J. Zool., Lond. (1997) **243,** 329–340

Development of electrical signalling in larvae of the African fish, *Pollimyrus adspersus* (Mormyridae, Teleostei): the patterns of interdischarge intervals

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(Accepted 8 January 1997)

(With 4 figures in the text)

The ontogenetic development of the overt motor and the electrical signalling behaviour in larvae of a West African elephantfish, *Pollimyrus adspersus*, were studied. At an age of 35–40 days, hovering in mid-water was first observed. Before that time, the larvae moved only occasionally and rested in the nest that was guarded by the male parent. The very low electric organ discharge (EOD) rate of 2.4 ± 0.9 Hz observed in 8- to 10-day-old larvae (that generate their first EODs on day 8) increased to an adult rate of 8.4 ± 1.7 Hz in 21- to 25-day-old larvae. Even 8- to 10-day-old larvae generated a trimodal inter-EOD interval distribution (with three distinct discharge rates), similar to that observed in adults, although larval interval modes were of much longer duration. For the first (high rate) mode, the trend towards shortening stabilized already at the age of 21–25 days, whereas for the second and third (low rate) modes, this occurred only at an age of around 61–70 days.

Inter-EOD interval patterns recorded during swimming behaviour of 8- to 10-day-old larvae closely resembled that observed in juveniles (exceeding 100 days): there was a single mode only, and EOD rate was increased (13.1 ± 3.2 Hz).

Artificial stimulation with natural inter-EOD interval patterns previously recorded from other larvae or the nest-guarding male did not evoke any responses in 14-day-old larvae, apart from a brief EOD stop response to stimulus onset. However, even in larvae as young as 11 days, Preferred Latency Responses of their EODs to an artificial series of stimulus pulses (constant rate of 5 Hz) were observed at a stimulus intensity of 120 $\mu V_{p\text{-}p}$/cm. In the youngest larvae, 36-ms latencies were most frequent; this shortened to 19 ms in 31-day-old larvae (approaching the adult value; Kramer, 1978). The time pattern of EOD generation in *P. adspersus* larvae resembled that in mature specimens even before the adult electric organ became functional.

Introduction

African weakly electric fish, the elephant- or snoutfishes (Mormyridae), are active during night and communicate with their electric organ discharges, EODs (reviews, Moller, 1995; Kramer, 1990*a, b,* 1994, 1996). The waveform of an EOD is constant for a given individual of a certain species; however, the sequence of discharge intervals varies from moment to moment (Lissmann, 1958).

As demonstrated both from observation and experiment, mormyrids have an interdischarge interval (IDI) code of communication, probably as a symplesiomorphic (common-to-the-group) character (Kramer, 1994). Using the sequence of EODs, members of certain species discriminate conspecifics from members of other mormyrid species (Kramer & Lücker, 1990; Kramer & Kuhn, 1994), exchange signals in territorial or agonistic conflicts (Kramer, 1979), and recognize mates (Bratton & Kramer, 1989; Crawford, 1991). The ontogenetic development of the interdischarge interval code is not known (except for a 6-h period on day 8 following the first recognizable larval EOD in *Pollimyrus isidori*; Westby & Kirschbaum, 1977). The present study aims to change this situation for *P. adspersus* (which appears to have not been discriminated from the very similar *P. isidori* in most studies of its behaviour

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and reproduction in the past 20 years; Crawford, pers. comm., 1995, based on Bigorne, 1990). Still earlier this species was (then correctly) referred to as *Marcusenius isidori* (Taverne, 1971*a, b*), and sometimes appears to have been misidentified as *Petrocephalus bovei* (Birkholz, 1969, 1970).

Pollimyrus adspersus (or *P. isidori*) was the first mormyrid to be bred in captivity (Birkholz, 1969, 1970; Kirschbaum, 1975, 1987) and its electric signalling and reproductive behaviour are well studied (e.g. Kramer, 1978; Lücker & Kramer, 1981; Crawford, Hagedorn & Hopkins, 1986; Bratton & Kramer, 1989).

Pollimyrus adspersus larvae hatch four days after spawning and emit their first EODs when 8 days old (Westby & Kirschbaum, 1977). After stabilizing within 3 days, the larval EOD is of approximately 10 times longer duration than the adult EOD (1.9 vs. about 0.2 ms) and of reversed polarity. Larval and adult EODs are generated by two distinct electric organs (Denizot *et al.*, 1978, 1982). The larval organ is bulky and located in the trunk; it begins to degenerate soon after the much more compact adult organ located in the caudal peduncle begins to become functional at an age of about 50 days (Westby & Kirschbaum, 1978). For about 40 days, both organs coexist when a peculiar double discharge can be seen, the larval EOD being followed by the adult EOD at a brief and constant interval (0.7 ms).

Larvae only 10 days old respond to stimulus pulses of low intensity (10 $\mu V_{p\text{-}p}$/cm) by a change of their interdischarge interval pattern (Postner & Kramer, 1995). Their electrosensory system, being 'tuned' to the larval EOD waveform of long duration, undergoes adaptive changes that makes it more suitable for the detection of the brief adult EODs, even before a larva's own adult electric organ is functional.

The present study focuses on: (1) the description of the ontogeny of the interdischarge interval patterns; (2) the question of whether there is phase-locking of larval EODs to stimulus pulses, that is, preferred latency responses similar to those observed in adults of this species (Kramer, 1978; Lücker & Kramer, 1981).

