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ORIGINAL ARTICLE

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Electrosensory basis for individual recognition in a weakly electric, mormyrid fish, *Pollimyrus adspersus* (Günther, 1866)

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Abstract *Pollimyrus adspersus* discriminates the individually variable waveforms of Electric Organ Discharges (EODs) of conspecifics of only 150–250 μs duration. We examined: (1) the discrimination threshold for artificially generated EODs of similar waveform, (2) the mechanism of signal analysis (spectral vs temporal) present, by determining the discrimination between different waveforms of identical amplitude spectra, and (3) the threshold field intensity and reach of discrimination. The triphasic *P. adspersus* EOD waveform was artificially generated by superimposing two Gaussians, one wide, the second narrow, inverted, and of threefold amplitude. The natural variability among individual EOD waveforms was simulated by phase-shifting one Gaussian relative to the other. The symmetrical waveform where the peaks of the two Gaussians coincided was used as a reference (phase shift=0, rewarded stimulus S+). Results were: (1) in food-rewarded conditioning experiments, trained fish (N=7) detected a phase-shift in artificial EOD stimuli as low as 2 μs (N=2 fish), 6 μs (N=1) and 10 μs (N=1). (2) All fish tested (N=3) discriminated between artificial EODs of identical amplitude spectra but different waveforms (hence, different phase spectra), demonstrating a temporal mechanism of signal analysis. (3) The maximum reach of waveform discrimination was 130 cm at 4.9 $\mu V_{p\text{-}p}$/cm and 100 μS/cm water conductivity (test signal generated at natural amplitude), that is, similar to the reach of EOD detection. Therefore, among the three kinds of electroreceptor organ present in mormyrids, we consider Knollenorgane the relevant sensory organs for EOD waveform discrimination.

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Introduction

The weakly electric West and Central African fish species *Pollimyrus adspersus* generates Electric Organ Discharge (EOD) pulses of triphasic waveform, ranging from 150 to 250 μs in duration. The first head-positive potential (P1) is followed, in turn, by a short and strong, head-negative potential (N) and another head-positive potential (P2). On a microsecond scale, there is considerable intraspecific waveform variability (Lücker and Kramer 1981; Westby and Kirschbaum 1982; Bratton and Kramer 1988; Crawford 1992), for example, in the relative amplitudes of the first and the second head-positive phases (Fig. 1A). The EOD waveform of a mormyrid individual is very stable for hours and days, and even over a period of weeks and months (Kramer and Westby 1985; Bratton and Kramer 1988; Crawford 1991). The stability of an EOD has previously been postulated to be an evolutionarily advantageous adaptation (Kramer, review 1996). Fish could use individually constant EOD waveforms as an important source of information, e.g. for individual recognition of conspecifics. In food-rewarded playback experiments, trained fish discriminated the small differences between natural (digitally recorded) EOD waveforms generated by different conspecifics, independent of stimulus amplitude (Graff and Kramer 1992).

Because the limits and mechanism of discrimination are still unknown, we here determine: (1) the discrimination threshold for EOD-like stimuli of similar waveform in *P. adspersus*. We also determine (2) which type of signal analysis is present: spectral analysis as commonly present in the mechanical senses, or true temporal analysis of waveforms (as in the weakly electric "wave" gymnotiform *Eigenmannia*; review, Kramer 1999). Additionally, we try to (3) estimate the reach for also identifying the relevant electroreceptor-organ system

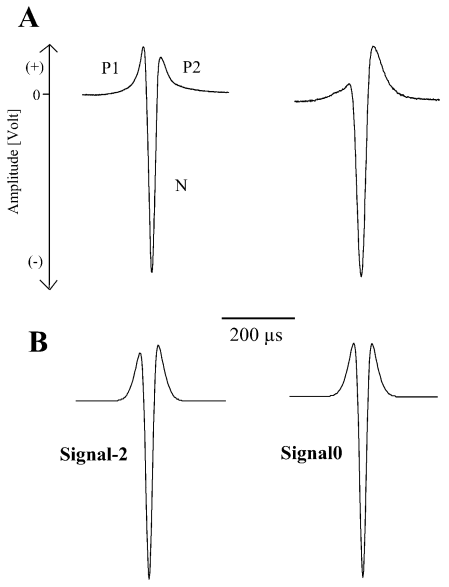

Fig. 1 **A** Electric organ discharges of triphasic waveform recorded from two *Pollimyrus adspersus* individuals. The amplitude of the first head-positive phase (*P1*) is higher than that of the second (*P2*) in the *left* waveform. The EOD on the *right* shows the opposite relationship. Discharges normalized to the same amplitude (peak-to-peak) (*N* head-negative phase). **B** Computer-generated stimulus pulses that were still discriminated by two trained fish. Compared to Signal0, in Signal-2 the N phase is advanced by 2 µs

among the three anatomically and physiologically different systems: the ampullary electroreceptor-organ system, the Knollenorgan and the mormyromast systems. Using artificial stimulus pulses, we determined discrimination in trained fish by conditioning techniques.

Methods

Animals and animal care

Experimental fish were obtained from a wholesaler who imported them from West Africa (Nigeria) direct. Originally, we had identified fish from the laboratory stock as *Pollimyrus isidori*. Bigorne (1990) recognized fish from a few West African coastal rivers east of the Volta as representing *P. adspersus* (Günther, 1866), which is also reported from Congo or Zaïre and Cameroon. In agreement with this species, but not *P. isidori*, our experimental fish had 12 scales around the caudal peduncle with the exception of fish Pa-1 (in which the number was 14 as has been observed in specimens of both species). By contrast, Pa-1's anal-fin ray count of 29 was specific for *P. adspersus* only (upper limit for *P. isidori*: 27). After completion of the experiments, the gonads of the fish were dissected and their sex determined. Pa-1, Pa-2 and Pa-6 were female, Pa-3, Pa-5 and Pa-7 male. For further detail, see our web site http://www.biologie.uni-regensburg.de/Zoologie/Kramer/index.htm.

Before training, the fish were kept in a communal tank of 720 l capacity and were fed on chironomid larvae (bloodworms) five to six times per week. The light/dark cycle was 12:12 h.

Experimental setup and design

Discrimination threshold for EODs of similar waveform

The experiments were conducted in two identical 120-l tanks (Fig. 2A). The tanks were illuminated by two incandescent light

