Chapter Eighteen

BEHAVIOR
OF MORMYRIDAE

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SUMMARY

There are over 200 species of fishes belonging to the African family Mormyridae, making it the largest single group of electrogenic fishes. All of the mormyrids produce weak electric discharges by a highly specialized electric organ in the tail, and all possess at least three major classes of electroreceptors: ampullary, used in prey detection and predator avoidance; mormyromasts, used for active electrolocation; knollenorgans, used for social communication. The mormyrids may be divided into three main subfamilies, based on external morphology and bone structure: there is 1 species in the Gymnarchinae; there are over 20 in the Petrocephalinae, which has a single genus, Petrocephalus; *and there are over 170 species in the subfamily* Mormyrinae. *Recent field recordings of the electric signals have made it possible to distinguish between sibling species. The diversity of electric discharges plays a vital role in species and in sex recognition.*

Mormyrids occur in virtually every type of freshwater habitat in Africa, but they are primarily river specialists. Many species migrate laterally from rivers or streams into flooded areas for reproduction. Little is known about the breeding and nesting behavior of mormyrids except for Gymnarchus, *which produces a large floating nest and has an elaborate system of parental care, and* Pollimyrus isidori, *which has been observed to build nests and show male parental care in aquarium observations.*

Electric communication is well developed in the mormyrids, and most of the species that have been studied appear to produce electric displays in fighting behavior. Little is known about electric signaling during courtship.

The active space of an electric discharge spans 1 or 2 m, depending on the size and orientation of the signaler and the receiver. Signals are composed of two parts: the stereotyped electric organ discharge (EOD) wave form and the variable sequence of pulse intervals (SPI). EOD durations vary from 200 μsec to 10 msec depending on the species. Males and females of many species have different EOD wave forms; usually the duration of the male's pulse is two to three times that of the female pulse.

There are four major types of patterns in the SPIs: cessations, frequency modulations, variations in tonic discharges, and interactions between pairs of discharging fish. Because of the technical difficulty of separating pulses from more than one individual, it has been difficult to analyze the context of SPI displays. Playback experiments have been useful for demonstrating discrimination of different SPIs.

Mormyrids may be unique among vertebrates in having a sense organ that is used primarily for sensing communication signals. The knollenorgan receptor is a putative communication sensor. Knollenorgans exhibit specific adaptations for sensing the EODs of other mormyrids. EODs of signalers are coded for by simple patterns of spikes with well-defined timing. Playback experiments have demonstrated that recognition of species-specific EODs depends upon the temporal properties of the EOD stimulus, not the power spectrum of the pulse. The temporal properties of the EOD wave form translate directly into the timing of spikes evoked in peripheral electroreceptors.

INTRODUCTION

Of all the known electric fish, the most remarkably diverse group is the freshwater fish of the family Mormyridae, to which *Gymnarchus niloticus*, the Nile knife fish, and several hundred species of mormyrids belong.* The Mormyridae are found in virtually every freshwater habitat in Africa south of the Sahara (including the Nile River basin) down to the northern part of South Africa: lakes, rivers, streams, and swamps. There are bottom dwellers, midwater fish, top feeders, inhabitants of deoxygenated swamps, and dwellers in the swiftest rapids of African rivers. In some places, the Mormyridae are the most abundant of all groups of fishes, making up over 65% of the fish biomass. Some of the mormyrids are famed for their long, elephant-like snouts, which serve as both a specialized feeding probe and a sensory appendage. *Gymnarchus* is known for its ability to swim forward and backward with equal ease by generating undulations of a long dorsal

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*Other authors in this book follow the older usage, which treats *Gymnarchus* as a family, the Gymnarchidae, and the rest of the group as the family Mormyridae, together comprising the order Mormyriformes.

fin; and of course, all mormyrids are widely recognized for their electrogenic and electroreceptive abilities. The Mormyridae is an example of spectacular adaptive radiation.

In spite of the size and importance of this group of fishes, knowledge of their behavior and of the diversity of their electrogenic and electroreceptive abilities is fragmentary and rudimentary. Most work has focused on a single species, *Gnathonemus petersii*, which has been a popular aquarium fish for the past 30 years. Studies have concentrated on both electrolocation and electric communication in this species. By comparison, little is known about nearly 200 other species of mormyrids. Yet, recent field and laboratory studies of the mormyrids have indicated that there is a wide range of specialized behaviors and a unique set of anatomical and physiological adaptations associated with the electric sense of these fish—adaptations that parallel those seen in the gymnotiform fishes of South America. For example, it now appears clear that the three distinct classes of electroreceptors in the mormyrids serve distinct behavioral functions: the mormyromasts are used for detecting objects by electrolocation; the knollenorgans for detecting conspecifics for communication; and the ampullary receptors for detecting predators, prey, and inanimate electric fields. This chapter is intended as a general introduction to the ecology, reproduction, behavioral biology, and especially electric communication of the Mormyridae, the largest and most diverse group of freshwater electric fishes.

THE FAMILY MORMYRIDAE

Mormyridae Are Members of the Osteoglossomorpha

The mormyrids belong to the most primitive group of living teleosts, the Osteoglossomorpha or "bony tongued" fishes (Fig. 1). Within this clade, many authors place *Gymnarchus* in a separate family from the mormyrids, but a recent cladistic analysis of all of the actinopterygian fishes by Lauder and Liem (1983) has placed them together, and that will be the convention followed in this chapter. The mormyrids are most closely related to the Notopteridae (the "knife fishes" of Africa and Asia) and the Hiodontidae ("mooneyes") to make up the Notopteroidei. Also included in this clade are the Osteoglossidae *(Pantodon, Osteoglossum, Scleropages)* and the Arapaimidae *(Heterotis* and *Arapaima)*, which occur both in South America and in Africa. The Mormyridae appear to be unique among the Osteoglossomorpha in their ability to produce electric discharges from an electric organ; electroreception is found in at least one African genus, *Xenomystus*, of the Notopteridae, but not in an Asian genus, *Notopterus* (Braford 1982; Bullock & Northcutt 1982). Otherwise no osteoglossomorph, other than the mormyrids, has electroreceptors (Bass 1982).
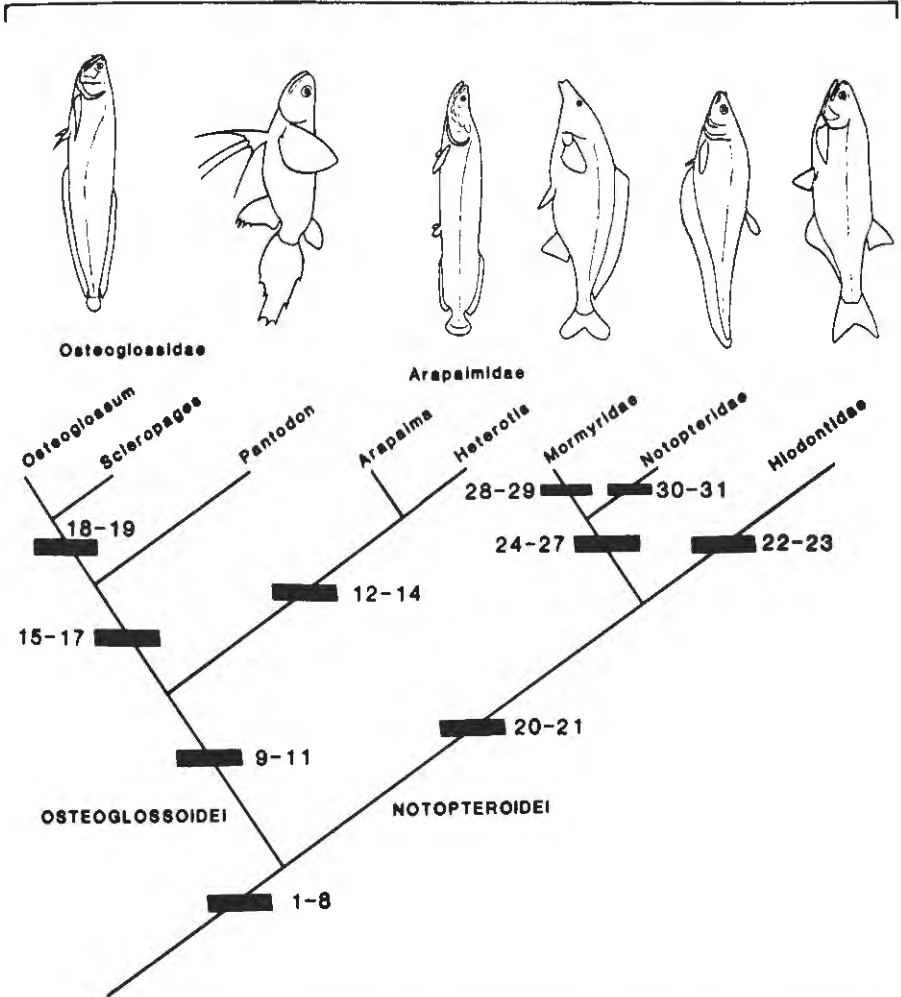
FIGURE 1. Phylogenetic relationships of the Osteoglossomorpha (bony-tongued fishes), a group of primitive teleosts to which the Mormyridae belong. Other osteoglossomorphs shown in this cladogram are the Osteoglossidae, *Pantodon*, the Arapaimidae, Notopteridae, and Hiodontidae. Phylogenetic relationships are based on the presence or absence of up to 31 different derived morphological characters, indicated by numbers. Character 24: the utriculus is completely separated from the sacculus and lagena. Character 25: the lateral line is without pores. Character 26: the brain has an enlarged cerebellum. Character 27: the dentary sensory canal is an open groove rather than enclosed. All of the Mormyridae and Notopteridae share these four characters. (For a list of remaining characters used in this phylogenetic analysis, see Lauder & Liem 1983.)

Mormyridae

The systematics of mormyrids are relatively well known. In addition to the major systematic studies of mormyrids by Marcusen (1864), Boulenger (1898, 1907, 1909–1916), and Poll (1957), Taverne (1967, 1968a,b, 1969, 1971a,b, 1972) has completed a detailed descriptive examination of the osteology of all of the major genera of mormyrids. Orts (1967) studied the anatomy of soft tissues, including the digestive tract, swim bladder, urogenital tract, inner ear, and gross anatomy of the brain. Quinet (1971) reviewed the structure of electroreceptors and their localization from the standpoint of systematics. Cranial morphology, studied extensively by Taverne (1972), has been crucial in determining differences between genera of mormyrids. Earlier classification schemes (Marcusen 1864; Boulenger 1898, 1909–1916) based largely upon external morphology differ from the present one principally in the organization of the older genus *Marcusenius* into the present *Hippopotamyrus, Pollimyrus,* and *Brienomyrus.* As interest in the mormyrids has increased in recent years, there have been many discoveries of new species and genera (Taverne & Géry 1968, 1975; Taverne et al. 1976, 1977a,b). We can expect new species to be described in the future.

The family Mormyridae can be divided into three main subfamilies (Table 1). The first, the Petrocephalinae, contains only one genus, *Petrocephalus,* with as many as 25 species. The second, the Mormyrinae, contains 16 genera with over 170 species. The third, the Gymnarchinae, has only a single species, *Gymnarchus niloticus.* A list of genera is given in Table 1. Taverne (1972) summarized anatomical characteristics in a phylogenetic tree that has been modified for Fig. 2. Selected comments on some of the genera of mormyrids are given below.

Mormyrus.   *Mormyrus* is the first genus of the Mormyridae to have been described (*M. cashive* Linné 1758). It is easily recognized by the very elongated dorsal fin, which can be more than twice the length of the anal fin. Many members of this genus possess an elongated tubular snout that is often associated with the mormyrids. Twenty-three species, listed by Taverne, have been described. Most are from Central Africa in the Zaire River Basin (see the map in Fig. 3). *M. rume,* a species from the Nilo-Sudan region of Africa, can attain lengths of 870 mm and 5200 g. *M. cashive* and *M. kannume* can reach over 1 m in length (Daget & Durand 1981) and can generate an electric field strong enough to be felt by humans if the fish is grasped near the electric organ either in or out of water. *M. rume* has been illustrated on many ancient Egyptian tombs and carvings (Kellaway 1946; also see Brier & Bennett 1979). *Mormyrus* is unusual among mormyrids in having mormyromast electroreceptors over the entire flank above and below the lateral line, where all other mormyrids lack electroreceptors (Quinet 1971). Reizer (1964) made a careful study of the systematics and descriptions of species of *Mormyrus* from central Africa. Bennett and

TABLE I. Mormyridae

Petrocephalinae
   Petrocephalus (Marcusen, 1854)—26 species and subspecies
Mormyrinae
   Mormyrus (Linné 1758)—23 species
   Mormyrops (Muller 1843)—28 species
   Paramormyrops (Taverne et al. 1977)—2 species
   Marcusenius (Gill 1862)—41 species
   Hyperopisus (Gill 1862)—3 species
   Gnathonemus (Gill 1862)—5 species
   Isichthys (Gill 1862)—1 species
   *Heteromormyrus** (Steindachner 1866)—1 species?
   Campylomormyrus (Bleeker 1874)—14 species†
   Myomyrus (Boulenger 1898)—3 species
   Stomatorhinus (Boulenger 1898)—12 species
   Genyomyrus (Boulenger 1898)—1 species
   Hippopotamyrus (Pappenheim 1906)—17 species
   Boulengeromyrus (Taverne & Gery 1968)—1 species
   Pollimyrus (Taverne 1971)—23 species
   Brienomyrus (Taverne 1971)—6 species
   Ivindomyrus (Taverne & Géry 1975)—1 species
Gymnarchinae
   Gymnarchus (Cuvier 1829)—1 species

*The taxonomic status of *Heteromormyrus* is uncertain (see Taverne 1972, p. 168).
†Revision in Poll et al. (1982)

Grundfest (1961) studied the mechanisms of discharge from the electric organ of *M. rume*, and Heiligenberg (1976) recorded patterns of electric discharges in nonsocial situations.

