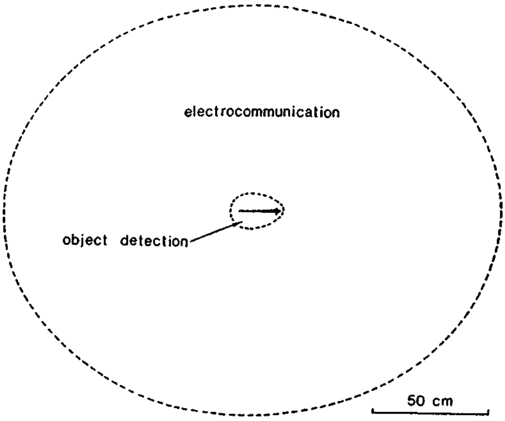


Fig. 4.5: The range of electrocommunication as compared with that of active electrolocation in *Eigenmannia,* in water of 500 μS/cm conductivity. The range of electrocommunication is inferred from electric field measurements and sensitivity data; the range of object detection is shown for a 2-mm plexiglass rod. (From Knudsen 1975)

In a small mormyrid, *Brienomyrus niger,* the behaviourally determined communication distance (its reach) was 135 cm (perhaps even 157 cm; or a field gradient of 10 μV/cm), as measured at a quite natural water conductivity of 52 μS/cm (Squire and Moller 1982). More recently, electrical communication between a pair of distant *B. niger* was demonstrated at a still lower field gradient of only 1 μV/cm (Moller et al. 1989). At an unnaturally high conductivity of 678 μS/cm the communication range was very much reduced to 22 cm (Squire and Moller 1982) (Fig. 4.6).

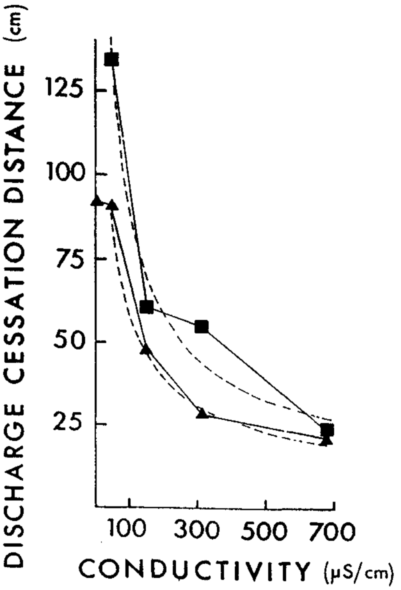


Fig. 4.6: Threshold distance of communication in *B. niger* depends on water conductivity (*abscissa*). *Ordinate* The distance at which a pair of fish first showed a behavioural response when their separation was slowly reduced by the experimenter. *Triangles* Shelter tubes in which fish resided were in end-to-end orientation; *squares,* parallel orientation. (From Squire and Moller 1982)

When one electrogenic teleost approaches another (or a dipole source) it does so by following the curved current lines (or field gradient). When starting its journey, the fish seems to know neither the location nor the distance of the target, but finds it by following the current lines by a trial-and-error strategy, similar to klinotaxis (Davis and Hopkins 1987; Schluger and Hopkins 1987; Hopkins 1993). There is, however, evidence that the pulse fish *Gymnotus carapo* approaches the source of unusual or non-conspecific electrical pulse waveforms by a more circuitous route compared to the source of conspecific EODs (Scudamore and McGregor 1993).

4.2.3 The Detection of Communication Signals

Besides their role in active object detection, the tuberous electroreceptors of weakly electric teleosts support electrocommunication. Elephantfishes (Mormyridae) have a low-threshold communication receptor, the Knollenorgan, while in gymnotiforms both types of tuberous receptor are probably involved.

Communication signals must be detectable, recognizable and memorable (Guilford and Dawkins 1991). Detectability depends on the response, or filter, properties of electroreceptors to electric stimuli, especially the tuning to a certain passband of frequencies (review, Zakon 1988). Generally, the range of frequencies transmitted by tuberous electroreceptors corresponds to the spectral properties of a species' EOD, that is, the range of frequencies with high amplitudes. In pulse-discharging fish, spectral filtering of the EOD tends to be weak (tuberous electroreceptor tuning-curves often being almost flat over most of the range of interest); this is not so in wave-discharging gymnotiforms, where tuberous electroreceptors (especially T units) may have filter slopes of up to about 50 dB/octave on the high-frequency side, of up to 20 dB/octave on the low-frequency side (Zakon 1987, 1988).

In contrast to the exceedingly sharp tuning of some auditory neurons in some higher vertebrates, very sharp filtering does not occur in tuberous electroreceptors, not even in wave fishes. For example, peripheral auditory neurons in bats may have filter slopes of up to 3500 dB/octave (Suga et al. 1976; Suga 1990). The relatively mild filtering by tuberous electroreceptors (virtually no filtering in some pulse fishes) affords the fish considerable advantages: the frequency range transmitted by the receptors is broad, and signal distortion by sharp filtering presumably minimal. Broad passbands in tuberous electroreceptors are useful in both intra- and interspecific social encounters because the intraspecific range of EOD frequencies (in wave fishes) or pulse durations (in pulse fishes) is often considerable. For example, the EOD frequency of the wave fish *Eigenmannia* varies by 2½ octaves at constant temperature among different individuals, while the of *Marcusenins macrolepidotus'* pulse discharge even varies by a factor of 13 (356 *vs.* 4779 μs; Kramer submitted).

To recognize a communication display involves the faithful transmission of the discharge rate modulations by tuberous electroreceptors, and analysis through higher neuronal mechanisms. Apart from the central-nervous blanking mechanism of a mormyrid's reafferent Knollenorgan responses to its own EOD (Bell 1989, 1993), very little is known about the Knollenorgane in mormyrids and M receptors in pulse-discharging gymnotiforms; this is also true for the T receptors in wave-discharging gymnotiforms (*Eigenmannia*), except in the context of the jamming avoidance response (see Chap. 5.4.2.2), usually involving only small frequency changes of a few Hz which do not appear to be social displays.

Behavioural discrimination performances have also been very little studied. The pulse-discharging mormyrid *Pollimyrus isidori* discriminates pulse trains of constant rate which differ by as little as 2%. These training experiments also tested for a good memory, because the alternative stimuli were not presented pairwise, but well separated in succession (Kramer and Heinrich 1990); therefore, the detection of a 2% variation is a remarkable result. Selected humans, when tested in similar fashion using sound clicks, did no better than non-selected *P. isidori* stimulated with electrical pulses (Kramer and Heinrich 1990).

In training experiments using bursts of sine waves alternating in frequency, that is, with direct comparison of the alternative stimuli, the wave-discharging gymnotiform *Eigenmannia* was able to discriminate frequency differences of as little as 0.52 Hz at a frequency which was close to its discharge frequency, about 400 Hz (Kramer and Kaunzinger 1991). A very similar value was found using the spontaneous jamming avoidance response (Kramer 1987; Chap. 5.4.2.2).

A frequency discrimination threshold of only 0.11% (0.17% in the worst case) in *Eigenmannia* is by far the lowest discrimination threshold for an octavo-lateralis line system. In a selected range of frequencies, this threshold is lower than the lowest value ever published for the human in the acoustic modality, which is 0.16% under optimal conditions using selected individuals (Wier et al. 1977); only 0.7% according to other authors under what appears to be more typical conditions (Zwicker 1982).

About the memorability of different communication displays very little is known. It appears that on the basis of the interindividual variation of discharge waveform, individual discrimination or even recognition is possible. Examples where this has been tested experimentally, with positive results, are: the mormyrid *Pollimyrus isidori* (Graff and Kramer 1989, 1992); another pulse-discharging fish, the gymnotiform *Gymnotus carapo* (McGregor and Westby 1992); and a wave-discharging gymnotiform fish, *Eigenmannia* (Kramer and Otto 1988). Play-back experiments of pre-recorded (or simulated) EOD activity, including pulse rate modulations as observed during rest or aggression in mormyrids (Kramer 1979) and the gymnotiform *G. carapo* (Black-Cleworth 1970; Westby 1974), evoked statistically significantly different rates of attack behaviour and other responses on the dipole model from the receiver fish; hence, the different display patterns used for play-back were probably discriminated by the fish.

Interspecific discrimination of natural, pre-recorded time interval sequences of EODs has been demonstrated in mormyrids when no other cues, except the artificial electrical pulses, were available. The discrimination of conspecific EOD activity from that of the members of other species appears to be based on the recognition of EOD time interval patterns characteristic for each species; the discrimination works even when the mean pulse rates and the statistical EOD interval distributions (or histograms) are identical for a pair of heterospecific EOD activities presented to a fish (Kramer and Lücker 1990; Kramer and Kuhn 1994).

In summary the little we know about frequency or pulse rate discrimination in weakly electric fishes suggests that weakly electric fishes are extremely sensitive to these kinds of signal variation. This includes the discrimination of different pulse interval sequences with identical mean pulse rates.

Weakly electric fishes tend to lock their EODs to a specific phase (or latency) within the discharge cycle of a conspecific; this has been observed in both pulse and wave fishes (Fig. 2.6). In mormyrids, for example, the preferred latency response is an echoing of the EOD pulses of one fish by those of another at a fixed latency of around 12 ms (at each discharge cycle, or occasionally skipping one or a few discharge cycles)(Kramer 1974; Russell et al. 1974; Bauer and Kramer 1974). The response also occurs in a negative form, the preferred latency avoidance (Kramer 1978). Its behavioural significance is not quite clear; sensory gating - keeping the degree of sensory adaptation constant by locking to the other fish's EOD at a fixed latency - seems to be involved (see Kramer 1990a).

Similar phase-related discharge behaviour was observed in some pulse-discharging gymnotiforms which discharge at more constant pulse rates compared to mormyrids; hence, periods of EOD coincidences, beats, would occur quite regularly and predictably in a pair of fish discharging at slightly different rates. To avoid such beating, fish may phase-couple their discharge to that of their opponent (Heiligenberg 1974; Heiligenberg et al. 1978; Westby 1975b, 1979; Langner and Scheich 1978; Gottschalk and Scheich 1979). A function in jamming avoidance and sensory gating has been demonstrated which is clearly important in the presence of sensory input from a neighbour's discharges tending to disrupt a fish's own sensory input.

5 Communication by Electric Organ Discharges: Strategies

In the skates, but especially the Mormyroidei and the Gymnotiformes, electrocommunication is rich and complex, and clearly an important factor in these fishes' lives. Electrocommunication seems of less importance, in strongly electric fishes. There are two phenotypes of EOD in the Mormyroidei and the Gymnotiformes, wave and pulse, both of which encode social signals as discharge rate modulations. The pulse EODs of certain species resemble the time course or waveform of an action potential of a muscle fibre. The wave EODs of other species are relatively broad pulses that are repeated at such a high and regular rate that they merge into a continuous wave (Fig. 2.6).

While a pulse fish, although discharging continuously, is silent most of the time (because the duration of an EOD is short compared to the inter-EOD interval), a wave fish's signal is always "on" (except on rare occasions, a brief "off" being a display of social significance).

We are still unable to identify the selection pressures which shaped the ancestors of certain Mormyroidei and certain Gymnotiformes to discharge their organs either in pulse or in wave form, with only one living species that may represent a transitional state (Fig. 3.18 of Kramer 1990a). Wave and pulse fishes are found on both continents which are home to weakly electric fishes: the Mormyroidei in Africa and the Gymnotiformes in South America. The intricate pattern of speciation in the tropics, leading to the highest degree of biodiversity on earth, is a subject of prime interest (Fittkau 1985; Colinvaux 1989; Terborgh 1991; Grabert 1991).

While in Africa the wave discharge type is represented by a single species, *Gymnarchus niloticus*, the only living member of the Gymnarchidae, there are two families of wave fishes in South America, the Sternopygidae, and the large family of Apteronotidae (with their neurogenic electric organs). In contrast to Africa, in South America wave species are far more numerous than pulse species (Kramer et al. 1981; Kramer 1990a).

Although it is not possible to clearly separate wave from pulse species by their modes of life or habitat selection, "advantages" and "draw-backs" of the two signal types can clearly be seen from a communication engineer's point of view.

The harmonic content of a periodic signal, such as the wave discharge of an *Eigenmannia*, is detected by spectral amplitude analysis, such as Fourier analysis. According to J. Fourier's theory of 1812, any periodic signal may be represented by a series of sine waves (see, for example, Herivel 1975; Bracewell 1986; Bracewell 1989). The sine wave of lowest frequency is the fundamental frequency, f_1 or first harmonic. One cycle of this sine wave (of longest duration, T) represents a full repeat of the complex signal waveform; T and f are related by $f=1/T$. Other sine-wave components are also detected the T values of which are of exactly one-half, one-third, etc., duration, and represent the so-called higher harmonics (or overtones in a sound signal); their frequencies are integer multiples of the fundamental frequency. Their relative amplitudes and phase relationships, that is, relative time delays, collectively define the waveform of a signal.

For the human the tone quality or timbre of a sound signal is determined only by the relative amplitudes of its harmonics. For example, the sound of a flute is poor in overtones (especially in the upper register); therefore, it sounds "dull" compared to a violin with its more "brilliant" tone which is due to its series of intense overtones.

A wave discharge, such as the one shown in Fig. 2.6, has a harmonic amplitude spectrum, in contrast to a pulse discharge which is broad-band. A harmonic spectrum shows energy only at the fundamental frequency, f_1, and its harmonics. A pulse discharge, by contrast, has a continuous spectrum ranging from very low to high frequencies, with a broad peak region. The sound of clapping one's hands, for example, produces a similar spectrum.

Because wave fishes generally discharge at higher frequencies (depending on the species, about 50-1800 Hz) compared to pulse fishes (from below 1 to about 65 pulses per second at rest), most wave fishes receive more sensory feedback per unit of time than do pulse fishes. However, in the context of active electrolocation, pulse fishes may be at an advantage: their broader amplitude spectra which also contain higher frequencies may be better suited to detect a wide range of capacitative impedances of objects (von der Emde 1990).

On the other hand, the harmonic spectrum of wave fishes strongly contrasts from the background noise which is especially high in tropical freshwater bodies because of an intense atmospheric activity combined with a low water conductivity that attenuates electric fields relatively weakly (Hopkins 1986).

To compensate for the low spectral contrast from background noise, weakly electric pulse fish have a rather strong EOD amplitude. A wave fish's EOD is so stable in frequency that it contrasts strongly from the background noise (Bullock 1970; Kramer 1987); for a reasonably good estimation of the frequency jitter a 10-MHz clock is needed. There is no need for a pulse fish to discharge at a particularly stable rate, although some do (for example, among the gymnotiform family Rhamphichthyidae). The Mormyridae are well known for their seemingly "irregular" EOD patterns at rest.

Both electrical phenotypes encode their social displays by discharge rate modulations. While those of the wave fish are rather simple (ranging from brief "offs" to frequency increases or decreases, followed by resuming to discharge at the original frequency), there may be a whole plethora of discharge rate modulations, or patterns of EOD intervals, in pulse fishes, especially the mormyrids (Chap. 5.2.).

Strategies of jamming avoidance, or behaviours facilitating the discrimination of a fish's own EODs from those of its neighbours, are found in both discharge phenotypes. In wave fishes this may consist of an EOD frequency shift away from the frequency of a neighbour's EOD that is too close (both physically and in frequency). The sensory problems associated with masking by "social noise" from conspecific wave fishes are turned into advantages by beat analysis. A pulse fish delays its own EOD in response to another fish's discharge. The coexistence of two or more individuals thus involves frequency-sharing of the electrical communication channel in wave fishes, time-sharing in pulse fishes (Chaps. 5.4.2.2 and 5.2.6; see also the recent review, Kramer 1994).

5.1 Rays - Batidoidimorpha

Electric rays (Torpedinidae). Electric rays, such as *Torpedo* or *Narcine*, discharge their strong electric organs in volleys only during prey capture behaviour, or during defence. An intraspecific communication function cannot be excluded, but as yet there is no evidence in support of such a hypothesis.

Prey capture is a stereotyped electrical and overt motor behaviour in *Torpedo marmorata*, an Atlantic ray of the French coast the behaviour of which was studied in great detail (Belbenoit 1970, 1986; Belbenoit and Bauer 1972). A ray is an ambush predator with a flattened, disc-shaped body (and short tail) that is usually buried under the sand, with only its eyes and spiracles visible. A ray will start its predatory attack whenever a fish (or an artificial object) comes sufficiently close to the front rim of its body (Fig. 5.1). Within half a second, the ray lifts itself up on its pectoral fins (forming a wide gate facing the potential prey), jumping up- and forward. The height of the ray's leap equals half the diameter of its disc-shaped body, while it moves forward for a distance of ⅔ the diameter of the disc. By leaping both upward and forward, in a successful attack the ray lands on top of a prey fish. By rocking movements involving its tail the ray tries to seize with its mouth the head of the prey fish captured and to swallow it; this can take from 7-24 seconds.

Despite the relative speed and precision of this remarkable prey capture behaviour, a ray normally would risk starvation because its prey, probably mainly teleost fishes, are just too smart and quick. It is the ray's strong electric discharge (with the voltage gradient vertically oriented; see Chap. 3.1.) which greatly enhances its success rate. The organ is fired 80 ms after the onset of a ray's jumping attack. The pulse volley can be as short as 0.1 s (when the prey has escaped) or as long as 24 s, corresponding to 20-340 discharges (this is in contrast to the very brief reflex discharge evoked by touching a ray with a wooden stick). The discharge rate is high and stable up to the moment of landing (140-290 pulses per second); afterwards, while the ray tries to manoeuvre its prey to its mouth, the pulse rate becomes low and unstable (<10 pulses per second after 3 seconds of discharging).

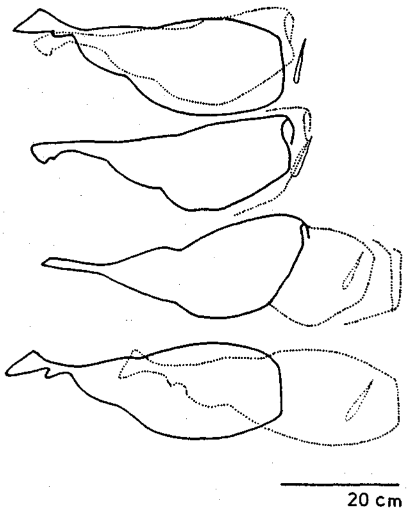


Fig. 5.1: A strongly electric ray's prey capture behaviour (redrawn from video recordings). Initially the ray is buried under sand and immobile (top panel, *line*). On receiving mechanical stimuli from a fish passing by the front rim of the ray's disc-shaped body, the ray rises on its lateral fins within half a second (top panel, *dotted line*), and leaps upward and forward (second panel, *line;* followed by next frame, *dotted line*). Its strong electric discharge volley appears only 80 ms after onset of this motor behaviour. In a successful attack a ray lands on top of its immobilized prey that has moved or has been moved horizontally (third panel). Lowest panel, total horizontal distance (*dotted*) from initial position (*line*). The whole sequence lasted 1.4 s in this example. A ray of 47 cm length and 30 cm disc diameter will rise to 15 cm above the bottom and land 20 cm ahead of its original position. (From (Belbenoit 1970, modified)

The effect of a ray's EOD volley on a prey fish can be quite devastating, even in prey which closely manage to escape. This includes partial immobilisation, a broken spinal column, or melanisation of one or both body sides, followed by early death (one or a few days thereafter). This is astonishing because the current density, as measured in sea water, is relatively feeble: 30 mA/cm^2, at 15 V. Measured in air the amplitude is 50 V and the power output at the peak of the pulse may exceed 1 kW. The duration of an individual EOD which is a monophasic, dorsal-positive pulse is about 5 ms.

Because the ray triggers its electric organ only *after* it started an overt attack, active electrolocation of the prey depending on EODs (as hypothesized by Baron et al. 1985) can be excluded. However, there could be passive electrosensory location of the prey by the field potentials emanating from any organism (as suggested by Belbenoit 1981). Experiments and observations in large tanks using natural prey fish and artificial objects have established that the mechanoreceptive stimuli associated with quick movement are sufficient to release a ray's attack behaviour; especially effective is an object passing by at 1.5-2 m/s (Belbenoit 1970; Belbenoit and Bauer 1972). Vision is unnecessary and probably not involved, for blinded rays continued to hunt successfully. The prey normally does not touch the ray; it must not be farther away than ½ a diameter of its disc-shaped body from the front rim of the disc to evoke an attack.

Skates (Rajidae). In contrast to the strongly electric rays, in the weakly electric skates an intraspecific communication function of their EOD may be assumed with great confidence (Baron et al. 1982; Bratton and Ayers 1987). Other possible functions, such as defence or prey capture, are unlikely in these fishes because of the weakness of their EOD. Active object detection dependent on their EOD, as hypothesized by Baron et al. (1982), also is an unlikely possibility because the skates discharge only rarely, not even when swimming or approaching an obstacle (Bratton and Ayers 1987).

Most often skates discharge during social encounters (Bratton and Ayers 1987). Often one skate lies on top of another, with the lower animal showing no avoidance behaviour. From isolated skates a "reflex discharge" may be obtained by gentle mechanical stimulation of the dorsal surface, or by electrical stimuli of head-positive polarity (D.C., or one half-wave of a 0.2 Hz sine wave, or monopolar square-wave pulses of about 5 pulses per second). Thus a skate's own EOD would not evoke a reflex discharge since the EOD is head-negative throughout the entire region of the ampullae of its own body (the electric organ is located in the long, extremely slender tail fin with the voltage gradient oriented in parallel to the spinal cord).

The EOD of skates seems to be of species-specific pulse duration, as shown for six species (Bratton and Ayers 1987; Bratton and Williamson 1992). The head-negative, monopolar pulses are of variable amplitude but regular waveform (Fig. 5.2). In *Raja erinacea*, for example, the EOD pulse duration is, on average, 70 ms while it is 217 ms in *R. ocellata* (the variability among individuals is so high that standard deviations may be up to 20% of the mean). In air the amplitude of the discharge is 1-1.5 V in both species (recorded between the base and the tip of the tail) while it is only 20 to 40 mV recorded in sea water of 23 $\Omega \cdot$cm resistivity.