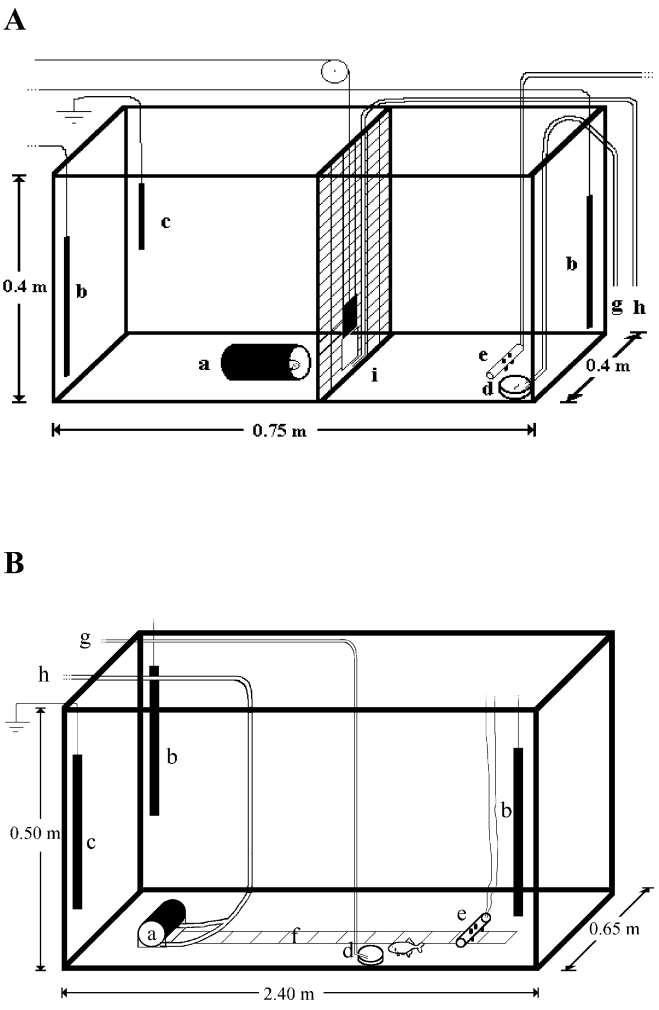

Fig. 2A, B Experimental tanks for the determination of waveform discrimination threshold (**A**) and the associated threshold field intensity (**B**). **B** shows a parallel arrangement of the porous pot (*a*) and the dipole (*e*) (*b*, *c*, recording and ground electrodes, *d* petri dish for food, *f* scale. *g* tubing for delivering food (reward), *h* tubing for delivering air as a mild form of punishment, *i* trapdoor with air tubing)

bulbs of 60 W. Water conductivity was kept almost constant at 100 µS/cm (96–104 µS/cm). Temperature varied between 25.7 and 28.5°C in tank 1 and 25.9 and 26.5°C in tank 2. A plastic mesh partition with an integrated trapdoor divided an experimental tank into two sections. One section of a tank contained a porous pot as a hiding place for the fish. The pot was orientated in parallel to the long axis of an aquarium. The other section of each tank held an electric dipole as an electric fish decoy, and a petri dish which served as a food tray. At feeding time, a bloodworm reward was flushed onto the petri dish via a fine PE tube and a glass pipe. Hiding and feeding places were separated by 46 cm in tank 1 and 49 cm in tank 2. The stimulus dipole consisted of a horizontal Plexiglas pipe (10 mm diameter, 120 mm length) with two vertically projecting graphite rods in the function of a dipole. The rods were 26 mm from each other to mimic a natural electric organ. Suckers were used to fix the dipole on the tank bottom. The longitudinal axes of the dipole and the porous pot formed a right angle. The minimal distances between the porous pot that faced the door-opening, and the dipole were 306 mm in tank 1 and 331 mm in tank 2. The opening of the trapdoor (45 mm wide and 50 mm high) allowed the fish to pass between tank sections easily. The experimenter opened and closed the trapdoor quickly by gently

pulling on an attached string. The distances between the centre of the dipole and the trapdoor were 186 mm in tank 1 and 185 mm in tank 2. When necessary, a negative stimulus (S−), a few air bubbles, was applied via a glass pipe ending at the trapdoor.

To monitor the electric signals emitted from both the fish and the stimulus dipole, recording electrodes were placed at diagonal cor- ners of an aquarium. Potential differences were amplified (differential amplifier, 1–100 kHz, ×10–100) and monitored using an os- cilloscope (Hameg HM 208). Stimuli were generated by our custom-made DAM, a digital-to-analog converter with memory and microprocessor (Kramer and Weymann 1987). This device was controlled by an IBM-compatible PC. To exclude disturbances of the fish by the experimenter and his actions, a black curtain was put between both.

Threshold field intensity and reach of discrimination

For this test, an aquarium of 2.4 m length and 0.65 m width was used (Fig. 2B). It was illuminated by three 100-W incandescent light bulbs. Conductivity was almost constant during the experimental period (97–104 μS/cm at 26.5–28.0 °C). The fish's shelter, a porous pot, was orientated normal to the longitudinal axis of the tank. The openings of a bifurcating plastic tubing were directed towards the ends of the porous pot, delivering, if necessary, a negative stimulus in the form of a brief pulse of air bubbles. The centre of the porous pot was placed at the beginning (zero point) of a distance scale along which the dipole was moved to specified positions. Whereas the dipole's position could be given exactly, the fish obviously remained mobile. By choosing a porous pot of just sufficient size for the fish (inner diameter, 42 mm; length 106 mm), the distance could be given with sufficient precision.

In additional experiments, the dipole was rotated by 90°; the dipole now was at a right angle relative to the fish. For the procedures of generating and monitoring signals, as well as giving rewards, see the previous section (discrimination threshold for EODs of similar waveform).

Stimulus pulse waveforms

Playbacks of natural EOD waveforms are unsuitable for studying the present questions because natural EODs vary among individuals in various parameters simultaneously. Rather than natural EODs, we decided to use precisely defined, artificial waveforms to examine the electrosensory system of *Pollimyrus*.

Generation and analysis of stimulus waveforms

Following Westby (1984), simulated *Pollimyrus* EOD waveforms were calculated using a Gaussian distribution with a large sigma value (p), from which a second Gaussian function with a small sigma value (n) was subtracted.

$$g(x) = \frac{r}{p\sqrt{2}\sqrt{\pi}}\, e^{\frac{-(x+v)^2}{10p^2}} - \frac{1}{n\sqrt{2}\sqrt{\pi}}\, e^{\frac{-(x-v)^2}{10n^2}} \quad (1)$$

The natural variability of EOD waveforms—though not duration—among individuals of *Pollimyrus* is generated with parameters set as follows:

- r=1 (weighting factor)
- p=6 (width of the positive Gaussian)
- n=2 (width of the negative Gaussian)
- $v \in \mathbb{R}$={−15, ..., +15} (phase shift)

At v=0, the maximum and the minimum of the curve coincide and the resulting waveform is symmetrical (Fig. 3, Signal0). A negative v advances the negative peak relative to the positive peak; a positive v has the opposite effect (delay of the negative peak). The continuous waveforms were digitized and scaled to fit the format required by our DAM stimulator (8 bit vertical resolution and 11 bit horizontal resolution). The sampling rate of the DAM was 500 kHz or 2 μs between adjacent points. Whereas Gaussian functions approach zero asymptotically (without ever reaching it), our discrete curves did reach zero according to the finite amplitude resolution of our digitization. Consequently, the duration of our calculated EOD pulse used for stimulation depended on the arbitrary (or machine-imposed) choice of amplitude resolution.