Material and methods

Mormyrid fish are an important component of local fish markets, but their conservation status is unknown. One hundred adult fish of Nigerian origin were obtained from a tropical fish importer as an unwanted 'by-catch' of commercially more interesting mormyrids such as *Gnathonemus petersii*. *Pollimyrus adspersus* is very similar to (and sometimes difficult to distinguish from) *Pollimyrus isidori*. Whereas *P. isidori* is found in most of West Africa, from Senegal to the Tchad, *P. adspersus'* distribution is much more restricted, and it seems to replace *P. isidori* where it occurs (a case of vicariance?). Bigorne (1990) reports the presence of *P. adspersus* in West African coastal drainage systems to the east of the Voltas, and in the coastal sections of the Niger System. *P. adspersus* ranges east as far as Cameroon; and its occurrence in Zaire was also reported.

Conditions under which reproduction occurred in our aquaria were described in Postner & Kramer (1995). Eggs were taken from the nests on the morning following a nocturnal spawning. Eggs were transferred to small rearing tanks (15 × 18 × 11 cm high) floating in 40-l tanks; water conditions were the same as those in which spawning had occurred (26 ± 1 °C; 250 ± 50 μS/cm). Unfertilized eggs turned white and were removed. Larvae hatched 4 days after spawning. When 12 days old, larvae were fed with live protonauplii of *Artemia salina* (Crustacea) twice a day. When the alevins had reached a total length of 20 mm, chopped *Chironomus* (blood-worm) larvae were added (from a deep-frozen supply). Partial water exchanges were made twice daily to remove food that had not been eaten.

The acrylic recording chamber was cylindrical (height, 80 mm; inner diameter, 43 mm; wall, 2 mm). Four small carbon electrode plates (diameter, 7 mm) were inserted in the wall at regular 90° intervals; opposing electrodes formed a pair for either recording or stimulating across the centre of the chamber. The 2 electrode pairs were thus oriented normal to each other.

To record interdischarge intervals from a larva, usually both electrode pairs were connected to a 2-channel, differential amplifier (×1–1000; 5 Hz ... 33 kHz). Separately amplified EODs were full-way rectified, summed, and the combined signal fed into a Schmitt trigger circuit that evoked one standard, computer-compatible TTL logic pulse for each EOD. By this procedure, amplitude changes and polarity reversals of the EOD associated with a larva's movements in the recording chamber did not affect the measurement of inter-EOD intervals that was based on the sequence of TTL pulses.

Inter-EOD intervals were measured by a counter interface inside a computer (IBM-compatible, 286 PC/AT). The interface (PITI board) had 2 input channels and 50 μs resolution for the measurement of time intervals; it operated under a custom-made program written in Turbo Pascal. Also, custom-made analysis and output routines were written in QuickBasic 4.5.

In order to restrict its movements during stimulation experiments, a larva was put into a small, cylindrical plastic mesh cage (diameter, 25 mm) that was placed in the centre of the recording chamber. Recording conditions were optimal when a larva's long axis was aligned with the pair of recording electrodes, whereas the pair of electrodes at its right and left were used for stimulation.

Bipolar, single-cycle sine-wave pulses (as shown in Fig. 1A of Postner & Kramer, 1995) of 1 ms duration were generated by a function generator (Hewlett Packard model 3312A or Exact model 126) that was externally triggered by the computer (via the output channel of the PITI board), to generate a series of 5 pulses/s for 3 min per experiment. The amplitude was adjusted using a Hewlett Packard model 350D attenuator the output of which was fed into a transformer (100 Hz ... 18 kHz) that isolated the stimulus from ground. Field amplitude in the chamber was 12–120 $\mu V_{p\text{-}p}$/cm.

The signal from the recording electrodes was differentially amplified (×1–1000; 5 Hz ... 33 kHz) and recorded on magnetic tape, track 1 (Revox A77 hifi recorder). On the second track the stimulus pulses were simultaneously recorded from the output of the function generator.

For measuring the sequences of inter-EOD and inter-stimulus pulse intervals with the 2-channel counter interface, the recording on the first track of the magnetic tape was first analysed by a 'window' circuit (WPI model 120): it separated stimulus and EOD by their difference in recorded amplitude. An alternative method yielding the same result consisted in first digitizing track 1, where both kinds of pulses were stored, then used the digitized record of the stimulus pulses on track 2 to remove those on the digitized record of track 1 by an off-line computer program.

A 2-channel oscilloscope served to monitor signal level and quality. EOD-to-stimulus latency histograms were calculated from files generated by the counter interface, using a custom-made program written in QuickBasic 4.5.

Results

Four days after spawning, the larvae hatched by breaking their embryonic membranes. This they achieved by tail stretching. After struggling themselves free, they were lying on their sides, usually without moving, on the aquarium bottom. When stimulated with a fine water jet or a flashlight, they were already able to move away. From day 5 on, all larvae gathered in the darkest corner of their tank; light of an intensity of 50 lx was sufficient to evoke negative phototaxis.

The first EODs occurred on the 8th day after spawning, as described by Westby & Kirschbaum (1977), at a rate of around 2 EODs/s (Table I). Larvae that were stimulated with a fine water jet showed a sharp increase of EOD rate associated with an escape response: in 8-day-old larvae, the shortest EOD intervals during an escape response were around 50 ms, shortening to 20 ms in 20-day-old larvae. Spontaneous swimming was first observed between days 12 and 15 when the originally prominent yolk sac had almost vanished. The larvae now began taking up food (Kirschbaum, 1987). Larvae of this stage were resting on their bellies in an upright position, supported by their well-developed pectoral fins.