During daylight the skates are usually inactive and buried under sand, with only their eyes and spiracles visible (Bratton and Ayers 1987). Sometimes the skates swim short distances. Skates observed in aquaria were more active during night than during day. Discharge trains were quite variable. In *R. erinacea* the duration of an average train was about 12-30 s, at about 5 pulses per second (less than 8 pulses per second). A discharge train consisted of a few to about 100 EODs. A resting animal, when disturbed by another, may give an EOD train of 5-10 s duration, at a constant interval pattern of 7-8 pulses per second. When several skates rested together, a rhythmic discharge sometimes occurred (regular accelerations and decelerations of discharge rate).

In *R. ocellata* the average train duration was similar to that of *R. erinacea,* but the pulse rate was only 1-2 pulses per second (Bratton and Ayers 1987). In pairs of skates pulse pairing, or echoing, was sometimes observed (at 400-600 ms latency from the EOD of one skate to the "echoing" EOD of the other). A skate approached by a conspecific may give several EOD trains which are correlated with the movements of the approaching skate. Although it is clear that there is a correlation between motor behaviour and electrical signalling in several *Raja* species, more detailed information, for example, an ethological study of the reproductive behaviour, is very much needed.

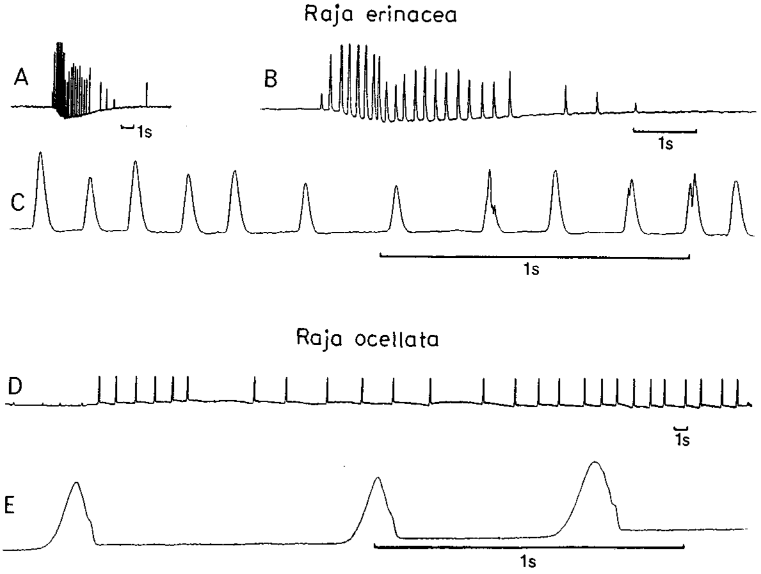


Fig. 5.2: Trains of electric organ discharges in two species of weakly electric skates. Head-negativity is up. Note monophasic, head-negative pulses in both species: the EOD of *Raja ocellata* is of longer duration and lower repetition rate (**D,E**) than that of *R. erinacea* (**A,C**). (From Bratton and Ayers 1987)

5.2 Elephantfishes - Mormyroidei

The Mormyroidei are African freshwater teleosts. They comprise two families: the monospecific Gymnarchidae and the Mormyridae. Of the many fish families endemic to Africa, the Mormyridae are the largest (about 200 species). The Mormyridae are predominantly tropically distributed; they do not occur in the northern Maghreb but are found in the Nile. Their southern limit is the Zambezi system (Skelton 1993).

The Mormyroidei are related to the xenomystines or African knifefishes two species of which are only known (see Fig. 1.2). In contrast to their notopterine Asian relatives, the xenomystines are electroreceptive; both do not possess electric organs and their behaviour is unstudied (Braford, Jr. 1986).

The systematics of the Mormyroidei (Daget et al. 1984, 1986) is well worked out, and keys are available for West and southern Africa (Lévêque and Paugy 1984; Lévêque et al. 1990; Skelton 1993). The most recent reviews about their communication behaviour are Kramer (1993, 1994).

5.2.1 Schooling and Group Cohesion

Most mormyrids are active during night and inactive during day when they seek cover. The smaller species (below about 20 cm) gather in schools close to the river bed or in the dense vegetation of small creeks, in crevices between rocks, near fallen trees or submerged bushes close to the river bank. There, fish may hide motionless during the day, often with their heads pointing downwards. Some schools are mixed in their species composition. Large species, like those found in the genus *Mormyrops*, live solitarily and defend a territory (Géry 1970; Moller et al. 1979).

Even during day, vision may be severely limited by a high turbidity of the water, due to its mud load or an intense blackish coloration from decaying plant material. Under these conditions of low visibility, the key factor enabling fish to maintain social contact, or social distance, is the EOD. This has been established experimentally in *Marcusenius cyprinoides* (Moller 1976) and *Gnathonemus petersii* (Kramer 1976a) with a surgically denervated electric organ.

In a group of "electrically silent" *M. cyprinoides* studied in the laboratory, the lack of EODs resulted in reduced locomotor behaviour and a decrease or elimination of social contact behaviours (such as "contact", "parallel lineup" and "single file swimming"), as compared to a group of intact fish (Moller 1976). Electrically silenced *G. petersii*, introduced into the aquarium of a dominant, territorial conspecific, evoked significantly less attacks (only ½) from the territory owner, compared to discharging conspecific or a mormyrid of another species, *Brienomyrus niger* (Kramer 1976a). These experiments performed in clear water during the light period showed that, even under conditions of excellent visibility, a fish's potential to arouse and to attract conspecifics critically depends on its giving off EODs (see also Moller et al. 1982; Teyssèdre and Moller 1982).

5.2.2. Species or Individual Recognition

Field observations have shown that different species of mormyrids tend to flock together separately; however, polyspecific groups were also reported (see previous Chapter). There are only a few experimental tests of species recognition.

One of these (Moller and Serrier 1986) used four species of mormyrids of four genera which were, therefore, not closely related (*Brienomyrus niger*, *Marcusenius cyprinoides*, *Mormyrus rume*, and *Gnathonemus petersii*; the first three of these are known to coexist in wide parts of West Africa). Two live conspecifics ("decoy fish") that were confined to a small peripheral compartment of a large circular tank, attracted strongest the freely roaming members of their own species; this result was obtained in all four species used. The freely moving fish of the other three species did, however, also respond to the presence of the "decoy fish", ranging from attraction to avoidance, depending on the species pairing. Although electric signalling was probably involved in these experiments performed in clear water during the light phase, other sensory modalities (vision, audition, mechanical - lateral line, olfaction) were not excluded; vision even being a likely possibility (Teyssèdre and Moller 1982).

The question of whether the natural EOD activity, as recorded from a mormyrid, may serve as the exclusive basis of species recognition (when all other sensory modalities, except the electrical, are excluded) was addressed in two ways because the EOD activity of mormyrids tends to be species specific in (1) the waveform of a single EOD pulse, (2) the sequence of inter-EOD intervals (see Fig. 5.3). This is treated in the following two chapters.

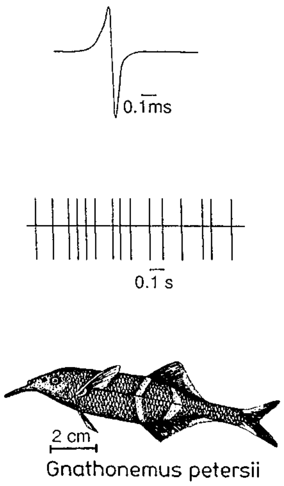


Fig. 5.3: Communication by electric organ discharges in mormyrids, such as *Gnathonemus petersii*, is based on properties of the waveform of a single discharge which remains almost constant over time (*top*), and on trains of EOD pulses (*below*). These pulse trains are highly variable and encode diverse messages. Note difference in time scales. (From Kramer 1985a)

5.2.2.1 Waveform of Electric Organ Discharge

In a species-characteristic manner, the pulse EODs of mormyrids differ widely in duration and waveform. There are almost purely monopolar pulses like those of *Hippopotamyrus ansorgii*, biphasic ones resembling single-cycle sine-wave pulses like those of *Marcusenius senegalensis,* and EODs with three or even more phases (for example, *Pollimyrus castelnaui* (local variety from Linyanti); see Fig. 5.4). The EOD durations vary by a factor of greater than 100, from below 0.1 ms in certain small species to greater than 30 ms in *Mormyrus lacerda.* It is not yet clear whether sympatrically living species always possess unique, non-overlapping EOD waveforms (Hopkins 1980, 1981); this question can only be addressed by studying natural populations, assessing the intraspecific *versus* interspecific variability of sympatric fish communities. In a recently studied community of mormyrids from the Zambezi system in Africa this is clearly the case (Fig. 5.4). This also includes one species with a sexually dimorphic EOD pulse waveform, *Marcusenius macrolepidotus.*

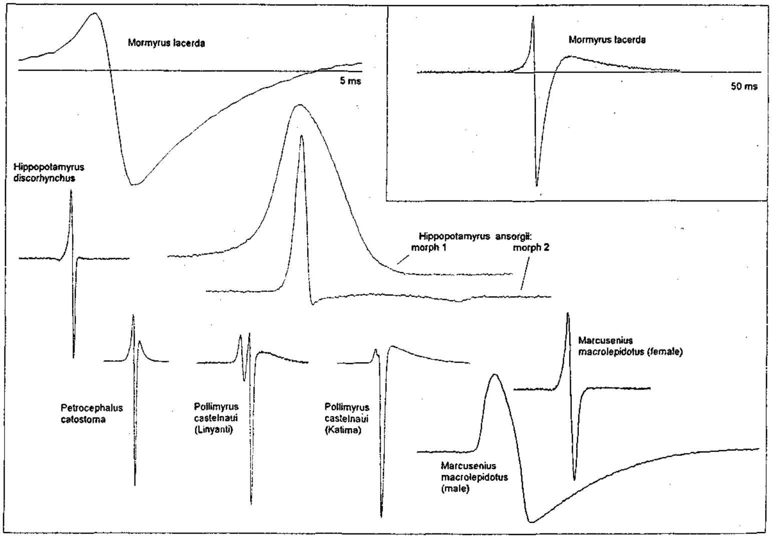


Fig. 5.4: EOD waveforms of several sympatric mormyrids from the Zambezi system (eastern Caprivi, Namibia). All waveforms digitized and stored in the field in the original stream water. All waveforms corrected to 25 °C, using a Q_{10} of 1.5 (Kramer and Westby 1985). All EODs scaled to the same oscilloscope sweep speed, as indicated for *Mormyrus lacerda* (duration of zero line, 5 ms); except *inset* showing *Mormyrus lacerda's* EOD of extremely long duration (zero line, 50 ms). Head positivity is up. Note that sympatric species show markedly different EOD durations and waveforms. *Hippopotamyrus ansorgii* has a most unusual monopolar, head-positive EOD pulse; two EOD morphs coexist syntopically (sibling species; “morph 1“ is a new species, van der Bank& Kramer, in press). In *Pollimyrus castelnaui* from two different localities (140 km apart with sporadic water connection) a pronounced diversification is apparent. The EOD waveform and duration of *Marcusenius macrolepidotus* differs markedly for adults of both sexes; juveniles and females have the same EOD. (Kramer, unpublished)

The huge diversity of EOD waveforms among different species could be the basis of species recognition in mormyrids (Kramer 1978; Hopkins 1980, 1981; Moller 1980a,b). However, to analyse the waveform of a brief pulse of - very often - much less than 1 ms simply appears to be impossible for any sensory system.

The best way to ask an animal whether it is able to discriminate two similar, but not identical, stimuli is the method of conditioned discrimination, introduced by Karl von Frisch in trained bees and fish (reviews, von Frisch 1938, 1967). Using this method, Hans Lissmann demonstrated active electrolocation in *Gymnarchus niloticus* even before electroreceptors were known (Lissmann 1958).

A dipole was used to play back previously digitized EODs (for method, see Kramer and Weymann 1987). Food-rewarded *Pollimyrus isidori* were able to discriminate the EOD waveform of their own species from that of *Gnathonemus petersii* (Graff and Kramer 1989, 1992). The trained fish even discriminated the slightly different EOD waveforms from different conspecific individuals. Because *P. isidori*'s electrosensory system can resolve the subtle intraspecific variability in EOD waveform, it is clear it can also detect the EODs of other species as being categorically different from its own, a much easier task.

From *P. isidori*'s remarkable sensitivity for the waveform of a very short pulse, its EOD, we may conclude that mormyrids are indeed able to use species-characteristic EOD waveform cues for species recognition. We do, however, not know whether (or when) they use this information in the natural context.

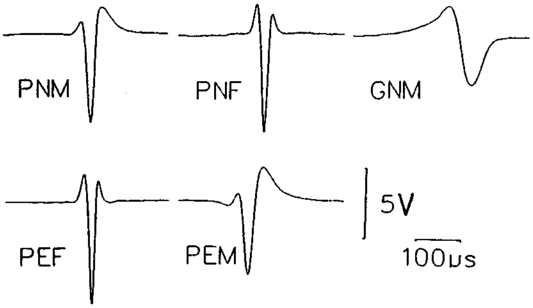


Fig. 5.5: Individual recognition in mormyrids by their electric organ discharges (EODs). Digitized EODs of different *Pollimyrus isidori* individuals, and of a *Gnathonemus petersii* (*GNM*; upper right), normalized for equal energy contents, as used for playback experiments. Trained *P. isidori* not only discriminated conspecific EODs from those of *G. petersii*, but also between the EODs of different conspecifics (two males, *PNM* and *PEM*, and two females, *PNF* and *PEF*). Individual recognition of EODs proved to be independent of stimulus amplitude that was varied at random during subsequent trials. (From Graff and Kramer 1992)

Hopkins and Bass (1981) have proposed an interesting sensory mechanism for the discrimination of long-duration EODs of a special, almost rectangular waveform that differ in duration by a factor of two to three both between and within three morphologically indistinguishable *Brienomyrus* species (in the *Brienomyrus brachyistius* triple complex of sibling species which needs systematic clarification). In this model, Knollenorgane, located on different sides of the fish's body, would mark the beginning and the end of EODs that are of different durations, the interval presumably being measured by the brain (the brain mechanism is purely speculative at present; Bell 1989). Such a sensory mechanism would, however, not work for *P.isidori*'s EOD waveform (see also Crawford 1992), nor those of most other species which also do not resemble a square-wave pulse, nor would it explain *P. isidori's* capability of discriminating between EODs so similar as those from different conspecific individuals (Graff and Kramer 1992).

In *P. isidori*, and probably other species as well, the sensory basis for the discrimination of the intraspecific variability of EODs, often so similar in waveform and duration, could be the differential phase sensitivity of the two sensory cell types which mormyromast electroreceptor organs carry (Bell 1990; von der Emde and Bleckmann 1992a; see Chap. 2.2). Additional tests are necessary to corroborate this hypothesis.

Besides species recognition, another biological function for sensing subtle EOD waveform differences could be mate recognition, provided there are sexually dimorphic EOD waveforms in the species considered. Unfortunately, the reports of sexually dimorphic EOD waveforms in the recent literature (as last reviewed in Landsman et al. 1990; see also Landsman 1993) suffer from insufficient information on one, or more often, several of the following points: (a) the species identity and/or place of origin of the individuals under study is unclear, the salient taxonomical differences in several mormyrid genera often being a matter for the expert (Lévêque et al. 1990); (b) a statistical population analysis of the character in question is lacking; (c) the reproductive behaviour has not been observed, nor the role of the presumed sexual EOD waveform character studied; (d) the water conductivity was unnaturally high or not specified (water conductivity may have a profound effect on the EOD waveform; see below); (e) stress (Landsman et al. 1987; Landsman and Moller 1993), for example, from intercontinental air transport or handling; (f) inadequate recording techniques. There are however, clear effects of androgen hormones on EOD waveform when administered to mormyrids, especially females which usually respond by increasing their pulse duration (Hopkins 1988; Freedman et al. 1989; Landsman et al. 1990).

A recent field study has revealed a case of sexual dimorphism in EOD waveform in a mormyrid which is both clear and certain (Kramer submitted). Adult male *Marcusenius macrolepidotus* from the Zambezi river of southern Africa have an EOD of up to 13x longer duration than females or juveniles (Fig. 5.4). An EOD of long duration was found in every big male (beyond about 15 cm) in a large (>80) sample of fish which had been caught in the presence and with the aid of the investigator; that is, with time and place of origin known.

Although field observations are still lacking, in *P. isidori* the information is sufficient to conclude that a weaker form of sex difference in EOD waveform is present. It seems only weak because the statistical distributions of the waveform character which differs significantly between males and females, the amplitude ratio of the two positive phases, or P1/P2 ratio (see Fig. 5.6), overlap widely (Bratton and Kramer 1988). However, in 14 fish which were in breeding condition this overlap was reduced: only five or six individuals overlapped, and near perfect separation was achieved on combining P1 amplitude with pulse duration in a two-parameter analysis (Crawford 1992); it is unknown, however, whether or not the fish perform a similar analysis.

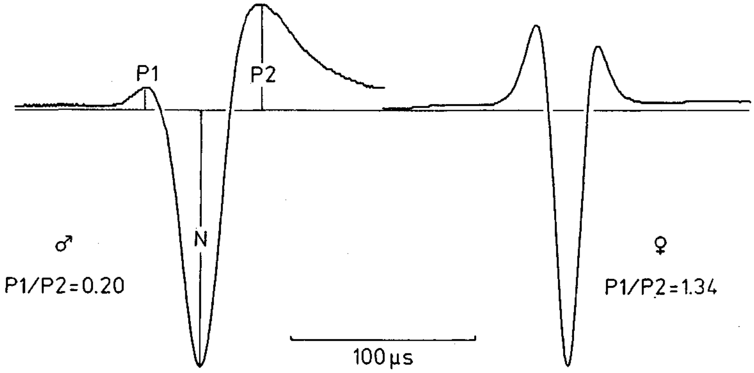


Fig. 5.6: Two examples for the great inter-individual variability in EOD waveforms in *Pollimyrus isidori.* Although there is considerable overlap between the two sexes, male EODs tend to have a small *P1* phase compared to *P2,* while in females the *P1* phase tends to be larger, often larger than *P2. N* Head-negative main phase of the EOD. Baseline indicates 0 V; water conductivity, 100 μS/cm. (From Bratton and Kramer 1988)

In spite of this tendency for a sex difference, EOD waveform does not seem to play any role in mate recognition in *P. isidori,* as observed both in undisturbed, breeding pairs of fish (Bratton and Kramer 1989), and determined experimentally in territorial, nesting males (Crawford 1991). Instead, it is the behavioural/ecological context including acoustic signalling (Crawford et al. 1986), and the sequence of inter-EOD intervals (Bratton and Kramer 1989; Crawford 1991), that are the salient features (see Chap. 5.2.4). The function of *P.isidori's* exceedingly fine EOD waveform discrimination, as demonstrated by conditioned discrimination (Graff and Kramer 1989, 1992), might be individual recognition not only of mates but also of territorial neighbours and rivals.

The EOD waveform of a mormyrid is affected by a change in water conductivity. Natural water conductivities vary widely in tropical Africa, from about 5-150 μS/cm (or a resistivity of about 7-200 kΩ · cm). A strong decrease in water conductivity may almost abolish the head-negative phase of a mormyrid EOD (which is electrically evoked; Bennett 1971a), making it very weak and of extremely long duration (Bell et al. 1976; Bratton and Kramer 1988; Kramer and Kuhn 1993). Therefore, a fish entering a stream of low water conductivity would experience a great loss in its electro-communication and location abilities when leaving a river of high conductivity (Bratton and Kramer 1988).

In two species of *Campylomormyrus* it has recently been shown that the electric organ is able to match its output as a voltage and current source, to water of a drastically changed conductivity within two days (Kramer and Kuhn 1993). After that adaption time the EOD waveform again is typical for the species, and similar to (although not exactly identical with) that displayed before the change in water conductivity. Possible physiological scenarios for this impedance matching of the electric organ are discussed by Kramer and Kuhn (1993).

5.2.2.2 The Sequence of Inter-Discharge-Intervals

In mormyrids, the sequence of inter-discharge intervals (SDI) is usually characterized by a high moment-to-moment variation. Any change of motor activity, or state of excitement, instantly shows in a change of EOD rate.

In order to address the question of whether there is an inter-discharge interval (IDI) code of communication in mormyrids which might serve the fish to recognize members of their own species, it is necessary to clearly define a sender fish's behavioural state, motor activity, circadian phase, recent history, etc. When these factors are kept constant species-characteristic differences in a fish's SDI emerge (review, Kramer 1990a; Figs. 5.7, 5.8).

Nine *Petrocephalus bovei* were separately tested for their spontaneous preference, or indifference, for one out of two simultaneously presented, artificially-generated SDIs in a T-maze paradigm, with symmetrically arranged stimulus dipoles to the left and right of a fish's hiding and resting shelter (Kramer and Lücker 1990). One type of SDI had previously been recorded from a conspecific, while the two other types of SDI were from other mormyrid species. To exclude EOD waveform cues, all stimulus pulses were identical single-cycle sine-wave pulses (3 kHz). Random assignment of the simultaneously presented stimulus patterns to the left or right dipole compensated for spatial learning or sidedness. Fish received neither reward nor punishment, and their preference for a specific SDI was measured as the time spent in a specified area close to a dipole.

Almost all fish spent significantly more time close to a dipole presenting a conspecific EOD pattern. This was true in both species pairings (*Petrocephalus bovei*, the experimental species, versus *Brienomyrus niger*; and *Petrocephalus bovei* versus *Pollimyrus isidori*), for both types of EOD activity presented (SDIs recorded during day-time resting or during night-time swimming activity). None of the experimental fish preferred any of the heterospecific EOD patterns compared to a conspecific one.