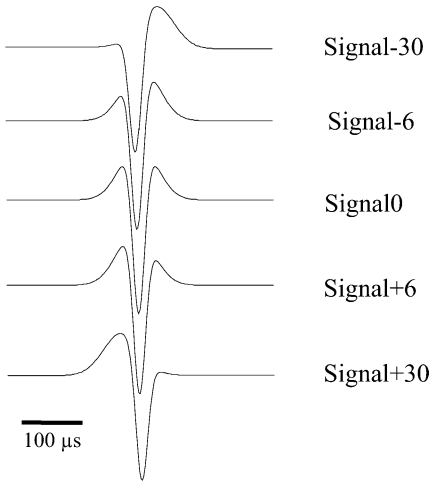

Fig. 3 Family of computer-generated stimulus pulses (calculated by superimposing two Gaussians), simulating one aspect of the natural variability in EODs of *Pollimyrus adspersus* by systematically varying the time shift of the N phase relative to P phase. The code number of each signal designates advance (-) or delay (+) in microseconds, relative to coincidence of peaks as shown in "Signal0"

To circumvent this problem, we chose a physiologically more relevant parameter as a measure for pulse duration. According to our proposed sensory mechanism (see Discussion), the rate of voltage change is of more importance than (the arbitrary) pulse duration. We chose a gradient of greater than or equal to +3 V/s to mark the start of an EOD-like pulse, and a gradient of greater than or equal to −3 V/s to mark its end (with the pulse played back head-positive, and amplitude standardized at 1 $mV_{p\text{-}p}$).

Stimulus pulses and natural EOD variability

By varying the delay between the two Gaussians, v, we generated a series of stimulus pulses that represent a good deal of the natural variability among *P. adspersus* EODs (Fig. 3 shows a few examples). In signal0, 14 discrete points or 28 μs fall between the zero-crossings of the N-Phase, as generated by computer (Fig. 4). The N-duration in natural EODs is in the range of 17.3–31.6 μs in *P. adspersus* for females (N=14) and 23.1–37.8 μs in *P. adspersus* for males (N=10), respectively (Bratton and Kramer 1988, at a water conductivity of 95–105 μS/cm and 26–28 °C). The interval between the two positive peaks in natural EOD waveforms is 44.20±6.53 (SD) μs for males (N=8) and 40.47±6.55 (SD) μs for females (N=6) according to Crawford (1992); the interval ranges from 28.9 μs to 60.9 μs according to Bratton and Kramer (1988). The interval of our computer-calculated EOD (48 μs for Signal0) thus was close to the centre of the natural range of variability.

During playback of synthetic EODs, pulse rate and amplitude were kept constant. A pulse rate of 10 Hz (as used in the present experiments) is close to the average EOD rate of resting *P. adspersus* (11.7±2.1 Hz; Bratton and Kramer 1989). Stimulus amplitude was chosen such that it exactly matched the EOD amplitude of a randomly chosen adult *P. adspersus* (standard length, 73 mm), as determined in the test aquarium. EOD waveform discrimination does not depend on a constant signal amplitude because fish are able to discriminate between EOD waveforms even when amplitudes vary randomly (Graff and Kramer 1992). We

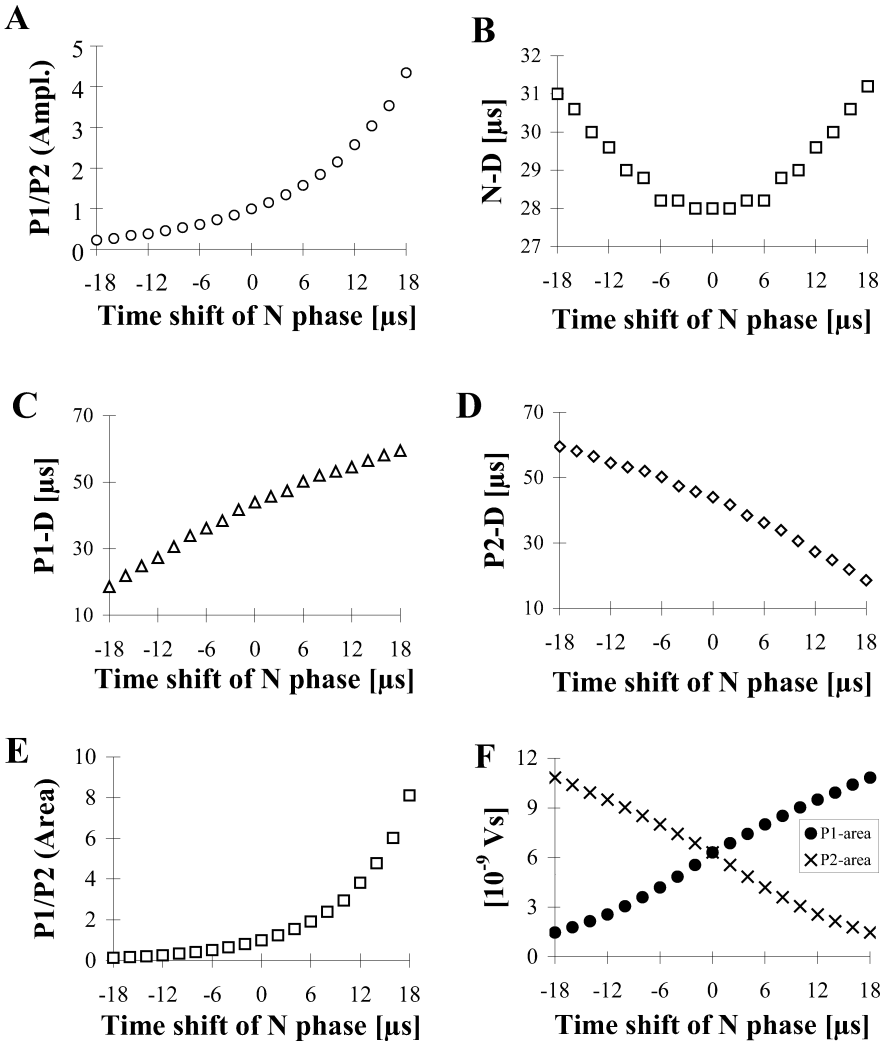

Fig. 4A–F Change of waveform parameters with time shift of the negative Gaussian relative to the positive one in microseconds (data calculated from waveform file). Abscissa, time shift in microseconds. Ordinate in **A**, P1/P2 amplitude ratio; **B** duration of N phase (*N-D*); **C** duration of P1 phase; **D** duration of P2 phase; **E** P1/P2 ratio of areas under curves; **F** P1 and P2 areas of pulses normalized to 1 $mV_{p\text{-}p}$. P1 duration was measured from the first occurrence of an intensity greater than or equal to +3 V/s (head-positive waveform, amplitude normalized to 1 $mV_{p\text{-}p}$) and the first zero-crossing of the N phase. P2 phase lasts from the second zero-crossing of the N phase to the first occurrence of an intensity greater than or equal to −3 V/s

compared the waveforms of stimuli as recorded from the water with the waveforms recorded from DAM output. Differences were negligible (see web site http://www.biologie.uni-regensburg.de/Zoologie/Kramer/index.htm).