At an age of 35–40 days, stationary hovering in mid-water was first observed which was accomplished by co-ordinated movements of all fins. Aggression among larvae was first observed at an age of 50–60 days, including circling around each other and biting (as also apparent from

TABLE I

*Development of electrical discharge (EOD) behaviour in larval **P. adspersus** during resting behaviour. Modes are the peaks of interdischarge interval histograms, and are shown as means ± S.D. in ms. '**n** fish' is the number of fish studied at a certain age, and the number coded by Σ shows the associated total of EOD intervals. The last column shows the mean discharge rate ± S.D. in Hz*

Age (days)	1st mode (ms)	2nd mode (ms)	3rd mode (ms)	4th mode (ms)	*n* fish *n* EODs	Discharge rate (Hz)
8–10	51 ± 19 *n* = 8	126 ± 40 *n* = 19	261 ± 57 *n* = 17	372 ± 72 *n* = 7	23 Σ5479	2.4 ± 0.9
11–15	33 ± 16 *n* = 21	235 ± 38 *n* = 17	335 ± 47 *n* = 7	—	44 Σ31116	5.3 ± 0.8
16–20	36 ± 13 *n* = 20	194 ± 48 *n* = 26	333 ± 50 *n* = 3	—	27 Σ13990	7.1 ± 1.2
21–25	19 ± 4 *n* = 22	172 ± 34 *n* = 21	—	—	22 Σ17575	8.4 ± 1.7
26–30	22 ± 7 *n* = 22	189 ± 46 *n* = 21	272 ± 92 *n* = 4	—	23 Σ18455	8.9 ± 2.4
31–40	19 ± 2 *n* = 21	165 ± 30 *n* = 13	242 ± 19 *n* = 7	—	21 Σ17425	9.4 ± 1.4
41–50	23 ± 5 *n* = 16	171 ± 30 *n* = 14	—	—	16 Σ10118	11.0 ± 1.4
51–60	20 ± 3 *n* = 6	172 ± 48 *n* = 5	—	—	6 Σ3490	11.2 ± 1.8
61–70	21 ± 2 *n* = 8	148 ± 32 *n* = 8	235 ± 42 *n* = 2	—	8 Σ5385	9.4 ± 1.0
71–80	21 ± 4 *n* = 5	113 ± 43 *n* = 4	—	—	5 Σ3254	10.9 ± 1.4
81–100	22 ± 4 *n* = 10	139 ± 39 *n* = 10	216 ± 67 *n* = 6	—	10 Σ7497	8.7 ± 1.8
101–150	20 ± 3 *n* = 9	136 ± 49 *n* = 10	236 ± 35 *n* = 9	—	10 Σ5921	7.9 ± 1.5
Adult	13 ± 2 *n* = 5	115 ± 8 *n* = 6	211 ± 29 *n* = 3	—	6 Σ4465	8.4 ± 0.9

damaged fins). This was the age when the adult electric organ had become functional and the larval electric organ was beginning to degenerate, with larval EOD amplitudes declining rapidly (Westby & Kirschbaum, 1978; Denizot *et al.*, 1982).

EOD pattern during resting. Larvae showed the lowest discharge rates when resting in the recording chamber. Very quickly, the exceedingly low rate of 2.4 ± 0.9 Hz observed in larvae 8–10 days old increased to an adult rate of 8.4 ± 1.7 Hz at 21–25 days (Table I).

Adult *P. adspersus* that are resting motionless in their day-time shelter (such as inside a ceramic tube, under a rock or root, when supported by their fins, or stabilized by dense, filamentous water plants) generate a pattern of long, medium, and short interdischarge intervals in a broad, trimodal distribution (Kramer, 1978). Surprisingly, even our youngest larvae showed a similar trimodal interval distribution with, however, corresponding interval modes of much longer duration (Table I).

At certain ages (Table I) the third mode (intervals of the longest duration) was not always present in the histograms, whereas the first and second always were. The change of these histogram modes with age is shown in Fig. 1.

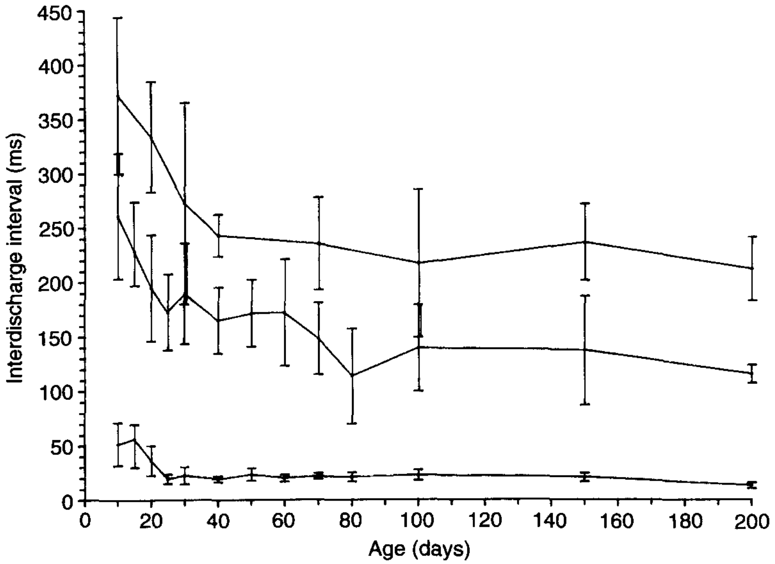

FIG. 1. Development of the discharge behaviour of *P. adspersus* larvae as observed during resting (no locomotion). The modes of interdischarge interval histograms, as computed from the inter-EOD intervals, shorten considerably with age. Histograms show three modes, and the means of the modes ± 1 S.D. are shown for larvae of different age (for number of fish, etc., see Table I).

The trend towards shortening of the first mode stabilized already at an age of 21–25 days at 19–20 ms; that range was still shown when the larvae were 101–150 days old, all discharging their adult electric organs. A slower development was observed for the second mode where the trend for shortening stopped around an age of 61–70 days (at 148 ms). The third mode (intervals of the longest duration) followed a similar time course. In still older fish (juveniles of an age of >200 days), however, all three modes were still shorter than in larvae 101–150 days old. These juvenile values were the same as those found for sexually mature adults (Bratton & Kramer, 1989).