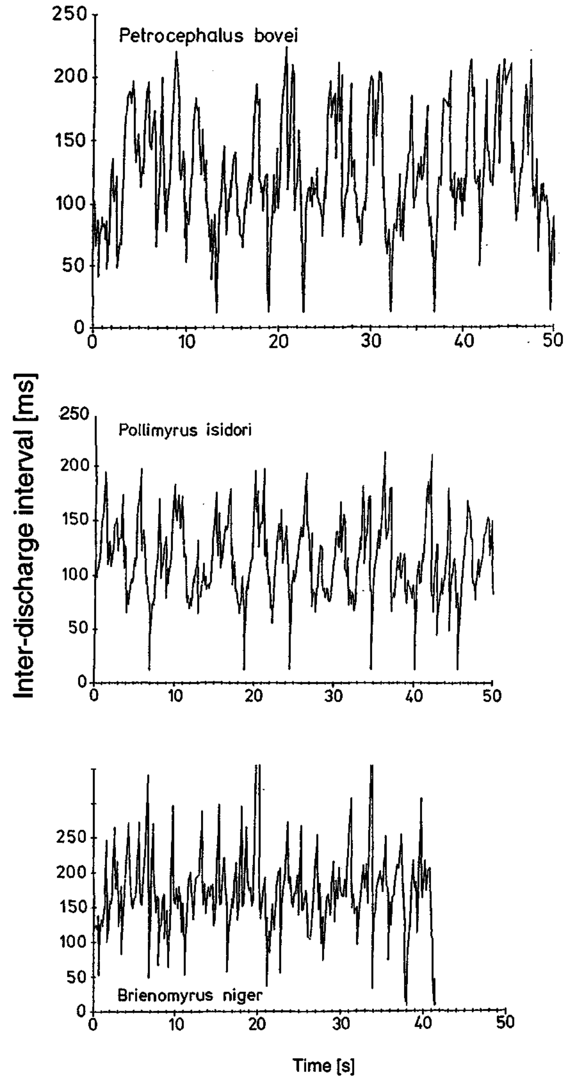


Fig. 5.7: Resting discharge activity of isolated individuals of mormyrids of three species, recorded during day-light hours when fish were completely immobile. Sequential representations of discharge activities. *Ordinates* Duration of individual inter-discharge intervals (ms); *abscissae* time (s). (From Kramer and Lücker 1990)

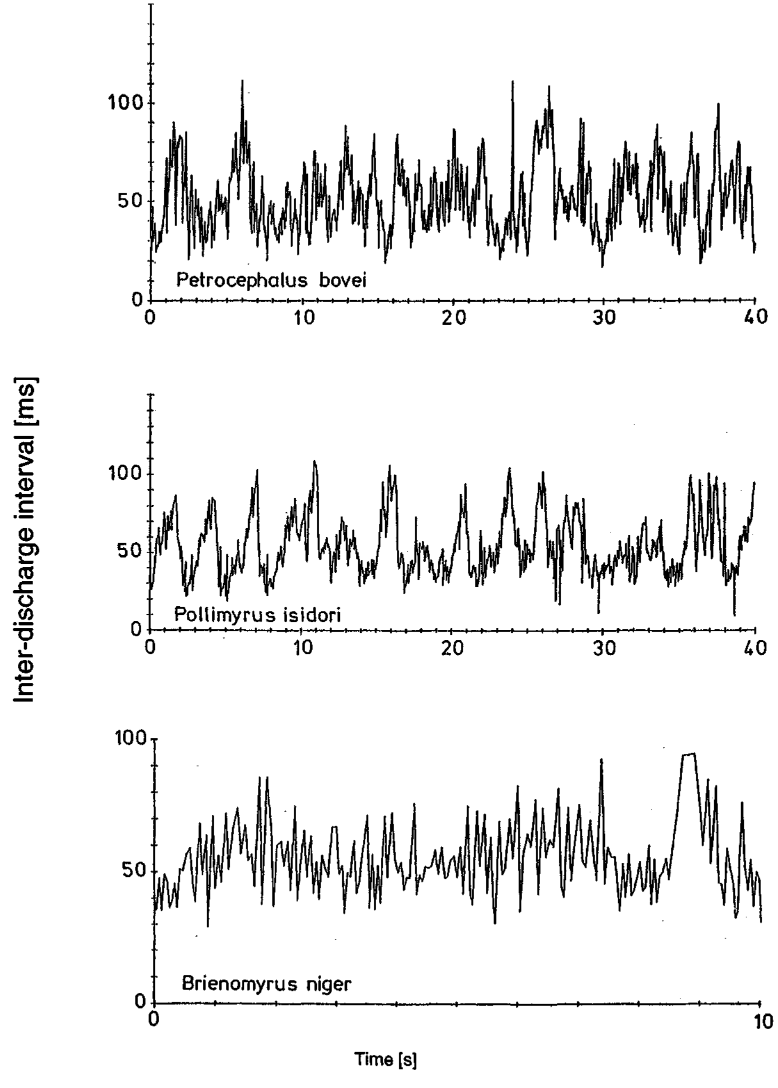


Fig. 5.8: Discharge activity of isolated individuals of mormyrids of three species, recorded during the nocturnal period of spontaneous swimming (no rest periods included). *Ordinates* duration of individual inter-discharge intervals (ms); *abscissae* time (s). (From Kramer and Lücker 1990)

The basis for this discrimination seems to be the presence of species-characteristic patterns of inter-EOD intervals found in each species' EOD activity, lasting a few seconds at most ("micro-patterns"; Kramer and Lücker 1990). This is also inferred from the observation that, in the above experiments, the fishes' frequency of first choices (after onset of stimulation) was significantly higher for a dipole that presented a conspecific SDI pattern than for an alternative dipole that presented the EOD pattern of another species.

These short patterns of EOD intervals, which clearly vary considerably (see Figs. 5.7 and 5.8), might perhaps be the rhythmical equivalent of a short musical phrase which humans recognize even if presented in strongly modified form or context (the so-called variations of a theme).

In an improved experimental paradigm two closely related mormyrids were tested, *Campylomormyrus tamandua* and *C. rhynchophorus*, in the roles of both senders and receivers (Kramer and Kuhn 1994). Fish had been imported from Zaïre where they live sympatrically. For each species, two SDIs which had previously been recorded from different individuals during their active night phase were used for playback via dipoles, in a similar arrangement as detailed above for *P. bovei*. The only difference was that, in addition to randomly switching the species roles of the two simultaneously active dipoles (similar to the experiments described above), there was another random choice among the two alternative SDI playback-patterns for each species. This further step was introduced to avoid relying, perhaps, too heavily on a single individual's idiosyncrasies in signal generation, and to get a result more representative for the species (Kroodsma 1989).

There are clear-cut differences in the SDIs of both species recorded in the same behavioural state (Fig. 5.9). Conforming to expectation, the four *C. rhynchophorus* available all preferred the conspecific SDIs compared to those from *C. tamandua*, measured as the time spent in a specified area close to a dipole. Independently, this result was significant for each fish tested ($P<0.05$ at least).

A different result was obtained in the reverse test. The five *C. tamandua* did not show any preference for their conspecific SDIs; one fish even found the *C. rhynchophorus* pattern more attractive than its own species' pattern ($P<0.05$).

This paradoxical result - one species does and the other does not prefer conspecific SDIs - might have a simple explanation. At the time of testing, the *C. rhynchophorus* were grown to almost half the maximum size reported for their species (which is 23 cm), while the *C. tamandua* were grown to only ¼ their maximum size (which is 43 cm; Gosse 1984). Field data for five mormyrid species show that a mormyrid usually reaches sexual maturity at somewhat below half maximum size (Blake 1977; Kolding et al. 1992). Thus the *C. rhynchophorus* probably were and the *C. tamandua* probably were not sexually mature at the time of testing. It would not be surprising if sexually mature fish had a more pronounced tendency to discriminate between

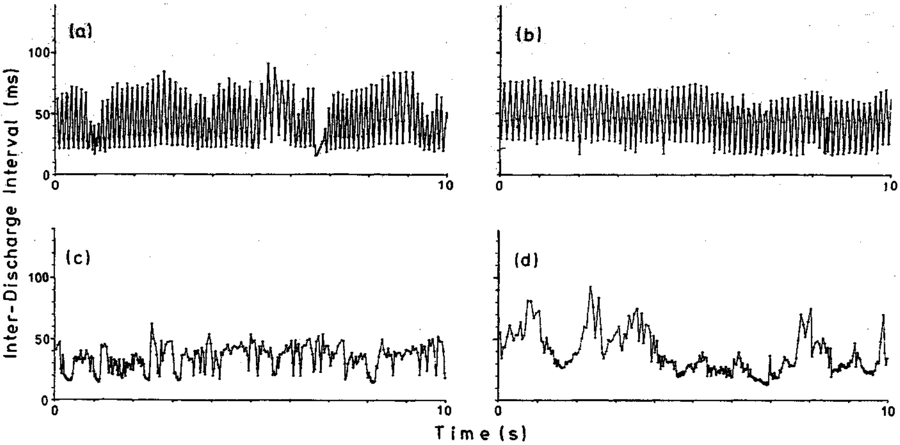


Fig. 5.9: Sequences of inter-discharge intervals in two *Campylomormyrus* species, *tamandua* [*(a),(b)*] and *rhynchophorus* [*(c),(d)*], during their nocturnal activity phase. *Ordinate* Inter-discharge interval (ms); *abscissa* time in s. Each point is one interval. For each species, the discharge activity of two different specimens is shown. Note strong contrasts and marked regularity in adjacent intervals in *C. tamandua*; usually smaller contrasts but higher variation in *C. rhynchophorus*. The statistical interval distributions and mean EOD rates were very similar for both species. (From Kramer and Kuhn 1994)

conspecifics and other fish, compared to immatures which might join mixed-species schools more readily (see Chap. 5.2.1). Therefore, it is concluded that one function of the IDI code of communication in mormyrids is species-recognition even if fish may show this only when sexually mature.

5.2.3 Agonistic Behaviour

Whether aggression in mormyrids occurs in nature, and, if so, for what reasons, is unknown. Aquarium observations indicate that aggression may be an important element in the life of mormyrids, occurring frequently in territorial disputes, during feeding, and courtship.

Immediate attack is the response of a hiding mormyrid on an intruder's attempt to enter its shelter in an aquarium. As in many other fishes, aggression of an especially high intensity occurs during the early stages of courtship (which is known from a single species only, *Pollimyrus isidori*).

In all mormyrids studied up to now, the motor behaviour of overt attack is announced by a transient, short-lived sharp increase in discharge rate which may be followed by a decrease (SID, Fig. 5.10; Bauer 1972). The correlation of overt behaviour with electric signalling is so strict that the SID may be considered an integral part of the motor behaviour of attack, the two components never occurring in

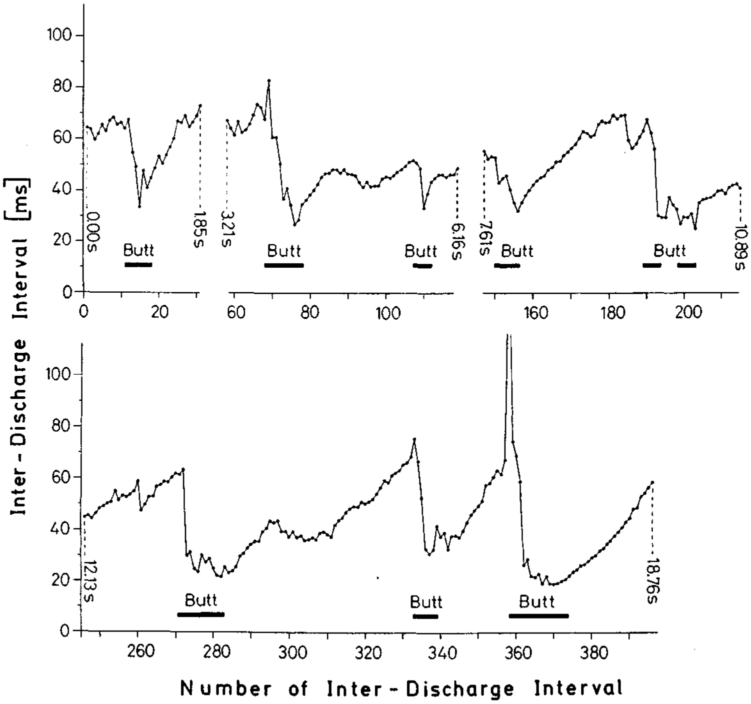


Fig. 5.10: Sequence of discharge intervals displayed by a *Brienomyrus niger* attacking another mormyrid (*butt*). *Ordinate* Duration of individual intervals; *abscissa* arbitrary number of discharge interval in the section shown. Each point is one interval. Note that, firmly associated with the motor behaviour of attack, there is a rapid decrease of EOD interval duration, or sharp increase of discharge rate, followed by a decrease (SID) to the level displayed before the attack behaviour. The time course in s is indicated as shown. (From Kramer 1976a)

isolation. Signalling during agonistic behaviour is an especially clear function of the IDI code of communication in mormyrids.

In a few species like *Gnathonemus petersii* and *Pollimyrus isidori*, an attacking fish's sharp increase in discharge rate (SI) usually is not followed by a decrease, but, instead, by a short period of a very high discharge rate (SI-HD). The steady-state, high discharge rate component (HD) may last up to 4 s in *G. petersii* (Bauer 1972; Bell et al. 1974; Kramer 1974; Kramer and Bauer 1976), and 1 s in *P. isidori* (Kramer 1978; Bratton and Kramer 1989). The steady-state character of the HD may be of two kinds: (1) all intervals are of the shortest possible duration for that species, or twice as long; both may be present in a single display; (2) the shortest possible and intervals of twice that duration alternate in a double pulse pattern (Fig. 5.11).

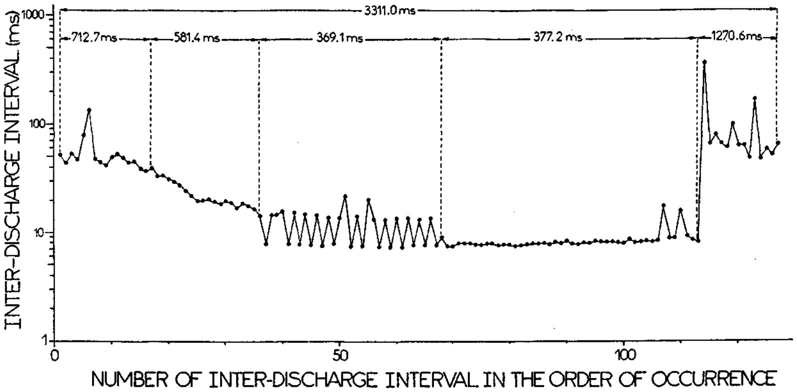


Fig. 5.11: Electric signalling during agonistic behaviour in the mormyrid *Gnathonemus petersii*. Associated with an attack on another fish there is a sharp increase (SI) of discharge rate (shown as the decrease of interval duration), followed by a steady-state, high discharge rate (HD), in this instance consisting of two portions. The HD component accompanies a lateral display directed at the attacked fish. *Ordinate* Duration of individual EOD intervals, represented by points; *abscissa* arbitrary number of interval in the section shown. (From Kramer 1985a)

In *G. petersii* the correlation of electrical and overt motor behaviour has been studied in detail (Kramer and Bauer 1976). During a territorial fish's aggressive lunge to butt or bite its opponent, physical contact usually occurs at the end of a sharp increase in EOD rate which is immediately followed by a high discharge rate (SI-HD). The HD component is accompanied by a lateral display, often in an antiparallel position and in close contact to the attacked fish. Compared to the discharge rate of the SI component at the moment of physical contact with the opponent, the HD usually is of twice that rate: up to about 150 EODs per s which is the maximum species rate (Bell et al. 1974; Kramer 1974; Kramer and Bauer 1976).

Multiple SI-HDs are observed in pairs of fish fighting about territorial dominance, with the HD component usually disappearing when one of the two opponents gives up. In *P. isidori*, attacks during territorial disputes (Fig. 5.12), as well as the so-called courtship attacks during the initial stages of courtship carry the high discharge rate component.

Most interesting is the behaviour of the subdominant fish fleeing from the repeated attacks of an aggressive persecutor. A fleeing fish usually increases its discharge rate during the moments of greatest danger of being bitten by a dominant fish, but, in contrast to the aggressor, its discharge rate remains well below the highest possible level (see Fig. 5.12B). Very often, these increases given by a fleeing fish immediately follow a short EOD cessation of up to 1 s, the contrast making the display still more conspicuous. The increase from the low-rate discharge activity of about 8 EODs per s (or even brief EOD cessation) between attacks usually occurs in

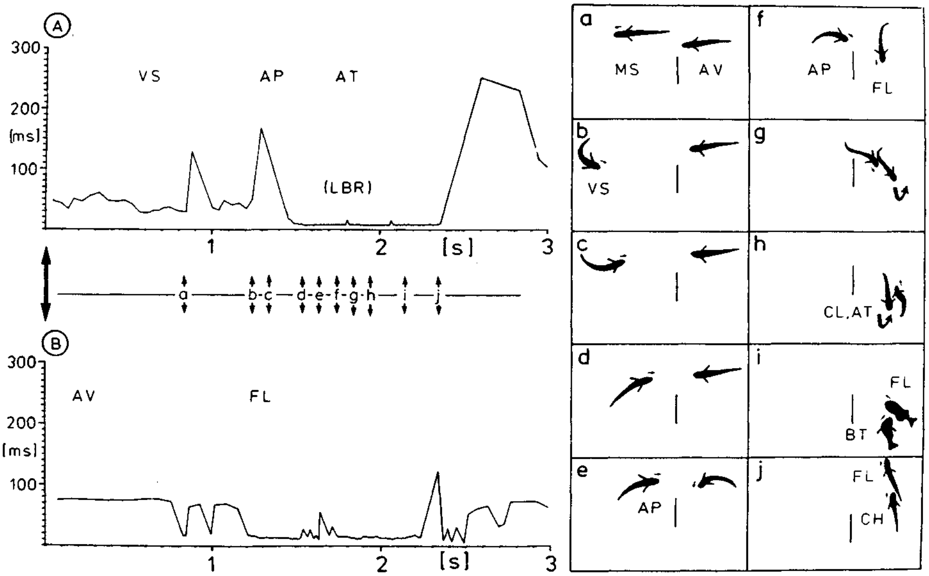


Fig. 5.12: Concurrent electric signalling during agonistic behaviour in two male mormyrids (*Pollimyrus isidori*). Attacking male's discharge activity is shown in **A**, that of the other fish in **B**. *Ordinate* Inter-EOD interval duration (although plotted individually, connecting lines may hide adjacent intervals of similar duration, especially when short); *abscissa* time in s. Low values indicate periods of high discharge rate. Letters *a-j* synchronize video frames (*right*) with electrical signalling activity. Motor behaviour recorded from underneath through glass bottom of aquarium; bar=5cm serves as a geographic reference. *VS* vigorous swimming; *AP* approach; *AT* attack; *AV* avoidance; *FL* fleeing; *LBR* long burst; *MS* moderate swimming; *CL* circling; *BT* immediately before bite; *CH* chase. Note that the attacking male increases its discharge rate during the approach phase which is followed by a high discharge rate during which the fish successfully tracks and finally bites its opponent, in spite of this fish's avoidance and fleeing manoeuvres. During these evasive actions the subdominant fish also displays an increased discharge rate for most of the time, although at a much lower rate than the dominant fish. (From Bratton and Kramer 1989)

a single step, or one inter-EOD interval, to up to about 55 EODs per s; that is, in a fleeing fish's display, there is usually no smooth discharge rate acceleration, in contrast to a SID or SI-HD given by an attacking fish (Kramer 1976b).

The displays given by a fleeing fish clearly have a threatening function, since they have been observed to sometimes discourage the attacker from finishing an already initiated aggressive lunge to bite or butt; this may occur repeatedly in certain pairs of fish (Kramer 1976b). A threatening function of the display would also correspond to the observation that its EOD rate is substantially higher and more regular than "normal", but, compared to the HDs observed in dominant, attacking fish, of much lower rate. Threat is thought to arise from a conflict between aggressive and escape tendencies when neither can find separate expression (see, for example, Manning and

Dawkins 1992). The conflict can be struck on any point along the attack-escape continuum of tendencies; with fish badly bitten and chased for some while stopping to discharge altogether, while still continuing to escape from the aggression of their relentless tormentor. For the reduced aggression evoked by electrically silenced conspecifics in *G. petersii*, see Chap. 5.2.1.

A further similarity between the signalling of escaping and aggressively pursuing fish, besides the EOD rate increases both fish display during each "hot" moment of an escape-pursue sequence, is that both fish tend to briefly stop their EOD immediately before each EOD rate increase, giving additional weight to the agonistic conflict hypothesis.

In playback experiments (Kramer 1979) resting, isolated *G. petersii* were stimulated with one of two discharge patterns, either previously recorded from a similarly resting, isolated conspecific, or a conspecific aggressively defending its territory and shelter against a threatening intruder (a big *Mormyrus rume*). Both stimulation patterns had a profound effect on the overt behaviour, as well as the discharge rate, of the experimental fish that differed significantly. For example, compared to the "rest pattern" the "attack pattern" evoked significantly more "intention movements" of a hiding fish to leave its shelter, as well as overt attacks on the dipole model which the fish severely hit with their heads or mouths.

The intention movements to leave the shelter were accompanied by SIDs of only moderate EOD peak rates, as also observed in aborted attacks on real conspecifics; the overt attacks on the dipole model were often followed by lateral displays. During the "attacks" on the dipole model, which were followed by lateral displays, the experimental fish displayed full SI-HD discharge patterns in correct physical and temporal context, as if the dipole model was a real conspecific opponent (Kramer 1979). ("Intention movements" in classical ethological theory are incomplete or aborted versions of a behaviour; see, for example, Manning 1979.)

These playback results show that in *G. petersii* electrical pulse patterns alone, presented via a simple, stationary dipole model, are sufficient to evoke complex social behaviours of high intensity, and that the "message" of the two natural stimulus patterns used in the last-mentioned study was different in the direction expected. Agonistic signalling clearly is one of the functions of the IDI code of communication in mormyrids.

5.2.4 Reproductive Behaviour

It was only after *Pollimyrus isidori* successfully reproduced in aquaria (Birkholz 1969, 1970; Kirschbaum 1975, 1987) that the reproductive behaviour of a mormyrid could be studied (Crawford et al. 1986); a breakthrough for the scientific enquiry of electrocommunication (Bratton and Kramer 1989).

Throughout the year captive *P. isidori* males tend to become territorial. Even in a big aquarium there is usually a single, dominant male which chases away all other fish from the aquarium bottom. The only place where the other fish are relatively secure from the high aggression of the "tyrant" is high up in the water column where plants, tubes, etc. are readily accepted for shelter by the subdominant fish.

The aquarium bottom is the place where the territorial male constructs a nest which is made from filamentous plant material anchored between rocks or stones. After dark and even before nest-building, the male begins to sing (Crawford et al. 1986; Bratton and Kramer 1989). In a quiet room, humans may hear the song without any electronic equipment. These songs, composed of elements called grunts, growls, and moans, are thought to attract females from a distance in the wild (advertisement call).