Different waveforms of identical Fourier amplitude spectra

To select stimulus pulse pairs of different waveforms with identical Fourier amplitude spectra, we Fourier-transformed function (1). The amplitude spectrum is as follows:

$$h(f)=\sqrt{5\left(r^2e^{\left(-5k^2f^2p^2\right)}+e^{\left(-5k^2f^2n^2\right)}-2r\cos(2kfv)e^{\left(-\frac{5}{2}k^2f^2\left(p^2+n^2\right)\right)}\right)}$$

$$k = 4\pi 10^{-6} \quad (2)$$

See Eq. 1 for the values of *n, p, r* and *v* (all constants were combined in *k*). For *v*-values of equal magnitude but opposite sign, only the argument of the cosine changes in Eq. 1. Since the cosine is a symmetrical function, the amplitude spectrum is unaffected. Therefore, a change in sign only affects the phase spectrum, but not the amplitude spectrum. Continuous Fourier amplitude spectra (CFT) were calculated according to Eq. 2. Figure 5A compares continuous Fourier amplitude spectra using as examples Signal-10 and Signal+10; they are identical. For each stimulus pulse, *N*=11 recordings from the experimental tank were Fourier-analysed (Fig. 5B, C). Between the discrete spectra for both types of stimulus pulses (Fig. 5B), there is no difference in the average frequencies of peak amplitudes, or their SDs (12.041±0.075 kHz for Signal+10, 12.060±0.078 kHz for Signal-10; difference in SDs not significant: F=1.099, P=0.442; also difference in average peak frequencies not significant: P=0.570, df=20, Student's t-test), and the spectra also closely resemble the continuous (theoretical) spectra (Fig. 5A). The associated discrete FFT-phase spectra shown in Fig. 5C are mirror images, symmetrical about 0° as expected.

Measuring electric field intensities

For determining electric field intensities, a single-cycle, bipolar sine-wave pulse of 2 ms duration generated by the DAM was used. Signal amplitudes were the same as already described. Electric field intensities were measured using a pair of glassy carbon electrodes for recording and an oscilloscope for monitoring the signals. The glassy carbon electrodes formed a dipole consisting of two vertically arranged, parallel carbon rods (Sigradur G) of 1 mm diameter separated by 1 cm (centre-to-centre), of 6 cm length which were insulated except for 10 mm at their tips. During measurements, this measuring dipole replaced the fish's shelter. All field intensities were recorded as voltage differences of the maximum amplitudes from peak-to-peak ($\mu V_{p\text{-}p}$/cm).

At greater distances, recorded field intensities were very weak and could not be measured precisely due to background noise. Using a sine wave (of 1000 Hz) rather than single-cycle sine-wave

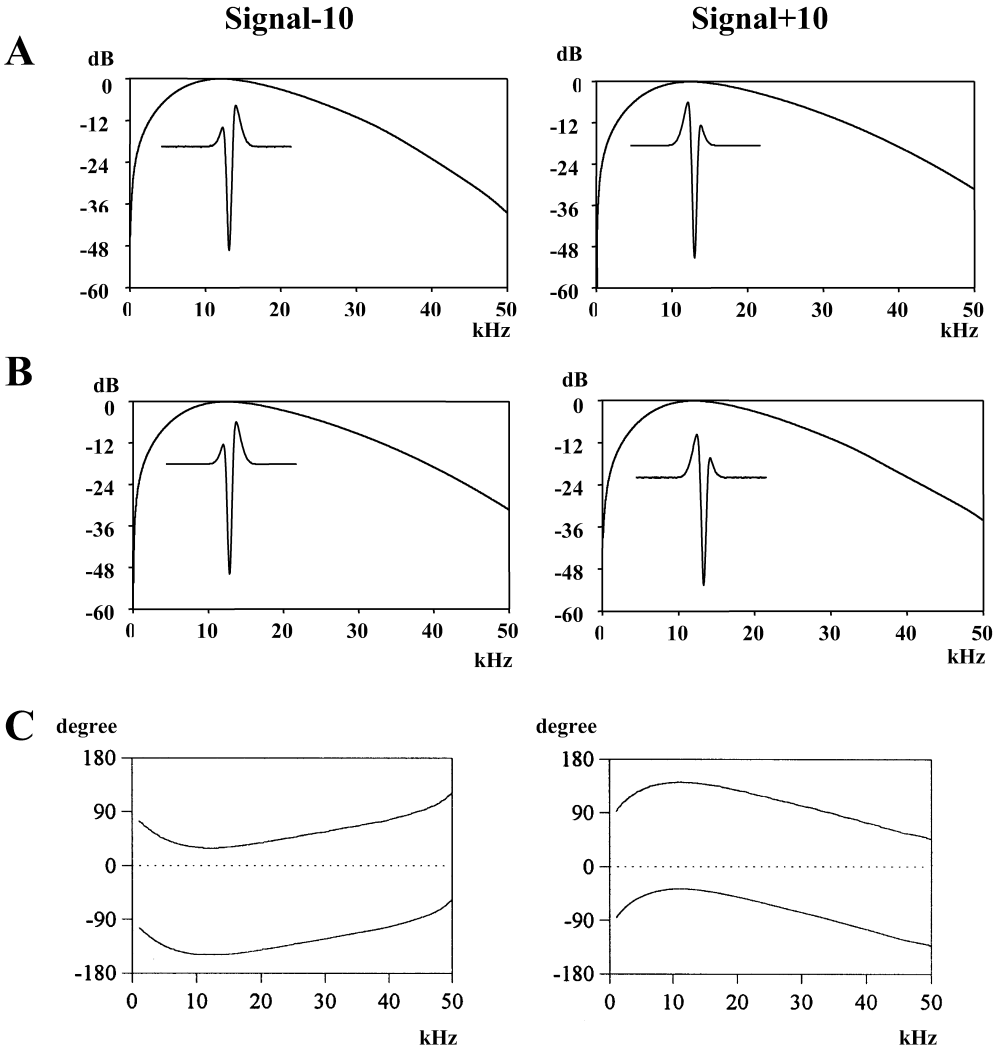

Fig. 5A–C Spectral analysis of Signal-10 (*left column* of panels) and Signal+10 (*right column* of panels). **A** Continuous Fourier amplitude spectra were calculated for the continuous waveform functions using Eq. 2, see text. Note that the two spectra are identical. **B** There is very little difference from the discrete amplitude (Fast Fourier) spectra for our real-world, discrete stimulus pulses, Signal-10 and Signal+10, as recorded from the water. Ordinates, relative amplitude (in dB) relative to strongest spectral component=0 dB; voltage for pulse waveform insets. Abscissae, frequency (kHz), time for insets. **C** As **B**, but discrete phase spectra for Signal-10 and Signal+10; ordinate, phase angle in degrees; abscissa, frequency (in kHz) (resolution: 0.95 Hz; frequency window: 125 kHz). Note that stimulus pulse waveforms (insets) are time-symmetrical mirror images, with the N phase advanced or delayed by the same amount (±10 μs). Therefore, phase spectra are also mirror images, symmetrical about zero degree. When going along the abscissa representing frequency, the associated phase angles alternate by a constant amount which causes the two seemingly independent lines in each graph. Spectral components below about 1 kHz were too weak to be resolved

pulses allowed sharp bandpass filtering with cutoff frequencies of both low- and high-pass filters set at 1000 Hz (Wavetek Rockland Model 452; 24 dB attenuation/octave). Signal attenuation of 6 dB was taken into account when calculating the field intensity. The dependency of the electric field intensity on distance was recorded prior to and after every experiment. Field intensities were measured for both dipole orientations, parallel and perpendicular (see above), relative to the fish. Therefore, we obtained five values for each distance and arrangement. The initial distance between stimulus and measuring dipole of 5 cm was increased in steps of 5 cm, until the electrical noise made measuring impossible.