Our attempts to record EOD patterns from single larvae resting in their undisturbed home nests proved to be very difficult for technical reasons (separation of EODs from those of other individuals). In two 11- and 13-day-old larvae, where we did succeed, EOD interval distributions were quite similar to those observed in larvae that had been transferred into the recording chamber prior to recording. There were, however, only two clear modes in two short sequences (at 80 and 45 ms for the first, and 265 and 275 ms for the second; Fig. 2).

EOD pattern during spontaneous swimming. Discharge rates of even the youngest larvae (age 11–20 days) closely resembled those that were at least 101 days old, including still older juveniles: 13.1 ± 3.2 Hz vs. 14.6 ± 2.8 Hz. Usually, there was only one mode in the interval distribution, as has also been observed in adult fish (Kramer, 1978; Bratton & Kramer, 1989). There was no clear systematic trend for a change with age like that observed for the EOD pattern generated by resting larvae (Table II).

Stimulation with natural EOD patterns. After transferring 14-day-old larvae into the recording chamber, they were stimulated with either larval EOD patterns or those from the nest-guarding adult male. The example in Fig. 3 (for a 21-day-old larva) shows an initial EOD stop response evoked by stimulus onset, followed by quick resumption of the normal resting discharge. Neither the first nor

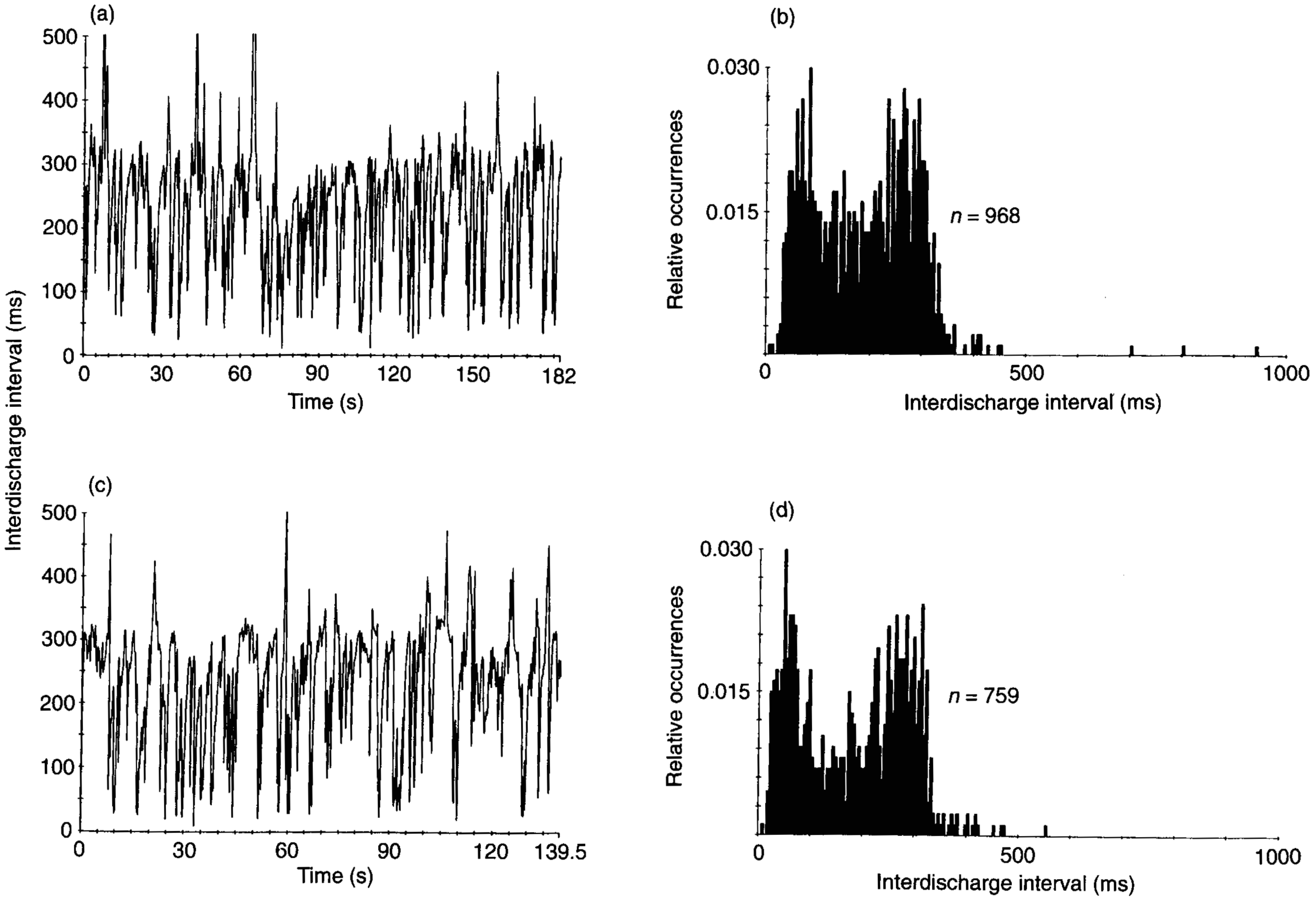

FIG. 2. Discharge activity of larvae of *P. adspersus* resting in the nest (no locomotion): (a, b) 11-day-old larva; (c, d) 13-day-old larva; (a, c) sequential interdischarge interval representations, showing trends of EOD interval duration over time (abscissa); (b, d) statistical interdischarge interval histograms, showing the proportion of intervals of each duration. The histograms were computed from the data shown to their left.