Hyperopisus.   Although three species of *Hyperopisus* have been described, they are probably simply geographical races of a single species, *H. bebe* (Lacépède). They are easily recognized by the long anal fin and comparatively short dorsal fin. Adults can reach 500 mm or more in length and 1240 g or more. This genus is restricted to the Nilo-Sudan zone of Africa.

Mormyrops.   *Mormyrops* is a large, diverse genus. The body is usually elongate. *M. deliciosus* is a large predatory species found in the Nilo-Sudan region that feeds on insect larvae when young and on fish when adult. Some specimens have achieved a total length of 1.5 m (6 kg). Along with *Gymnarchus*, *M. deliciosus* is one of the few piscivorous mormyrids; we know little about its habits. *M. zanclirostris,* found in the Lower Guinea zone of Africa, and *M. boulengeri* both have elongated tubular snouts that appear suited for probing for insect larvae among rocks on the river bottom. The pattern of innervation of the electric organ in at least one species,

M. zanclirostris, is inverted and the pulse appears inverted in polarity compared to other species of mormyrids (see Chapter 2).

Campylomormyrus.   The most spectacular of the long-tube mouth mormyrids are represented by *Campylomormyrus*. Even the names of species such as *C. rhynchophorus*, *C. elephas*, *C. ibis*, and *C. phantasticus* are suggestive of the most remarkable feeding specializations known for fish. Most of the species occur in the Zaire region (Fig. 3). Poll et al. (1982) present a recent survey of this genus with revisions of nomenclature. Little is known of the behavior of these species.

Isichthys.   There is only one known species of *Isichthys*, *I. henryi*, from the lower Niger, Cameroon, and Gabon. Its distinctive elongated body form and anal and dorsal fins are reminiscent of the long fins of *Gymnarchus* or some of the gymnotiforms.

Marcusenius, Pollimyrus, Hippopotamyrus, Ivindomyrus, Brienomyrus, Boulengeromyrus, **and** *Paramormyrops.* With the exception of *Boulengeromyrus*, *Paramormyrops*, and *Ivindomyrus*, which have been recorded only from Gabon, these genera are represented widely in Africa. This is a complex group of genera; its members can be distinguished from one another only by their osteological characters. *Brienomyrus* has been an important genus for behavioral studies and will be discussed further below.

Stomatorhinus.   Recognized as a distinct genus by Boulenger in 1898 because of the unique position of the external nares, one of which lies next to the mouth, this genus now appears to be restricted to the Zaire and the Lower Guinea regions of Africa. There are 12 species known from these regions. The electric organ in *Stomatorhinus* attains a complexity not seen in other species (doubly penetrating and nonpenetrating stalks), and the electric organ discharge wave form is one of the most complex, as well as the shortest in duration, known for any mormyrids (Hopkins 1981; Chapter 2, this volume). Most of the species are small (80–100 mm).

Gnathonemus.   According to Taverne's (1972) classification, *Gnathonemus* is restricted to five species, all of which, like *G. petersii*, have a single fleshy mental appendage *(Schnauzenorgan)* attached to the lower jaw which is covered with mormyromast and ampullary electroreceptors. Most likely it is a sensory structure used to probe crevices between rocks for food.

Myomyrus **and** *Genyomyrus.*   *Myomyrus* is represented by three species and *Genyomyrus* by only one. Although these species are known to systematists and appear in museum collections, no physiological or behavioral studies have been done on either genus.
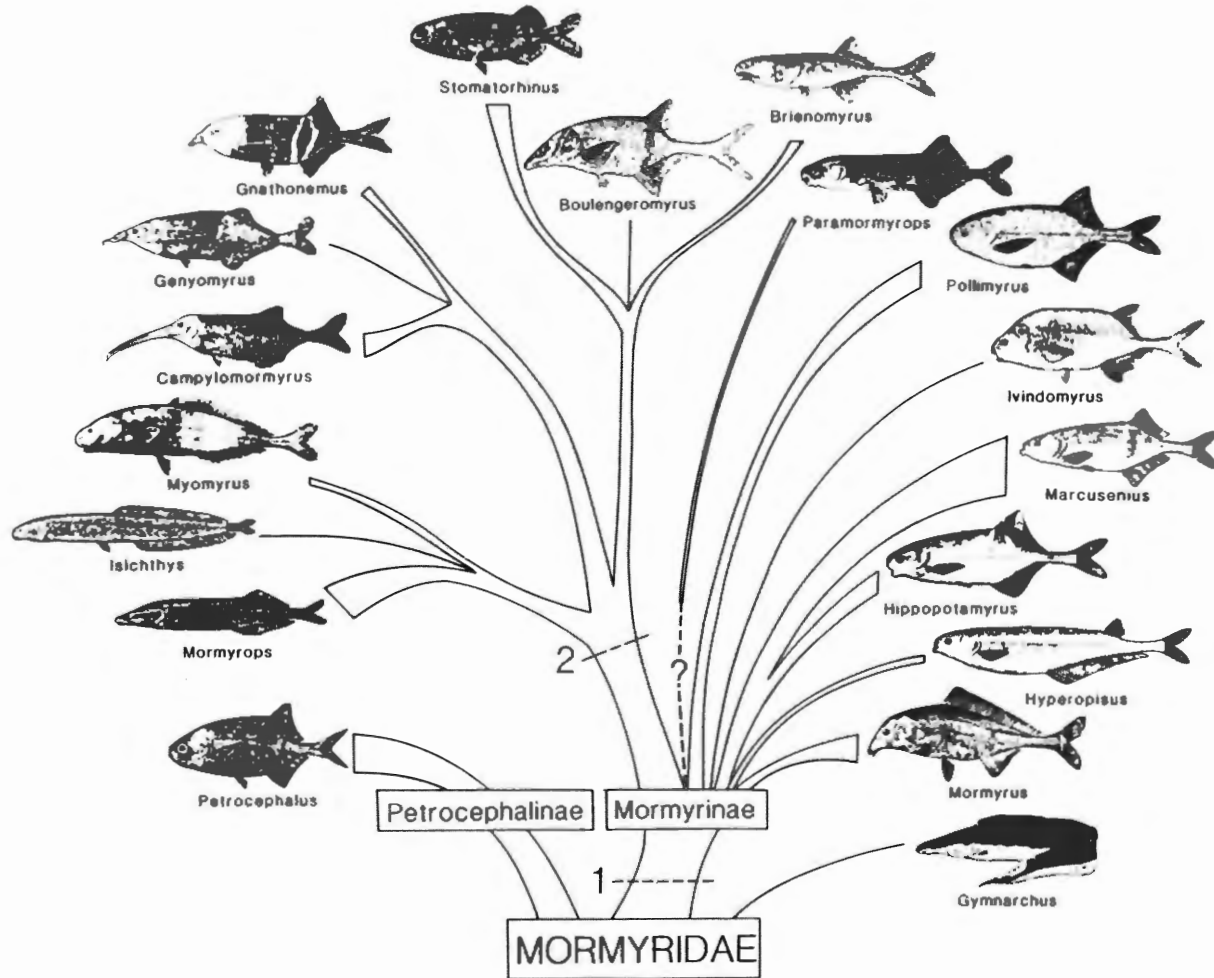
FIGURE 3. Map of African rivers showing Roberts' (1975) biogeographical analysis of current fish distributions. Each of the 12 zones has a distinctive fish fauna; mormyrids are not found in the Cape and Maghreb zones of Africa.

Petrocephalus.   *Petrocephalus* is a large genus (with over 25 species) that occurs throughout Africa. All of the species have rather shortened body forms. They frequently are silver colored, and many travel in large schools. The subfamily, Petrocephalinae, is distinguished from the rest of the mormyrids by its cranial morphology; by the proximity of the nares to each other, close to the eye; by the position of the mouth directly below the eye (Taverne 1969); and by unique "rosettes" of electroreceptors on the body surface in three positions on the head around the eye (Harder 1968a,b).

Gymnarchus.   Although most authors place *G. niloticus* in a separate family, Lauder and Liem (1983) put this species in a subfamily of the Mormyridae. The body form is unique because it is extremely elongated and possesses a single dorsal fin. Anatomically and physiologically, the species is comparatively well known (see the review by Hopkins 1983a). It is the only mormyrid with a wave-like electric discharge; all other mormyrids produce brief pulse discharges separated by comparatively longer intervals. *Gymnarchus* is restricted to the Nilo-Sudan region of Africa. Aspects of its reproductive behavior will be discussed below.

FIGURE 2.   Phylogenetic tree based on Taverne (1972), showing the three main groups within the family, Petrocephalinae, Mormyrinae, and Gymnarchinae. The Mormyrinae all lack a small bone in the anterior part of the skull above the mouth, the basisphenoid (character 1). Within the Mormyrinae, the left branch (*Mormyrops* to *Brienomyrus*), all species lack a lateral ethmoid, another small bone in the skull below the nares (character 2). The width of the branch is proportional to the number of species within a genus.

Electric Organ Discharges Are Useful Taxonomic Characters

In addition to the clear distinction between wave and pulse discharges already mentioned for *Gymnarchus* and the remaining mormyrids, the electric organ discharge (EOD) of the pulse mormyrids is a stable, stereotyped, species-typical, and often species-specific electrical event that may be described in terms of the polarity, number of phases, inflection points, duration, and spectrum of each pulse from the electric organ.

Unlike the gymnotiform fishes, in which the electrocytes of the electric organ are spread out along the entire axis of the fish's body, and in which there is considerable variability from one cell to the next in the wave form of the discharge (Bennett & Grundfest 1961; Bennett 1971a), mormyrid electric organs (with the exception of *Gymnarchus*) are compacted into the caudal peduncle to make a very short dipole source. The electrocytes discharge synchronously, with a uniform EOD wave form for each cell. The mormyrid EOD approximates a perfect dipole much better than the gymnotiform EOD, and as a consequence, the wave form of the EOD is constant for nearly all recording distances and directions (Hopkins 1983a; see Fig. 1 in Bass & Hopkins, 1985). The gymnotiform wave forms are highly variable, depending on the recording electrode position. When samples of EODs are collected from an individual that is turning with respect to the recording electrodes, the wave forms may be shown to superimpose almost exactly once the peak-to-peak amplitudes are scaled to the same value (see Fig. 2 in Hopkins 1983b). Figure 4 illustrates the diversity of EOD wave forms from a population of mormyrids from the Ivindo River district of Gabon (Lower Guinea region). Because the EOD is so stereotyped for a given species, it is possible to illustrate a single EOD (or two EODs in cases where the sexes differ) for each species. It is clear, from brief inspection of this figure, that within a given geographical area the EOD is highly diversified in terms of duration, number of phases, inflection points, polarity, and other features. Chapter 2 of this volume discusses the differences in the structure of the electric organs that give rise to the diversity of wave forms.

Sibling Species May Be Distinguished by EODs

Collections from Gabon include several species of mormyrids that hitherto had been virtually indistinguishable morphologically or had shown such broad overlap in morphological characters that they had been confused by researchers without access to records of the EOD wave forms. One such confusing case is *Brienomyrus brachyistius* (Gill) from West Africa (see the discussion in Trewavas 1974). Although the forms of *Brienomyrus* are highly variable, Trewavas placed all of them from Cameroon into a single species, *B. brachyistius*. In Gabon, where it has been possible to collect specimens and record the EODs from each, it is clear that there are four distinct patterns to the EODs of individuals resembling the original *B.*

brachyistius (Gill) (see Hopkins 1980); these patterns undoubtedly represent distinct species. One species has a monophasic EOD and occurs mainly in deep rivers and larger streams; a second has a 0.6-msec biphasic discharge and inhabits streams and rivers alike; a third, with a triphasic discharge varying in duration from 0.8 to 2.5 msec, inhabits only shallow streams. A fourth species has an 0.8 to 1.5 msec biphasic discharge and is found in both shallow streams and streams reaching 1 m depth. Although there is wide overlap, these species do show distinct habitat preferences. Only rarely would all four species occur in a single habitat. Without the aid of the EOD, these species would have remained indistinguishable. A discussion below outlines experiments showing that some of these mormyrids make behavioral discriminations between EODs in the process of species recognition.

Bass et al. (1983) have examined the morphology of each of these four electric organs to show that three of the species (biphasic, long biphasic, and triphasic) have similar types of electric organs (i.e., a single penetrating stalk that arises on the anterior side of the electrocyte); the monophasic species has a simple nonpenetrating stalk (see Chapter 2). Further taxonomic work is now needed to describe these species of mormyrids and to clarify the evolutionary relationships between them.

Sex Differences in EODs of Many Species of Mormyrids

The first case of a sex difference in an electric discharge was noted for one of the gymnotiforms with a wave discharge, *Sternopygus macrurus* (Hopkins 1972). Sex differences in a pulse fish were noted for three of the mormyrids from Gabon (Hopkins 1980), *Stomatorhinus corneti*, *Brienomyrus brachyistius* (triphasic), and *B. brachyistius* (long biphasic). Sex differences in *Stomatorhinus* were confirmed by Moller (1980). Westby and Kirschbaum (1982) have also reported on sex differences in *Pollimyrus isidori*, one of the first species of electric fish to be bred in the laboratory.

More recently, Bass and Hopkins (1983, 1985), and Bass (Chapter 2) have succeeded in imitating the natural development of sex differences in the EODs of several mormyrids by administering testosterone or testosterone derivatives to female fish or to juveniles of the species. Interestingly, Bass has been able to induce a change in EOD in many species previously not known to have a natural sex difference. Importantly, for one species known *not* to have a sex difference in EOD in the field (*B. brachyistius* [biphasic]), testosterone administration causes no change in the EOD of females or juveniles (Bass & Hopkins 1983).