Conditioning procedures

Prior to training, the fish were kept isolated in the experimental tank for 4–27 days. Basic training consisted of training the fish to swim to the feeding station on stimulus onset (S+) in one smooth movement. Signal0 was chosen for the rewarded stimulus (S+). Stimuli were presented every second minute for a period of 30 s. Initially, the trapdoor was left open permanently; later, it had to be closed after a fish's return to its shelter in order to prevent it from checking for food all the time (without stimulus). Therefore, the door was only opened immediately before stimulation, and closed after the fish had returned to its shelter. Because training was conducted during the light period, fish returned to their shelter spontaneously.

Conditioned discrimination training started when an unrewarded stimulus, S–, was added to the stimulus regime. Initially, the

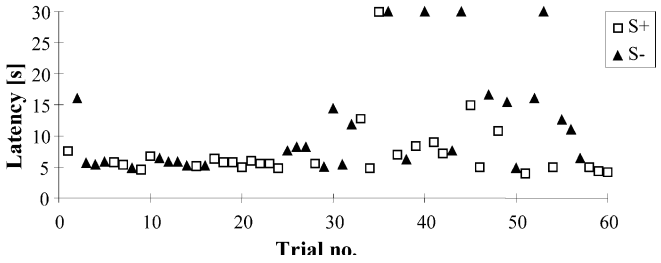

Fig. 6 Example of a learning curve for fish Pa-2 which eventually discriminated signal-2 (the *S*-) from Signal0 (the *S*+), as demonstrated by increasing latencies for the *S*-. Ordinate: response latency in seconds; abscissa, trial no.

stimulus Signal-30 was chosen for an S− in order to facilitate discrimination conditioning. Our response criterion for estimating a fish's performance in discriminating stimulus pulse waveforms was the latency from stimulus onset to the time when the fish put its snout into the petri dish. However, when determining threshold field intensities, latency was defined as the time from signal onset to the time when the fish had left its shelter completely, that is, when all of the fish became visible in an overhead mirror (including its tail when leaving the shelter by swimming forward, the head when backing out). Latencies were measured using a stop-watch, at an accuracy of ±0.2 s.

Stimuli were delivered only when the fish had assumed a defined position and orientation within its shelter. When the latencies for (S+) and (S−) stimuli clearly started to dissociate, data collection for statistical analysis started (5–20 days after basic training had stopped; Fig. 6). Therefore, the experimental procedure had to be standardized as follows. A training session consisted of 46 trials, the first 6 of which were an identical sequence of introductory stimuli (2 S+, 1 S−, 2 S+ and 1 S−). The sequence of the next 40 stimuli followed a randomized blocks design (Table 15.7 from Cochran and Cox 1968). Every fourth trial was a "test" trial that was followed by neither reward nor punishment. The results in this paper are based exclusively on test-trials.

Randomization of the sequence of stimuli was restricted as follows: (i) a maximum of 3 positive (rewarded) or 3 negative (unrewarded) punished trials in a row; (ii) 20 positive and 20 negative trials made up 1 session. Every fish went through one or two sessions per day. Training sessions stopped when the fish appeared to lose appetite.

Statistical analysis

Latencies were analysed by the Wilcoxon matched-pairs signed-ranks test. *P* values are one-sided since latencies for (S+)-stimuli were expected to be either shorter or of similar duration (no difference) as compared to those for (S−) signals. Data were obtained from the same individuals and were therefore related. When for at least five sessions the S− was significantly discriminated from the S+ at $P \leq 0.05$, a new, more similar waveform was used as an S−, or the sender-receiver distance was increased when studying discrimination reach. If after five sessions significance was not reached, this was considered evidence for the fish's inability to discriminate between the two stimulus waveforms tested. We refer to a single approximation of the (S−) signal to the reference signal (Signal0) as a series of experiments. In a series of experiments, the negative stimulus, Signal-30 or Signal+30, was made more similar to the reference signal first by large steps, and later on by increasingly smaller steps.

Results

Discrimination threshold for EODs of similar waveform

Food-rewarded playback experiments were conducted to determine the discrimination threshold for synthesized EOD-like stimuli of similar waveform, using Signal0 as the rewarded stimulus, S+. During the initial series of experiments that started using Signal-30 as an (S−) stimulus, fish Pa-1 and Pa-2 eventually discriminated Signal-6 from the S+ ($P<0.0001$ and $P=0.0034$, respectively; Table 1); Pa-4 discriminated Signal-10 ($P=0.0273$) from the reference signal S+, and Pa-3 excelled in discriminating even Signal-2 ($P=0.0177$). In Pa-3 and Pa-4 only one series of experiments were carried out.

To determine the extent to which learning and training affected the discrimination, the training of Pa-1 and Pa-2 was continued, approaching discrimination threshold from different "directions". For Pa-1, the first S− used was Signal+30, for Pa-2 once again Signal-30. The apparent discrimination threshold in Pa-1 was already reached at an S− of Signal+10 (which is difficult to understand because in the previous series of trials, it had been Signal-6 in this fish). In order to exclude the possibility that the training and testing series had simply been too long for this fish, we started the next four series with a smaller difference from S+, using Signal+12 as the most dissimilar S−. Eventually, the fish discriminated even Signal+6 from the reference S+ ($P=0.0031$), repeating its initially shown discrimination performance for the other "side" of testing. A similar improvement was seen

Table 1 Discrimination thresholds for EOD-like stimuli differing in waveform: latency and test statistics (t_{S-}, t_{S+} mean latencies ±SD in seconds for S- and S+ stimuli, respectively; *N* number of matched pairs in a test series, as used for a Wilcoxon matched-pairs signed-ranks test). Signal0 was used as an S+ in all tests. The test series started with signal-30 in all test series where the N phase of the stimulus pulse was advanced; with signal+30 when the N phase was delayed. Mean latencies of Pa-1 on signal+6 were quite short and SD, accordingly, small

Fish	(S-)-signal	t_{S-} [s]	t_{S+} [s]	*N*	Sum of signed ranks	Sum of positive ranks	Sum of negative ranks	*P* value
Pa-1	Signal-6	12.1±8.1	3.9±4.2	15	120	120	0	<0.0001
	Signal+6	2.6±2.8	1.6±0.1	20	74	82.5	−8.5	0.0031
Pa-2	Signal-6	18.7±10.2	9.2±7.3	12	−58	4	−62	0.0034
	Signal-2	11.4±8.3	7.3±5.0	30	−230	74	−304	0.0030
Pa-3	Signal-2	22.1±7.6	14.9±7.9	15	−74	23	−97	0.0177
Pa-4	Signal-10	26.3±5.3	18.2±9.6	10	−28	4	−32	0.0273
Pa-2	Signal-1	7.2±3.2	6.8±3.8	20	−22	84	−106	0.340
Pa-3	Signal-1	9.5±6.8	13.4±9.7	25	100	212	−112	0.091

Table 2 Discrimination between waveforms with identical Fourier amplitude spectra: latency and test statistics (t_{S-}, t_{S+}mean latencies ±SD in seconds for S- and S+ stimuli, respectively; *N* number of matched pairs in a test series, as used for a Wilcoxon matched-pairs signed-ranks test). Signal+10 was used as an S+, signal-10 as an S-

Fish	t_{S-} [s]	t_{S+} [s]	*N*	Sum of signed ranks	Sum of positive ranks	Sum of negative ranks	*P* value
Pa-2	21.3±11.9	10.7±9.9	10	−37	4	−41	0.0137
Pa-3	26.6±7.7	13.8±9.2	5	−15	0	−15	0.0313
Pa-4	19.4±11.1	7.4±6.6	15	−79	20.5	−99.5	0.0108

in Pa-2: in the first series of experiments, this fish discriminated Signal-6 from the S+. Subsequently, test series started using Signal-8 as an S−. In the sixth series, the fish discriminated even Signal-2 from the S+ (*P*=0.0030; Fig. 6). These results show that the fish discriminated increasingly similar waveforms with continued learning and training (especially when the difference the fish had to go among S− stimuli was not too great, or the time not too long). In Pa-1, the discrimination threshold of 6 μs shift of the N phase of an S− was independent of whether the shift was an advance or a delay relative to the positive Gaussian.