TABLE II

*Development of modes in the interdischarge interval histograms of larval **P. adspersus** during swimming behaviour (modes given as means ± S.D. in ms). For explanations, see Table I*

Age (days)	1st mode (ms)	2nd mode (ms)	*n* fish *n* EODs	Discharge rate (Hz)
11–20	60 ± 14 $n = 13$	—	13 Σ14626	13.1 ± 3.2
21–30	52 ± 11 $n = 19$	—	19 Σ17466	14.9 ± 2.1
31–40	51 ± 6 $n = 18$	—	18 Σ19493	15.0 ± 1.2
41–50	57 ± 12 $n = 16$	—	16 Σ12274	14.6 ± 1.8
51–60	46 ± 11 $n = 9$	—	9 Σ8123	17.2 ± 1.9
61–70	60 ± 16 $n = 16$	—	16 Σ9514	14.2 ± 2.1
71–80	63 ± 14 $n = 8$	100 ± 28 $n = 2$	8 Σ4783	12.2 ± 2.7
81–100	61 ± 17 $n = 18$	—	18 Σ14093	12.6 ± 3.2
101–adult	36 ± 6 $n = 4$	52 ± 14 $n = 12$	12 Σ10616	14.6 ± 2.8

the second mode in the histograms of the stimulated larvae were affected by the stimulus pattern (Table III).

Preferred Latency Responses. Even in larvae as young as 11 days, clear latency responses were obtained to a series of stimulus pulses presented at 5 Hz and an amplitude of 120 μV_{p-p}/cm, but not at weaker amplitudes (12 and 1.2 μV_{p-p}/cm tested). Most latency histograms were of the 'valley-followed-by-peak' type; that is, in a certain latency range, the larvae tended to delay their discharge by several milliseconds (Fig. 4). Thus most latency histograms resembled the type found in adult females (Kramer, 1978; Lücker & Kramer, 1981).

TABLE III

*Effect of stimulation with natural EOD patterns on histogram modes of 14-day-old larvae. The larval EOD pattern used for stimulation had been recorded from a resting 14-day-old larva, the adult pattern from a nest-guarding male. Histogram modes given as mean values in ms (± S.D.); **n**, number of larvae tested. Stimulus amplitude, 120 μV_{p-p}/cm. **P** values based on two-tailed **t**-test*

Stimulation with larval EOD pattern		Stimulation with adult EOD pattern	
1st mode (ms)	2nd mode (ms)	1st mode (ms)	2nd mode (ms)
26 ± 9 $n = 10$ $P = 0.40$ $P > 0.05$[†]	267 ± 36 $n = 10$ $P = 0.68$ (not significant re: stimulation with adult pattern) $P > 0.05$[†]	23 ± 7 $n = 10$ $P > 0.05$[†]	259 ± 38 $n = 10$ $P > 0.05$[†]

[†] Not significantly different from resting pattern of undisturbed larvae (Table I)