Recent physiological studies suggest that androgens act directly on the tissues of the electric organ to produce the differences in discharges between males and females. Bass and Hopkins (1983) first demonstrated that the descending command signal from the pacemaker to the electric organ is identical for males, females, juveniles, and testosterone-treated individ-
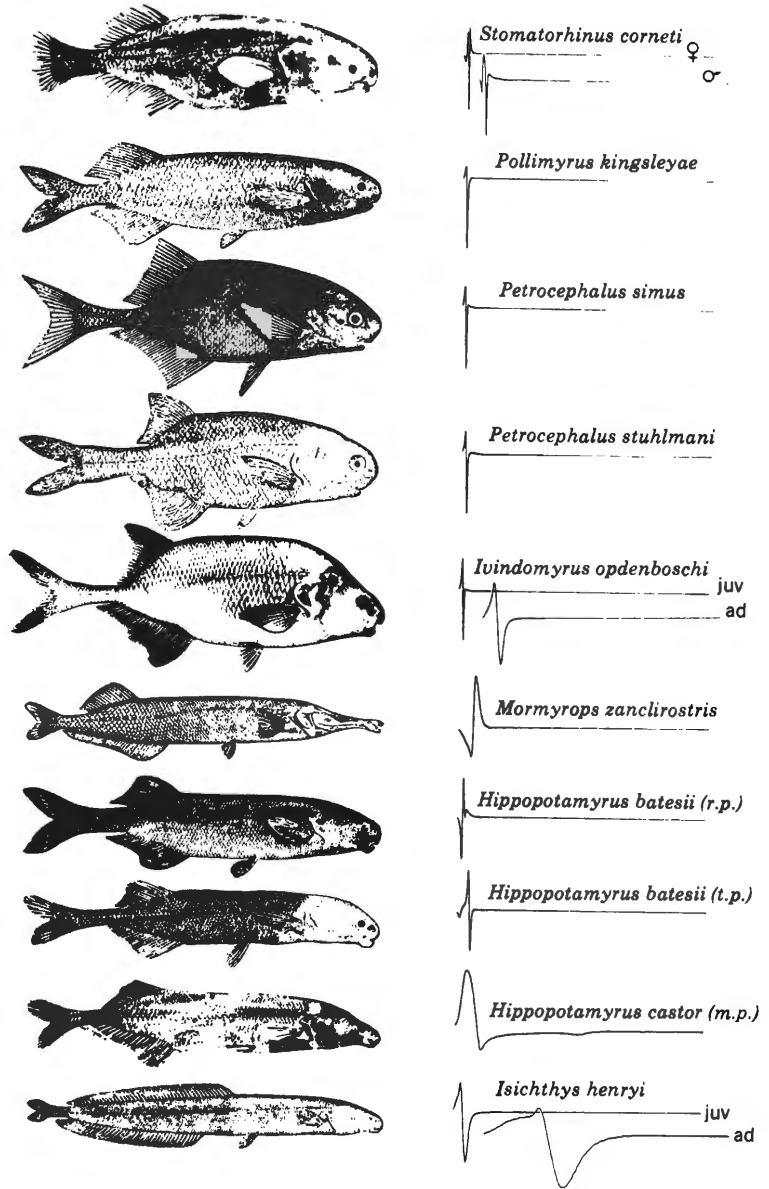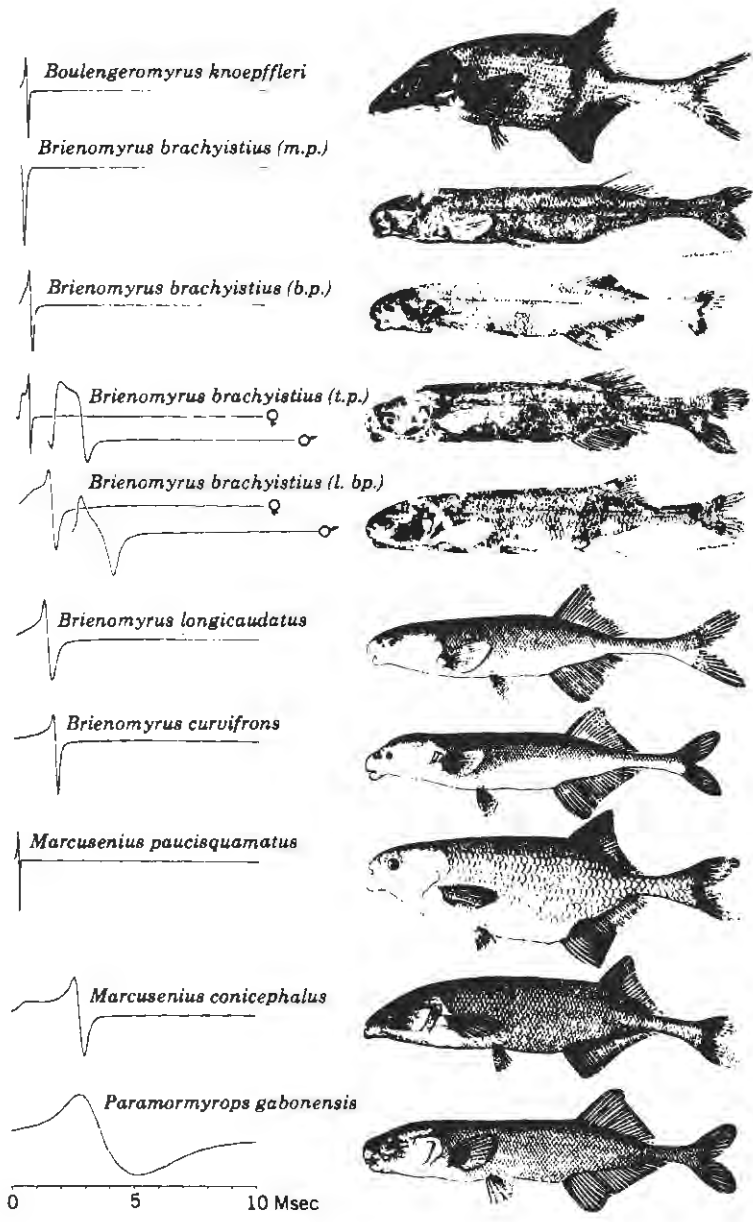
FIGURE 4. Mormyridae captured in the Ivindo River and surrounding streams in Gabon, part of the Lower Guinea ichthyofaunal province. The fish are arranged by genus, and each species' EOD is illustrated. All EODs are recorded with head positivity going upward on the trace. In cases where the sexes differ in the shape of the EOD, or where adults and juveniles differ, more than one trace is presented. One may conclude from an examination of EOD diversity that EODs may be important in both species and sex recognition in mormyrids. Since the EOD is produced regularly as the animal moves about in the environment, it is an example of a tonic communication signal.

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Boulengeromyrus knoepffleri

Brienomyrus brachyistius (m.p.)

Brienomyrus brachyistius (b.p.)

Brienomyrus brachyistius (t.p.) ♀ ♂

Brienomyrus brachyistius (l. bp.) ♀ ♂

Brienomyrus longicaudatus

Brienomyrus curvifrons

Marcusenius paucisquamatus

Marcusenius conicephalus

Paramormyrops gabonensis

0   5   10 Msec

uals. This finding strongly suggests that the sex difference must originate within the electric organ, not the electromotor pathway in the central nervous system. Bass and Volman (1985) have observed a two- to threefold increase in electrocyte spike durations of testosterone-treated females compared to control or cholesterol-treated females. Hagedorn and Carr (1985) recorded from testosterone-treated electrocytes of the gymnotiform *Hypopomus* and found changes in the shape of the action potentials recorded from the anterior face of some electrocytes.

One of the mormyrids with a sex difference, *Pollimyrus isidori*, has a complex EOD that has three phases in females and two in males (Westby & Kirschbaum 1982). Reasoning that the EOD wave form results from the sum of action potentials on the anterior and posterior faces of electrocytes in the electric organ, Westby (1984b) modeled the wave form of *P. isidori* as the sum of two Gaussian-shaped action potentials with slightly different durations and latencies and opposite polarities. He simulated the sex change in EOD by progressively delaying the latency of the second action potential compared to the first. Westby (1984b) suggests that natural EODs and sex differences in EODs may be accounted for by changes in the latency between the onset times of pulses generated in the caudal and rostral faces of the electric organ. Bass (Chapter 2) discusses these and other theories of EOD wave form generation in mormyrids and their development with sexual maturation.

In pulse fish with a sex difference in EODs, the male's pulse is always longer in duration than that of the female. In fact, pulse durations are increased by 100–200% in males of some species of mormyrids, and, as a consequence, the Fourier transforms have a peak energy at lower frequencies for males than for females (Bass & Hopkins 1985). This generalization holds for the gymnotiforms too, both for *Hypopomus occidentalis* (Hagedorn & Carr 1985), a pulse species, and for one wave species *Sternopygus macrurus* (Hopkins 1972; Meyer 1983) [The only exception to this rule is *Apteronotus leptorhynchus*, a gymnotiform, in which males discharge in the 1-kHz range at a slightly higher frequency than females (J. H. Meyer, M. Leong & C. H. Keller personal communication)]. For signaling purposes, contrast could be achieved with equal efficiency and effectiveness if males had shorter, not longer, pulses than females, yet we rarely find this situation. The reason for the similarity between gymnotiforms and mormyrids may become clearer when we understand the typical physiological effects of androgens on membranes and the exceptional cases.

ECOLOGY OF MORMYRID FISHES

Essential to an understanding of behavior is the ecological context in which it occurs. To appreciate fully the behavior of mormyrids, we must first know something about the distribution of different species in Africa, what

kinds of habitats they choose, how many species occur in a given habitat, what they eat, and where and when they reproduce. These and other questions will be reviewed in the section to follow.

Biogeography

Mormyrid fishes, like many African freshwater fishes, are distributed widely throughout Africa south of the Sahara and north of the Cape zone in South Africa. Roberts (1975) and Poll (1957) surveyed the distributions of all African freshwater fishes, taking into account present-day and ancient river drainage patterns to come up with different biogeographical ichthyofaunal provinces in Africa (Roberts' zones are illustrated in Fig. 3). Each zone is characterized by a distinct fish fauna, although some species are found in more than one zone. Each zone is typified by a number of endemic species (and genera). For example, *Gymnarchus niloticus* and *Hyperopisus* spp. are found only in the so-called Nilo-Sudan province in Africa, which includes the Nile River basin, and the entire southern border of the Sahara from Senegal and the Gambia on the west coast, to the Sudan, Ethiopia, and Somalia on the east coast. *Boulengeromyrus*, *Paramormyrops*, and *Ivindomyrus* appear to be endemic to the Lower Guinea ichthyological province (Gabon, southern Cameroon), while *Genyomyrus* and *Myomyrus* are endemic to the Zaire province. Other genera of Mormyridae, by contrast, are distributed throughout Africa except in the Sahara, the Maghreb zone bordering the Mediterranean, and the Cape zone in South Africa, where no mormyrids are found. *Brienomyrus*, *Pollimyrus*, *Petrocephalus*, *Marcusenius*, *Mormyrus*, *Gnathonemus*, and *Hippopotamyrus* are all fairly widely distributed throughout several of these provinces. Biogeographical information is sketchy for many regions of Africa; the Nilo-Sudan region is the best known (see Daget & Durand 1981). Useful guides to the literature on African freshwater fishes are found in Roberts (1975), Lowe-McConnell (1969), and Appendix 1, this chapter.

Mormyrids Are Primarily Riverine Species

Lake habitats are rare in Africa compared to river habitats, with the exception of the great lakes, which formed several million years ago. Not surprisingly, the mormyrid fishes, being a primitive group, appear to have speciated primarily in rivers, not lakes (Lowe-McConnell 1969). In the Zaire and Niger rivers, mormyrids account for 18% and 14% of the total fish species, respectively. In Lakes Rudolf, Victoria, and Malawi, they account for less than 2% of the total fish species; in other great lakes such as Lake Tanganyika, they are absent altogether. Lake Albert is represented by a comparatively rich mormyrid fauna. Some mormyrids have become specialists for lake environments (e.g., *Petrocephalus bane* and *Pollimyrus isidori*; see Lek & Lek 1978), but the majority of species occur in riverine habitats.

The creation of artificial lakes in the past three decades has provided an

opportunity to see how freshwater fishes adapt to lake environments. Volta Lake was studied by Petr (1967, 1968) both before and after construction. Mormyrids underwent the most dramatic drop in population as a result of the lake filling, nearly disappearing completely from the fish catches in the southern part of Volta Lake (less than 2% of the biomass of total fish catches), and maintained themselves only in the northern part of the lake, where they had access to river feeding conditions. Before the construction of the dam, the Black Volta River mormyrids comprised over 65% of dry season catches (biomass). A similar decline in mormyrids was noted for the Niger River after the creation of Kainji Lake in Nigeria (Blake 1977c). Both in the Volta Lake and the Kainji Lake, mormyrids appear to be restricted to the extensive reed beds on the lake shores.

Except for *Gymnarchus niloticus* (Förg 1853) most mormyrids appear to lack specialization for air breathing (Orts 1967); they may thus be poorly adapted to living on deoxygenated lake bottoms. Since many mormyrids appear to feed exclusively upon bottom-dwelling insect larvae, this situation may make lacustrine environments unsuitable in many cases. Petr (1968) reports that most Volta River/Lake mormyrids appear to prefer ephemerid, chironomid, trichopterous, and odonatan larvae, which live predominantly in rapids and in quickly-moving, highly oxygenated water.

Most of the larger tropical rivers are extraordinarily diverse in habitat structure. Regions with rapids house a different fauna from regions of slower-moving water. Roberts and Stewart (1976) report on the presence of *Campylomormyrus* in the rapids of the Zaire River. The long snouts of these fishes may be important in probing for insect larvae attached to rocks in the fast-moving rapids.