Next we investigated whether the two fish that had shown the best discrimination performances, Pa-2 and Pa-3 (see Table 1), were also able to discriminate between Signal-1 (as an S−) and Signal0 (as an S+), testing a phase shift of only t_v=1 μs. However, both fish failed to discriminate the two waveforms (*P*=0.340 and *P*=0.091, respectively).

In summary, best discrimination performances were as follows (Table 1): Pa-1 discriminated Signal+6 and Signal-6 from the S+, and Pa-4 Signal-10. Both Pa-2 and Pa-3 showed the best performances among all fish, discriminating even Signal-2 from the S+.

The electric field intensities associated with discrimination were 0.76 mV_{p-p}/cm and 1.56 mV_{p-p}/cm at the near end of the porous pot and at the trapdoor, respectively, as measured in tank 1 (see Fig. 2). In tank 2, field intensities were 0.31 mV_{p-p}/cm and 1.32 mV_{p-p}/cm, respectively.

Comparison of natural EOD waveform variability with stimulus pulse waveforms at discrimination threshold

The waveform differences between Signal-2 and Signal0 that were discriminated by fish Pa-2 and Pa-3 are surprisingly small (Fig. 1B), especially when compared with natural EOD waveform variability. A variation of P1/P2-amplitude ratio of 0.148 as present in our stimuli is 15 times less than the variability among natural EODs (range, 0.04–3.33), and a variation of the interval between P1 and P2 peaks of 1 μs is 32 times less than the natural variability range, 28.9–60.9 μs. The N duration of natural EODs ranges from 17.3 to 31.8 μs whereas there is no variation at all between Signal0 and Signal-2 in this parameter. The same holds true for Signal-2 and Signal0 in the interval between P1 and N peaks (no difference), but natural variability ranges from 15.8 to 28.9 μs. A negligible variation of our test pulses of only 35 Hz in peak amplitude frequency of amplitude spectra (CFT of the function) contrasts with a natural range of peak amplitude frequencies of greater than 16 kHz (from 8.8 kHz to 25.0 kHz; Bratton and Kramer 1988). The P1 phase of Signal0 lasts 44.0 μs and is 2.3 μs shorter than that of Signal-2 (data for waveform file; see definitions for P1 and P2 duration). The duration of the P2 phase in Signal0 (44.0 μs) was slightly shorter than that of Signal-2 (45.7 μs).

Discrimination of waveforms with identical Fourier amplitude spectra

Amplitude spectra and pulse durations of Signal+10 and Signal-10 are identical, and both signals differ only in their waveforms and phase spectra (Fig. 5). Signal+10 was the rewarded stimulus, Signal-10 the unrewarded one. All three fish tested discriminated between the two stimuli after a few sessions only (Table 2). In Pa-2, two sessions (*P*=0.0137), in Pa-3, a single session (*P*=0.0313) and in Pa-4, three sessions (*P*=0.0108) were required to establish discrimination. Electric field intensities were the same as those used for determining discrimination threshold. In additional tests, the fish also discriminated between Signal-8 and Signal+8. We conclude that *Pollimyrus adspersus* discriminates easily between waveforms of identical amplitude spectra and identical pulse duration, provided waveforms (or phase spectra, Fig. 5) are different.

Reach and threshold field intensities of waveform analysis

We determined the maximum distance from the stimulus dipole at which four fish still discriminated waveforms. The individuals used were Pa-2, Pa-5, Pa-6 and Pa-7.

Signal-8 and Signal+8 had been discriminated by the fish already in the previous tests (see first section on discrimination thresholds). Playback experiments using this pair of stimuli (Signal-8 for S− and Signal+8 for S+) started at a stimulus dipole-fish distance of 30 cm. After fish had successfully discriminated between the two signals, we moved the dipole 15 cm further away from the fish, and continued testing. This procedure was repeated until the fish failed to discriminate between the two

Table 3 Reach and threshold field potentials for discrimination between two pulse waveforms: latency and test statistics (t_{S-}, t_{S+} mean latencies ±SD in seconds for S- and S+ stimuli, respectively; *N* number of matched pairs in a test series, as used for a Wilcoxon matched-pairs signed-ranks test; *perpend* perpendicular). Signal+8 was used as an S+, signal-8 as an S- in all tests

Fish	Arrangement	Distance [cm]	Field potential [μV_{p-p}/cm]	t_{S-} [s]	t_{S+} [s]	*N*	Sum of signed ranks	Sum of positive ranks	Sum of negative ranks	*P* value
Pa-2	Parallel	130	12*	27.3±6.3	8.8±5.6	7	−28	0	−28	<0.0001
Pa-5	Parallel	60	79	17.4±11.0	11.5±8.3	25	−162	69	−231	0.0107
Pa-6	Parallel	50	123	19.7±10.0	12.9±10.3	25	−145	90	−235	0.0264
	Perpend.	55	37*	28.8±2.8	15.9±8.0	5	−15	0	−15	0.0313
Pa-7	Parallel	90	29*	15.7±8.8	8.6±6.8	10	−39	8	−47	0.0244
	Perpend.	110	4.9*	10.9±7.9	7.6±5.3	30	149	128.5	−277.5	0.0460

* Threshold electric field intensities were determined by extrapolation from a regression line.

stimuli. In this case, the dipole was moved back 5 cm closer to the fish. Depending on whether or not the fish discriminated between the two stimuli at this closer distance, we either increased the distance by 15 cm or reduced it by another 5 cm. When the dipole had to be moved back closer to the fish two times in succession, we defined the greatest distance at which the fish significantly discriminated between the two signals as the reach of its waveform discrimination. Maximum distances for both dipole-fish arrangements were determined.

For the parallel arrangement, reaches determined in this way ranged from 50 cm in Pa-6 to 130 cm in Pa-2 (Table 3). The related field intensities varied from 12 μV_{p-p}/cm (130 cm) to 123 μV_{p-p}/cm. For the perpendicular arrangement, maximum distances of waveform discrimination were similar (55 cm and 110 cm, 37 μV_{p-p}/cm and 4.9 μV_{p-p}/cm, respectively, determined in two fish).

For distances greater than about 60 cm, the associated electric field intensities were too low to be measured. The electric field intensity was approximately inversely proportional to the cube of the distance (see Knudsen 1975), and regression analysis yielded straight lines on double log plots (log y=−2.42 logx+3.21 for the parallel arrangement, and log y=−2.94 logx+3.69 for the perpendicular arrangement). Therefore, field intensities for long distances were extrapolated from the regression results (see Squire and Moller 1982).

