Species recognition by the sequence of discharge intervals in weakly electric fishes of the genus *Campylomormyrus* (Mormyridae, Teleostei)

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Abstract. In two *Campylomormyrus* species, *tamandua* and *rhynchophorus* from Central Africa, the electric organ discharge (EOD) activity was studied during the nocturnal activity phase in the laboratory. Both species have a pulse-type EOD of less than 200 μs duration and similar waveform; the sequence of inter-discharge intervals, however, differed characteristically: *C. tamandua* displayed a 'micro-pattern' encompassing nearly the whole range of intervals in a sequence of only three intervals (long–intermediate–short), while in *C. rhynchophorus* adjacent intervals tended to be more similar in duration. Four *C. rhynchophorus* and five *C. tamandua* were tested for their preference of conspecific pulse sequences rather than those of the other species, respectively, in playback experiments. These were performed in a T-maze paradigm such that two pulse patterns, one from each species, were simultaneously presented via two electric fish dipole models. Two pulse sequences recorded from different individuals were used to represent each species; the natural EOD waveform was replaced by a square-wave pulse of approximately natural duration. The pattern pairings and the sequence of stimulus patterns followed a randomized blocks design. Each of the four *C. rhynchophorus* had significantly higher preference scores for the conspecific pulse patterns than for those of *C. tamandua*, while in *C. tamandua* no such discrimination was observed. It is suggested that the juvenile *C. tamandua* used would probably have joined mixed-species schools as reported to exist in the wild, while this appears unlikely in the more mature *C. rhynchophorus*. One of the functions of the inter-discharge interval code of communication in mormyrids is species recognition although this may be seen only in sufficiently mature fish.

Mormyrid fish use their electric organ discharges (EODs) for active electrolocation (for a review see Bastian 1990) and communication (for reviews see Moller 1980; Hopkins 1986, 1988; Kramer 1990a, b, 1994). The electric organ discharge of a mormyrid is a brief pulse repeated at usually less than 10 per s (pulses/s or Hz) at rest during the day, and, depending on the species, even greater than 100 pulses/s during vigorous activities such as attack.

The sequence of discharge intervals, or interval patterns, accompanying resting, locomotion, agonistic behaviour and reproduction changes characteristically in several species; this has been found both descriptively and experimentally, using playback (for a review see Kramer 1990b). The occurrence of context- as well as species-specific discharge interval patterns accompanying overt activities has led to the hypothesis of an inter-discharge interval code of communication as a symplesiomorphic group character (i.e. one that is primitive and shared between taxa) in the Mormyridae (Kramer 1994).

Species recognition is one of the suggested functions of the inter-discharge interval code for which there is experimental support. Thus, members of a mixed-species group of mormyrids, tested during daylight, preferred caged conspecifics to mormyrids of other species (Moller & Serrier 1986); several sensory modalities, including the electrosensory, were probably involved (Moller et al. 1982; Teyssèdre & Moller 1982). An exclusively electrosensory preference for the sequence of discharge intervals recorded from conspecifics rather than those from *Pollimyrus isidori* or *Brienomyrus niger* was experimentally demonstrated in *Petrocephalus bovei* (Lücker 1982, 1983; Kramer & Lücker 1990). The EOD has been shown to be important for the cohesion of schooling mormyrids even when tested during the day (when many mormyrids hide) (Moller 1976); it is probably of still greater importance

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during the night when mormyrids migrate (Moller et al. 1979).

Species recognition among mormyrids has, up to now, been tested only using members of different genera where fairly large differences, including the inter-discharge interval code, may be assumed because of their phylogenetic distance. Here we report evidence for an exclusively electrosensory species recognition by the sequence of discharge intervals in members of the same genus, *Campylomormyrus tamandua* and *C. rhynchophorus*. Very little, if anything, is known about the behaviour and ecology of these fish (except a recent paper by Kramer & Kuhn 1993).

METHODS

Study Species

The genus *Campylomormyrus* Bleeker 1874 comprises 14 species (Gosse 1984) all of which possess trumpet-like snouts of sometimes spectacular dimensions; among all Mormyridae, these are the true 'elephantfishes'. Their forceps- or probe-like trumpets are regarded as adaptations to specialized feeding habits within the ecological type 'bottom-oriented micropredator' (Daget & Durand 1981). The genus is of Central African distribution with *C. tamandua* also widely occurring in West Africa (Lévêque & Paugy 1984).