Stream Habitats

From the main rivers, mormyrids have invaded smaller streams, some taking up permanent residence as stream specialists. Knowledge of microhabit selection in stream mormyrids has been facilitated by the opportunity to census streams for mormyrids with electrodes and portable oscilloscopes. Electrode samples taken during the daytime indicate positions of individual mormyrids on a day-to-day basis. EOD wave forms indicate the species and often the sex. Hopkins (1980) illustrated the positions and spacing of several species of mormyrids from Gabon and demonstrated that species with long-duration EODs tend to be spaced farther apart than species with short-duration EODs. Stream censuses are also useful for estimating the distribution of males and females in species with a sex difference in EOD. A study area 280 m long from a small stream in Gabon is mapped in Figure 5, and the positions of individual unidentified male *Brienomyrus brachyistius* (tp) are indicated on separate map sketches below. The density of males remains relatively constant from day to day: from 7.2/ 100 m to 9.0/100 m over 7 sample days spaced over 1 month. Certain
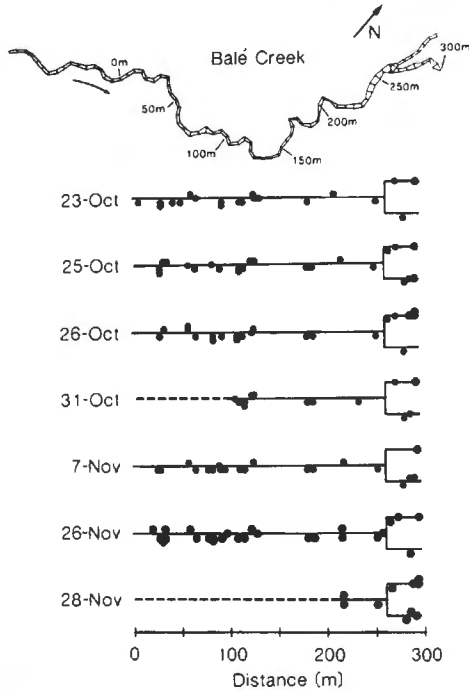
FIGURE 5. Male mormyrids show site attachment in a small stream habitat. Map of 280 m of a small stream in Gabon near the Ivindo River (above) for which routine censuses of mormyrids were taken over a period of 1 month. Each *Brienomyrus brachyistius* (triphasic) male is shown as a dot on the schematic of the maps (below), one map for each census day. Censuses were conducted during the daytime when the fish did not move from their hiding places under the banks, tree stumps or roots, and rocks. Inspection of the positions of individuals reveals many sites with a high degree of occupancy; others are occupied only rarely. The density of males ranged between 7.2 and 8.97 per 100 m during this study.

favorable sites are occupied day after day, probably by the same individual. Other less preferred sites serve as resting places for 1 day only. Males are often spaced apart by more than 5 m and are rarely seen within 2 m of each other.

Breeding Biology of Mormyrids

To date, little is known about the natural breeding seasons of mormyrids except that they tend to coincide with the period of maximal flooding and rainfall. Rainy seasons vary from region to region in Africa. Some sub-Saharan regions like the Ivory Coast receive rain in a single season; others have two rainy seasons per year. DeMerona (1979–1980) and Albaret (1983) found a single prolonged breeding season for most mormyrids in the Ivory Coast. Albaret (1983) and Blake (1977a) found as many as three different egg sizes in developing mature female mormyrids, which suggests that

they may spawn several times during a breeding season. In the Senegal and Gambia rivers, a single rainy season promotes synchronous breeding of mormyrids including *Gymnarchus* toward the begining of the flooding season. Females are seen to be filled with developing eggs prior to the rains.

Many mormyrids appear to be anadromous. They leave large lakes or rivers to migrate into smaller streams and flooded areas for spawning. Observations of the breeding behavior of mormyrids in Lake Victoria (Corbet 1960; Okedi 1969) suggest that mormyrids such as *Marcusenius* and *Gnathonemus* sp. aggregate near the mouth of large rivers emptying into the lake, and make a river ascent during the time of peak flood conditions. These fish may be migrating into the flooded swamps adjacent to these main rivers. Juvenile mormyrids are then captured in the rivers and pools next to these habitats at the beginning of the dry season. *Hippopotamyrus pictus* also shows anadromous behavior in the Niger River and Lake Kainji (Blake 1977a). Daget (1957) reports the same for *Marcusenius elongatus* from the Niger River.

Little is known about the reproductive behavior of mormyrid fishes, with the exception of *Gymnarchus niloticus*, which has been observed in the field, and *Pollimyrus isidori*, which has been bred in the laboratory (Kirschbaum 1975; Crawford et al. 1985).

Pollimyrus isidori. *Pollimyrus* males become highly territorial in aquaria, and individual males may occupy and vigorously defend a territory that may be as large as 1 m in diameter (Hopkins personal observation; Kirschbaum 1984; Crawford et al. 1985). Territorial defense appears to be most vigorous at night. During the day, intruding individuals are tolerated. Isolated males build nests by weaving a 2- to 5-cm-diameter spherical ball out of filamentous algae or macrophytes. The male brings the vegetation to the nest site in his mouth. The nest is pushed into crevices between rocks or inside pieces of tubing provided in an aquarium. A male may build several nests on his territory. Females, attracted to the male's territory, are then courted by the territorial male; spawning takes place (at night) over a period of 2–3 hours. Spawning bouts are separated by about 2 weeks. Spawning is accompanied by elaborate courtship behavior which includes the production of an acoustic song by males (described in Crawford et al. 1985). Eggs hatch in 4 days and slowly develop into juvenile fish over the next 2 months (Kirschbaum & Westby 1975, personal observation). After spawning, the male continues to defend the nest with very active circling. Upon occasion, he can be seen to push the eggs or wriggling larvae back into the mats of plants that make up the nest with his head. Both unhatched eggs and larvae are found in the nest. The male is highly territorial against members of his own species, even the female with whom he has just spawned. He fans the eggs and larvae during the early stages of development. Nest defense persists for 1–2 weeks after the original spawn-

ing, but by then the larvae are free-swimming. We have observed no attempt to eat the young by the parents. Kirschbaum and Westby (1975) report that larval *Pollimyrus* have a peculiar, long-duration EOD which arises from a special larval electric organ consisting of four longitudinal masses of electrocytes that extend from the base of the skull to the caudal peduncle. One tube of electrocytes lies dorsal to the spinal cord, and the other lies ventral to it (Kirschbaum 1977; Westby & Kirschbaum 1977, 1978; Denizot et al. 1978). The larval electric organ degenerates within 3 months after hatching, and the adult electric organ takes over the discharge function by about day 60.

Gymnarchus niloticus.   Budgett (1901) provides a complete description of the nest of *Gymnarchus niloticus* in natural habitats on the Gambia River. *Gymnarchus* constructs an elliptical floating nest measuring 60 × 90 cm in the outer diameter and 30 × 15 cm in the inner diameter. Nest construction begins immediately after the river banks flood, and spawning probably occurs within 10 days after flooding (Svensson 1933). The nest floats in open water or may be suspended by stalks of grasses to which it is attached in water that is usually no more than 1 to 1.5 m deep. The nest is constructed from a dense mat of vegetation and mud; it projects from the surface 4 to 5 cm on all sides except near the nest entrance. Budgett reports that about 1000 large spherical eggs 10 mm in diameter are laid in the nest and states that these eggs hatch in approximately 5 days. The young larvae carry a large, drawn-out yolk sack, which gradually becomes absorbed; the young have external blood-red gill filaments, and they travel from the nest bottom to the surface to gulp air to fill their lung-like swim bladder from about 10 days after hatching until they leave the nest at age 18 days. Nests built by *Gymnarchus* in Lac de Guiers (Senegal) containing advanced stages of larvae (over 3 weeks old, according to Budgett's estimate) are actively patrolled by adults (Hopkins unpublished). The larvae are electrically silent while in the nest.

ELECTRIC COMMUNICATION

One of the more fascinating aspects of mormyrid behavior is social communication via the unique electrical modality. Although detailed descriptions of electric communication signals are lacking for most species, available evidence indicates that some mormyrids have a very elaborate repertoire of electric displays that are important to social communication. Electric communication occurs when one fish (the signaler) emits an electric signal that evokes a behavioral response from another fish (the receiver). Electric communication is used in aggression, courtship, and appeasement, and in identifying the sex, species, and individual (see the reviews in Hopkins 1974, 1977, 1983a). The introduction below reviews,

first, basic principles of the electric communication modality and, second, the recent literature on electric communication in mormyrids.

Active Space of Electric Signals

One of the most important features of the electric communication system in fishes is the active space of a signal, that is, the range at which signals can be detected by a recipient so as to evoke a change in behavior. Receivers may be conspecifics, predators, parasites, or other species. The active space is affected by three variables: (1) the amplitude of the signal at the source, (2) the rate of attenuation with distance during transmission, and (3) the sensitivity of the receiver to signals embedded in background noise. For electric fish, this space is typically ellipsoid shaped, with the greatest range parallel to the long axis of the fish.

Empirical measures of the active space of mormyrid electric signals were made in a large laboratory tank by Moller and Bauer (1973) and Squire and Moller (1982) by passively moving one mormyrid toward another until one or the other produced a silencing response. By moving an empty fish holder, Squire and Moller controlled for mechanical effects and concluded that they were measuring active space for the EOD itself. One *Brienomyrus niger* can detect another at a maximum distance of 135 cm as long as the two fish are favorably positioned in an end-to-end orientation, facing in the same direction, at low water conductivity (52 μmho/cm). Oriented antiparallel or parallel but side by side, the maximum distance of communication is cut to about 50% of this distance. The active space shrinks in size dramatically, while retaining the elipsoid shape, as the water conductivity is raised. The amplitude of the electric field near a fish is reduced when the conductivity increases (Bell et al. 1976; Squire & Moller 1982). There are no field observations of active space that have analyzed the effects of vegetation between sender and receiver, water depth, natural variations in water conductivity, size of the signaling fish, and a range of possible relative orientations of signaler and receiver. Squire and Moller's data fit expected communication distances based on physical measurements of field strength from electric fish (Knudsen 1975) and on behavioral thresholds to species-specific signals. A 1- to 2-m active space for electric communication contrasts dramatically to the active distance of electrolocation, determined to be about 5–10 cm from 1-cm objects (see the review in Heiligenberg 1977).

To date, the best measurements of electric field attenuation around an electric fish are those made by Knudsen (1975), who tethered various gymnotiform fishes in a cloth bag suspended in a large pool of water over which he suspended an electrode positioning device for measuring voltage and electric fields. Knudsen's measurements were conducted in a large container where the distortion of the electric field by the container wall was minimal. Monopolar recordings of peak-to-peak voltages of EODs were

used to map the scalar magnitude of the electric potential around the fish in reference to an electrode located essentially at an infinite distance. Equipotential lines look dipole-like at distances greater than the fish's body length. Voltage drops off according to the inverse square of the distance for all distances beyond 10 cm and according to the cosine of the angle between the main body axis of the fish and the recording probe. The magnitude of the electric field vectors falls off according to the inverse cube of the distance. The orientation of the field matches that of a simple dipole field for distances greater than 20 cm. In the near field, the electric field is distorted by the body itself (Heiligenberg 1975; Bacher 1983).

The principal reason for the rather small active space for electric communication is the rate of signal attenuation in a volume conductor. Because the magnitude of the electric field vector attenuates according to the inverse cube of the distance, a fish with a discharge amplitude, a, that can be detected at a maximum range, d, should be able to boost its active space to twice this distance only if the amplitude is increased eightfold. Surely the fish cannot continue to produce signals that are nearly an order of magnitude larger for each distance doubling it hopes to achieve for communication! Instead, the fish probably compromises on a maximal distance of communication where there is a trade-off between the metabolic costs of signal production and the behavioral benefits of social communication.