Discussion

Sensory limits

Westby's approach of generating artificial *P. adspersus* EODs by superimposing two Gaussians (that was adopted here, see Methods) follows the physiology of the electric organ where a neuronally evoked, broad P potential is split into two by a brief, strong N potential that is electrically evoked by P current from the opposite, non-innervated cell faces (Westby 1984). In varying N delay, characteristic features of the natural variability of the *P. adspersus* discharge, such as P1/P2 amplitude ratio that varies for the two sexes, is simulated (Westby 1984).

As shown in the present paper, discrimination performance is astounding. Fish detect a time shift of N phase relative to P phase as small as 2 μs, resulting in a change of P1/P2 amplitude ratio of only 14.8%. The change of time difference between the P1 and P2 peak is only 1 μs. Fish also discriminated between pairs of waveforms of identical amplitude spectra that differed only in phase spectra (because stimulus pulse waveforms were time-symmetrical mirror images), demonstrating a temporal (as opposed to a spectral) mechanism of signal analysis.

In addition to the discrimination limen and the mechanism of signal analysis, both of which were unknown to Graff and Kramer (1992), we here present the reach of waveform discrimination (with a bearing on the relevant receptor system, see below). Here we have shown that the reach varied from 50 to 130 cm, depending on the individual fish and dipole orientation (Table 3). The variation among individuals may be explained by differences in motivation that are also known from other conditioning experiments. Our longest reaches measured were 110 cm (field intensity: 4.9 μV_{p-p}/cm) for the perpendicular arrangement, and 130 cm (field intensity: 12 μV_{p-p}/cm) for the parallel arrangement of dipole and fish, and these are quite long in comparison to the small size of the fish (SL, 7.5 cm and 8.1 cm, respectively). While our study provides the first determination of the reach of waveform analysis in mormyrids, the reach of signal detection had previously been determined in *Brienomyrus niger*, a mormyrid of slightly larger maximum size (Squire and Moller 1982; Moller et al. 1989). Interestingly, the reach of EOD detection, as determined by recording evoked discharge rate changes in untrained fish, is similar to our estimate for the reach of EOD discrimination determined in trained *P. adspersus*. Therefore, the reach of signal discrimination, as a specific form of communication, and the reach of signal detection are about the same.

Relevant receptor system

Mormyrids possess three distinct electroreceptor organ systems, namely the ampullary receptor organs and two types of tuberous receptor organs, Knollenorgane and

mormyromasts. The afferent fibres of ampullary receptors fire permanently, have the lowest stimulus thresholds among all electroreceptors, and are most sensitive between 10 Hz and 30 Hz (electrophysiologically determined in *Gnathonemus petersii*, Dunning 1973 in Zakon 1986). Therefore, ampullary organs can be excluded for the discrimination of EOD waveforms, with spectral amplitude maxima ranging from 8 to 25 kHz (Bell and Russell 1978; spectral amplitude maxima determined by Bratton and Kramer 1988). Ampullary receptors would, however, respond to brief electrical pulses (50–200 μs) if these had a noticeable DC-component, which was not the case in the present study. [The DC-component of our triphasic stimulus waveform is theoretically zero (r=1 in Eq. 1), and deviations from theory as recorded in our synthetic pulses were <0.5% when weighing the combined areas of the positive phases against the area of the N-phase.]

The second class of electroreceptor, mormyromasts, are also unsuitable for the detection of the fine detail of EODs generated by conspecifics, because a motor-command-related brain mechanism, the electric organ corollary discharge (EOCD), facilitates only reafferent, but blanks exafferent mormyromast responses (Bell 1989; Bell and Grant 1992; Bell et al. 1992). The relatively insensitive mormyromasts are also unlikely receptors in the present context because of the low electric field intensity of 4.9 $\mu V_{p\text{-}p}$/cm at which waveform discrimination was still observed (Table 3), even when considering that behavioural thresholds usually are at least 10 times lower than electrophysiologically determined ones (Bennett 1971; Squire and Moller 1982; Postner and Kramer 1995). Therefore, we regard the Knollenorgan system as the one involved in EOD waveform discrimination, as studied in the present paper.

The behaviourally determined electrosensory threshold of *P. adspersus* larvae to EOD-like stimuli is only 2.4 $\mu V_{p\text{-}p}$/cm (Postner and Kramer 1995) whereas electrophysiologically determined thresholds are much higher (0.1–1.0 mV, Zakon 1986). The afferents of Knollenorgane respond to outside-negative to positive-going transients of a stimulus by a single action potential of almost constant latency (Bennett 1965, 1967; Szabo and Fessard 1974; Hopkins and Bass 1981). The action potential is generated by the receptor cell itself (Bennett 1967). Knollenorgan responses to a fish's own EODs are blanked in the nucleus of the electrosensory lateral line lobe by an EOCD from the EOD command nucleus (Zipser and Bennett 1976a, 1976b; Russell and Bell 1978; Bell 1989; Bell et al. 1995). Because of this central-nervous gating mechanism and their low threshold, Knollenorgane appear to be specialized for the detection of exafferent EODs. The Knollenorgane also appear to be the relevant receptors for waveform analysis as studied in the present paper.

P. adspersus larvae possess a larval electrosensory system that is morphologically distinct from the adult system (Denizot et al. 1998). This system is "tuned" to the monopolar, larval EOD waveform of long duration, and possesses a *v*-shaped threshold/frequency curve of low sensitivity (Postner and Kramer 1995). In older larvae, threshold curves to exafferent EOD-like stimuli change to the adult form (broad-band, high-sensitivity characteristics up to 20 kHz) immediately before the advent of their bipolar, brief adult discharge. This corresponds well to the spectral amplitude maxima of *Pollimyrus*-EODs (8–25 kHz; Bratton and Kramer 1988).

Sensory mechanism of waveform analysis

Hypothetical sensory mechanisms in mormyrids that discriminate different EOD waveforms were discussed controversially (Hopkins and Bass 1981; Westby and Kirschbaum 1982; Crawford 1992) long before the phenomenon was established as a fact (Graff and Kramer 1992). Hopkins and Bass (1981) suggested a discrimination mechanism by detecting pulse-duration differences, whereas Westby and Kirschbaum (1982) favoured differences in spectral energy distributions. Crawford (1992) considered waveform discrimination by a temporal mechanism (like that of Hopkins and Bass 1981) unlikely in *P. adspersus* because of an unsuitable EOD waveform and too little variability in relevant parameters. Differences in temporal waveform parameters (such as the interval between P1-N and N-P2 peaks) would overlap among individuals and it would therefore not be possible to discriminate between them reliably.

The sensory mechanism suggested here for *P. adspersus* follows Hopkins and Bass (1981) whose hypothetical mechanism discriminates between short and long EOD pulses of almost monopolar, square waveform, as recorded from some members of the *Brienomyrus brachyistius* species complex. In *P. adspersus*, EODs are much shorter, the triphasic EOD waveform is more complex and bipolar, and inter-individual differences much smaller (a sexual dimorphism is lacking; there are no two alternative forms); all factors that make intraspecific EOD waveform discrimination more difficult. We suggest sensory discrimination in *P. adspersus* might work as follows: Knollenorgane respond to the positive-going slope of a stimulus pulse by an action potential of constant latency. The Knollenorgane of the right and left body side receive an electrical stimulus with reversed polarity (Fig. 7A). Therefore, at suprathreshold stimulation, the receptors of one body side will respond earlier (to the rising slope of the P1-phase) than the receptors of the other side (to the rising slope of the N-phase). The time difference between the action potentials of both sides would code for P1 duration of the stimulus.