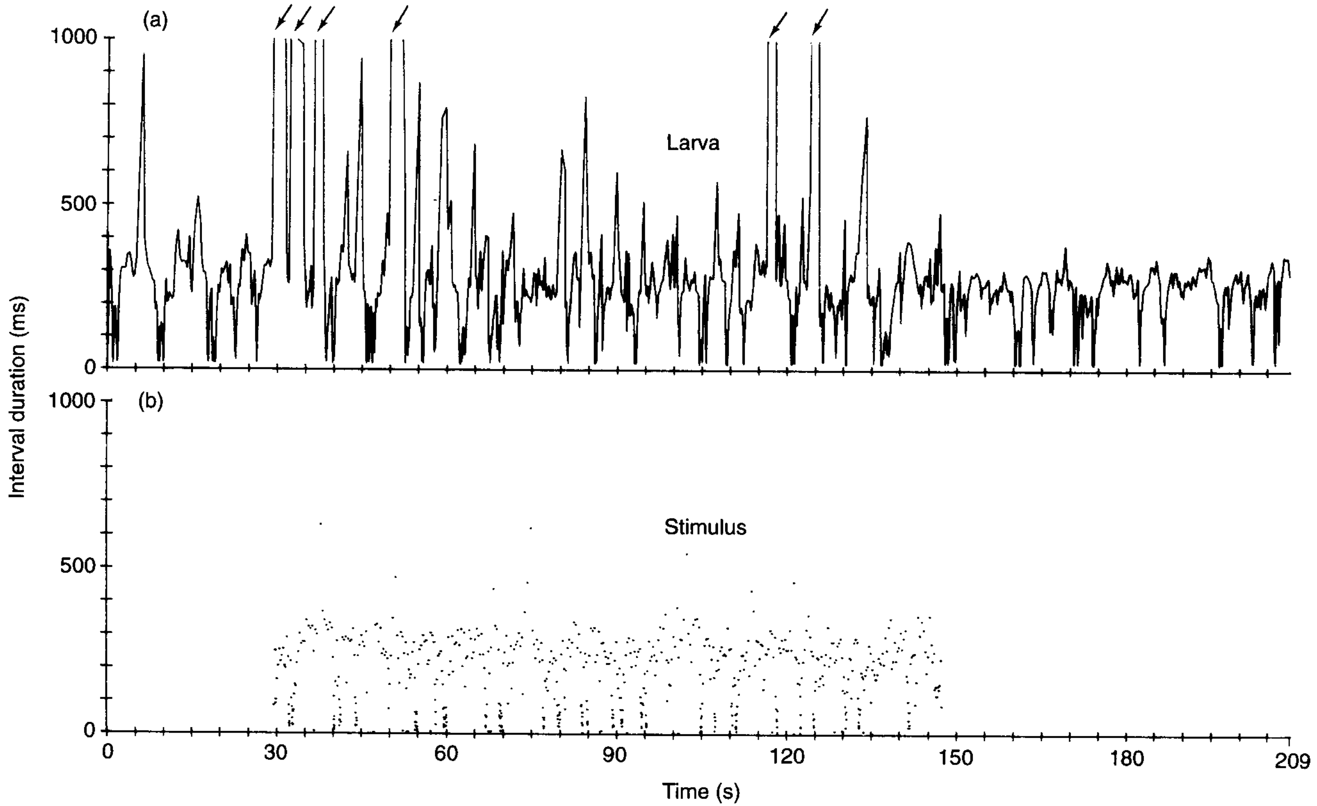

FIG. 3. Inter-EOD interval responses of a 21-day-old *P. adspersus* larva (a) to artificial, electrical stimulation (b). For the stimulus, points not connected by lines. Stimulus pulses were biphasic, single-cycle sinusoids of 1 ms duration and 25 $\mu V_{p\text{-}p}$/cm amplitude; the stimulus time pattern was that recorded from another larva of the same age while resting. Stop responses (arrows) occur at stimulus onset and also later at diminishing frequency.

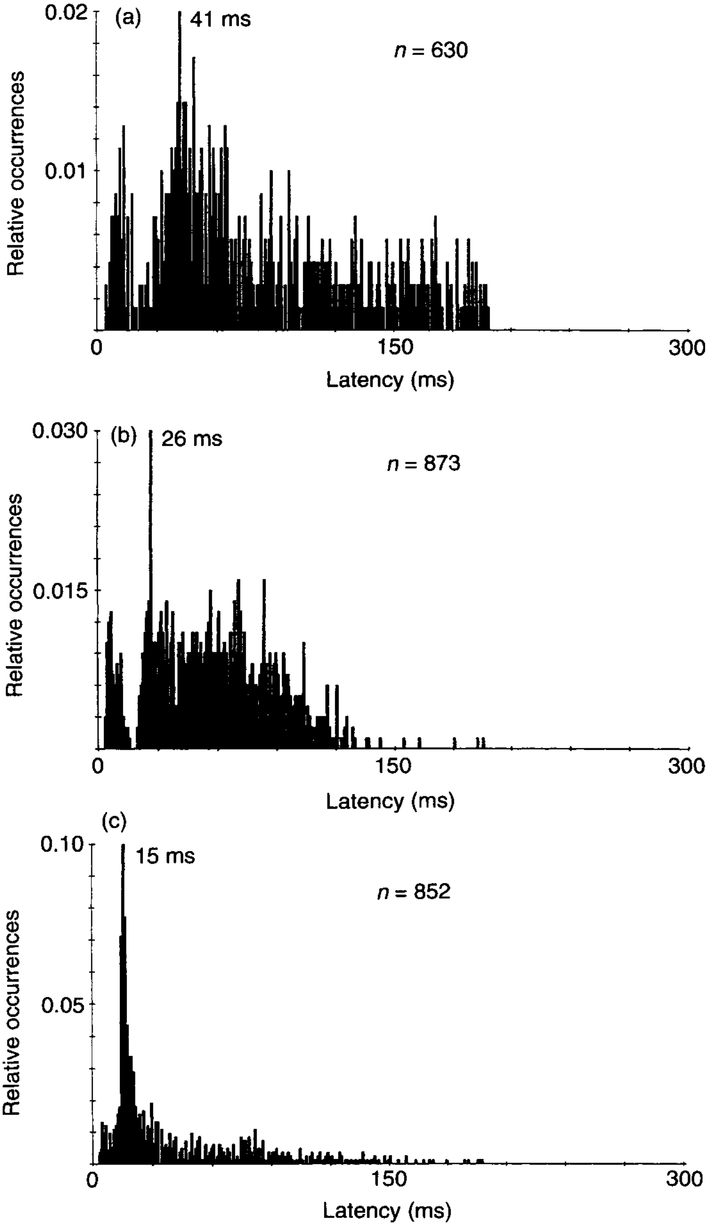

FIG. 4. Preferred latency responses of larvae of *P. adspersus* to artificial stimulation. The latencies of the first EOD to a stimulus pulse only are shown; latencies shorter than 3 ms not shown for technical reasons (*n*, number of latencies for a histogram). Stimuli were biphasic, single-cycle sinusoids of 1 ms duration repeated at 5 Hz, and 120 $\mu V_{p\text{-}p}$/cm amplitude. (a) 11-day-old larva; (b) 31-day-old larva; (c) 64-day-old larva.

TABLE IV

Development of Preferred Latency Responses (shown as minima or maxima in latency histograms) of larval EODs to trains of stimulus pulses (5 Hz). ***n****, number of histograms with a minimum or maximum the mean values of which are given in ms (±S.D.). Stimulus amplitude, 120 $\mu V_{p\text{-}p}/cm$*

Age (days)	minimum (ms)	maximum (ms)	*n* larvae
11	19 ± 2 *n* = 4	36 ± 5 *n* = 11	23
12	20 *n* = 2	32 *n* = 1	10
31	12 ± 2 *n* = 5	19 ± 5 *n* = 8	10
58	11 ± 1 *n* = 12	16 ± 1 *n* = 12	12
64	12 ± 3 *n* = 2	18 ± 5 *n* = 10	10

Both valley and peak occurred at the longest latencies in the youngest larvae: 19–20 ms for the valley, 36 ms for the peak. With increasing age, both values declined rapidly. At an age as early as 31 days, the values were within the adult range and changed only slightly in still older larvae (12 and 19 ms; Table IV).