Squire and Moller's measures of active space were made in a laboratory environment, but in nature an electric fish has to detect a signal in the presence of electric noise from other electric fish in the environment, which varies from one habitat to another and emanates from inanimate sources like distant lightning discharges (Hopkins 1973, 1981). Lightning discharges produce enormous local currents and give rise to electromagnetic radiation that propagates both through the earth and from reflections off the ionosphere. A high-impedance amplifier connected to electrodes in water, like the ones used for fish detectors, picks up clicks, tweeks, spherics, and other well-known atmospheric phenomena described for lightning discharges (Fig. 6). Measurements of the field strength of the discharges from lightning at sites in South America and Africa (Hopkins 1973, 1981) indicate that (1) the amplitude of signals, although usually below the threshold of sensitive electroreceptors, does reach threshold levels several times per second at night; (2) the frequency spectrum of the signals from lightning has a peak in the power spectrum at 1–2 kHz, which is a prominent range of sensitivity for knollenorgan electroreceptors; and (3) electrical noise from lightning increases during the night, when electric fish are active, probably because the ionosphere forms at night and permits reflection of very distant discharges. The noise is erratic and pulsatile. Figure 6 shows wave forms from lightning discharges and the discharges of electric fish on the same time scale for comparison. Some electric fish may be able to hide in the electrical noise by giving the pulsatile discharge an erratic rhythm. Alternatively, they may come out of hiding by "regularizing" their
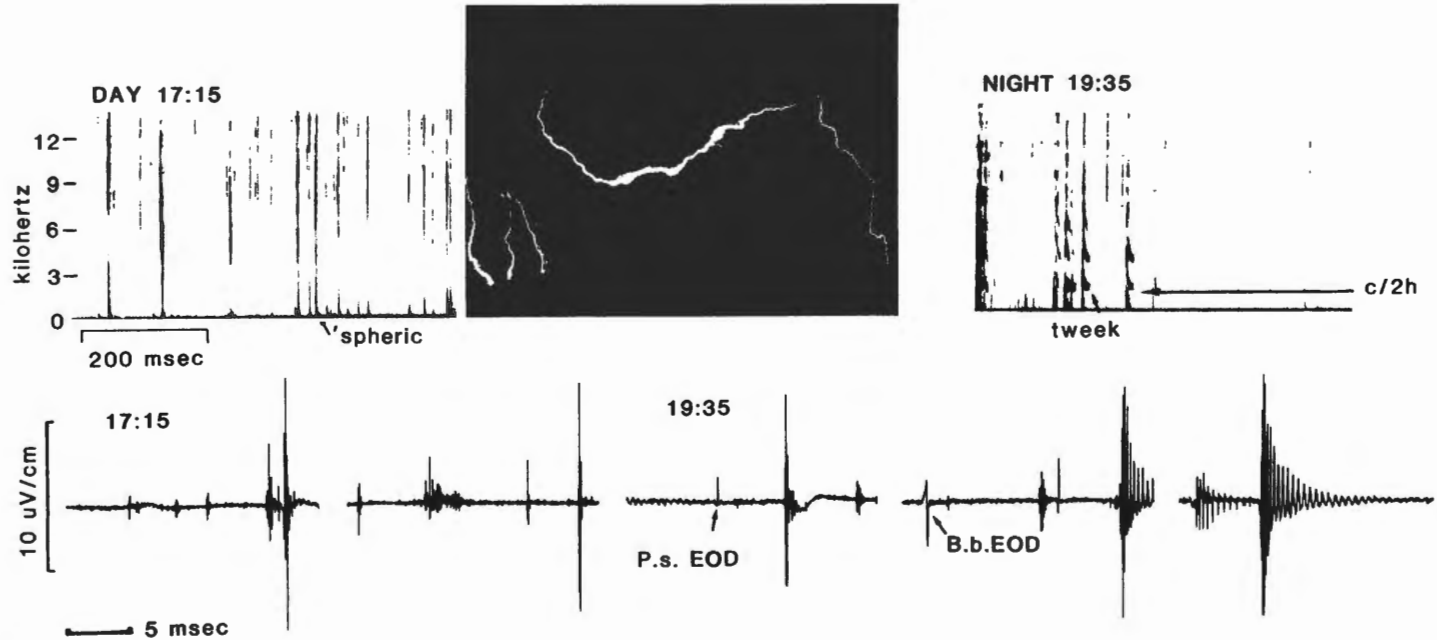
FIGURE 6. Lightning is a major source of background noise for electrical communication. The oscillograms (below) and the spectrograms (above) show typical electrical recordings made from a small stream in Gabon in the late afternoon (17:15, 45 minutes before sunset) and at 19:35, well after sunset, on a typical evening without thunderstorm activity in the immediate vicinity. Electrical activity is recorded with a bipolar Ag/AgCl electrode immersed in the water and is recorded after amplification on a high-quality audio tape recorder. During the day, distant lightning flashes show up as brief clicks called *spherics* (see Malan 1963). At night, the spherics take on a ringing quality due to resonance set up between the earth and the ionosphere. The resonant frequency is approximately 2 kHz, which matches the waveguide theoretical resonant frequency of $c/2h$, where c is the speed of light (3×10^8 m/sec) and h is the height of the ionosphere (70 km). The EODs of two mormyrids, *Petrocephalus simus* and *Brienomyrus brachyistius* (biphasic), are shown in these oscillograms: they are well below the amplitude of the lightning.

discharges, which makes the signal far more conspicuous in the presence of the noise (see the discussion of regularization below). Much more needs to be learned about the importance of natural background noise for the active space of electric communication, both from lightning and from other electric fish.

Electric Signals Have Two Features: EOD and SPI

The electric signal produced by a mormyrid is composed of a fixed EOD wave form separated by a highly variable sequence of pulse intervals (SPI) (Fig. 7) which is under central control by the pacemaker. *Gymnarchus* is unusual for mormyrids, since it produces a wave-like discharge at about 300–500 Hz (Lissmann 1958), but all other mormyrids produce brief pulses separated by long intervals. Both EODs and SPIs define the structure of signals; hence they will be treated separately below.

The EOD Wave Form in Communication

The EOD wave form, already seen to be of value to taxonomists, also appears to play a vital role in species and sex recognition by the fish themselves. When my work on mormyrids began, the idea that the EOD wave form might carry useful information seemed remote. The signals appeared too brief to carry much information or diversity, and it was unclear what mechanisms could be used to discriminate between the brief wave forms. Most investigators working on mormyrids had viewed the EOD simply as a carrier of the message embedded in the rhythm of the discharge.

The best experimental evidence for a communicative significance of the EOD comes from field playback experiments in which EODs were played to male mormyrids (*Brienomyrus brachyistius* [triphasic]; Figs. 4 and 5) during the breeding season, and electric courtship displays were counted as responses to signals (Hopkins 1981; Hopkins & Bass 1981). Males of this species can be distinguished from females (and from other species) by the
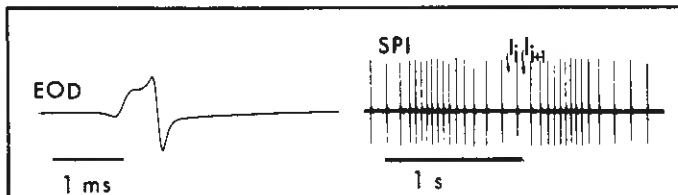

FIGURE 7. Electrical communication signals have two components, one fixed and the other variable. The EOD wave form is the fixed part of the discharge, since it is determined by the anatomy and physiology of the electric organ and does not appear to be under voluntary control. The variable part is the Sequence of Pulse Intervals (SPI), which is controlled by the pacemaker in the medulla. SPIs are highly variable and are used to generate a rich variety of social signals.

wave form of the EOD. During the breeding season, males become attached to, and probably defend, well-protected hiding places in shallow streams, and will give courtship calling responses to passing females. The courtship call is a burst of EODs at 100–150 Hz, in a stereotyped display called a *Rasp*. Experiments were conducted in which EODs were played into the water while the discharges of the male were monitored. The number of Rasps recorded was a good indicator of the male's unconditioned responses to the signals presumably interpreted to be a female fish.

The preliminary experiment of this type demonstrated that electric signals recorded from females and juveniles of the same species were much more effective in evoking Rasps than the discharges of males or of other species living in the same habitats (Hopkins 1981). Because the EOD and the SPI were reproduced intact in this experiment, however, it was unclear whether the fish was attending to the EOD or the SPI.

A second experimental series was designed to test the relative importance of the EOD versus the SPI in species and sex recognition (Hopkins 1983b). Stimuli were created by computer by digitizing EOD wave forms and storing interval sequences separately, and then putting them together in various combinations. For example, the EOD of a male might be the carrier for an SPI taken from a female of a different species. When EODs and SPIs were tested separately with these synthetic stimuli, males gave their courtship response when presented with the EOD from the female of the species, but not when presented with the male EOD or the EODs of other species that were living in the same habitats. The SPI recorded from the female of the species was ineffective as a stimulus if it was not paired with the correct EOD. Further experiments showed that the natural SPI of a female was as effective as a completely "scrambled" SPI of the female— as long as the EOD was unaltered. Hence, in terms of species and sex recognition, the EOD, not the SPI, seems to be of major importance for sex recognition in this species.

In the absence of definitive playback experiments, it is still too early to estimate how important the EOD is for species or sex recognition for other species. The increasing number of mormyrid species with sex differences in EOD is suggestive of a major, dominant role, perhaps universal. It is likely that EOD recognition is available and important to all species that have a male–female difference in EOD wave forms. In some species— particularly the small riverine species of *Petrocephalus* and some of the *Pollimyrus*, which tend to move in large mixed-species schools, at least as juveniles—species recognition may be accomplished not by a unique EOD wave form but rather by the SPI. This is not to say that the EOD is unimportant or that EOD recognition does not occur. For example, Hopkins (1980) has speculated that convergence upon exactly the same EOD wave form might be an adaptation to promote group cohesion in cases where mixed-species schools occur. For species with identical EODs, species recognition is undoubtedly accomplished by reliance upon other cues, such as

the SPI, or nonelectric cues like tactile signals, odors, or even sounds. (Crawford et al. 1985 reported elaborate acoustic song production in *Pollimyrus isidori* in laboratory breeding tanks. Sounds produced by males play a role in calling females to nest/spawning sites from a distance.)

Sequences of Pulse Intervals (SPIs) in Communication

Although the most conspicuous signal variable in mormyrid communication is the SPI, it has been one of the most difficult to study and interpret in the context of communication. The problem is largely due to the experimental difficulty of separating out and recording the electric pulses from individuals interacting in a social group. It is comparatively easy to record the discharge intervals from a single mormyrid (Harder et al. 1964; Heiligenberg 1976); however, when two or more fish are placed together, their pulses become confused. A second reason for the difficulty is that there is a high degree of variability of SPIs in a social context. Mormyrids can modulate the repetition of their EOD interval by interval rather than produce a regular SPI like the pulse gymnotiforms.

SPIs from Single Isolated Fish

The interpulse interval histogram for a mormyrid is characteristically very broad, with intervals ranging between 10 and 500 msec. Depending upon the species and time of day, the interpulse interval histogram may have one, two, three, or even more peaks (Harder et al. 1964; Bauer 1974; Bell et al. 1974; Heiligenberg 1976; Kramer 1976). Unlike the pulse gymnotiforms, which have a narrow distribution of interpulse intervals highly correlated with each other, a typical mormyrid joint-interval histogram shows a great deal of scatter, especially for intervals of long duration (Bauer 1974; Heiligenberg 1976). Mormyrids are typically inactive during the day, yet they produce low-frequency random pulse intervals separated by bursts of high-frequency discharges of much shorter intervals. At night the discharge is typically at a higher frequency with more regular intervals. Figure 8 shows interpulse interval histograms for the day (above) and night (below) activity of two individuals of *Brienomyrus brachyistius* (triphasic). The day histograms are bimodal (trimodal for some species), with one peak for short intervals contributed by the burst and one long interval peak representing the average interval of the random low-frequency discharge.

Three methods have been used to overcome the difficulty of separating out EODs from two or more interacting individuals. In the first, Bell et al. (1974) attached a fine wire to the caudal peduncle of one *Gnathonemus petersii* and let it interact with another unwired individual during staged dominance trials. Since the electric signal from the wired fish was relatively constant in amplitude and larger in magnitude than that from the unwired opponent, Bell et al. were able to segregate signals from the two fish. The wired fish did not appear to suffer from the attachment of the wire, and
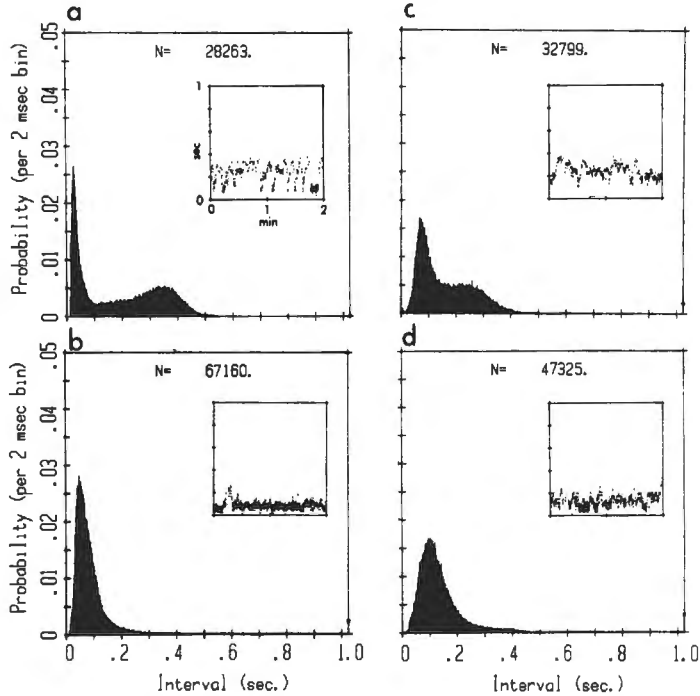
FIGURE 8. Typical histograms of inter-EOD intervals (main graphs) and short samples of typical SPIs (insets) for one *Brienomyrus brachyistius* (triphasic) male (left) and one female of the same species (right) during daylight (above) and at night (below). For the main graph, the abscissa is the interval in seconds, and the ordinate is the probability that an interval will fall within a 1 msec bin (1024 bins on this histogram). The insets show 2-minute samples of intervals as a function of time. During the day, both the male and the female produce 200- to 500-msec intervals at irregular frequencies, interspersed with bursts of pulses at 20–40 msec. At night, both produce more regular discharges at a mean interval of 50–100 msec.

they won as many fights as they lost. Lewis (1982) and Lewis and Hopkins (1979, in preparation) have made a detailed study of discharge patterns during agonistic behavior in *B. niger* using this technique. In the second method, Kramer (1974) observed interactions between two individuals of different species so chosen because they had EODs sufficiently different from one another that the pulses could be separated electronically. Using a third method, Crocket (1983) studied interactions between one normal individual mormyrid and another that had been electrically silenced by spinal cord sectioning. Although the discharge of the normal individual could thus be studied without interference and confusion caused by the second individual, these studies do not permit analysis of EOD interactions.

Bell et al. (1983) have identified at least three medullary nuclei as part of the control network determining the firing pattern of the electric organ in mormyrids. There is a putative command or pacemaker nucleus which

projects to a relay nucleus in the medulla; this relay nucleus then sends output directly to the spinal cord. The command nucleus also sends output to the relay nucleus via a loop involving the third area, the bulbar command-associated nucleus, which receives input from the command nucleus and sends output back to the relay nucleus. There also appear to be mesencephalic cell groups involved in the control of the discharge—a precommand nucleus—located in the tegmentum. These tegmental cells and the ventroposterior nucleus of the torus send information to the medulla and may be responsible for determining the pattern of firing of the electric organ.