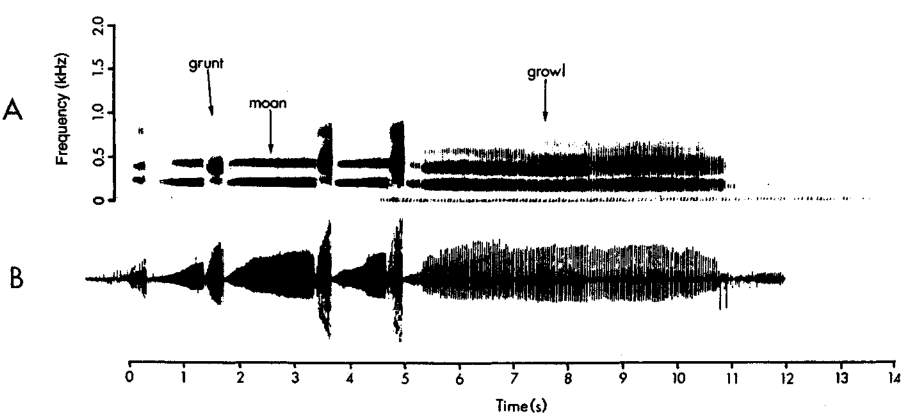


Fig. 5.13: Courtship vocalization of a male *Pollimyrus isidori*, as recorded with a hydrophone. **A** sonagraphic, **B** oscillogram representations of the same song. The *ordinate* in **A** is sound frequency in kHz, in **B** sound pressure. Note the tonal quality of the "moan" (consisting of a fundamental frequency of about 220 Hz and its harmonic of twice that frequency) which contrasts strongly with the much more broad-band "grunt" and "growl" signals. (From Crawford et al. 1986)

The reason why in *P. isidori* acoustic rather than electric signals seem to take over that role may be biophysical - a longer reach. If we consider the singing fish a point source, sound intensity is inversely proportional to the square of the distance between source and receiver (Hassall and Zaveri 1979), while the electrical field gradient (a vector, measured in µV/cm) generated by a dipole falls off with the inverse cube of the distance (Knudsen 1974). In addition, *P. isidori*'s very short EOD is weaker than that of *B. niger* of similar size, in which the electrical signal's reach, or communication distance, was determined as about 1.6 m at a conductivity of 52 µS/cm, commonly encountered in tropical waters (Squire and Moller 1982; Moller et al. 1989). Therefore, *P. isidori*'s song probably propagates farther than its particularly weak EOD.

Early on a spawning night, a female signals her readiness to mate by a unique sequence of EOD intervals of low rate and constant duration (histogram peaks between 80 and 140 ms) which is completely devoid of the short bursts which are so characteristic for all other sustained EOD patterns of *P. isidori* (Bratton and Kramer 1989). This constant discharge pattern of low rate seems to attenuate the male's aggression which is 10-20 attacks of high intensity in the first hour after darkness, and less than 4 per hour afterwards. The reduced aggression allows the female to advance, without discharging, into the bottom region repeatedly for brief periods, at first without contact to the male.

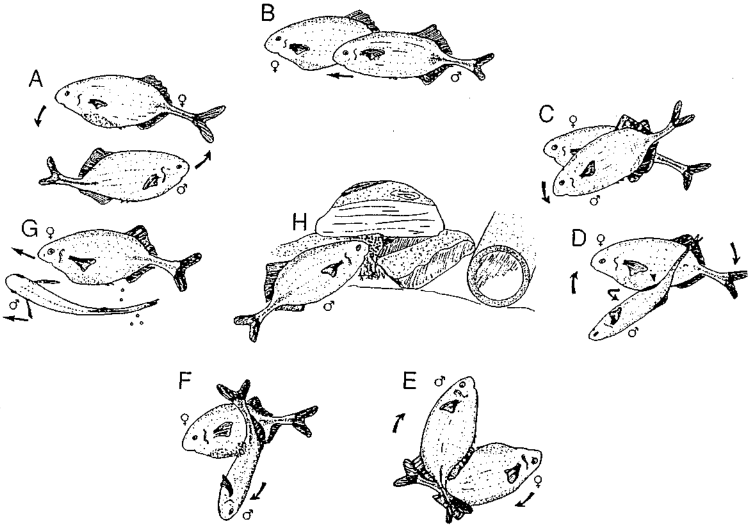


Fig. 5.14: Nocturnal courtship (**a-f**) and spawning (**g**) behaviour in *P. isidori*, as drawn from infrared video recordings. During courtship the male approaches the female and (**a**) Head-to-tail Circling (*HC*) occurs. **b** The male arrives alongside of the stationary female, **c** becomes coupled Vent-to-Vent (*VV*), **d** then turns laterally, **e** as both fish pivot around each other, **f** in one complete rotation (*RO*). The male then separates and the female swims away. Courtship bouts may be repeated for about 2 hrs on a spawning night, at a rate of 1-2 per minute. When spawning (*OP*) begins the rotation is deleted and (**g**) follows directly on (**d**). After each spawning bout the male quickly picks up the eggs (*ET*) in his mouth and (**h**) places them into the nest. (From Bratton and Kramer 1989)

P. isidori's courtship behaviour is one of the most complex among fish (Fig. 5.14). The female swims to near the male's hiding place (or even into it; for example, a tube). There she waits from 1-3 s. Even before the female's arrival in his territory, the male switches from a high sporadic rate discharge pattern (mean rate of about 18/s, containing many bursts) to a medium uniform rate (MUR pattern of 3.3-12.5/s, locking into the same discharge pattern of constant intervals at very low rate) which is displayed by the female (Fig. 5.15). In an antiparallel position, the two fish circle around each other very rapidly, discharging at surprisingly low rates. After several head-to-tail-circling (HC) episodes, interrupted by the female's quick retreat, often provoking courtship attacks and intense singing by the male, he is able to approach the female from behind and to position himself in parallel to the female while continuing his MUR discharge pattern. The female, however, displays a low to medium sporadic rate of still lower discharge rate, characterized by many discharge breaks. The male pitches head downward 20-40° to the female and rolls sideward after coupling itself tightly to the female by their anal fins. While remaining coupled ventrally, both fish, especially the male, move their caudal fins which cause them to perform one full rotation, resembling a slow (3-4 s) somersault in tandem. On completing the rotation the female returns to her hiding place, usually without discharging; the male immediately switches back from his MUR pattern to the high sporadic rate he displayed before the female's visit. Her brief visits recur every 30-60 s.

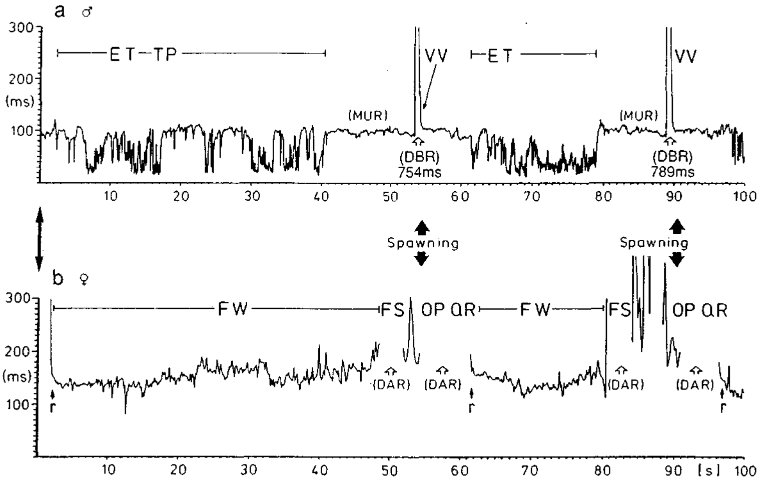


Fig. 5.15: Concurrent electric signalling during two nocturnal spawning bouts of (**a**) a male and (**b**) female *Pollimyrus isidori*. *Ordinate* inter-discharge interval duration (ms); *Abscissa* time in s. Record begins with the female just returning to her remote shelter (*r*) and waiting (*FW*), and the male patrolling within his territory (territory patrolling, *TP*, *ET*). Note that shortly before the female returns to the male's territory (*FS*) the male switches to a regular, low-rate medium uniform rate (*MUR*) contrasting with its high sporadic rate as shown during territory patrolling (*TP*) when the female is away. The male's MUR pattern is similar to the pattern the female displays throughout a whole courtship and spawning night until the last egg has been laid. During their times of close contact both fish stop discharging briefly in the male (discharge break, *DBR*), and for longer times in the female (discharge arrest, *DAR*). Other abbreviations see Fig. 5.14. (From Bratton and Kramer 1989)

During the courtship period which typically lasts from 2 to 5 h after dark the male's singing activity wanes; he is completely silent during the later stages of courtship and the whole subsequent spawning period, except for rare courtship attacks.

The behaviour preliminary to spawning is essentially an abridged version of courtship. On the female's arrival at the spawning site, the male immediately positions himself laterally, stimulating her anal fin region with a quivering motion of his anal fin, followed by oviposition (a few eggs per visit), fertilizing and egg transport to the nest. Head-to-tail-circling and the elaborate somersault part are omitted.

The male swims away first, while the female returns to her hiding place. The male returns quickly to pick up the eggs (as many as 4 at a time), which he transfers to the nest. The average time interval between spawning bouts is 72 s while the average duration of a spawning bout is 13 s (Bratton and Kramer 1989).

Spawning continues for 2-6 h during which period 50-192 eggs are laid. Male aggression is very low; during the whole spawning period the male attacks the female less than 5 times (1-3 per h).

On having released all eggs the female stops returning to the male's territory; this is the time when her discharge pattern changes abruptly from a MUR to a RAL pattern which is a regular alternation of high and low rate, with short bursts of high rate occurring at 2/s. The male's aggression towards the female returns immediately (over 12 attacks per h); this is accompanied by intense singing.

The male's main postspawning activity is tending to the nest, retrieving eggs, and covering the front with plant material. The male remains near the nest also during daylight and constantly checks the eggs during the first two weeks (nest nudging). Males may care for the eggs of more than one spawning or maintain two nests simultaneously. Over a period of 384 days the mean spawning cycle was 24 days; the shortest period between spawnings by the same female was 6 days (Bratton and Kramer 1989).

The male invests heavily into reproduction (nest-building, territorial defence, brood-care), and holds important resources (territory, nest); most likely, the male is polygynous. Therefore, a mating system called "resource defence polygyny" seems the most appropriate term for *P. isidori* (see Clutton-Brock 1991; Alcock 1993).

5.2.5 Ontogenetic Development of Communication

Larvae of *Pollimyrus isidori* hatch four days after spawning and emit their first EODs at an age of 8 days, or 8 mm total length (Kirschbaum 1975; Kirschbaum and Westby 1975; Westby and Kirschbaum 1977). After another 3 days the larval discharge has

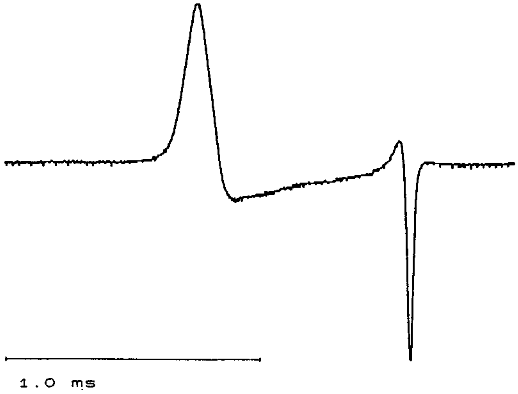


Fig. 5.16: Oscillogram of a larval followed by an adult EOD in a 53-day-old *Pollimyrus isidori*, as occurring during a short transitional time when the larval organ has not yet degenerated while the adult organ is becoming functional. The larval EOD is almost monophasic and head-positive, while in the adult EOD the head-negative phase is most prominent and the duration of the discharge much shorter. (Kramer, unpublished)

stabilized to the waveform (Fig. 5.16) which is seen throughout its existence for about 60 days (Westby and Kirschbaum 1978).

The larval EOD is an almost monophasic, head-positive impulse of about 330 µs duration which is followed by a weak, head-negative potential (total duration of the EOD, about 1.9 ms (Fig. 5.16). The triphasic adult EOD is of about 1/10 that duration; its main deflection is of the opposite, head-negative polarity. Owing to the great difference in duration, the amplitude spectra of larval EODs peak at low frequencies (on average, 964 Hz at 26 °C; see Fig. 5.19; Postner and Kramer 1995), while the amplitude spectra of adult EODs have their peaks at much higher frequencies (8-25 kHz, depending on the individual; on average, 15.15 kHz for adults of both sexes; Bratton and Kramer 1988).

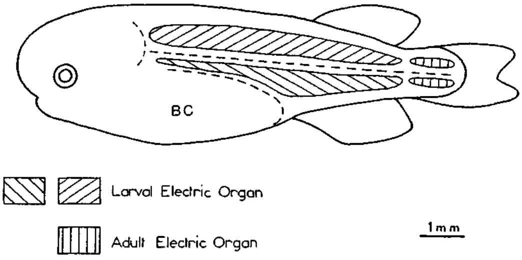


Fig. 5.17: *Pollimyrus isidori* larva with larval and adult electric organ (12 mm, 32 days old). *BC* Body cavity considerably limits the ventral part of the larval electric organ, the electrocytes of which are oriented at an oblique angle, as indicated (From Denizot et al. 1978)

Larval and adult EODs are generated by different electric organs (Fig. 5.17; Denizot et al. 1978, 1982). Also in 12 mm-larvae of the mormyrid *Stomatorhinus corneti* a larval discharge of much longer duration (3 ms) compared to the adult EOD has been described (Heymer and Harder 1975). The larval organ is ready very early in life but begins to degenerate when the adult organ begins to become functional (Fig. 5.18; Westby and Kirschbaum 1978). Compared to the adult organ, the larval organ is of rather irregular and bulky construction and, despite its considerable size, extending from just behind the skull to the caudal peduncle, generates a particularly weak EOD. The electrocytes composing the larval electric organ are morphologically very similar to true muscle cells in their vicinity, being only slightly shorter and thicker than these. Relative to the horizontal they are inclined by 45°, with the cells in the two upper tubes of the organ pointing downward (in rostral direction), and those within the two lower tubes pointing upward (as do the other cells of the respective myotomes). Therefore, the upper and lower rows of electrocytes form a right angle, leading to considerable cancelling of the voltage generated in rostro-caudal direction. Also, the 45° inclination of each electrocyte relative to its horizontal tube leads to only partial summation of the voltages over the length of the electric organ. Local currents within the larval organ are not prevented because there are no connective tissue barriers as observed in the adult organ (Denizot et al. 1978).

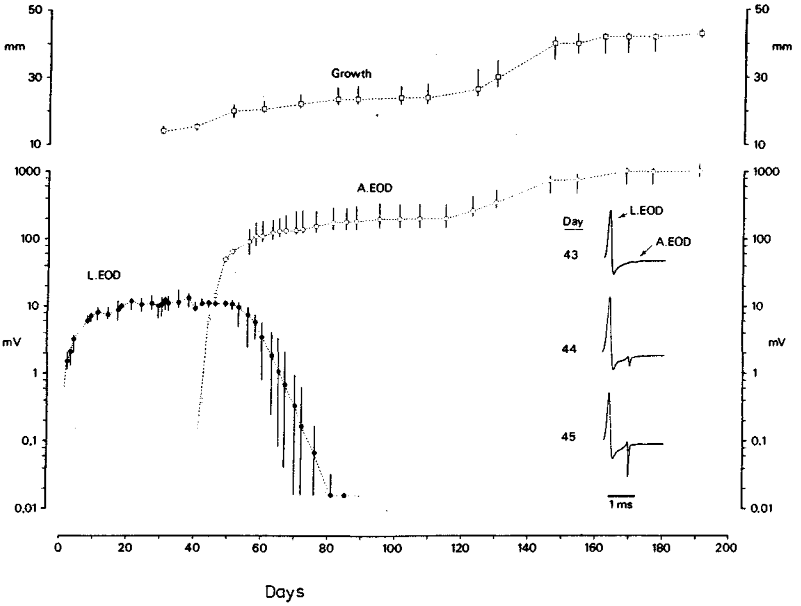


Fig. 5.18: Development of larval and adult EOD in alevins of *Pollimyrus isidori*. *Abscissa* days from first EOD; add 8 days for age. **Lower diagram** The *ordinate* is amplitude in mV (peak to peak). *Filled circles* and vertical bars show the medians and ranges of the larval discharge (L.EOD), *open circles* and vertical bars show the same for the adult discharge (A.EOD). *Inset* shows the amplitude increase of the adult discharge during three consecutive days in a certain individual. **Top diagram** Shows the growth curve (alevin length in mm). Note that shortly after the onset of the adult discharge, the larval discharge rapidly decreases in amplitude and finally disappears. (From Westby and Kirschbaum 1978)

The adult organ begins to differentiate in fish of only 10 mm total length and operates in 18 mm fish (60 days) with the adult discharge just detectable (Denizot et al. 1982). In fish between 18 and 20 mm both organs are functional as can be seen from a peculiar double discharge which is present for about 20 days (Fig. 5.16). With each neural command, the adult discharge follows the larval discharge by 0.7 ms, corresponding to the more caudal position of the adult organ. During their coexistence the relative amplitudes of the two discharges change dramatically: the larval discharge decreases and is no longer present in fish of 25 mm length (84 days) while the adult EOD increases to a strong amplitude (Westby and Kirschbaum 1978).

Compared to the larval organ, the adult organ is a highly efficient, compact precision structure. It is located in the caudal peduncle. Its large cells are very thin plates oriented normal to the long axis of their (horizontal) tube; that is, in the optimal way for voltage generation and summation in rostro-caudal direction. Although the numbers of electrocytes per column are the same in both organs (about 100), the adult organ of a larva in which both organs are functional is only 1/5 the length of its larval organ.

The main deflection of the adult organ is of opposite polarity compared to that of the larval organ; it is generated by the anterior, uninnervated faces of the electrocytes which are electrically excited by the current generated by the posterior, innervated faces. Larval electrocytes are also posteriorly innervated but their anterior faces are inactive. The reason for this inactivity may be (1) the current generated by the innervated posterior faces is too weak; (2) the anterior faces are electrically inexcitable. The latter case is found in *Gymnarchus niloticus* (Bennett 1971a), the only African wave fish of the monotypic family Gymnarchidae. The larval organ of *P. isidori* resembles the electric organ of adult *Gymnarchus* by its position and length; both generate head-positive impulses of similar wave form. The electric organ of *Gymnarchus* appears to be homologous to the larval organ of *P. isidori* (Kirschbaum 1977). The larval organ might thus represent a historical remnant that is functionally replaced during ontogeny by a more efficient adult organ. Is the larval organ useless?

There are several conceivable functions for the larval organ for a limited period early in life, for example: (1) autostimulation of a larva's own electroreceptors from the very beginning might be required for the normal development of its electrosensory system, thus providing time for the development of a more efficient adult electric organ that is used later in life; (2) to clearly signal "inedible" to the brood-caring male; (3) to facilitate the retrieval of lost larvae by the parental male; (4) to facilitate cohesion among the larvae of one nest.

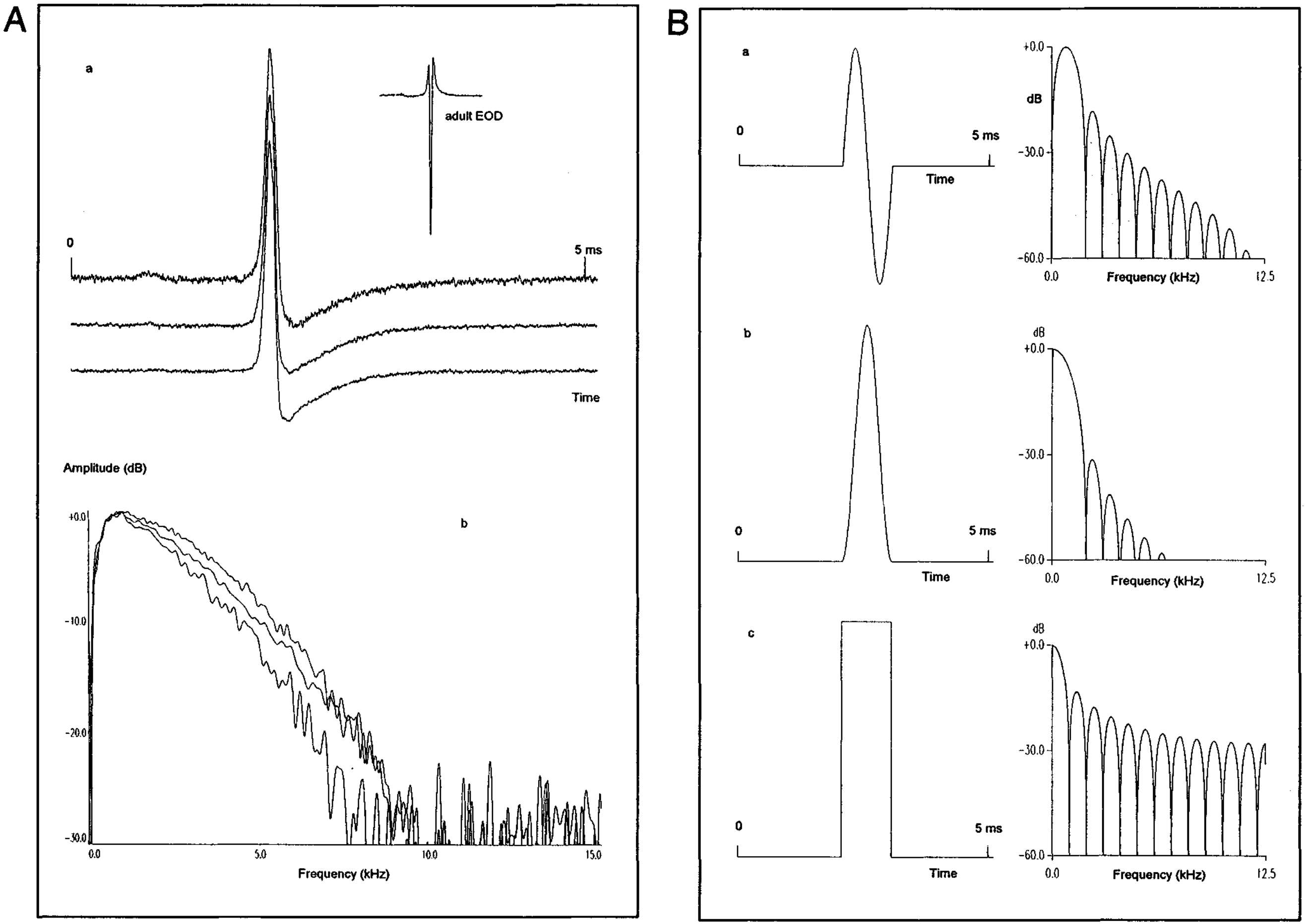
Hypothesis no. 1 is strongly favoured by Postner and Kramer (1995); however, the other hypotheses might also hold some merit, as any straying fry is immediately taken back to the nest in the male's mouth; the male may also switch the fry from one nest to another. Eggs and even larvae of up to 15 mm length which already had an adult discharge have been observed to be eaten by adult *P. isidori* (Postner 1992), and the male's high aggression towards adult conspecifics, even its mate before and immediately after spawning, may be necessary to prevent cannibalism that has also been observed in many other fishes (FitzGerald 1992).