Some fishes' EOD with an exceptionally weak P1-phase that is almost non-existent represent a problem for this mechanism. In these EODs, the Knollenorgane would be fired by the rising N-phase (early) and the declining N-phase (late) on opposite body sides, respectively (Fig. 7B). In this case, the N duration of the waveform is represented by the time difference between action potentials from right and left body sides.

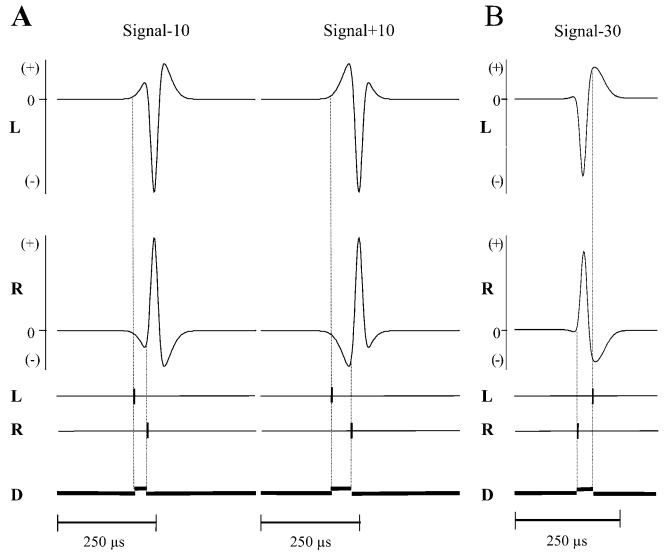

Fig. 7A, B Hypothetical sensory mechanism for **A** the discrimination between Signal-10 and Signal+10, and **B** for EOD-like stimulus pulses with very small P1-amplitudes (e.g. Signal-30). Because the Knollenorgane of the right and left body sides face in opposite directions, they receive the electrical signal with opposite polarities (*L*, *R*). Receptors respond only to transients from outside negative to positive by one action potential; therefore, there is a delay between the responses from receptors of both body sides (*D*). **A** A central nervous mechanism detects a perceived duration of the P1 phase of 30.6 μs for Signal-10 and 53.2 μs for that of Signal+10, under the arbitrary assumption that the Knollenorgane fire an action potential when the rate of voltage change is greater than or equal to +3 V/s. **B** The P1 phase would go undetected and the first response would be evoked by the rising N phase whereas receptors from the opposite body side would mark its decrease. The time interval between action potentials from both body sides (*L*, *R*) would be 32 μs in this example

To the best of our knowledge, this Knollenorgan mechanism is compatible with all observations, past and present. Our pair of least different stimulus waveforms that are still discriminated, Signal0 and Signal-2, differ by only 2.3 μs in P1 duration when applying our (arbitrary) criterion of minimum rate of voltage change of 3 V/s that is required to evoke an action potential. Sensitivity for temporal differences as small as these is known from binaural hearing in barn owls (Moiseff and Konishi 1981; Takahashi et al. 1984), and in the context of the jamming avoidance response in "wave" electric fishes, such as the gymnotiform *Eigenmannia* sp. (Rose and Heiligenberg 1985; Kaunzinger and Kramer 1995, 1996) and the mormyriform *Gymnarchus niloticus* (Kawasaki and Guo 1996).

Also, *Eigenmannia virescens*, an almost constant-frequency "wave" electric fish, discriminates the EOD waveform differences present in conspecifics, even when, in artificial stimuli, spectral amplitude cues are excluded (review, Kramer 1999). Both for the mechanism of waveform discrimination and the supporting Jamming Avoidance Response, a purely temporal sensory mechanism (that is presumably based on the T receptor system) has been demonstrated by behavioural studies (Kramer 1999). Among tuberous electroreceptors in wave gymnotiforms, T receptors best correspond to Knollenorgane in mormyrids: there is only one action potential per EOD, and timing is both precise (half a microsecond) and critical; sensory pathways use electrical synapses (Carr et al. 1986).

Individual recognition by waveform analysis

For individual recognition of EOD waveforms, the waveform must be stable over time. At a Q_{10} of only 1.5, temperature influences EOD pulse duration only little (determined in *Gnathonemus petersii*; Kramer and Westby 1985). However, a sudden, strong decrease in water conductivity strongly affects the EOD waveform in the short term (Bratton and Kramer 1988 in *P. adspersus* and *Petrocephalus bovei*; Kramer and Kuhn 1993 in *Campylomormyrus rhynchophorus* and *C. tamandua*) but waveform is restored within less than 2 days, even when the low conductivity is maintained (Kramer and Kuhn 1993). Long-term temporal constancy of EOD waveforms has been demonstrated over periods of hours or days, with very little variation even over weeks or months (Kramer and Westby 1985; Bratton and Kramer 1988; Crawford 1991). Also required for individual recognition is that intraspecific variability should exceed the fish's discrimination performance. Intraspecific waveform variability (see above, and Lücker and Kramer 1981; Bratton and Kramer 1988; Crawford 1992) is considerable in *Pollimyrus adspersus,* and fish are capable of discriminating even EODs that closely resemble each other (Graff and Kramer 1992). Our results presented here corroborate these findings and add discrimination limits for synthesized waveforms varying in N-phase delay. The amazingly long memory for waveforms we observed in nearly every *Pollimyrus adspersus* individual studied shows EOD waveform discrimination to be an important element in these fishes' behaviour.

In what ways could this advanced sensory capacity benefit *Pollimyrus adspersus*? A few other mormyrid species tend to school (chapter 11.4 in Moller 1995), e.g. *Marcusenius senegalensis* (Scheffel and Kramer 1997) or *Cyphomyrus discorhynchus* (Scheffel and Kramer 2000). In *Pollimyrus adspersus*, schooling or group formation has not yet been observed although it is suggested for the sister species *Pollimyrus isidori* on the basis of field studies (Moller et al. 1979). *Pollimyrus isidori* is believed to migrate to spawning grounds in flooded areas (Crawford et al. 1997). The males build a nest made of loose plant parts in a territory of 1–2 m^2 (Crawford et al. 1997). The behaviour of *Pollimyrus adspersus* has not yet been studied in the field but is assumed to be similar (Crawford et al. 1997). In captivity, males of *Pollimyrus adspersus* will spawn with any gravid female on successive nights, and are extremely territorial (e.g. Kirschbaum 1987). Individual recognition among established territory neighbours would be mutually beneficial because of a lower cost for defence. An individual-specific EOD-waveform

that is discriminated from other individuals' EODs would have a similar function as bird song (e.g. Krebs et al. 1978 in *Parus major*). Interestingly, untrained *Gymnotus carapo* (Gymnotiformes) discriminate between familiar and unfamiliar EODs when played back from adjoining territories, by the strength of their responses (McGregor and Westby 1992).

During nocturnal spawning, the female enters and leaves the male territory hundreds of times during one spawning night (Kirschbaum 1987; Bratton and Kramer 1989). Obviously, a breeding male that discriminates between its mate and other, potentially predatory females (which have been demonstrated in other freshwater fish with similar breeding system, resource defence polygyny), would have a significant adaptive advantage.

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