Discussion

The ontogenetic development of interdischarge interval patterns was very rapid in *P. adspersus*: (i) from the very beginning, the interdischarge interval distributions (trimodal in resting and unimodal in swimming larvae) appeared similar to the adult ones for the same behavioural states; (ii) mean discharge rate and histogram modes, especially the first (high rate) one, were virtually mature at around day 30; (iii) the same held true for the Preferred Latency Response; (iv) fin co-ordination was sufficiently advanced for the larvae being able to hover in mid-water around days 35–40; (v) aggression among larvae was recorded at days 50–60.

A similarly rapid development had been noted for the electrosensory stimulus-intensity thresholds: the adult characteristics of high sensitivity combined with broad-band tuning properties were found at an age of only 54–60 days, as opposed to low sensitivity and narrow-band properties in 10- to 15-day-old larvae (Postner & Kramer, 1995).

Compared with this rapid development of the electrosensory and the neural electromotor command system, the development of the effector organ, the adult electric organ (that becomes fully functional only around day 80) appears slow (Denizot *et al.*, 1982). The components of the electrosensory-motor system seem to need electrical autostimulation much earlier for their co-ordinated development to take place, especially the electrosensory afferences and their central nervous projections (Bell, 1986, 1989, 1990*a*, *b*, *c*, 1993; Bell & Szabo, 1986; Bell & Grant, 1992; Bell, Grant & Serrier, 1992), and the command-generating pacemaker circuits (Elekes *et al.*, 1985; Grant, Bell & Clausse, 1986; Grant, 1993) and their projections down to the electric organ. The larval electric organ that is fully functional already at day 11 appears particularly adaptive for the normal development of the electrosensory-motor system in *P. adspersus* because the adult organ is so slow to mature.

Specific responses of the larvae to electrical stimulation, either natural as occurring in the nest or artificial, in terms of the interdischarge interval pattern could not be discerned. However, preferred latency responses were observed already in 11-day-old larvae. This is surprising as much older juvenile, subadult fish had not shown any preferred latency responses (Lücker & Kramer, 1981); only in sexually mature fish did these authors confirm sexually dimorphic latency responses (the Preferred Latency Response and the Preferred Latency Avoidance) that had been observed by Kramer (1978).

The presence of latency responses in larvae suggests that, for an unknown reason, Lücker & Kramer (1981) had failed to demonstrate latency responses in subadult juveniles, although (in light of the present report) fish are probably capable of showing them. Especially *P. adspersus* females and juveniles tend to be shy, and latency responses are sometimes difficult to evoke experimentally (pers. obs.).

The presence of latency responses, even in the youngest of our larvae (11 days), underlines the significance of this behaviour that occurs in many species of mormyrids, although its function is still unclear (reviews Kramer, 1990*a*, 1996; Moller, 1995). However, even the youngest larvae of *P. adspersus* are able to discharge alternately in a group, a mechanism of time sharing of the communication channel. This seems especially adaptive for larvae: (i) because the noise from the other larvae sharing the same nest must be intense; and (ii) because the larval EOD is of about 10 times longer duration than the adult one, increasing the probability of discharge coincidences.

This study was supported by the Deutsche Forschungsgemeinschaft through grant SFB4/H1 to BK; MP held a research assistant position from this grant. Mrs B. Otto assisted in the care of the larvae.

REFERENCES

Bell, C. C. (1986). Electroreception in mormyrid fish. Central physiology. In *Electroreception*: 423–452. Bullock, T. H. & Heiligenberg, W. (Eds). New York: John Wiley.

Bell, C. C. (1989). Sensory coding and corollary discharge effects in mormyrid electric fish. *J. exp. Biol.* **146:** 229–253.

Bell, C. C. (1990*a*). Mormyromast electroreceptor organs and their afferent fibers in mormyrid fish: I. Morphology. *J. Comp. Neurol.* **286:** 391–407.

Bell, C. C. (1990*b*). Mormyromast electroreceptor organs and their afferent fibers in mormyrid fish: II. Intra-axonal recordings show initial stages of central processing. *J. Neurophysiol.* **63:** 303–318.

Bell, C. C. (1990*c*). Mormyromast electroreceptor organs and their afferent fibers in mormyrid fish: III. Physiological differences between two morphological types of fibers. *J. Neurophysiol.* **63:** 319–332.

Bell, C. C. (1993). The generation of expectations in the electrosensory lateral line lobe of mormyrid fish. *J. Comp. Physiol. A* **173:** 677–680.

Bell, C. C. & Grant, K. (1992). Sensory processing and corollary discharge effects in the mormyromast regions of the mormyrid electrosensory lobe. II. Cell types and corollary discharge plasticity. *J. Neurophysiol.* **68:** 859–875.

Bell, C. C., Grant, K. & Serrier, J. (1992). Sensory processing and corollary discharge effects in the mormyromast regions of the mormyrid electrosensory lobe. I. Field potentials, cellular activity in associated structures. *J. Neurophysiol.* **68:** 843–858.

Bell, C. C. & Szabo, T. (1986). Electroreception in mormyrid fish. Central anatomy. In *Electroreception*: 375–421. Bullock, T. H. & Heiligenberg, W. (Eds). New York: John Wiley.

Bigorne, R. (1990). Révision systématique du genre *Pollimyrus* (Teleostei, Mormyridae) en Afrique de l'Ouest. *Rev. Hydrobiol. trop.* **23:** 313–327.

Birkholz, J. (1969). Zufällige Nachzucht bei *Petrocephalus bovei*. *Aquarium* **3:** 201–203.

Birkholz, J. (1970). Nachwuchs bei *Petrocephalus bovei*. *Aquarium* **4:** 340–342.