SPIs as Communication Displays

Although observations of SPIs produced by mormyrids are limited to unusual situations that are either invasive (one fish is tethered to a wire) or restrictive (one fish interacts with another fish of a different species), we can broadly classify the known SPI patterns into four major categories. Three display categories are produced by a single individual, and one requires an interaction between two or more individuals. The displays are shown in Table 2, along with bibliographical sources.

Discharge cessations are either short (less than 1 second) or long (more than 1 second) interruptions in the otherwise continuous pulse train. Short cessations appear to be important in aggressive behavior and frequently accompany attacks or antiparallel display swimming. Some authors have seen abrupt, short-duration cessations associated with a smooth increase in frequency by one individual just prior to an attack. Long cessations often accompany the approach of a dominant fish or occur in response to playback of artificial stimuli (see references in Table 2).

Frequency modulations (FMs) are defined as transient modulations in the discharge frequency (typically an acceleration of the rate). Authors have used different terms to refer to these FMs. *Brief Accelerations, Bursts, Buzzes, SIDs*, and *Rasps* are all variations on the same basic pattern, as illustrated in Table 2 and in Figure 9. Many of the displays shown in Figure 9 may, in actuality, be part of a continuum of graded signals. Graded signals are often used in signaling threats and agonistic displays. In contrast, the Rasp display given by territorial male *Brienomyrus brachyistius* (triphasic) during courtship and nesting appears to be a discrete display category that is unlike any other FM display. The fish produces a burst of EODs at 150–100 Hz in a descending FM sweep. The display is stereotyped and easily recognized, and it serves in courtship calling by territorial males.

Tonic Discharge Patterns

Mormyrids are capable of changing the baseline frequency and regularity of their discharge without producing discrete FM patterns recognizable as displays. Long-term shifts in discharge frequency are termed *tonic discharge*

TABLE 2. Patterns in the Sequences of Pulse Intervals: Mormyridae

PATTERNS IN THE SEQUENCES OF PULSE INTERVALS: Mormyridae

List of different types of displays and signals patterned into the sequence of pulse intervals of different species of mormyrids. Representative diagrams of inter-EOD interval as a function of time are illustrated to the left of each display category. (Scales: ordinate 0 to 100 msec., abscissa: 0 to 1 second).

ELECTRIC DISPLAY	CONTEXT
DISCHARGE CESSATIONS	
SHORT CESSATIONS (duration < 1 s)[1]	Attack; antiparallel display; after smooth increase in frequency.
LONG CESSATIONS (duration > 1 s)[2]	After approach by dominant conspecific; response to playback of agressive pulse trains.
PATTERNED FREQUENCY MODULATION	
BRIEF ACCELERATION[3]	Swimming; object exploration; response to attack.
BURST[4]	Antiparallel swim; attack.
BUZZ[5]	Various stages of agressive behavior
SID: Sudden Increase in frequency followed by Decrease [6].	Intense agression, attack, antiparallel display.
SMOOTH ACCELERATION[7]	Attack (head butt)
RASP[8]	Courtship of female by male on territory (several species of *Brienomyrus*) .
TONIC DISCHARGE	
RANDOM INTERVALS[9]	All phases of resting, hovering.
REGULARIZED INTERVALS[10]	After detection of conspecific, or intruder.
PULSE PAIRS[11]	Intense aggression, overt attack (*G. petersii*).
DISPLAYS INVOLVING INTERACTION BETWEEN TWO FISH	
ECHO RESPONSE[12]	Response to external electric pulse stimulation; occurs at all phases of agonistic interaction.
PREFERRED LATENCY AVOIDANCE[13]	Female's response to an EOD stimulus (in *Pollimyrus*); response to electric pulses when EOD rate is low.
PHASE LOCKING (ALTERNATION)[14]	All stages of agonistic behavior.

100 ms

1 s

554

patterns here. For example, mormyrids often change their discharge from random (irregular) to regular intervals simply by switching from trains with a high degree of randomness to those with regularity. This shift may or may not accompany a change in discharge frequency. Moller (1970) recognized regularization as an important aspect of social signaling. Some species of mormyrids typically discharge their EODs in pairs or triplets and produce a characteristic pattern on an interval versus time diagram (Table 2, Fig. 9).

Displays Involving Discharges from Two or More Fish

The final category of temporal patterns involves duetting between one individual and a nearby conspecific. One individual produces a pattern of discharges that influences the timing of the pulses from a second fish. The most common duetting behavior is a strict alternation of EODs by two fish; first one fish fires its EOD, then the other, and so on (Bell et al. 1974). Alternation duetting may be physiologically possible because of the Echo Response—a reflex like firing of the EOD in response to an electric discharge from a conspecific or from a pulse generator after a precise delay, for example, 12–14 msec in several species. It has been described for fewer than five species of mormyrids.

Echo Response

First described by Russell et al. (1974) and Bauer and Kramer (1974), the Echo Response is characterized by an extremely short-latency firing of the EOD of one mormyrid in response to the EOD of a conspecific at close range. Latencies vary from 12 to 14 msec for *Gnathonemus petersii* under

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[1] Lewis (1982); *gap* in Kramer and Bauer (1976); Bell et al. (1974).

[2] Moller and Bauer (1973); *stop* in Moller (1970); *discharge break* in Kramer (1979); Serrier (1973); Bell et al. (1974).

[3] Lewis (1982); *burst activity* in Bauer (1974); *step-like decrease in interval* in Kramer (1976a); *rate acceleration* in Kramer (1976b).

[4] Lewis (1981).

[5] Lewis (1982).

[6] Bell et al. (1974); Kramer (1974); *attack discharge* in Kramer (1979).

[7] Kramer (1976b); Bell et al. (1974); *gradual decrease in interval* in Kramer and Bauer (1976).

[8] Hopkins and Bass (1981); Hopkins (1981).

[9] Lewis (1982); Moller (1970); Moller and Bauer (1973).

[10] Moller (1970); *constant frequency* in Bauer (1972); Bauer (1974); Kramer (1976a); Kramer and Bauer (1976); *fast* and *medium* in Lewis (1982).

[11] Bauer (1972); *discrete changes in intervals* in Bell et al. (1974); Bauer and Kramer (1976); Kramer (1974); Kramer and Bauer (1976).

[12] Russell et al. (1974); *preferred latency response* in Kramer (1974, 1979).

[13] Heiligenberg (1977); Lücker and Kramer (1981).
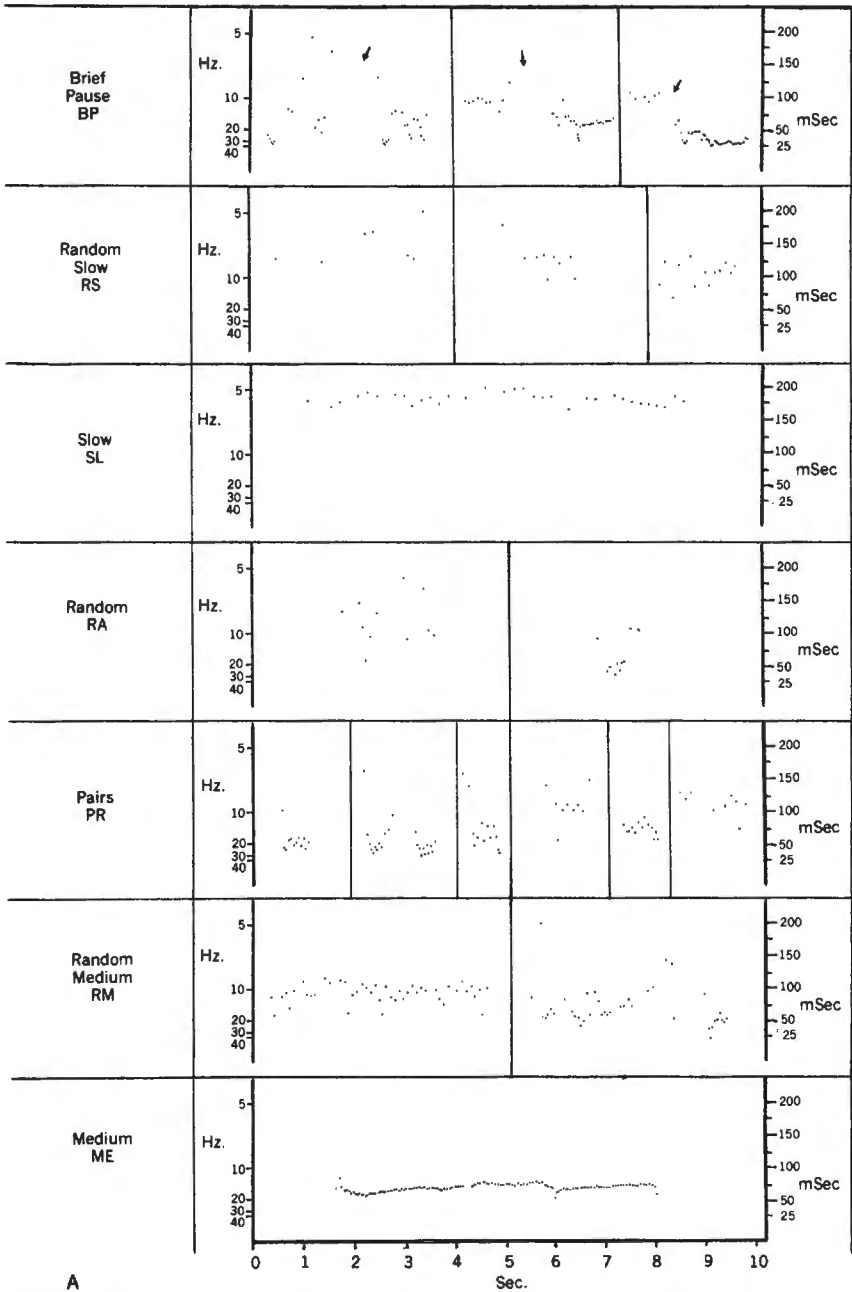
[14] Bell et al. (1974); Kramer (1974).

FIGURE 9. Catalogue of the SPI displays of *Brienomyrus niger* recorded during agonistic behavior in the laboratory. Each dot shows the time of occurrence of a single EOD. The vertical axis shows the time interval since the previous EOD. Patterns that have a slow or medium average discharge rate are shown in part A, those with a rapid rate in part B. Brief pauses are simply cessations of discharges for a short interval. Random slow, slow, random
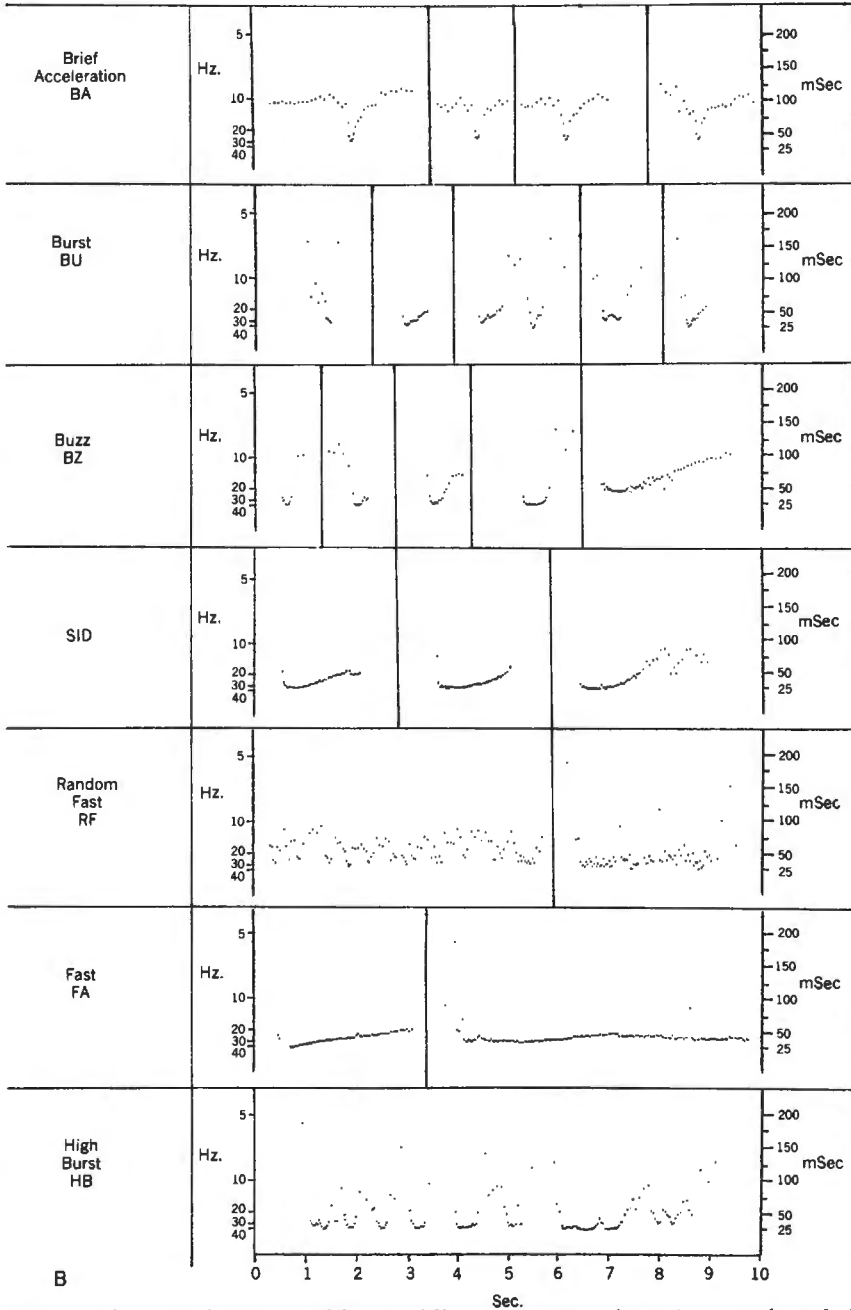
medium, medium, random fast, and fast are different patterns in the tonic rate and regularity of firing. Pairs occur when a fish discharges two pulses with a short interval separated by a longer interval. Brief Accelerations, Bursts, Buzzes, SIDs (Sudden Increases in frequency followed by Decreases) (SIDs), and High Bursts are all phasic frequency modulations. (Data from Lewis 1982.)

favorable conditions and from 20 to 22 msec in *Mormyrus rume*, a mormyrid with a longer-duration EOD and a generally slower repetition rate (Heiligenberg 1977). Russell et al. (1974) speculated that the echo response of mormyrids is mediated by electroreceptive input from mormyromast electroreceptors. The echo response is unaffected by lesions in *G. exterolateralis* (Moller, personal communication). They also speculated that the response may have a function in avoiding jamming of the EOD used in electrolocation, for the following reason: in a species that can generate pulses at a rate of 40–50/sec (i.e., 25- to 20-msec intervals), two individuals together, each echoing the other's discharges, tend to alternate rather than overlap in time. The echo response, then, might be viewed as a sophisticated mechanism for avoiding coincident discharges by a reflex that enhances time sharing between adjacent conspecifics. Mormyrids do appear to suffer a reduction in object-locating ability—measured in terms of maximum object-locating distances—when they are jammed by coincident EODs from conspecifics, but there is only a negligible decrease in the probability of coincident discharges produced by the echo response itself (Heiligenberg 1976).