The development of a larva's electrical behaviour (Postner 1992; Postner and Kramer 1992; Kramer and Postner, submitted) begins on the eighth day after spawning with its first EOD. From the tenth day on the larva will respond to mechanical stimulation by vigorous swimming bouts. Bouts of spontaneous swimming occur between the 12th to the 15th day, coinciding with the beginning of feeding (the egg yolk is largely absorbed by that time). Hovering in mid-water, a behaviour often observed in adult fish, occurs from days 35-40 on, and it is only in 50- to 60-day-old larvae that aggression is seen (these older larvae often have an adult discharge in addition to their larval discharge).

Larvae 8-10 days old discharge at a low rate of, on average, only 2.4 EODs per s; an adult resting discharge rate of about 8/s is reached very soon, at 21-25 days. Also the statistical distributions of inter-EOD intervals resembled those in adults (Kramer 1978) by being trimodal (that is, there were three "preferred" intervals in a broad distribution), although individual differences were more pronounced in the larvae; from about day 40 on, the agreement among different larvae as to the positions of histogram modes resembled that observed among adults (measured in standard deviations of the means). The discharge activity accompanying bouts of spontaneous swimming resembled the corresponding adult pattern from its very beginning (on day 11). The same holds true for the EOD pattern accompanying hovering, beginning on days 35-40. Already larvae 11 days old responded to artificial stimulation with a preferred latency of a mean 19-20 ms which shortened to a mean value of 12 ms on day 31, hence was in the adult range of 10-16 ms (for adults, see Kramer 1978; Lücker and Kramer 1981). Taken together, the motor part of the electric system seems mature at day 40, that is, before the onset of the adult electric organ discharge (Postner 1992; Kramer and Postner, submitted).

Is this also true for the sensory part of electrocommunication in *P. isidori*? An unconditional EOD-stop response on stimulation with pulse trains allowed to examine this question. A stimulus train consisted of 10 pulses at a rate of 5/s (that is, the duration of a train was 2 s). The inter-train interval was 15 s; ten trains were presented during one trial, the duration of which was thus 152 s. The onset of each stimulus pulse train (of 2 s duration) within a trial evoked a discharge arrest of at least 1 s; the larvae resumed discharging before or immediately after the end of a stimulus pulse train. Waveform, duration, and intensity of stimulus pulses were systematically varied and thresholds determined (Postner and Kramer 1995).

Larvae 10-15 days old already responded to electrical stimuli of well below 100 μV_{p-p} /cm, which is clear proof of a functional electrosensory system. Among the artificial pulse waveforms used (single-cycle, monopolar square-wave pulses; single-cycle, bipolar sine-wave pulses; and single-cycle, monopolar sine-wave pulses) only the


A
a
adult EOD
0
5 ms
Time
Amplitude (dB)
b
+0.0
-10.0
-20.0
-30.0
0.0
5.0
10.0
15.0
Frequency (kHz)
B
a
0
5 ms
Time
+0.0
dB
-30.0
-60.0
0.0
Frequency (kHz)
12.5
b
0
5 ms
Time
dB
+0.0
-30.0
-60.0
0.0
Frequency (kHz)
12.5
c
0
5 ms
Time
dB
+0.0
-30.0
-60.0
0.0
Frequency (kHz)
12.5

latter resembled the larval EOD (Fig. 5.19). For these, the monopolar sine-wave pulses, there was clear tuning to an optimal pulse duration of 1 ms, with a significantly lower threshold (10.9 $\mu V_{p\text{-}p}$/cm) than observed for any bipolar sine-wave pulse (Fig. 5.20). The curve for square-wave pulses did not significantly deviate from a monotonical decrease of threshold with pulse duration, that is, there was no tuning for this kind of pulse. The larval electrosensory system is well tuned to the reception of larval EODs with their spectral peak close to 1 kHz (Fig. 5.19A), not adult EODs with spectral peaks between 8-25 kHz.

Larvae 54-60 days old had lower thresholds (2.4 $\mu V_{p\text{-}p}$/cm) and broader tuning compared to the younger larvae (Fig. 5.20B). Like these, they proved more sensitive to monopolar, single-cycle sine-wave pulses than to bipolar ones. Compared to the young age group, the older larvae showed considerably broader tuning, with "best" stimulus pulse durations in the range from 0.1-1 ms, demonstrating a sensitivity increase in the spectral high-frequency range. This is amazing because these (older) larvae did not yet have an adult EOD (which is much shorter than the larval EOD) but continued to discharge their larval organ, with the waveform unchanged (see Fig. 5.19A).

In addition to conventional spectral tuning the results support the notion of tuning to the larval EOD waveform in the young age group of larvae: monopolar sine-wave pulses of 1 ms duration proved more effective stimuli than bipolar ones of any duration, and, as shown by regression analysis, the filter slope for pulses of decreasing duration (shorter than 1 ms) was significantly steeper for monopolar than for bipolar sine-wave pulses (Fig. 5.20A) (Postner and Kramer 1995).

These observations show that there is, if any, very little delay between the maturation of the motor and the sensory parts of the electric system. Already 11-day-old larvae are sensitive to stimuli in the 10 $\mu V_{p\text{-}p}$/cm range, and posses a larval discharge. During the first 60 days of their life behavioural tuning to the duration of stimulus pulses changes in an adaptive way, and sensitivity increases markedly, up to the values observed in adults.

Knollenorgane are the most likely receptors involved in the reception of stimulus pulse trains of low intensity, as described above. Knollenorgane of an apparently functional nature, containing glycogen, were already seen in 8-day-old larvae

Fig. 5.19: **A** Larval EODs of *Pollimyrus isidori.* (**a**) Oscillograms of EODs (from top) of 11-, 20- and 41-day-old larvae. *Inset:* an adult EOD shown at the same oscilloscope sweep speed. (**b**) Fourier amplitude spectrum of the three larval EODs shown in (**a**). *Ordinate* Amplitude in dB relative to the frequency of strongest amplitude; *abscissa* frequency in kHz. **B** Oscillograms of the waveforms (*left* hand diagrams) and Fourier amplitude spectra (*right* hand diagrams, as in **A,b**) of single-cycle pulses used for stimulation. (**a**) Bipolar, single-cycle sine-wave pulse; (**b**) monopolar, single-cycle sine-wave pulse; (**c**) monopolar, single-cycle square-wave pulse. Both types of sine-wave pulse comprise a full cycle or 360°, but the monopolar sine-wave pulse starts at a phase of 90° and ends at 450° (instead of 0° and 360° as in the bipolar sine-wave pulse), with the base-line adjusted accordingly. (From Postner and Kramer 1995)

(Kirschbaum and Denizot 1975). (Mormyromasts and ampullary organs are added only on the 13th day; Denizot, pers. comm.) The number of Knollenorgane is below 20 in 10-day-old larvae; they are located on the head (Postner 1992). Adult *Pollimyrus fasciaticeps* of similar size compared to adult *P. isidori* carry 105 Knollenorgane (Quinet 1971).

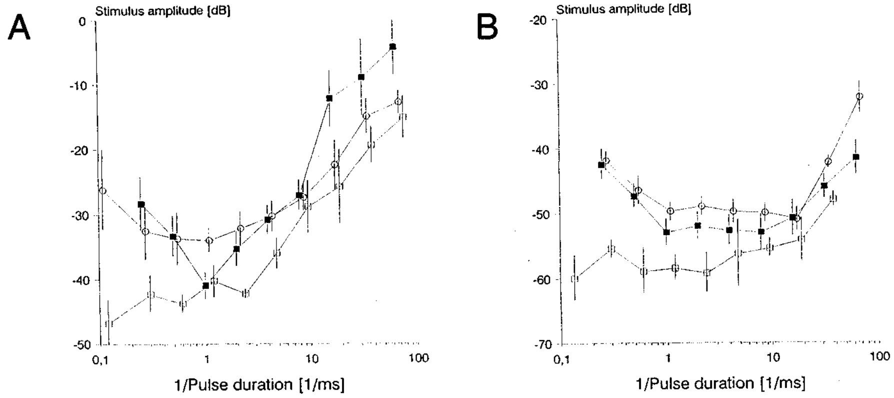


Fig. 5.20: Behavioural tuning to electrical stimulus pulses of variable duration in 10- to 15-day-old larvae of *Pollimyrus isidori* (**A**), and 54- to 60-day-old-larvae (**B**); both with a larval discharge and no adult discharge yet present. The *ordinate* is the threshold stimulus amplitude (peak-to-peak) that evoked an unconditional discharge stop-response. Stimulus pulse duration is shown on the *abscissa*; the scale with dimension 1/ms would read in kHz if the stimulus pulses had been continuous. Stimulus pulses were either ■ single-cycle, monopolar sine-wave pulses, ○ single-cycle, bipolar sine-wave pulses, or □ single-cycle, monopolar square-wave pulses (as shown in Fig. 5.19). Points for ○, □ are slightly displaced to the right in order to allow standard error bars to be shown. **A** Sharpest tuning (at 1 ms pulse duration) is for monopolar sine-wave pulses while there is no tuning for square-wave pulses. **B** Note broad-band sensitivity extending to high frequencies for sine-wave pulses in the older age group of larvae. (From Postner and Kramer 1995)

Therefore, the sensitivity increase during ontogeny may be explained by an increase in both Knollenorgan density and body size (larger fish sample a greater potential difference in an electric field). However, an increase in body size seems to contribute to sensitivity during the earliest stages of development only, because the older age group of larvae had adult sensitivity despite their tiny size (Postner and Kramer 1995).

For the change in spectral sensitivity during *P. isidori*'s early ontogeny, however, other explanations than a mere increase in Knollenorgan number must be sought. There are at least two possible hypotheses: (1) Before the onset of the adult discharge, a second type of Knollenorgane, tuned to higher frequencies, might be added. There is evidence for two types of differently tuned Knollenorgane in adults of the mormyrid, *Brienomyrus brachyistius* (Bass and Hopkins 1984). (2) Alternatively, the tuning properties of a single class of Knollenorgane would change during ontogeny (that is, broaden towards higher frequencies). In adult weakly electric fish (both gymnotiforms and mormyrids) a change in receptor tuning was evoked by administering hormones (dihydro-testosterone in most cases; Bass and Hopkins 1984; Keller et al. 1986; Zakon 1987; Meyer et al. 1987). However, the hormonal hypothesis seems remote in larvae younger than 60 days.

Unlike adult mormyrids and gymnotiforms where a fish's tuberous electroreceptors are tuned to its own EOD frequency by entrainment (Meyer and Zakon 1982; Bass and Hopkins 1984), larval Knollenorgan electroreceptors are not entrained in 54- to 60-day-old *P. isidori* because the change to adult tuning properties *preceded* the advent of the adult organ discharge (Postner and Kramer 1995).

5.2.6 Preferred Latency Responses

In certain species, both vertebrate and invertebrate, many individuals gather in one place to signal collectively; for example, choruses of birds, bats, frogs, cicadas, or the "flash-light" communities of certain tropical fireflies (Schwartz and Wells 1983; Zelick and Narins 1985; Popp 1989; Landa et al. 1990). Intense interference from the signals of (conspecific as well as heterospecific) neighbours may reduce the effectiveness of an individual's signalling; special tactics (like duetting, or antiphonal singing) have evolved to cope with this noise by partitioning broadcast time (Greenfield and Roizen 1993).

Mormyrids discharge throughout their lives and many are social; that is, there must be intense interference from the EODs of other animals, especially during daytime when fish hide under often crowded conditions (pers. field observations using an electro-acoustic "fish-detector"). One way to minimise that interference for a fish *A* would be to couple its own EOD to that of another fish *B* at a short interval of time; shorter than the time *B's* next EOD was expected. This is seen in the preferred latency response (also called “echo” response).

The preferred latency response (PLR) has first been observed in *Gathonemus petersii* during agonistic behaviour towards mormyrids of other species (Bauer and Kramer 1974; Kramer 1974; Russell et al. 1974; Kramer 1976a); it may be the most rapid form of communication in the animal kingdom. An aggressive, territorial *G. petersii* shows a strong tendency to respond to the EODs of an opponent by delaying its own EODs by 12 ms; the response occurs only during the variable, low-rate EOD activity between attacks. PLR (“echo”) responses were also observed in intraspecific contests with one *G. petersii* tethered by a thin wire for signal separation (Russell et al. 1974). Groups of 6 and of 14 *G. petersii* also showed the PLR without any aggression, although an individual signal identification was not possible (Serrier 1982).

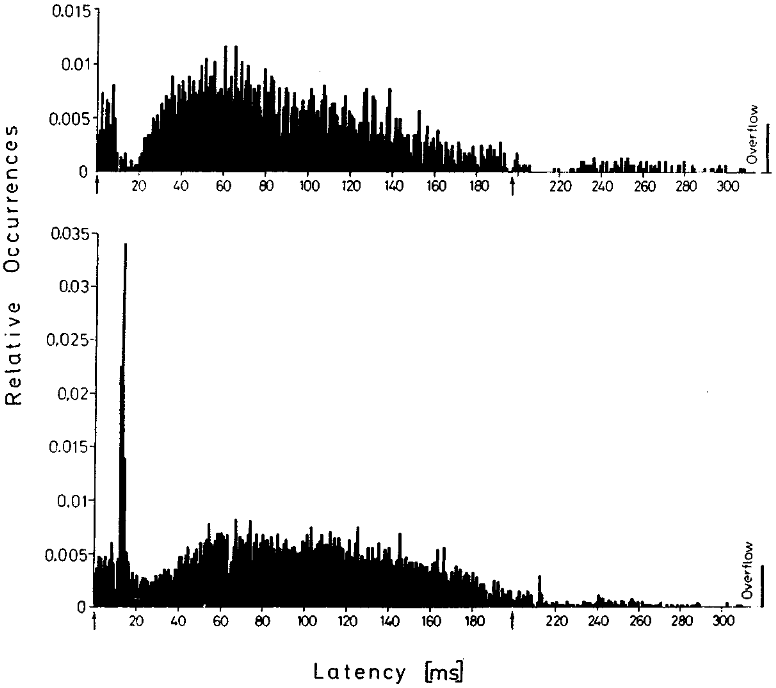


Fig. 5.21: Post-stimulus time histograms of the discharge latencies of a female (**top**) and a male (**below**) *Pollimyrus isidori* to stimulus pulses repeated at a rate of 5/s (arrows). The stimulus pulses imitated a conspecific's discharges as to field geometry and intensity. Note that in the male there is a strong tendency to lock its discharges to the stimulus pulses at a delay of 12-14 ms (preferred latency response), while the female delays its discharge to a variable time beyond 20 ms, resulting in a depression in the histogram from about 10-20 ms (preferred latency avoidance). (From Kramer 1978)

The PLR response was also found in several other species (more complete review, Kramer 1990a). In *P. isidori* there is a sexual dimorphism: males show the PLR and females the opposite response, preferred latency avoidance (PLA), which consists in avoiding a latency range from 10-20 ms (Lücker and Kramer 1981; Kramer 1978). Subadult, juvenile *P. isidori* neither showed PLR nor PLA responses; only after sexual maturity latency responses were observed (either PLR or PLA for any one individual). It is astonishing that 11-day-old *P. isidori* larvae did show the PLR (see previous chapter; Postner 1992); when and for what reason the response disappears later during life, only to reappear at sexual maturity, is unknown.

Latency responses have also been seen occurring spontaneously in pairs of resting mormyrids (Kramer 1978; Bratton and Kramer 1989), and may be evoked by using artificial stimulation (Kramer 1976b, 1978). Clear PLR or PLA responses have been observed in *Marcusenius senegalensis* (10-25 ms), *Petrocephalus simus* (8-23 ms), *Brienomyrus niger*, and *Hippopotamyrus psittacus* (Focke 1990), as well as *Petrocephalus bovei* (Lücker in Kramer 1990a).

Apparently most, if not all, species have some kind of latency response, although fish not always show it. In *G. petersii* the response seemed mediated by the less sensitive type of tuberous electroreceptor organs, the mormyromasts, because this form of communication was limited to an inter-fish distance of about 25 cm (Russell et al. 1974). However, as recognized only later (Bell 1989), another fish's EOD (an exafference) is not transmitted by the mormyromast pathway that is specialized on reafferences, and the rapidity of the response would also argue for the alternative (Knollenorgan) pathway with electrical synapses (Bauer and Kramer 1974). The Knollenorgan hypothesis receives support from recent observations in *Brienomyrus niger:* this fish's PLA response was still present at 60 cm distance from a stimulus dipole adjusted to generate a conspecific's field strength (97 μV/cm at 100 μS/cm water conductivity), and in one specimen even at 80 cm (34 μV/cm; Lamml and Kramer, in prep.). These field intensities are too low to support the mormyromast hypothesis.

The function of the PLR or PLA responses might be the reduction of the probability of EOD coincidences (Bauer and Kramer 1974), a time sharing strategy of signalling like that found in certain frogs or insects. However, the short duration of the EODs of most mormyrids, together with the high variability of much longer inter-EOD intervals (that is, a low duty cycle), in itself represents a most efficient mechanism guarding against that possibility (Lücker and Kramer 1981).

More likely seems an alternative hypothesis of "sensory gating" which sees the PLR or PLA as a motor mechanism protecting a fish's own sensory feedback (or reafference) for active electrolocation, from the disrupting effects of other fishes' EODs (or exafferences). This conclusion follows from electrophysiological studies of mormyromast afferences: adaptation, or reduced responsiveness, was still found 165 ms after an EOD-like stimulus pulse (Kramer-Feil 1976). The PLR/PLA responses could help keeping reafferent feedback from mormyromasts more constant in the presence of the disturbing EODs of other fish, as it is not possible to have the other fish "shut up". However, a role in social communication cannot be ruled out at present, especially for the species with highly variable latency responses, or a sexual dimorphism in latency response.

5.3 Catfishes - Siluriformes

There is only one member of the Siluriformes with an identified electric organ, the strongly electric catfish *Malapterurus electricus,* the only representative of the family Malapteruridae (however, Howes 1985 considers two valid species, *M. electricus* and a very similar fish, *M. microstoma*, as "generally accepted"). The electric catfish is a large (up to 1.2 m), nocturnal predator of almost pan-African distribution. It occurs in both rivers and lakes. The electric organ discharge is a monopolar, head-negative pulse of 1.3 ms duration at 28 °C. It is under the command of two giant electromotor cells in the first segment of the spinal cord (Schikorski et al. 1992).

The electric catfish's discharge activity occurs mainly in three behavioural contexts (Bauer 1968; reviewed and extended by Rankin and Moller 1992): when (1) responding to disturbances (disturbance volleys); (2) during prey capture (feeding volleys); and (3) in response to an attacking predator (defensive volleys). Disturbance volleys are brief (3-67 EODs) and of low frequency; they are effective in chasing away most intruding fish, and are also evoked by a human prodding the fish with a stick. Feeding volleys are long, high frequency volleys (14-562 EODs; average EOD repetition rate: 300/s) and accompany the catfish's prey attacks. When, however, an electric catfish is itself being attacked by a larger predator (such as a catfish of the genus *Clarias*) it may give off still longer EOD volleys of still higher pulse rate: up to 438/s peak rate within a volley (Rankin and Moller 1992).

The electric catfish's discharge is evoked by gustatory or mechanical stimuli; a possible role of the catfish's ampullary electroreceptors still being unclear. However, an "ordinary" non-electric catfish's, the brown bullhead's *(Ictalurus nebulosus)*, sensitivity for impedance inhomogeneities ventrally to the fish has been demonstrated (Peters and van Wijland 1993). The bullhead does not possess an electric organ; however, like any live organism, it generates a bioelectric D.C.-field accompanying the regulation of its ionic balance. Using this self-generated electric field the bullhead may detect conductivity anomalies, such as those caused by prey buried in the sand, by active electrolocation (Peters and van Wijland 1993); a sensory mechanism until now thought to be present in weakly electric fishes, exclusively (Chap. 4.2.1.).

A surgically denervated electric catfish unable to discharge has a drastically lowered success rate in prey capture (Bauer 1968). An electric catfish sometimes discharges "voluntarily", apparently in order to stir up prey by its low-frequency "chase volley" which is composed of 1-10 EODs (Bauer 1968; Moller et al. 1979; Belbenoit et al. 1979). Moving prey may then be detected by mechanical or gustatory cues.

In contrast to its interspecific communication function, the catfish's electric organ appears to have little significance for intraspecific communication. Social interactions among strongly electric catfishes are strictly non-electrical (Rankin and Moller 1986). The only exception from this is extreme distress, for example, an electric catfish being severely bitten or swallowed by another may give off EOD volleys even from inside a larger one (Bauer 1968; Rankin and Moller 1986).

Weak electrical activity was recorded from a few other African catfishes: three small species of synodontid Mochokidae or squeaker (Hagedorn et al. 1990), and the big sharptooth catfish *Clarias gariepinus* (Clariidae) (Baron et al. 1994). In one of these synodontids, *S. nigrita*, as well as in an additional one, *S. schall*, Baron et al.

(1994) report electric signals of variable amplitude and waveform. These authors consider the electrical activity of these fishes to represent weak EODs; the associated weak electric organs are thought to represent dorsally located tissue derived from sonic muscle in the synodontids (Hagedorn et al. 1990), whereas there is no information yet in the case of *Clarias*. *Synodontis obesus* was the squeaker that generated the strongest signals (field strengths of 2-4 mV/cm); this is comparable to "weak" weakly electric fish (wave-type). This squeaker discharged only when disturbed; discharges also occurred when the fish did not vocalize (Hagedorn et al. 1990). The sharptooth catfish generated pulses of variable duration (5-260 ms) and similar strength; the activity occurred during intraspecific aggression only.