Bratton, B. O. & Kramer, B. (1989). Patterns of the electric organ discharge during courtship and spawning in the mormyrid *Pollimyrus isidori*. *Behav. Ecol. Sociobiol.* **24:** 349–368.

Crawford, J. D. (1991). Sex recognition by electric cues in a sound-producing mormyrid fish, *Pollimyrus isidori*. *Brain Behav. Evol.* **38:** 20–38.

Crawford, J. D., Hagedorn, M. & Hopkins, C. D. (1986). Acoustic communication in an electric fish, *Pollimyrus isidori* (Mormyridae). *J. Comp. Physiol. A* **159:** 297–310.

Denizot, J., Kirschbaum, F., Westby, G. W. M. & Tsuji, S. (1978). The larval electric organ of the weakly electric fish *Pollimyrus (Marcusenius) isidori* (Mormyridae, Teleostei). *J. Neurocytol.* **7:** 165–181.

Denizot, J., Kirschbaum, F., Westby, G. W. M. & Tsuji, S. (1982). On the development of the adult electric organ in the mormyrid fish *Pollimyrus isidori* (with special focus on the innervation). *J. Neurocytol.* **11:** 913–934.

Elekes, K., Ravaille, M., Bell, C. C., Libouban, S. & Szabo, T. (1985). The mormyrid brainstem. II. The medullary electromotor relay nucleus. An ultrastructural HRP study. *Neuroscience* **15:** 417–430.

Grant, K. (1993). Motor control of signal generation compared in mormyrid and gymnotiform fish. *J. Comp. Physiol. A* **173:** 729–731.

Grant, K., Bell, C. C. & Clausse, S. (1986). Morphology and physiology of the brainstem nuclei controlling the electric organ discharge in mormyrid fish. *J. Comp. Neurol.* **245:** 514–530.

Kirschbaum, F. (1975). Environmental factors control the periodical reproduction of tropical electric fish. *Experientia* **31:** 1159–1160.

Kirschbaum, F. (1987). Reproduction and development of the weakly electric fish, *Pollimyrus isidori* (Mormyridae, Teleostei) in captivity. *Environ. Biol. Fishes* **20:** 11–31.

Kramer, B. (1978). Spontaneous discharge rhythms and social signalling in the weakly electric fish *Pollimyrus isidori* (Cuvier et Valenciennes) (Mormyridae, Teleostei). *Behav. Ecol. Sociobiol.* **4:** 61–74.

Kramer, B. (1979). Electric and motor responses of the weakly electric fish, *Gnathonemus petersii* (Mormyridae), to play-back of social signals. *Behav. Ecol. Sociobiol.* **6:** 67–79.

Kramer, B. (1990*a*). *Electrocommunication in teleost fishes: Behavior and experiments.* Berlin: Springer-Verlag.

Kramer, B. (1990*b*). Sexual signals in electric fishes. *Trends Ecol. Evol.* **5:** 247–250.

Kramer, B. (1994). Communication behavior and sensory mechanisms in weakly electric fishes. In *Advances in the study of behavior*: 233–270. Slater, P. J. B., Rosenblatt, J. S., Snowdon, C. T., Milinski, M. (Eds). San Diego, CA: Academic Press.

Kramer, B. (1996). *Electroreception and communication in fishes. Progress in Zoology.* **42.** Stuttgart: Gustav Fischer Verlag.

Kramer, B. & Kuhn, B. (1994). Species recognition by the sequence of discharge intervals in weakly electric fishes of the genus *Campylomormyrus* (Mormyridae, Teleostei). *Anim. Behav.* **48:** 435–445.

Kramer, B. & Lücker, H. (1990). Species recognition by EOD interval pattern. In *Electrocommunication in teleost fishes: behavior and experiments*: 157–170. Kramer, B. (Ed.). Berlin: Springer-Verlag.

Lissmann, H. W. (1958). On the function and evolution of electric organs in fish. *J. exp. Biol.* **35:** 156–191.

Lücker, H. & Kramer, B. (1981). Development of a sex difference in the preferred latency response in the weakly electric fish, *Pollimyrus isidori* (Cuvier et Valenciennes) (Mormyridae, Teleostei). *Behav. Ecol. Sociobiol.* **9:** 103–109.

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

Postner, M. & Kramer, B. (1995). Electrosensory thresholds in larvae of the weakly electric fish *Pollimyrus isidori* (Mormyridae, Teleostei) during ontogeny. *J. exp. Biol.* **198:** 783–791.

Taverne, L. (1971*a*). Ostéologie des genres *Marcusenius* Gill, *Hippopotamyrus* Pappenheim, *Cyphomyrus* Myers, *Pollimyrus* Taverne et *Brienomyrus* Taverne (Pisces Mormyriformes). *Ann. Mus. r. Afr. Centr. (Tervuren, Belgique). Sér. Sci. Zool.* **188:** 1–144.

Taverne, L. (1971*b*). Note sur la systématique des poissons Mormyriformes. Le problème des genres *Gnathonemus* Gill, *Marcusenius* Gill, *Hippopotamyrus* Pappenheim, *Cyphomyrus* Myers et les nouveaux genres *Pollimyrus* et *Brienomyrus*. *Rev. Zool. Bot. Afr.* **84**(1–2): 99–110.

Westby, G. W. M. & Kirschbaum, F. (1977). Emergence and development of the electric organ discharge in the mormyrid fish, *Pollimyrus isidori*. I. The larval discharge. *J. Comp. Physiol. A* **122:** 251–271.

Westby, G. W. M. & Kirschbaum, F. (1978). Emergence and development of the electric organ discharge in the mormyrid fish, *Pollimyrus isidori*. II. Replacement of the larval by the adult discharge. *J. Comp. Physiol. A* **127**: 45–59.