A second possibility, originally mentioned by Russell et al. (1974), is that the echo serves in social communication, and that different species of mormyrids might use different echo latencies much like fireflies that recognize their own species by the species-specific flash-answer latency (Lloyd 1971). This possibility needs to be explored in detail, since the majority of commercially available mormyrids that have been tested have similar echo latencies of 10–14 msec. Nevertheless, pending a thorough comparative study of the echo response in mormyrids, the potential for species-specific echo responses remains uncertain. A reasonable alternative primary function of the echo response could well be to mediate duetting during close encounters such as fighting or courtship.

Preferred Latency Avoidance

A second response, similar to the Echo, termed the *preferred latency avoidance response (PLA)*, first described by Heiligenberg (1977) for *Mormyrus rume* and recently by Lücker and Kramer (1981) for *Pollimyrus isidori* females, is a specific avoidance of a discharge at a fixed latency following an electric stimulus from a conspecific EOD. Heiligenberg (1977) noted that *Mormyrus* responds to an external discharge by going silent for 10–20 msec following an external EOD, followed by a preferred latency of firing—a longer-duration echo than that seen for *Gnathonemus petersii*. Lücker and Kramer (1981) reported a similar finding for *Pollimyrus*. These authors also noted that the PLA is characteristic of sexually mature females, but not of males, which produce a typical 10- to 12-msec echo. Lücker and Kramer have suggested that sex recognition in *Pollimyrus* may be mediated by the PLA. If a male *Pollimyrus* approached a conspecific and produced a burst of

pulses with intervals of 20–30 msec, this action would tend to evoke a burst of pulses *in alternation* from a conspecific male who was echoing; but it would evoke a burst of pulses *in synchrony* from a conspecific female who was producing a PLA. Hence a male *Polimyrus* may be able to probe other fish with bursts of pulses in order to determine their sex. Much experimental work needs to be done on this interesting system to explore these possibilities further.

Experimental Tests of SPI Functions

Just as playback experiments have been invaluable in assessing the importance to species recognition of a diversity of EODs, they have also been useful in studying SPIs. One study (Kramer 1979) compared the responses of *Gnathonemus petersii* to a playback of tape recordings of a sequence of discharges recorded from either a resting or an attacking fish. Not surprisingly, the attack pattern, which was composed of many more bursts of pulses and which had a higher mean firing rate than the resting SPI, elicited a greater arousal response and a higher rate of attacks on the dipole playback electrode. Kramer did not examine the significance of different components of the attack pattern in order to assess the responses separately.

In a similar study, Teyssèdre (1983) and Teyssèdre and Serrier (1986) examined the approach response of *G. petersii* to a playback of tonic discharge patterns recorded during three nonsocial activities: slow swimming, investigative swimming, and feeding. In all cases, there were clear statistical differences between the stimuli; again, there was no attempt to isolate specific SPI displays or to integrate these playback responses with agonistic or reproductive behavior. Teyssèdre also compared responses to natural SPIs with sequences of intervals in which the order of the same intervals had been scrambled by computer. *Gnathonemus* approached an electrode more often when it played natural rhythms than it did when a scrambled rhythm was played.

In a field study of events triggering courtship responses of *Brienomyrus brachyistius* (triphasic), Hopkins (1983b) demonstrated that the SPI of one species can be substituted for the SPI of a second, sympatric species, with little effect on the level of courtship responses (rasps) produced, as long as the EOD is kept constant. Scrambling the SPI similarly had no decremental effect on the strength of the courtship response evoked from nonmated males.

Convergence of Electric Signaling Behavior

Because the mormyrids and gymnotiforms are thought to have evolved tuberous electroreceptors and electric organs independently, similarities in the structure and physiology of electroreceptors and electric organs are usually explained by convergent evolution (see examples in Lissmann

1958; Bennett 1971a,b). There has also been convergence in electric signaling behavior in the two groups (Hopkins 1977). The most remarkable example is the signaling behavior of *Gymnarchus niloticus*, which converges on that of the gymnotiform, *Eigenmannia*.

Gymnarchus is the only mormyrid with a wave discharge. At rest, individuals produce a modified sinusoid at 200–500 Hz. During aggressive interactions, they produce two types of modulations of the constant discharge: discharge cessations and FMs. *Eigenmannia* produces an analogous constant discharge and analogous modulation patterns. *Gymnarchus* and *Eigenmannia* both produce brief cessations of the discharge prior to attacks during fighting. The display appears to be effective in repelling conspecifics of both species. There is a similar use of very subtle FMs in the otherwise steady discharge. In *Gymnarchus*, downward FMs of 1–30 Hz are given by subordinate individuals during fighting behavior. These modulations accompany retreats from fights and may be used as submissive signals during normal fighting bouts. *Eigenmannia* produces a similar display. In fighting, subordinates produce upward FMs (long rises), and during breeding, females produce warbling FMs upward and downward from their constant frequency. The frequency excursion is 1–30 Hz. Convergence in the physical forms of these displays and in the contexts in which they are used is described in Hopkins (1977). In addition to these displays, subordinate *Gymnarchus* also produce long-duration cessations, whereas *Eigenmannia* do not. The display is probably effective in concealing the subordinate electrically. This display is homologous to the long cessations produced by the Mormyridae. Also, *Eigenmannia* produces interruptions at a high rate during courtship (called *Chirps* by Hagedorn in Chapter 17) that have not yet been seen for *Gymnarchus*.

Convergence is also noted for the pulse mormyrids and gymnotiforms. In both groups, bursts of pulses serve as aggressive threats; high-frequency bursts, called *Rasps*, appear to be used in some courtship sequences; long-duration cessations are used in both groups by submissive fish during fighting and as a response to a novel electric stimulus. Patterns of discharges are summarized in Hopkins (1974).

Although Hopkins (1977) has argued that discharge interruptions may be conspicuous attention-getting displays for a fish that is otherwise producing a constant tone discharge, and that they are therefore adapted for use as threat signals, this and other ideas about the adaptive significance of electric displays are highly speculative. Convergence between mormyrids and gymnotiforms on the same electric displays remains one of the most fascinating mysteries of electric communication.

Additional Functions of Electric Communication

In addition to the recognition function of electric communication—either at the level of species or sex—mormyrids generate signals to warn of impend-

ing attack, to signal submission, to signal courtship, and for schooling. These functions are reviewed by Hopkins (1974, 1977) and Moller (1976).

SENSORY BASIS OF ELECTRIC COMMUNICATION

Mormyrids have three classes of electroreceptors: ampullary, mormyromast, and knollenorgan (see the reviews of morphology and physiology in Szabo 1965; Bennett 1971b; Moller & Szabo 1981; Hopkins 1983a; Chapter 4, this volume). Of these three, it is the knollenorgans that appear to play the most important role in the reception of electric communication signals. This conclusion is based on the following four observations:

1. Knollenorgans are sufficiently sensitive to detect the distant, highly attenuated EODs of other fish, unlike mormyromasts, which are much less sensitive (Bennett 1965, 1971b; Hopkins 1977).

2. Knollenorgans are tuned to match the power spectrum of the EODs of the species (Hopkins & Bass 1981; Bass & Hopkins 1984), unlike ampullary receptors, which are tuned to 1–10 Hz (Bennett 1971b), and mormyromast receptors, which appear to be tuned to 100–500 Hz (Hopkins 1981).

3. The central command to fire a fish's EOD also serves to blank sensory throughput from knollenorgans to the mesencephalon for a few milliseconds after the command. This action effectively makes a mormyrid "deaf" to its own EOD while leaving unaffected the response to other fish in the vicinity, since they fire mainly between the EODs of other fish. Blanking occurs in the nucleus of the electrosensory lateral line lobe by an unknown mechanism (Zipser & Bennett 1976).

4. Lesions in the midbrain areas that receive input from knollenorgans (ganglion mesencephali exterolateralis), and its cerebellar projections abolish responses of one fish to the electric signals from another (the "silencing" response of Moller 1970; Moller & Szabo 1981). The lesions apparently do not affect electrolocation performance—as expected, since electrolocation is mediated through the mormyromast receptors that project more medially in the midbrain.

It is possible, but improbable, that ampullary and mormyromast receptors also encode electric communication signals. Ampullary receptors are tuned to 10 Hz or lower and are therefore outside the bandwidth of most EODs; Bell and Russell (1978a) showed that they do respond to EOD-like stimuli, but only when given at high intensity, comparable to a fish receiving its own EOD. Mormyromast receptors are insensitive compared to knollenorgans (Szabo 1962; Bennett 1965, 1971b; Hopkins 1980), and at least some of the central units become facilitated, not inhibited, by the command signal from the fish's pacemaker.

Tentatively, therefore, knollenorgans are the putative electric communication sensor for mormyrids. This is an important conclusion, since the central pathways for knollenorgans are distinct from those of other electroreceptors and other senses (Bell et al. 1983). Receptors functioning in communication appear to be segregated both at the periphery and in the central nervous system. We now turn to a discussion of the physiology of knollenorgans and their role in coding of species-specific EODs (see also Chapter 4).

Temporal Coding of Species-Specific Wave Forms

Knollenorgans rectify and band-pass filter incoming electric stimuli. They fire a single phase-locked spike on an outside positive-going voltage step (Bennett 1965; Hopkins & Bass 1981) but do not respond to the reverse polarity (outside negative going voltage step). When a single EOD is used as a stimulus, spike probability is highest for segments of the EOD wave form where there is a transition from outside negative to outside positive. Thus, for some wave forms, there is a single preferred latency of firing for each polarity, while for others there may be several preferred latencies (Fig. 10).

In nature, a fish receiving the EOD of a nearby signaling electric fish will experience, at any instant during the stimulus EOD, current flowing inward through one half of its body and outward (180° out of phase) through the opposite half (Fig. 11). Consequently, different patches of skin on the two halves of the body will receive the EOD wave form in both normal and inverted polarities simultaneously. To understand fully what the brain will receive from different parts of the body, we routinely present single knollenorgans with normal and inverted polarities of each stimulus.

Figure 10 shows a male *Brienomyrus brachyistius* (triphasic) knollenorgan's responses to the EOD of a female of the same species. The organs are most sensitive to the inverted polarity of the EOD (−), which triggers a single spike phase locked to the transition between the second and third phases of the wave form. Having the lowest threshold and the lowest jitter, this spike latency probably serves as a time reference for other phase-locked response latencies. The positive polarity (+) evokes a single spike 0.4 msec before this time reference. Note that the threshold and jitter are both slightly higher for the positive polarity of the stimulus. As the amplitude of the stimulus increases, the spike latency decreases, but the decrease in latency for one stimulus polarity tracks that for the opposite polarity, resulting in a constant 0.4-msec time difference between the two spike latencies.