Kalmijn (1974) gives an account of action potential fields recorded near freshwater fish. For example, oscillograms of muscle action potentials recorded from the vicinity of an African non-electric catfish are shown by Lissmann (1958, 1963). The strength of potentials originating from the sonic muscles of vocalizing toadfish (*Opsanus*) that were also recorded externally to the fish was tens of millivolts (Bennett 1970).

5.4 South American Knifefishes - Gymnotiformes

The Gymnotiformes are the sister group of the Siluriformes (Chap. 5.3.); see Fig. 1.2. Whereas the latter are distributed worldwide, the former occur in South America only (with a few Central American exceptions ranging as far north as Guatemala). The centre of distribution of the Gymnotiformes is the Amazonian drainage system with the Rio de la Plata being the southern limit.

The systematics of the Gymnotiformes is still rather confused with the exception of a few genera; there may be about 108 species [J. Albert, pers. comm; see also brief review in Kramer (1990a) and the literature cited therein]. According to Mago-Leccia (1978) there are six families placed in two suborders. Mago-Leccia (1994) and J. Albert rearrange these in the following way: the Sternopygoidei comprise the families Sternopygidae and Apteronotidae which are all wave-discharging. The suborder Gymnotoidei has four families which are all pulse-discharging, the Gymnotidae, Electrophoridae, Hypopomidae and Rhamphichthyidae. All are weakly electric, with the electric eel, or electric knifefish (*Electrophorus electricus*), being able to also generate dangerously strong EODs. This fish is "le gymnote électrique" of the 19th century literature mostly written in French (for example, von Humboldt 1819). The most recent reviews of their communication behaviour are Kramer (1993, 1994).

5.4.1 Knifefishes with a Pulse Discharge

Like most other gymnotiforms, knifefishes with a pulse discharge tend to rest during the day. Discharge rates are low (depending on the species, from below 1 to about 65 pulses per second), and successive inter-EOD intervals are of almost equal duration. The standard deviation may be almost as low as 1% of the mean during quiet periods; in a few species even lower.

From a behavioural point of view the pulse gymnotiforms may be divided into two groups: (1) The species in which any change in state of excitement or motor activity (even the periodic gill movements; Westby 1975b) are reflected in a change of EOD rate which may be followed by a decrease to the resting level (for example, *Gymnotus carapo),* and (2) the fewer species which do not change their discharge rate even to strong stimuli or during vigorous motor activity (for example, *Steatogenys elegans).* The latter group also displays the most constant EOD rates at rest. The two groups do not appear to be systematic groups, as both behavioural types are found, for example, among the Hypopomidae as well as the Rhamphichthyidae.

The most conspicuous EOD rate display (only shown by fish of the "variable EOD rate group") is the SID [sharp increase of EOD rate followed by a decrease to the original level in a time course sometimes resembling an exponential decay (Black-Cleworth 1970); Fig. 5.22]. The SID display may accompany attacks on conspecifics, or prey fish in predatory species like *Gymnotus carapo,* and in response to adverse stimuli (Black-Cleworth 1970; Westby 1975a). There is, however, no absolute linkage between the electrical display and a specific motor pattern (unlike the Mormyridae, where a specific EOD rate display is an obligatory part of probably any social behaviour; Chap. 5.2). In certain other social situations also EOD rate decreases and stops occur.

Hypopomus occidentalis displays the "decrement burst" during aggression and courtship (Hagedorn 1988; Fig. 5.23). A few additional EODs of smaller amplitude are added to the normal, uninterrupted sequence of EODs of full amplitude (between 3-11). These displays are also given by female *H. occidentalis* (Hagedorn 1988) when stimulated with trains of EOD-like pulses of male duration (Shumway and Zelick 1988). Both sexes have an EOD waveform approximately resembling a single-cycle sine-wave pulse. This is also found in *Hypopomus pinnicaudatus* which displays a morphological sexual dimorphism in the tail region (Hopkins et al. 1990), similar to the one found in *H. occidentalis* (Fig. 5.24; Hagedorn and Carr 1985).

Two male *H. occidentalis* put into a small aquarium with a single refuge tube will aggressively compete for the tube. Usually it is the fish with the EOD of higher amplitude and longer duration that wins possession of the tube. The experience of being a winner or loser further enhances the differences of EOD duration and amplitude within two days; winners changing to more male-like and losers to more female-like EODs (Hagedorn and Zelick 1989).

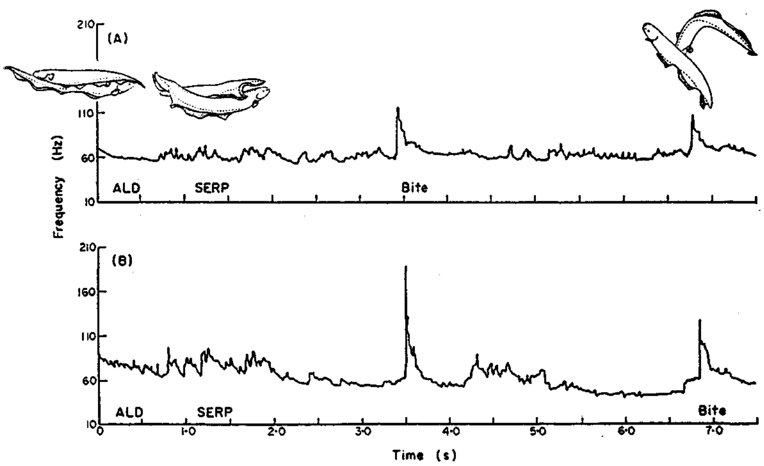


Fig. 5.22: Plots of concurrent discharge rates of two *Gymnotus carapo* engaged in a dominance struggle. *Ordinates* are the instantaneous discharge rates of each fish (that is, the reciprocal of each inter-discharge interval plotted individually). At around 3.5 s fish A bites fish B and displays a SID (*s*harp *i*ncrease in discharge rate followed by a *d*ecrease to the resting level) which in turn evokes a large SID in fish B. Shortly before 7 s a similar episode happens with reversed roles of the fishes. *ALD* anti-parallel lateral display; *SERP* serpentining (which are other forms of agonistic behaviour). (From Black-Cleworth 1970)

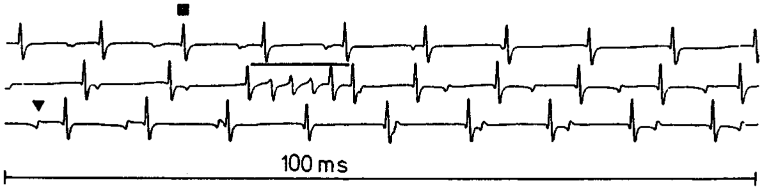


Fig. 5.23: An electrical display seen in attacking or courting *Hypopomus occidentalis* is the decrement burst which consists of a few (3-11) additional EODs of lower amplitude interspersed in the normal, steady firing of the electric organ (middle trace, *bar*). Each line = 100 ms. *Square* male EODs; *triangle* female EODs. (From Hagedorn 1988)

Individual recognition by EOD pulse waveform has recently been shown in *G. carapo* (McGregor and Westby 1992). This species shows a considerable intraspecific variability in EOD waveform. When the neighbour of a territorial fish residing in a fairly large aquarium was removed, and the neighbour's pre-recorded EOD pulses played back from the experimental fish's "incorrect" side (with respect to the neighbour's former position), the experimental fish attacked the dipole used for generating the playback signals significantly more often compared to the "correct" side (compare with the demonstration of individual recognition by EOD waveform in the mormyrid *Pollimyrus isidori,* Chap. 5.2.2.1).

Detailed EOD interaction between pairs of pulse gymnotiforms and mutual sensitivity to stimuli occurring during specific phases of their discharge cycles has also been reported. This seems to be related to dominance struggles but is also discussed in terms of sensory physiology (for review, see Kramer 1990a).

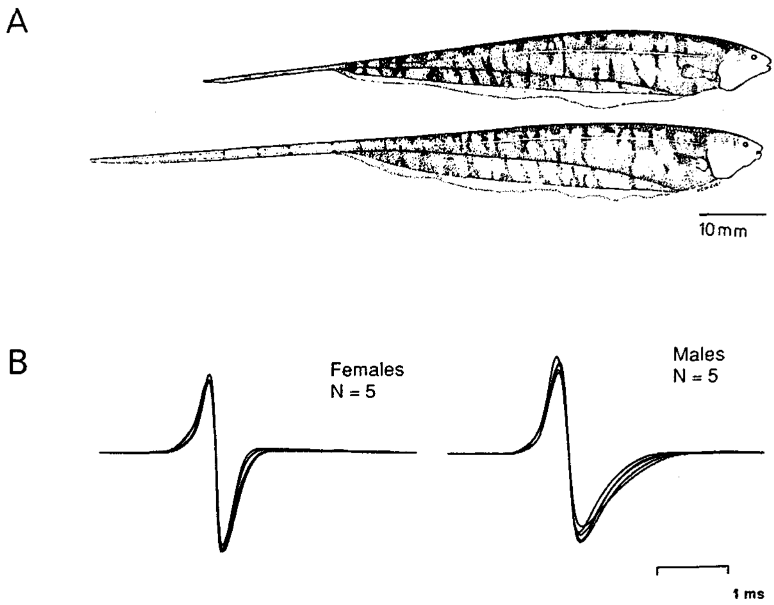


Fig. 5.24: A Male *Hypopomus pinnicaudatus* have a longer and broader tail filament compared to females (*top*) even when of the same body length (from snout to end of long anal fin). Also the average body length (without tail filament) of adult males is significantly above that of females. The electric organ extends into the tail filament; even the size of electrocytes (not shown) is greater for males than for females. **B** The waveform of the electric organ discharge shows a sex difference. Superimposed are oscillogram traces of the EODs of five individuals for each sex. Note head-negative phase of long duration and relatively lower amplitude in male EOD. These differences were significant for a natural population of fish recorded in the field. (From Hopkins et al. 1990)

5.4.2 Knifefishes with a Wave Discharge

Knifefishes with a wave discharge comprise two families. The Sternopygidae (at least 24 species) and the Apteronotidae (at least 45 species; J. Albert, pers. comm.) generate the most constant biological signals known: the standard deviation of 1000 EOD intervals of a mean of about 1 ms may be as small as 0.14 μs or less (Bullock

1969, 1970; Bullock et al. 1975; Kramer 1987). Discharge frequencies range from low to high in sternopygids (15 to about 800 Hz), and from medium to very high in apteronotids (about 500 to 1800 Hz). During the day these fish seek shelter and become active during night; their EOD frequency does not seem to change in a circadian rhythm (unlike some pulse gymnotiforms; Lissmann and Schwassmann 1965; Schwassmann 1978).

Apart from their constant discharge frequencies the stability of the EOD waveforms of the Sternopygidae and Apteronotidae is remarkable. EOD waveform differs widely between species (Kramer 1990a) and is variable within a species; this has been shown to be important in intraspecific communication. EOD waveforms and frequencies as related to communication will be treated in turn.

5.4.2.1 Signalling of Sex by EOD Waveform

The EOD waveform of *Eigenmannia lineata*, and probably other *Eigenmannia* species as well, is sexually dimorphic (Kramer 1985b) (Fig. 5.25). The differences are seen both in the time domain (waveform) and the frequency domain (harmonic content), that is, relative intensities of overtones or harmonics, as shown in an amplitude spectrum.

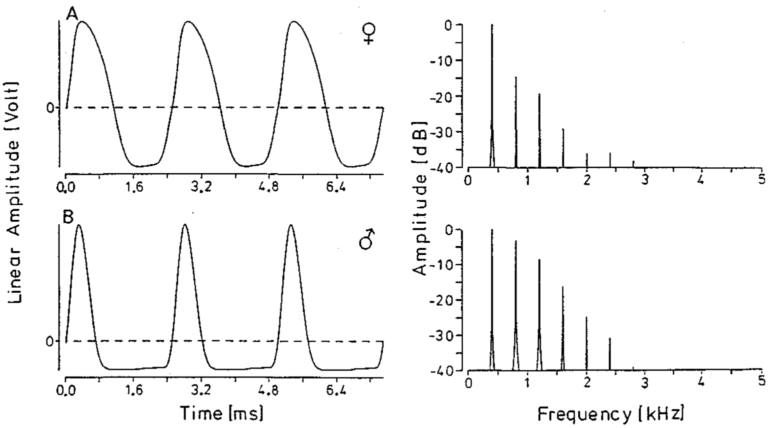


Fig. 5.25: *Eigenmannia*'s electric organ discharge of the wave type is sexually dimorphic, as seen in oscillograms (*left*) and Fourier amplitude spectra (*right*). Note that a female's EOD waveform (**A**) is closer to a sine wave and, therefore, weaker in higher harmonics than an adult male's EOD (**B**). (From Kramer 1985b)

The EOD waveform of juveniles and of adult females, as compared to that of adult males, is closer to that of a sine wave; hence, the intensity of overtones is lower in female and juvenile EODs. Trained *Eigenmannia* discriminate artificially generated

(Kramer and Weymann 1987) male and female EODs, with neither intensity nor frequency being factors (Kramer and Zupanc 1986). Naïve, untrained fish prefer dipoles playing back female EODs over those playing back male EODs (Kramer and Otto 1988).

Because female and male EODs differ both in waveform and harmonic content the question of which one of these properties the fish detect remained open. Analysing the spectral amplitudes of a signal would be sufficient for discrimination; similar to the ear of the human that is capable of discriminating audio playbacks of male and female *Eigenmannia* EODs by their difference in timbre (which is due to their difference in harmonic content).

Therefore, artificially generated signals were used as stimuli for both trained and naïve fish (Fig. 5.26A,E; Kramer and Otto 1991). A pair of artificial signals was synthesized using a sine wave of fundamental frequency, f_1, and its overtone, f_2 (of, for example, 400 and 800 Hz). The strong f_2-component was 3 dB lower in amplitude than the f_1-component in both signals, similar to the EOD of an adult male *Eigenmannia*. The pair of artificial signals differed in the phase relationships

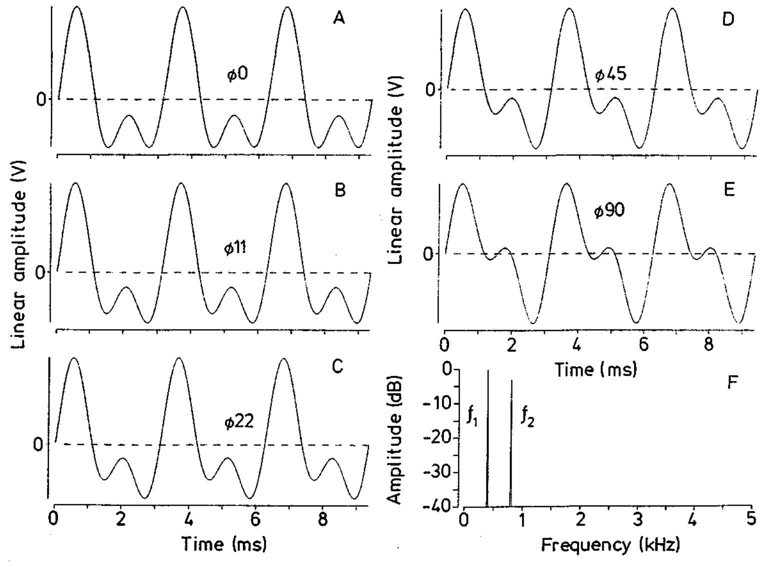


Fig. 5.26: A family of signal waveforms as used in conditioned discrimination experiments in *Eigenmannia*. The waveforms are all composed of two harmonics of identical intensity, the fundamental frequency, f_1, and its harmonic, f_2; their only difference is in phase relationship between these two harmonics. **A** Zero degree phase difference (relative to amplitude peaks); **B**, 11°; **C**, 22°; **D**, 45°; **E**, 90°. **F** Fourier amplitude spectrum is identical for all waveforms (*A-E*). Their second harmonic, f_2, is 3 dB weaker than their first, f_1. (From Kramer and Teubl 1993)

between their f_1 and f_2 components such that the waveform difference was maximal (0° *versus* 90°).

Audio playbacks of these signals are indistinguishable for the human. Trained *Eigenmannia*, however, did discriminate electrical dipole playbacks of the two signals (Kramer and Otto 1991). However, a possible (unwanted) cue for the discrimination could be amplitude: when presented at equal energy contents, the signals differ in peak-to-peak amplitudes; this is an unavoidable consequence of their difference in spectral phase relationships. (Shifting the f_2 component of the signal ø0 of Fig. 5.26 by a value of 90° causes the amplitude to rise by 14%.) Additional experiments clearly showed that fish detected "pure" waveform (time domain) differences in a pair of signals even when differences in spectral amplitudes or, alternatively, peak-to-peak amplitude of the signals, were excluded as factors by the experimental paradigm (Kramer and Otto 1991).

One of the two artificial signals (Fig. 5.26A) resembles an *Eigenmannia* EOD more closely than the other (Fig. 5.26E, which is a fairly good representation of an *Apteronotus albifrons* EOD). The question was studied whether one artificial signal was more effective than the other in attracting socially isolated, naïve animals (which received neither reward nor punishment) when used for stimulation.

Among eleven fish studied five showed a statistically significant preference for the artificial waveform which resembles *Eigenmannia*'s EOD more closely than the other (P at least smaller than 0.05, as tested for each fish individually; two-tailed test). The other fish did not show a significant preference for either signal (although two of these fish came close to significance in the same direction) (Kramer and Teubl 1993).

Using a totally different approach this experiment confirmed the validity of the conditioned discrimination results.

For the above experiments, the difference in phase relationships between the spectral components of the two artificial signals (Fig. 5.26A,E) had been chosen to be maximal (90° or $\pi/2$; 180° representing a simple polarity reversal without any change in waveform). However, fish can also discriminate pairs of signals with much smaller differences in spectral phase relationship which are, therefore, more similar to each other in waveform (Kramer and Teubl 1993). This has been shown for pairs of signals with a 45°- and a 22°-difference; a difference as small as 11°, however, proved too difficult for the fish to discriminate (Fig. 5.26). The threshold for a spectral phase difference between the first two harmonics of a signal is, therefore, assumed between 22 and 11° (Kramer and Teubl 1993).

The sensory mechanism responsible for the detection of a "pure" waveform difference among signals was addressed by (Kramer and Otto 1991). The EOD of an *Eigenmannia* is represented by the sensory responses of P and T electroreceptors (see Chap. 2.2). The T receptors which mark the zero-crossings of a fish's own EOD fire in phase throughout its body because they "see" the stimulus with the same polarity

(Fig. 5.27A). However, the T receptors of both sides of the fish's body experience the EOD of another fish with opposite polarities (Fig. 5.27B), as has also been observed in mormyrid pulse fish (Hopkins and Bass 1981).

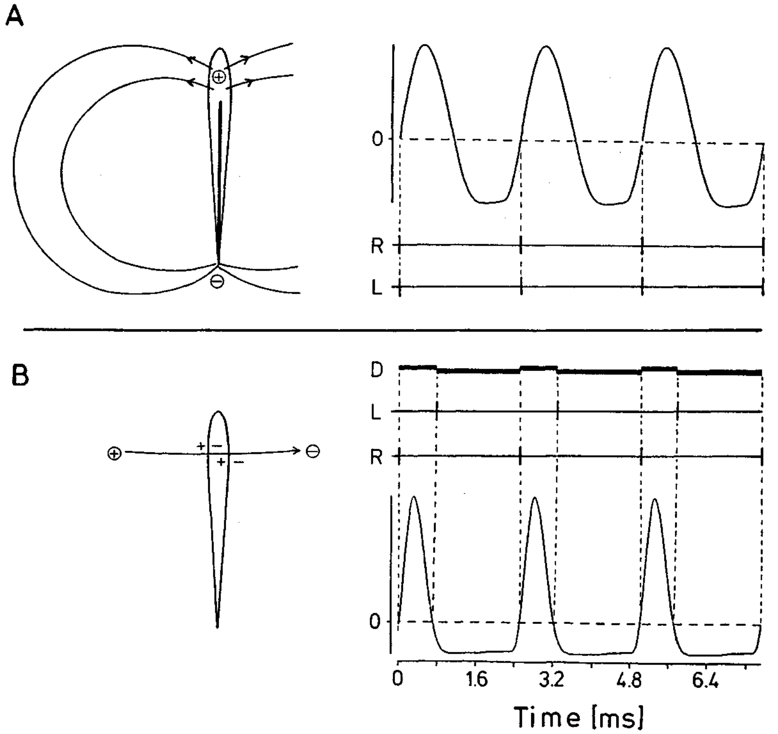


Fig. 5.27: Schematic responses of T afferences to own and conspecific's EODs in *Eigenmannia*. **A** Synchronous action potentials for both body sides (*R* right, *L* left) are phase-locked to the zero-crossings of the fish's own EOD. **B** Another fish's EOD is of opposite polarity for left and right side electroreceptors; hence, right and left receptor afferences would be out of phase as shown in traces *L* and *R* if the fish's own EOD was quiet (or for receptors located near the middle of the schematic electric organ bar). By centrally comparing the arrival times of afferences from the right and the left, the fish could assess an individually variable waveform parameter, the relative durations of head-positive and head-negative half-waves of another fish's EOD (*D*). (From Kramer and Otto 1991)

Unlike a pulse fish, a wave fish cannot sense its own EOD nor that of a conspecific in pure form, because both are "on" 100% of the time; both electric fields are seen superimposed by a local electroreceptor, according to their relative amplitudes, polarities, and frequencies. Because of the polarity difference of a conspecific's EOD for a fish's right and left side electroreceptors, the superimposition (of a fish's own and a conspecific's EOD) is additive for one body side and subtractive for the other (Fig. 5.28, top). For a local electroreceptor, a fish's own EOD is normally much stronger than a conspecific's EOD. There are substantial phase differences between the zero-crossings of both superimposed signals; the magnitudes of phase modulation between left and right side reflect the waveform of the signal being superimposed (Fig. 5.28, below). In this analysis, one cycle of the other fish's EOD is "stretched" to a full beat period, as determined by the frequency difference between the two fishes' EODs; this means a very great reduction of the speed requirements for the sensory system. If the fishes' discharge frequencies happen to be too close to each other (for example, a difference below 1 Hz) one or both fish may perform a jamming avoidance response which normally is directed such that the frequency difference increases to a few hertz (see Chapter 5.4.2.3.).

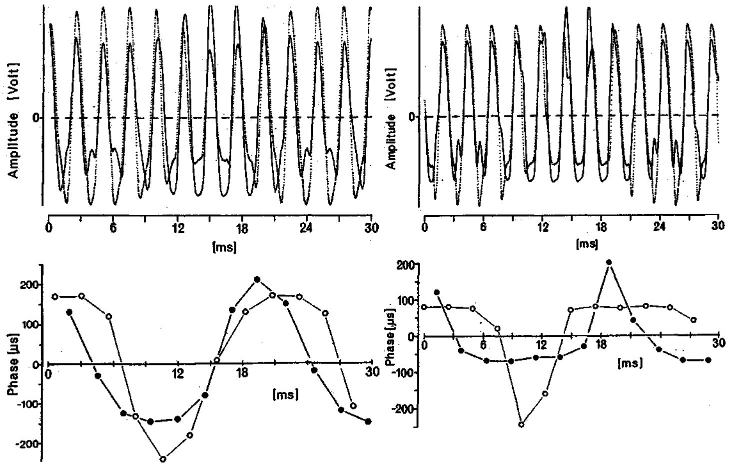


Fig. 5.28: Waveform detection by beat analysis in the wave fish *Eigenmannia.* **Top** A female *Eigenmannia's* EOD of 400 Hz is superimposed by another fish's EOD of 30% amplitude and 450 Hz, that is, modulated both in amplitude and in time of zero-crossings at a beat frequency of 50 Hz, corresponding to a beat cycle of 20 ms (centred). *Left* The other fish's EOD is a female, *right* 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** 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,* male for the *right* 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 and Otto 1991)

The T-receptor system is a fast one where electrical synapses are present; it faithfully preserves time information up to the midbrain (torus semicircularis; Szabo

1967). A neural circuit has been described which compares left and right (as well as tail and head) T-receptor information which might be the place of emergent phase sensitivity (Carr et al. 1986a,b; review, Carr 1990). This circuit appears to resolve phase differences in the range of below 1 µs (Rose and Heiligenberg 1985; Kawasaki et al. 1988); a value small compared with the phase modulation seen in Fig. 5.28.

5.4.2.2 Signalling by EOD Frequency Modulation

In wave fishes, even a small change of EOD frequency contrasts sharply from the extremely stable resting frequency (see Chap. 5.4.2). In an *Eigenmannia* discharging at around 400 Hz, a frequency change of as little as a fraction of 1 Hz may be statistically significant. In several species frequency modulations of various kinds have been observed during social behaviour, especially at night (for example, Hopkins 1974a). These modulations are correlated with overt behaviour and clearly serve as signals (Hopkins 1974a).

At night a courting male *Eigenmannia* displays short EOD interruptions (from about 20 to about 80 ms), called chirps, at a rate between one per minute and five per second (Hopkins 1974a; Hagedorn and Heiligenberg 1985). A gravid female will only spawn when a male has chirped at her site for at least an hour. The male may be replaced by an electrical dipole playing back male chirps (Hagedorn and Heiligenberg 1985). Chirps also occur in an agonistic context. In response to the mild attacks of a courting male a female may smoothly raise her discharge frequency by a few to several hertz over a period of a few to tens of seconds. Long rises may stimulate a courting male's rate of chirping and occur also in a purely agonistic context where they are thought to be submissive signals. Both sexes may also display "short rises" during the night of spawning.

Sternopygus macrurus males and females observed in the wild at night during their reproductive period tend to discharge at frequencies one octave apart (Hopkins 1974b). It is not known whether a mating pair engage in "active phase coupling", a behaviour especially seen in certain high-frequency apteronotids but also known from *Sternopygus* in experimental condition (Langner and Scheich 1978; Gottschalk and Scheich 1979). During active phase coupling, fish reduce their frequency difference and maintain frequency identity at a specific phase relationship for a few seconds to up to 4 minutes. The ethological or sensory significance of this behaviour is still unclear.

5.4.2.3 The Jamming Avoidance Response

The jamming avoidance response (JAR) has been studied mainly in the wave-discharging fish *Eigenmannia sp.* (Watanabe and Takeda 1963; Bullock et al. 1972 a,b), and is exclusively known from the laboratory using an unnatural (transversal) stimulus geometry; the function of the response is debated (see below). A stimulus of a frequency sufficiently close to a fish's EOD frequency may evoke a frequency change (even in an unrestricted fish quietly remaining in its electrically transparent shelter; Kramer 1987). According to the original report by Watanabe and Takeda in 1963 the response is always in the direction away from the stimulus frequency (Fig. 5.29); *Eigenmannia* behaving "as if to escape from the applied frequency" in order to "distinguish between its own signal and those of its neighbours" for better object detection (Watanabe and Takeda 1963). The sensitivity of the response is extraordinary (in the µV/cm range) and appears to be limited by that of the tuberous electroreceptors (see review Kramer 1987) of which there are two kinds.

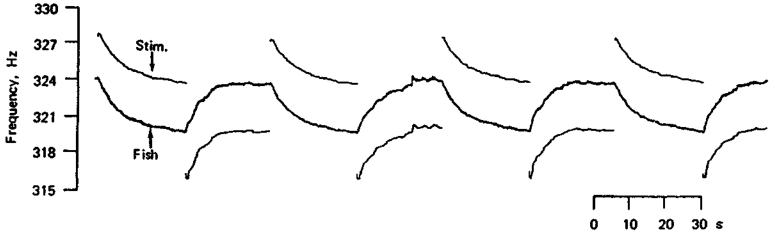


Fig. 5.29: Jamming avoidance response in *Eigenmannia*. *Stim.*, sine-wave stimulus of ΔF = ±4 Hz, held dynamically constant for 25 s by an electronic frequency clamp, then switching to the opposite sign. Note that the fish changed its EOD frequency *(Fish)* as if to escape from the stimulus frequency. (From Bullock et al. 1972a)

The sensory and neural mechanisms of signal detection, and of how the fish determines the frequency difference between its own EOD and the stimulus (ΔF-assessment), were studied in great detail (Bullock et al. 1972a,b; Scheich and Bullock 1974; Scheich 1977a,b,c; Heiligenberg et al. 1978; review of part of the subsequent work, Heiligenberg 1991). A fish would try to minimise the disrupting effect of another fish's EOD on its own electrolocation performance by increasing the beat frequency such that a more constant sensory input is achieved through "fusion" (similar to flicker fusion in vision). This hypothesis does, however, not address the problem that the stimulus field geometry routinely used in JAR experiments has, for technical reasons, been quite unnatural, with the stimulus electrodes symmetrically arranged to a fish's right and left. For the fish, this comes close to a homogeneous or uniform field, even when rod-shaped rather than plate-shaped electrodes were used. Uniform A.C. fields stimulate all receptors at the same time and are not biologically interpretable to electroreceptive organisms that cannot move (Peters and Buwalda 1986) because of their being caged or (pharmacologically) immobilized in the experiment.

Heiligenberg et al. (1978) have proposed a model of ΔF-assessment that relies on the joint activity of amplitude-encoding P- and phase-encoding T-receptors the afferences of which converge in the brain (the "amplitude-phase state-plane model" based on the Lissajous principle of difference frequency analysis that has already been envisaged by Watanabe and Takeda (1963). For years, the JAR has been said to represent the vertebrate behaviour the neural organization of which is best, almost completely, understood, from receptor responses to motor command (for example, Heiligenberg 1991). However, this model cannot explain, and its proponents seem to deliberately ignore (for example, Heiligenberg 1991, 1993), incompatible evidence such as (1) clear JARs to stimuli of ΔF=0 Hz that are frequency-clamped to the EOD (Kramer 1987, confirmed and extended by Kaunzinger and Kramer 1995, 1996); according to theory this stimulus should be ineffective because it does not amplitude- or phase-modulate the fish's EOD; (2) JARs to stimuli of threshold intensity (that is, field strengths of about 1 μV/cm), when one parameter thought to be essential, amplitude modulation, is below detection threshold (Kaunzinger and Kramer 1995, 1996); (3) Adult *Eigenmannia* males do not show a JAR, and females only respond in one direction (Kramer 1987); (4) No or little impairment of observed electrolocation performance in the presence of jamming stimuli.

Kaunzinger and Kramer (1995) argue that a contribution of the relatively insensitive P-receptors in ΔF-assessment is unlikely in the threshold range, because the amplitude modulation of a fish's EOD by a stimulus of threshold intensity is only 0.03%. (P-receptors are less sensitive than T-receptors by about 30 dB; Hopkins 1976.) These authors present an alternative sensory model (Fig. 5.30) that is exclusively based on the phase modulation of zero-crossings in the beating signal (phase modulation relative to a fish's unaffected EOD); a signal parameter that is encoded by the more sensitive T-receptors. For this new model to work (1) there should be (at least) two populations of T receptors, locking onto different phases of the EOD cycle; for example, one population to positive-, the other to negative-going zero-crossings. Secondly, a fish's natural EOD waveform has to be the "carrier" signal, with its asymmetries in waveform both in amplitude and time. To experimentally replace a fish's EOD by a sine wave (as has been customary practice in studies based on the amplitude-phase state-plane model) causes all differences in the phase modulation of zero-crossings for identical ΔF-values of opposite sign to vanish; hence, discrimination would not be possible (see Fig. 5.30; and next Chap.). This is the reason why the amplitude-phase state-plane model needs the P-receptors which, in the threshold range, simply do not contribute from all what is known about their sensitivity.

A role of the higher harmonics of *Eigenmannia's* EOD in ΔF-assessment has already been suggested by Scheich (1977a-c) who noted that the amplitude envelope of beat patterns for identical ΔF-values of opposite sign were time-symmetric mirror images. (These amplitude asymmetries reflect, of course, a similar asymmetry in the modulation of zero-crossings times, as shown in Fig. 5.30.) The importance of higher harmonics was refuted by Heiligenberg et al. (1978) who showed that the JAR (as judged from a pacemaker-derived, central-nervous signal) was still performed correctly when an anaesthetized fish's EOD was replaced by a sine wave applied through an electrode placed in the fish's stomach in order to better approximate the field geometry of a fish's own EOD. These authors concluded that higher harmonics were unnecessary for the JAR. [However, JAR results as shown in Fig. 4 of Heiligenberg et al. (1978) were only schematically summarized and do not represent truly quantitative data in this rather theoretically-oriented paper.]

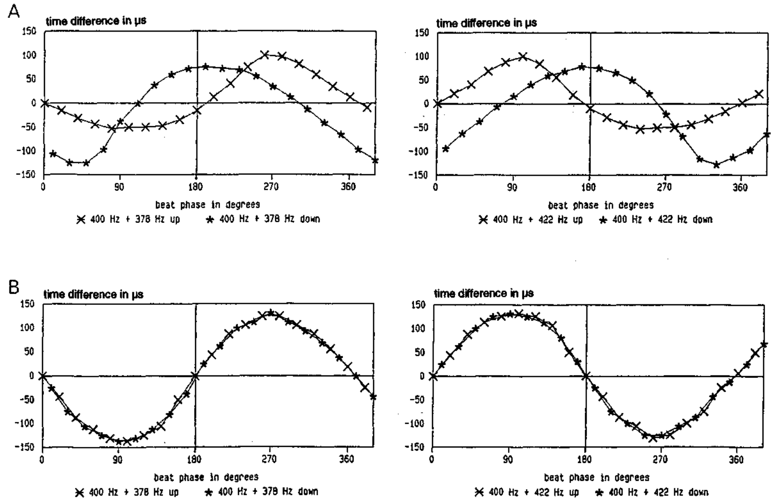


Fig. 5.30: **A** *Ordinates* Modulation of the zero-crossings times of an *Eigenmannia* wave-EOD by a superimposed sine wave of either plus or minus ΔF=22 Hz, at 30% amplitude of the EOD. *Abscissae* Time expressed as the phase of one beat cycle (360° corresponding to 1/22 s). **Left** ΔF is positive; **right** ΔF is negative. *(✕)* Positive-going zero-crossings; *(✱)* negative-going zero-crossings of superimposed EOD. In this model, zero-crossings times are reported by two populations of T electroreceptors. Note that it is not possible to collapse the two graphs into a single one by shifting one pair of curves along the abscissa; that is, the modulation patterns for identical ΔF-values of opposite sign are characteristically different. For an unequivocal ΔF-assessment beat-cycle phase information is unnecessary when, such as here, the "carrier" signal is a natural EOD rather than a sine wave. **B** Like **A**, but both carrier and superimposed signals are sine waves; note that patterns are identical for +ΔF and -ΔF except for their phase within a beat cycle. (Kramer and Kaunzinger, unpublished)

Higher harmonics are certainly not required for a stimulus to be effective in evoking a JAR; on the contrary, from a complex stimulus function such as "sawtooth", triangle or square, and an apparently infinite variety of others including playbacks of male and female EODs, *Eigenmannia* extracts the frequency difference and intensity of a single harmonic only, that which is closest in frequency to its own

EOD fundamental, f_1, and completely disregards all higher or lower harmonics (Kramer 1985). There is no difference between a JAR to a "naked" sine wave and to one hidden in a complex wave that contains higher and/or lower harmonics, as long as the two sine wave components are of identical intensity. A stimulus harmonic close in frequency to one of the higher harmonics of the EOD was effective only if the stimulus did not possess a lower harmonic close to the fish's EOD fundamental.

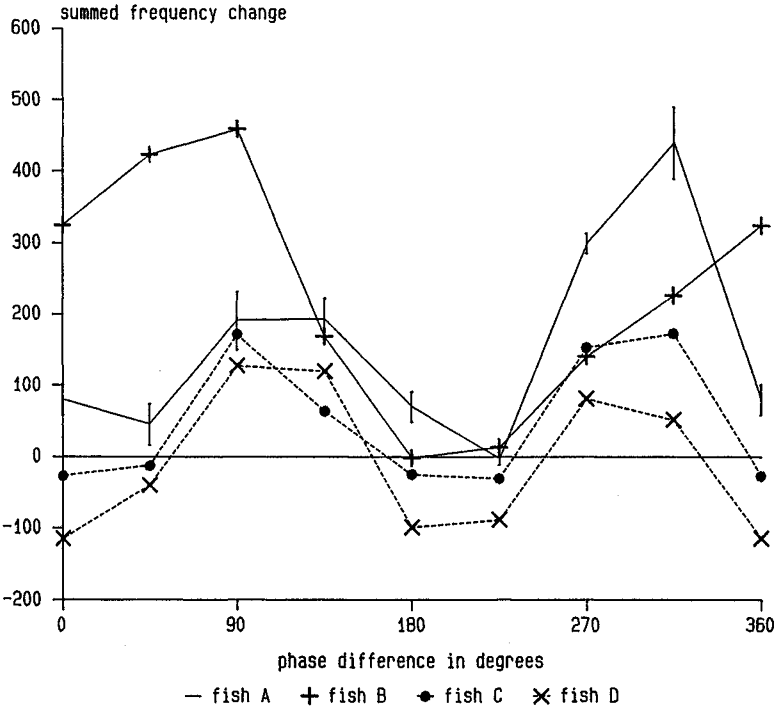


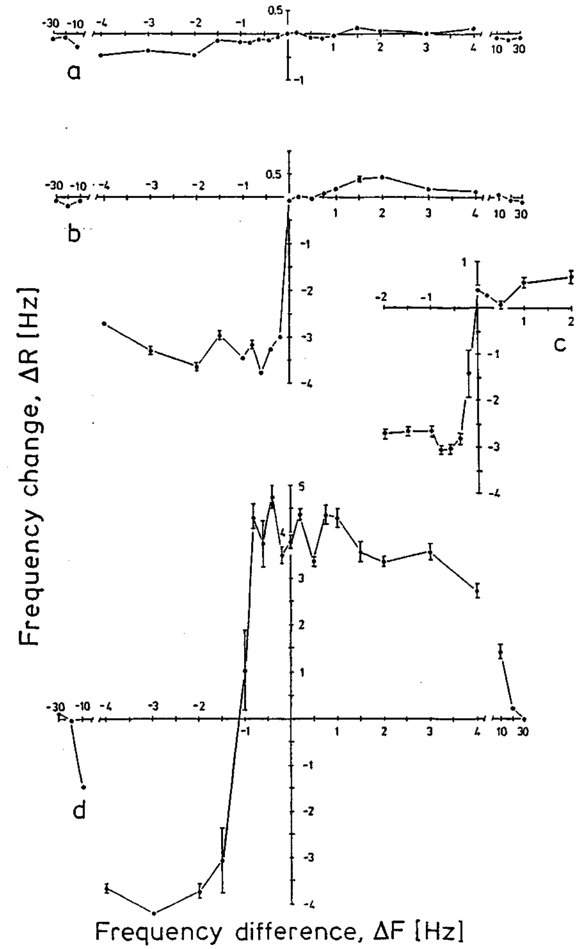
Fig. 5.31: JARs to supra-threshold sine-wave stimuli of ΔF=0 Hz that were both frequency-clamped and phase-locked (cycle by cycle) to the EOD of four different *Eigenmannia. Ordinate* Summed frequency change from resting frequency during a stimulus-on time of 60 s (area under curve); a positive value of 200 represents a mean frequency increase of about 1 Hz. *Abscissa* Phase difference of stimulus cycle relative to the fish's EOD cycle, with one EOD cycle corresponding to 360°. As the 0°-reference point positive-going zero-crossings were chosen. Each point is the mean of 10-20 tests; standard error bars are shown for one fish. Stimulus intensity, 500 μV_{p-p}/cm, about 30 dB above threshold. Note that strongest JARs were evoked by stimulus phase differences that caused the largest time shifts of zero-crossings in the superimposed EOD (see Fig. 5.35B). (After Kaunzinger and Kramer 1996)

For the "carrier" signal, however, we believe that Scheich's (1977a-c) suggestion concerning the relevance of higher harmonics of a fish's own EOD for its JAR should be reconsidered, although we now regard the phase modulation of zero-crossings times to be the salient parameter, not the amplitude modulation (Kaunzinger 1994, Kaunzinger and Kramer 1996). The significance of the modulation of zero-crossings times (that is, T-receptor responses rather than those from P-receptors) is demonstrated by JAR experiments using weak stimuli of ΔF=0 Hz that were both frequency-clamped and phase-locked to the EOD (Kaunzinger 1994, Kaunzinger and Kramer 1996). Significantly lower thresholds were associated with phase values that caused a notable time shift of zero-crossings (delay or advance) in the superimposed signal rather than with phase values that caused the amplitude to change (Fig. 5.31).

In the JAR literature we have the paradoxical situation of a behaviour thought by some to be completely understood in neuronal terms but clearly not as to its function; this is a contradiction in itself. The proposed function of the JAR is not compatible with the observation of little or no impairment of electrolocation performance in the presence of stimuli of EOD frequency (ΔF=0 Hz) and very high intensity (Heiligenberg 1977), in spite of the fact that the JAR is so exceedingly sensitive it is evoked already at threshold intensity (see above). Similarly, in spite of not showing a JAR, the electrolocation performance of *Sternopygus*, a related species with similar EOD waveform which does not seem to have a JAR, was only impaired by a stimulus intensity 50 times its own near-field EOD intensity (Matsubara and Heiligenberg 1978). It is unlikely that a fish ever encounters a wave signal of such a high intensity in nature.

That there must be more to the JAR than a mere supporting function for active electrolocation is also indicated by the observation of sexual dimorphism in JAR, which implies developmental change, in *Eigenmannia* (Kramer 1987). Adult males do not show the response (or extremely little; Fig. 5.32a); adult females only decrease their discharge frequency in response to slightly higher stimulus frequencies, and do not normally respond to stimuli lower than their own discharge frequency when they "should" give a frequency increase (Fig. 5.32b); perhaps the reason for this selective unresponsiveness is the similarity of a frequency increase with a long rise, a presumed submissive signal (see preceding Chap.). About half of the juveniles may respond in both directions according to whether the stimulus is of higher or lower frequency compared to their EOD frequency (Fig. 5.32d); the other half responding like females, that is, by giving frequency decreases only (Fig. 5.32c). The juveniles of the former group tend to increase rather than decrease their EOD frequency in response to stimuli up to about one hertz higher than their EOD frequency (Fig. 5.32d). Kramer (1987) did not find a single individual showing a JAR response profile approximately symmetrical about ΔF=0 Hz, as would be optimal under the hypothesis of an electrolocation function of the JAR (and as originally reported when the available electronic apparatus was less advanced). There was a disconcertingly high inter- and sometimes intra-individual variability, as well as strong habituation (Kramer 1987). The small amount of the frequency shifts associated with the JAR (a few hertz at most) has always been disappointing, and difficult to reconcile with the implied function of "jamming avoidance".

Fig. 5.32: The frequency change (ΔR) displayed by four *Eigenmannia* individuals in response to sine-wave stimuli similar in frequency to their own resting frequency (stimuli *not* frequency-clamped). ΔR is measured as the fish's response frequency minus its resting frequency; it is plotted here as a function of the frequency difference (ΔF), that is the fish's resting frequency minus the constant stimulus frequency. Each point is the mean of 12 measurements, ±1 SE. Large males (**a**) barely responded at all, even at increased stimulus intensities (+10 and +20 dB; not shown). Adult females (**b**) readily lowered their frequency to negative ΔFs, but showed no or only weak responses to positive ΔFs. Juveniles or subadults responded in both directions; however, those that were presumably females (**c**) only gave weak frequency increases to positive ΔFs, while the other type of juvenile (**d**), which was probably male, gave strong responses to both positive and negative ΔFs, including ΔF=0 Hz. This type of juvenile even increased their frequencies when the stimulus frequency was slightly higher than their own (negative ΔFs of small absolute values up to about 1 Hz). (From Kramer 1987)



Therefore, Kramer (1987, 1990a,b) and Kramer and Otto (1991) have proposed that by giving a JAR a fish changes the beat frequency of the superimposed signal (composed of its own EOD and that of another fish) such that it can better analyse the stimulus both in waveform (see Chap. 5.4.2.1) and in frequency. The fish actually must shift its EOD frequency because at exactly ΔF=0 Hz, its electrosensory threshold rises steeply and it is rather insensitive to another fish's EOD (see next Chap.). Although fish are perfectly capable of doing so (Kramer 1987), it would be disadvantageous for a fish to maximise the frequency difference between its own and another fish's EOD: it is a small frequency difference rather than a big one that yields a high temporal resolution because of a longer duration of the beat pattern. Under the hypothesis reviewed here, a fish would try to maximise the effect of another fish's EOD "riding" on its own by giving a JAR, that is, a *small* frequency change just sufficient to get out of the needle-like frequency region of "blindness" (see Fig. 5.33), in order to improve its sensory acuity for the reception of another fish's EOD. This is the opposite of the traditional jamming-avoidance hypothesis, where a fish would try to minimise the "deleterious" effect from a jamming signal by giving a JAR; under the jamming hypothesis the fish should give a *big* frequency change (which is not the case). Therefore, a different name for the JAR, such as "active beat response", would seem more appropriate [this is in analogy to "active phase coupling" which has also been observed in *Eigenmannia* (Langner and Scheich 1978; Gottschalk and Scheich 1979)].