In nature, when the male detects the female's EOD (Fig. 11), half of his body surface responds at the earlier latency, but with more jitter and higher threshold, while the opposite half responds 0.4 msec later with less jitter. Because the temporal structure of the EOD is so simple, this is essentially the only information that the fish has about the stimulus EOD.
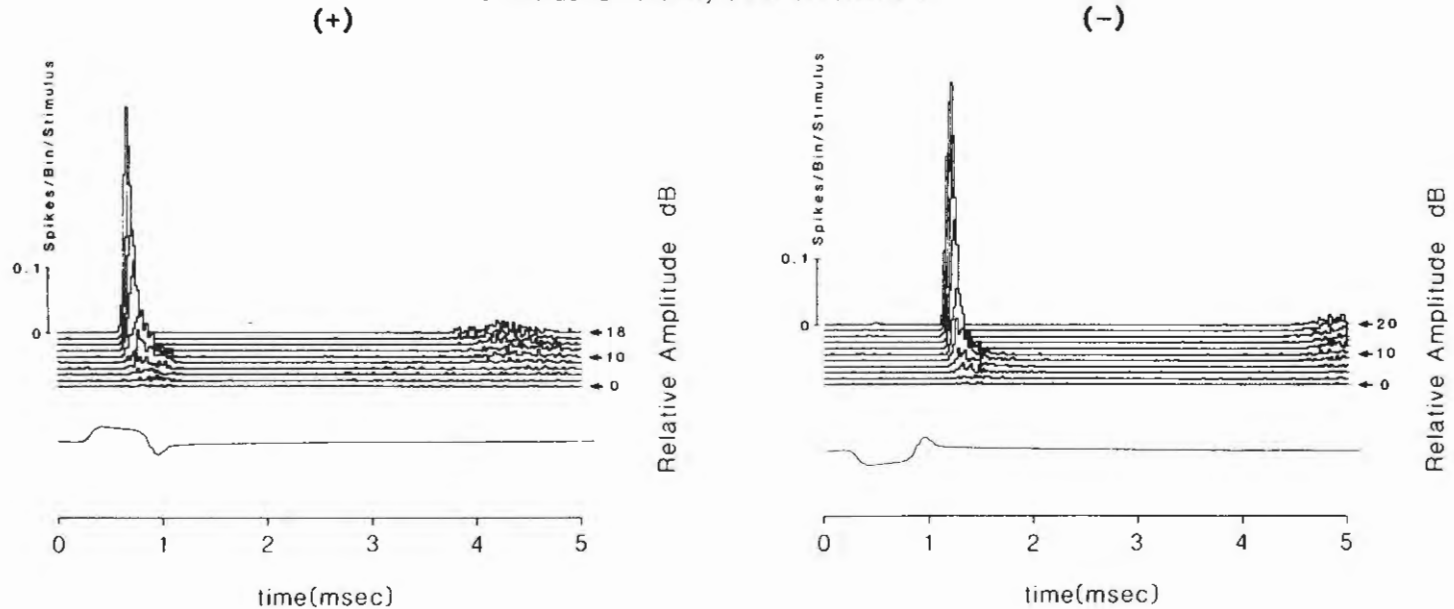
Stimulus *B. brachyistius* (TP)female

FIGURE 10. Poststimulus time histograms showing spike latencies from a single knollenorgan stimulated with a natural EOD wave form. The stimulus wave form (lower trace) is the female *Brienomyrus brachyistius* (triphasic) EOD, both in the normal polarity (left), such as that experienced in one part of the skin, and in the inverted polarity (right), such as is seen by a different patch of skin. Multiple histograms are superimposed to show the effect of stimulus amplitude (in decibels) on spike latency. Spikes are recorded from a knollenorgan on the surface of the skin of a *B. brachyistius* male while current is passed through the recording electrode by the use of a bridge amplifier. There is a latency difference of 0.4 msec between the (+) stimulus and the (−) stimulus polarity.
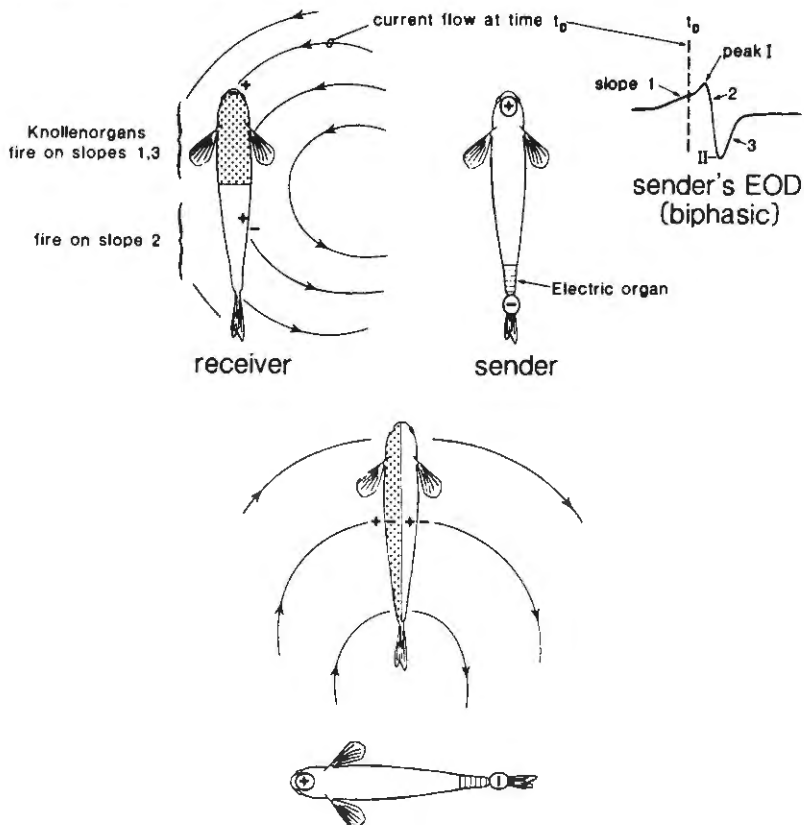
FIGURE 11. Detection of an EOD wave form by an electric fish differs from sound signal detection because the current flows through the body of the receiver. Hence electroreceptors in one patch of skin sense current flowing inward, whereas those in a different patch may sense current flowing outward. The sender in the diagram above produces an EOD such as the one shown to the right. At time, t_0, the signaler's head is positive with respect to its tail, and the current lines will be flowing from head to tail and will pass through the receiver's body, as shown by the current lines to the left. The anterior part of the receiver's body will detect current flowing inward across its receptors, while the posterior part will sense the same current lines flowing outward. Hence the anterior skin senses the (+) polarity of the stimulus, and the posterior skin senses the (−) polarity. When the sender and receiver are perpendicular (as in the diagram below), the polarity of the received EOD inverts on the receiver's midline.

Such a simple code for a species-specific signal should be easily mimicked, and Hopkins and Bass (1981) successfully substituted a rectangular wave form 0.4–0.6 msec in duration that evoked similar responses from knollenorgans and also evoked the courtship calling of males in the field situation. A summary of a series of playback experiments using rectangle functions is given in Figure 12. This figure shows that the male's response is "tuned" to rectangle durations of 0.4–0.6 msec, which matches
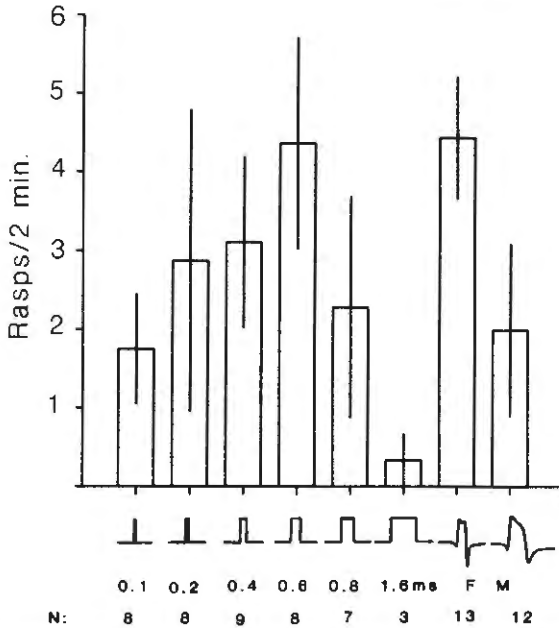
FIGURE 12. Results of field playback experiments in which rectangular wave forms, used as EOD models, are presented to isolated *Brienomyrus brachyistius* (triphasic) males. The EOD is repeated at intervals determined by a natural SPI for the female of this species. Males respond to these electrical stimuli with an electrical display—a rasp display—which is interpreted to be courtship calling. Male responses to female (F) and male (M) EODs are shown in the last two columns. Standard errors of the means for *N* experiments with two males are indicated by error bars. The male's courtship response to the female EOD does not differ significantly from the response to 0.6-msec rectangles. These males appear to be tuned to 0.4- to 0.6-msec rectangles, a good match to the intervals expected from the responses to the natural female EOD shown here and in Figure 10.

very well the interval between spikes triggered by the natural female's EOD. The rectangle function can be considered as an example of the classical "sign stimulus" in the Lorenz and Tinbergen sense. Rectangles of longer or shorter duration were less effective; these rectangles perhaps imitated the EODs of males or of other species.

Hopkins and Bass (1981) have argued that the sign stimulus is effective as a substitute for the natural EOD because the EOD is coded as a time domain code rather than as an equally likely alternative based on the spectral properties of the EOD. Additional experiments tested responses to EODs that had been modified by computer to be reversed in time or to have the phase spectrum advanced by 30°, 60°, or 90°, while not affecting the power spectrum of the pulse. Mormyrids clearly discriminated between EODs that had had their phase spectra modified in such a way as to leave the power spectrum unchanged.

Frequency Tuning of Knollenorgans

Although the evidence from playback experiments strongly supports the hypothesis that EOD recognition is mediated through a time-domain code for the EOD wave form, Hopkins (1983b), Hopkins and Bass (1981), and Bass and Hopkins (1984) found that most mormyrids have more than one class of knollenorgan based on frequency tuning curves. One patch of organs lies on the head near the operculum and another on the underside of the head, where the tuning curve has a minimum threshold (best frequency) near 500–1000 Hz, depending upon the species. The majority of the knollenorgans located on the trunk, on the rest of the head, and running on the dorsal and ventral midline back to the origin of the dorsal and anal fins, respectively, are tuned to 1000–3000 Hz, again depending upon the species. We refer to these low- and high-frequency knollenorgans as type II and type I, respectively (Bass & Hopkins, 1984).

Hopkins (1983) and Arnesen and Hopkins (1985) have shown that low- and high-frequency knollenorgans code the EODs of some species differently. In particular, the low-frequency organs tend to respond to slower and more gradual transitions in the wave form, while the high-frequency organs prefer to fire on the more rapid transitions [compare the response of low- and high-frequency organs to the discharge of female *B. brachyistius* (triphasic) males in Figure 13]. Hopkins and Bass (1982) suggest that knollenorgans have evolved tuning matched to the power spectrum of the EOD to ensure some noise immunity, and that the diversity of tuning has evolved to increase the complexity of the temporal code used in species or sex recognition of EODs. Additional playback experiments (Hopkins, unpublished) have revealed further complexities in the coding of species-specific wave forms in the periphery and give clues to the nature of central processing of EODs.

CONCLUSION

No discussion of electroreception and electric fish would be complete without an introduction to one of the most diverse and remarkable groups of electric fish, the Mormyridae. Mormyrids are well known to electrophysiologists for their complex electric organs and the diversity of their electroreceptor types, but they are also well known to systematists and ecologists for their explosive speciation in African rivers and their adaptation to a wide variety of riverine habitats. A new and fertile area of research is the exploration of reproductive behavior and communication in mormyrids, for all the mormyrids appear to be exploiting a remarkable modality of communication using their electric sense, and peripheral sense organs and central projections from these sense organs are specialized for a communication function. Mormyrids generate electric signals that can be analyzed into two components: a fixed part, the EOD, generated by the electric
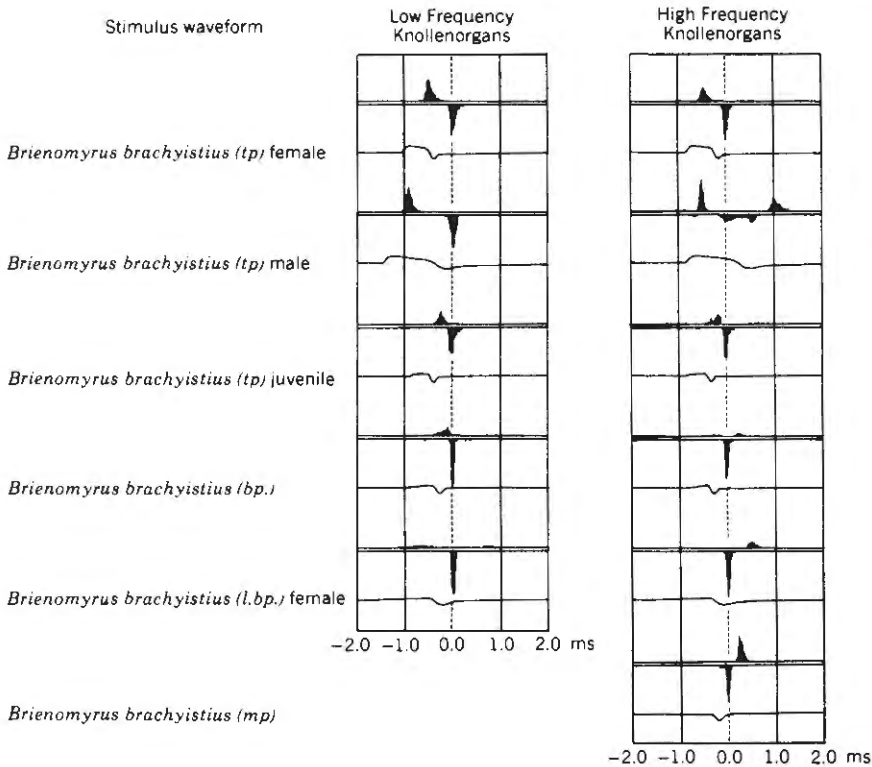
FIGURE 13.   Compound poststimulus time histograms of low-frequency (tuned to 500–1000 Hz) knollenorgans (left column) and high-frequency knollenorgans (tuned to 1.5–3 kHz) from *Brienomyrus brachyistius* (triphasic) for a variety of natural EOD stimuli. Each compound histogram shows responses to the positive polarity of the stimulus wave form (upward-directed) and to the negative polarity of the stimulus (downward-directed). Each of the stimuli would be encountered by this species in its natural environment in Gabon. The compound histograms for the species' own EODs are unique, thereby providing a unique temporal code for EOD recognition.

organ, and a variable part, the sequence of pulse intervals, generated by the pacemaker. The mormyrids studied so far appear to code EODs in a temporal pattern of nerve spikes by the knollenorgan electroreceptors and to recognize species-specific EODs by the timing of these patterns. Electric communication functions in species and sex recognition, in agonistic behavior, and in courtship.

ACKNOWLEDGMENTS

APPENDIX 1

Introduction to the Literature on Systematics and Ecology of Mormyridae

General

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