5.4.2.4 Frequency and Phase Sensitivity

The low-frequency wave fish's *Sternopygus* sensitivity to wave signals declined by 30 dB when its EOD was surgically abolished, and intact *Sternopygus* were significantly less sensitive to stimuli of exactly their own frequency or a higher harmonic than to neighbouring frequencies (Fleishman et al. 1992; Fig. 5.33). Using stimuli frequency-clamped to the EOD, a similar "needle-like" sensitivity decline was also found in *Eigenmannia* (Kaunzinger and Kramer 1993, 1995), a wave fish with similar discharge but higher frequency. The frequency band of reduced sensitivity was extremely narrow, filter slopes being up to 5000 dB/octave (Kaunzinger 1994, Kaunzinger and Kramer 1995). If two *Eigenmannia* happened to discharge at identical (or nearly identical) frequencies neither would be able to analyse the EOD waveform of the other because the two electrical fields would not beat against each other (or too slowly; see Chap. 5.4.2.1).

This may have been the key selection pressure to evolve a frequency difference sensitivity that is one of the highest in the animal kingdom. On the basis of JAR experiments *Eigenmannia's* frequency assessment close to (but not identical with) its own EOD frequency was 0.6 Hz (Kramer 1987). This was confirmed by training experiments where the minimal frequency difference resolved by *Eigenmannia* close to its own discharge frequency was 0.52 Hz, at 30 dB sensation level (Kramer and Kaunzinger 1991).

At both higher and lower stimulus frequencies compared to a fish's EOD frequency the sensitivity for frequency differences declined. The loss at higher frequencies was, however, only small when related to the stimulus frequency (Fig. 5.34).

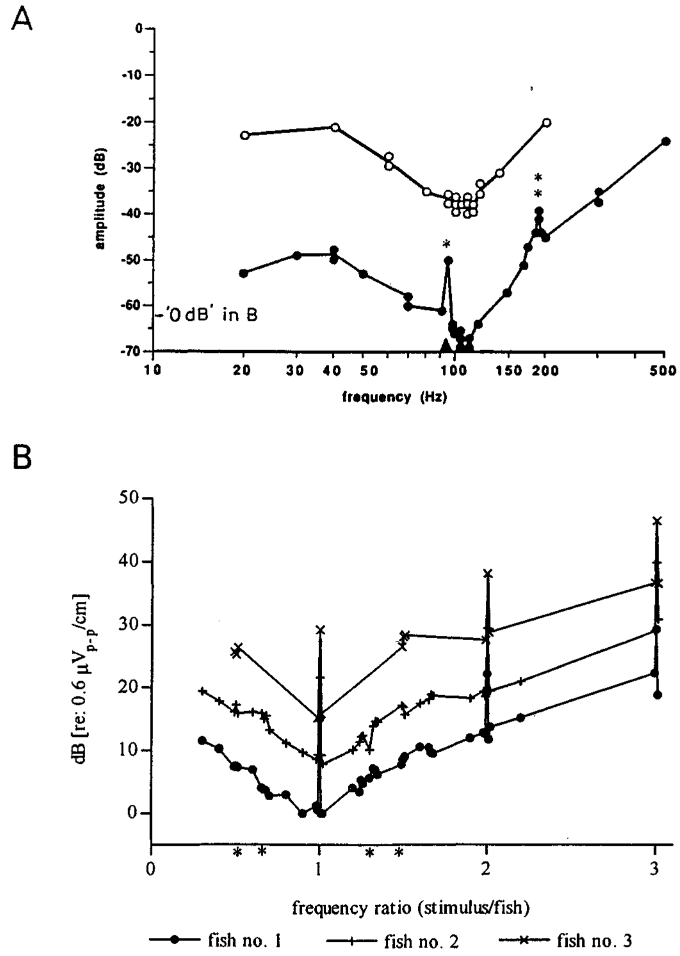


Fig. 5.33: Electrosensory threshold curves for a conditioned response in two species of wave-discharging gymnotiforms. Threshold for sine-wave stimuli defined as 70% correct "go" responses in a go/no-go choice. **A** An individual *Sternopygus macrurus*, **B** three *Eigenmannia sp.*. *Ordinates* Stimulus amplitude; *abscissae* stimulus frequency. **A** The average EOD frequency of the fish is indicated by a *triangle*; stimulus intensity, 0 dB=0.8 mV/cm. *Empty dots* Fish silenced by lesioning the central nervous pacemaker of the electric organ. Note marked decrease of overall sensitivity in a fish unable to discharge. *Full dots* Intact fish; note notches of reduced sensitivity at a stimulus frequency exactly equal to, or exactly twice, the fish's EOD frequency (*asterisks*). **B** like **A**, but *ordinate* scaled to lowest threshold (0.6 $\mu V_{p\text{-}p}$/cm=0 dB), and stimulus frequency referenced to EOD frequency (corresponding to 1 by definition). Ordinate values are correct for fish no. 1 (●); reduce curves for fish no. 2 (+) by 5 dB, for fish no. 3 (X) by 10 dB. Note that also in *Eigenmannia*, at stimulus frequencies representing exact integer multiples (1, 2, 3) of a fish's EOD frequency, threshold rose sharply compared to closely neighbouring frequencies. While this was true for stimulus

Eigenmannia's electrosensory frequency difference resolution is so high it is in the range of the most sensitive mammals (such as the human) for audition, and considerably superior to other acoustico-lateral senses in lower vertebrates for which difference thresholds are known (audition, Fay 1988; water surface waves, Bleckmann et al. 1989, Bleckmann 1995; Elepfandt et al. 1985). In contrast to *Eigenmannia* for electroreception, mammals have a highly specialised peripheral frequency analyser for audition, the cochlea.

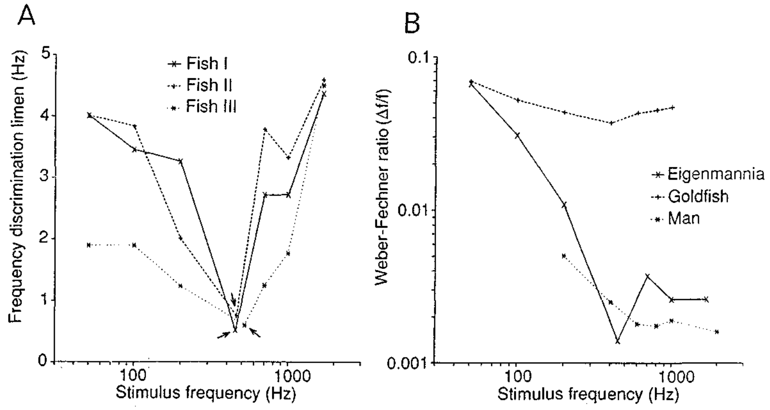


Fig. 5.34: Frequency difference sensitivity in *Eigenmannia*; sine-wave stimuli *not* frequency-clamped. **A** Frequency discrimination thresholds as a function of the stimulus frequency. Note that the lowest discrimination thresholds were observed close to each fish's individual discharge frequency (*arrows*; three fish). Lowest thresholds ranged from 0.52 to 0.79 Hz. **B** Comparison of electrosensory and auditory frequency discrimination in three vertebrates (*Eigenmannia*, electrosensory; N=3). Relative frequency discrimination is expressed as Weber-Fechner ratios ($\Delta f/f$) as a function of stimulus frequency (Hz) at similar sensation levels (*Eigenmannia*, 30 dB; goldfish, 35 dB; human, 40 dB). Note that the lowest difference threshold occurs in *Eigenmannia*, at a stimulus frequency close to its discharge frequency of 450 Hz. *Eigenmannia*'s electrosensory frequency resolution shows, however, a dramatic decline at lower frequencies compared to the frequency of best resolution; at higher frequencies, its frequency resolution remains remarkably high. (Goldfish data from Fay 1970, 1988; human data from Wier et al. 1977; *Eigenmannia* data from Kramer and Kaunzinger 1991)

Unlike other vertebrates which have to cope with signals as they occur, of a huge range of frequencies and intensities, *Eigenmannia* and similar fish detect a signal as the modulation (beating) of their own, extremely stable EOD. Tuberous electroreceptors are tuned to the frequency and intensity of a fish's own electric organ

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frequencies exactly equal to, and higher octaves of the EOD frequency, no sensitivity decrease was found at frequencies a fourth x 1.33) or a fifth (x 1.5) above EOD frequency, nor at ½ or ²/₃ of the EOD frequency (*), that are also characterized by standing wave patterns of the superimposed EOD. EOD frequency was around 500 Hz in these fish; each point represents the mean of at least 10 tests. In one fish the 50-90% range of correct responses is shown. (**A** from Fleishman et al. 1992; **B** from Kaunzinger and Kramer 1995) discharge. The receptors have a narrow working range only, and may thus specialise in a high difference sensitivity. This "functional" cochlea affords *Eigenmannia* a frequency difference sensitivity just as high as a "real" one; if not rather a higher one. In addition, *Eigenmannia* is sensitive for signal waveforms (spectral phase differences) in a way not known in the mechanical senses (see Chap. 5.4.2.1.).

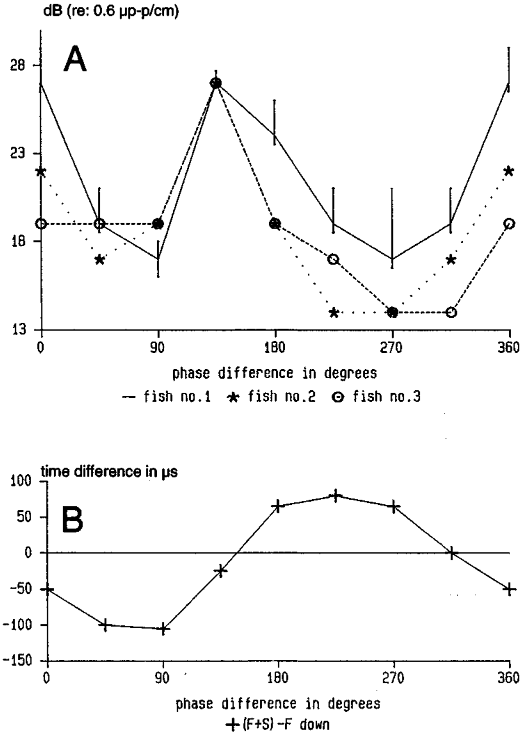

Fig. 5.35: Electrosensory thresholds to sine-wave stimuli of ΔF=0 Hz that were both frequency-clamped and phase-locked (cycle by cycle) to the EOD of three different *Eigenmannia*, as determined by a conditioned response. Threshold defined as 70% correct "go" responses in a go/no-go choice. *Abscissae* Phase difference between stimulus cycle and EOD cycle, one full EOD cycle corresponding to 360°; the 0°-reference point of a signal cycle is its positive-going zero-crossing. **A** *Ordinate* Electrosensory thresholds as field strength (0 dB=0.6 $\mu V_{peak\text{-}to\text{-}peak}$/cm). **B** *Ordinate* Time difference in μs between (negative-going) zero-crossings of the superimposed EOD (*F*+*S*) that is modulated by the stimulus (*S*), relative to the undisturbed EOD (*F*). For this electronically generated simulation stimulus amplitude was set to 30% of the EOD amplitude. Note that threshold in **A** is low where the zero-crossings time difference as shown in **B** is high (in absolute terms). (After Kaunzinger and Kramer 1996)

Additional experiments have shed light on the sensory mechanism of frequency discrimination (both in JAR experiments, see preceding Chap., and in tests using fish trained to receive a food reward on a correct behavioural response). The use of stimuli frequency-clamped to the EOD at ΔF=0 Hz that were locked to a specific phase of the EOD cycle, showed that threshold in trained fish depends on stimulus phase (Kaunzinger 1994; Kaunzinger and Kramer 1996). Phases that advanced or delayed the zero-crossings of the superimposed signal (EOD plus stimulus) relative to the "pure" EOD were detected at significantly lower threshold than stimuli of other phases (Fig. 5.35). It is probably the change of zero-crossing phases during the rise time of the stimulus that is detected.

As indicated, beat patterns where a natural EOD rather than a sine wave is the "carrier" signal display patterns of phase modulation of zero-crossings that are characteristically different for identical ΔF-values of opposite sign (Fig. 5.30). Therefore, ΔF can be determined unequivocally by using T-receptor information alone; we do not yet know, however, whether fish actually use this possibility. To look for such a sensory model was necessary because stimuli of threshold intensity modulate a fish's EOD only by 0.03% in amplitude (Kaunzinger 1994, Kaunzinger and Kramer 1995) which seems far too weak for a detectable change in P-receptor responses; the associated phase modulation of zero-crossings, however, is 0.26 µs (Kaunzinger and Kramer 1996); that value doubles for a left/right comparison of receptors located on opposite body sides (as discussed by Kramer and Otto 1991 and in Chap. 5.4.2.1). This is in the threshold range of *Eigenmannia* (Rose and Heiligenberg 1985).

5.5 Stargazers - Perciformes

The exclusively marine stargazers (Uranoscopidae) comprise some 18 genera and over 70 species (Pietsch 1989; Okamura and Kishimoto 1993). Members of the genus *Astroscopus* (*y-graecum*, *guttatus*, and *zephyreus*) possess electric organs, the best studied species being *Astroscopus y-graecum* (Dahlgren and Silvester 1906). These stargazers are the only marine group of electrogenic teleosts.

Stargazers demonstrate that it is possible for a fish to evolve electric organs without possessing electroreceptors. The lack of electroreceptors excludes an electrolocation or communication function of the electric organ. Stargazers are the group of electrogenic fishes the least well-studied, despite early interest in the unusual morphogenesis of the electric organ (White 1918), its electrophysiology (review, Bennett 1971a), the fishes' ecology (Dahlgren 1927), and their prey capture and discharge behaviour (Pickens and McFarland 1964).

Stargazers are somewhat flattened dorsoventrally with their eyes on the dorsal surface of the head, looking straight upward. Buried in the sand except for their eyes, they lie in ambush for smaller fish passing by which are engulfed by a quick opening of the wide mouth. During prey capture a stargazer may move a little upwards but quickly disappears in the sand again. Associated with the prey capture is a discharge volley which is evoked by visual and mechanical cues.

Members of the genus *Astroscopus* have two electric organs which are derived from extraocular muscle and lie behind the eyes (Dahlgren 1927); among all electrogenic fishes, these stargazers have the most "exotic" origin of their electric organs. The organs are innervated by the large oculomotor nerve and are fired synchronously. The electric organs consist of large flattened cells, vertically stacked on top of each other. They are innervated on their dorsal surface and generate a vertically directed field gradient (in agreement with these fishes' prey capture behaviour). About 150-200 cells form one column.

The discharges of the electric organ are monopolar pulses of about 5 ms duration (PSPs). The dorsal side of a fish becomes negative during an EOD. The EOD amplitude is up to 5 V recorded from a large *Astroscopus* (51-76 cm) with its dorsal surface in air (smaller values are measured with the fish totally submerged; Bennett 1971a).

A discharge volley usually consists of two parts: an initial high frequency "burst" of pulses lasting for about 100 ms which is followed by a low frequency train of pulses lasting several seconds. Discharge frequencies may reach 50 to 100/s. Prey are captured within 150 to 300 ms (Pickens and McFarland 1964).

Although the effectiveness of the EOD in prey capture has never been demonstrated a prey-stunning function is a reasonable assumption in species like *A. y-graecum*: (1) this stargazer discharges only during prey capture (or in defence while handled); (2) Even a small stargazer can cause mild discomfort, especially when hands are wet and have a number of minor cuts (Bennett 1971a).

Among all strongly electric fishes, *Astroscopus* stargazers are the weakest. Much weaker signals still were recorded from the Black-Sea stargazer *Uranoscopus scaber*; these signals were 50 times bigger in amplitude than signals recorded from ordinary, nonelectric fish (Baron and Mikhailenko 1976). *U. scaber* is thought to represent a "transitional form in the evolution of electric organs in fish" (Baron and Mikhailenko 1976); however, an electric organ has not been identified. Within the Uranoscopidae, the genus *Uranoscopus* is only distantly related to the genus *Astroscopus* (Pietsch 1989).

Outlook

The present review has shown that by the combined efforts of scientists from different disciplines, the field of electroreception and electrocommunication developed within the last three or four decades; a field that was inexistent to human knowledge before. Despite this remarkable progress, huge areas where we are still totally ignorant have also been identified in the foregoing chapters; all being promising areas of future research.

One would like to see more activity in certain areas that are currently not in the mainstream of reductionist analysis, essential as it is. For example, the phylogeny of electroreception is unfinished; especially studies among or beyond members of the "lower" and "upper" ends of primitively aquatic vertebrates would be of great general interest (Agnatha, Amphibia, and even Mammalia). The study of adaptation mechanisms of signal detection and signal generation, dealing with both proximate and ultimate causation, is an especially fruitful area. Adaptations are found from the membrane level of electroreceptor cells or electrocytes onwards up to the behavioural level. This leads to speciation processes that will need biogeographical/systematical and population genetics support. A corollary of this is wildlife conservation, as many of the freshwater species covered in the present review are stenotopic (Paterson in McEvey 1993) and will be the first pushed to extinction by human activities such as river impoundment (a worldwide, thriving business).

A well-adapted parasite never kills its host; let us try not to destroy the habitats our study-subjects live in so that future generations, especially the local people, may also profit from these fish as sources of protein food, as allies against malaria and onchocerciasis (Lévêque et al. 1988; Heeg and Kok 1988), or simply for enjoyment in angling and scientific studies.

Appendix:
Subphylum Vertebrates and Its Electroreceptive and Electrogenic Members

AGNATHA: jawless vertebrates

1 Myxini

1.1 Myxiniformes: hagfishes (32 species)

2 **Cephalaspidomorphi**

2.1 **Petromyzontiformes:** lampreys (41 species)

GNATHOSTOMATA: jawed vertebrates

PISCES: jawed aquatic vertebrates

3 **Chondrichthyes:** cartilaginous fishes

3.1 **Holocephali:** chimaeras (or ratfishes; 30 species)

3.2 **Elasmobranchii:** elasmobranchs (763 species)

3.2.1 **Selachimorpha:** sharks (339 species)

3.2.2 **Batidoidimorpha:** rays (424 species)

3.2.2.1 **Rajiformes** (424 species)

3.2.2.1.1 ★ **Torpedinidae:** electric rays (38 species)

3.2.2.1.2 ★ **Rajidae:** skates (190 species)

4 **Osteichthyes:** bony fishes

4.1 **Actinopterygii:** ray-finned fishes

4.1.1 **Cladistia:** polypteriform fishes (bichirs; 11 species)

4.1.2 **Actinopteri:** actinopterians

4.1.2.1 **Chondrostei:** chondrosteans (sturgeons and paddlefishes; 25 species)

4.1.2.2 Neopterygii: neopterygians

4.1.2.2.1 Ginglymodi: ginglymodes (gars; 7 species

4.1.2.2.2 Halecostomi: halecostomes

4.1.2.2.2.1 Halecomorphi: bowfin *Amia calva,* 1 species

4.1.2.2.2.2 Teleostei: teleosts (20 812 species), including the ***Xenomystinae*** (2), ★ ***Mormyroidei*** (200), ***Siluriformes*** (2211); including ★ ***Malapterurus electricus*** and

★ ***Synodontis obesus,*** ★ ***Gymnotiformes*** (108), and
Uranoscopidae: ★ Astroscopus(3 species)

4.2 **Sarcopterygii:** lobe-finned fishes

4.2.1 **Actinistia:** actinistians or coelacanths. ***Latimeria chalumnae,*** 1 species

4.2.2 **Dipnoi:** dipnoans (lungfishes; 5 species)

TETRAPODA: jawed terrestrial vertebrates

5 **Amphibia:** amphibians

5.1 **Urodela:** salamanders

5.2 Anura: frogs and toads

5.3 **Gymnophiona:** caecilians

6 Mammalia: mammals

6.1 ***Monotremata:*** monotremes

6.1.1 ***Ornithorhynchidae:*** platypus

6.1.2 ***Tachyglossidae:*** echidna

6.2 Marsupialia: marsupials

6.3 Placentalia: higher or „advanced“ mammals

7 Reptilia: reptiles

8 Aves: birds

Table 1. This classification of the vertebrates has been adapted to the needs of the present review. All living classes of vertebrates have been included (classes have one digit only). Latin names are followed by common names, if such exist. **Bold type**, electroreceptive by primitive ampullary receptor; ***bold face in italics***, secondarily electroreceptive (at least the immediate ancestors had lost electroreception); other print types: not electroreceptive (these codes are used on the Latin names only).★, possesses electric organs. Species numbers are approximate. (The presentation mainly follows Nelson 1984, Rosen et al. 1981 with its cladistic presentation of the Osteichthyes; and Northcutt 1986 for electroreception in nonteleost bony fishes). The Myxini are not considered vertebrates by some authors (e.g., Blieck 1992); therefore, it is probably justified to show both Agnatha and Gnathostomata in bold type.

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This concise review focuses on recent advances in the function and mechanism of electroreceptive systems in lower aquatic vertebrates and elucidates the sophisticated principles of communication, prey detection and orientation in these organisms.

An introduction into electroreceptors, electric organs and sensory functions is followed by a review of electrocommunication and its behavioral physiology. Throughout each section, one finds a wide range of examples, from sharks, rays and skates to catfishes and stargazers, including also strongly and weakly electric fishes from tropical freshwater bodies.

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