Eight *C. tamandua* (Günther 1864) and four *C. rhynchophorus* (Boulenger 1898) were obtained from a tropical fish dealer near Frankfurt/Main (Germany) who had imported the fish direct from Kinshasa (Zaïre), specifying the location of origin as an 'affluent of the Stanley Pool, 150 km north of Kinshasa'. The fish are not endangered and are eaten in large numbers by the local population.

The species were determined using the keys by Poll et al. (1982), Lévêque & Paugy (1984) and Lévêque et al. (1990). Eleven morphological characters were analysed, among them the number of scales around the caudal peduncle, the number of rays of the dorsal and anal fins, the relationship between total length and snout length and the angle of inclination of the snout. Apart from the markedly different coloration, which is a chequered pattern of dark and light brown as described for juvenile *C. tamandua* (Lévêque et al. 1990), versus an almost uniform dark (almost black) in *C. rhynchophorus*, the most clear-cut
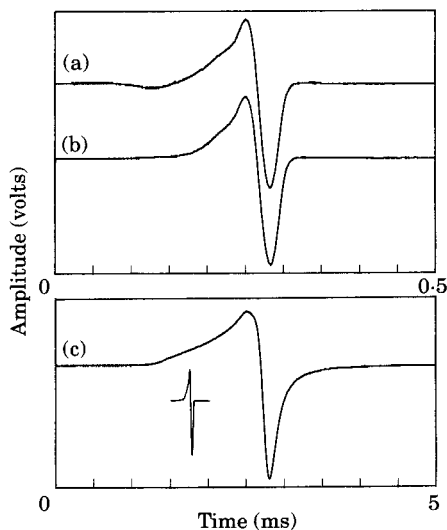

Figure 1. Waveforms of electric organ discharges, all of the pulse type, of (a) *C. tamandua*, (b) *C. rhynchophorus*, and (c) the exceptional *C. rhynchophorus* number 3 with the extremely long duration discharge. Each trace starts at zero volts; head-positive is up. For comparison, the inset of (c) shows the *C. rhynchophorus* discharge of (b) at the lower resolution time scale of (c).

morphological difference between the two species is the number of scales around the caudal peduncle: 16 in *C. rhynchophorus* and 12 in *C. tamandua* (confirmed in all our fish).

Our *C. rhynchophorus* were 8·9–10·0 cm long (standard length); the *C. tamandua* were of similar size (8·6–11·8 cm) except for one bigger fish of 14·0 cm. Thus the *C. rhynchophorus* were approaching half-maximum size (maximum total length, 22 cm; Gosse 1984) while most *C. tamandua* were closer to a quarter maximum size (maximum standard length, 43 cm; Gosse 1984).

All *C. tamandua* had similar waveforms of their EODs (Fig. 1a): two main phases, the head-positive P and the head-negative N phase, of a mean total duration of 133 ± 2 μs (SE; $N=6$ fish), were preceded by a weak pre-potential of widely varying duration (15–83 μs; at a water conductivity of 70 μS/cm as often encountered in tropical rivers). The discharges of all but one *C. rhynchophorus* closely resembled those of *C. tamandua* but for their lack of a pre-potential (Fig. 1b); total mean duration of the *C. rhynchophorus* EOD was 140 ± 4 μs (SE; $N=3$ fish; see Kramer & Kuhn 1993).

One *C. rhynchophorus* had a deviant discharge lasting 3·3 ms, about 20 times longer than that of its conspecifics (Fig. 1c). According to the key by Poll et al. (1982) this fish is clearly a *C. rhynchophorus*, in spite of a somewhat longer snout than the other three fish (22 mm versus 15–18 mm), a snout a little less inclined relative to the body long axis (40° versus 43°–49°), and a somewhat larger eye. All these measures were, however, within the variability described for the species *C. rhynchophorus* (Poll et al. 1982). A similar situation (totally different EODs in fish classified as members of the same species on morphological grounds) was observed in *Mormyrops curviceps* (Moller & Brown 1990).

The fish were kept in 360-litre communal aquaria at 27 ± 1°C with water conductivity 100 µS/cm and a 12:12 h light:dark cycle. The food was *Chironomus* larvae from a frozen supply.

Recording EOD Sequences

The fish were transferred from larger holding tanks to a recording aquarium (250 litre, $100 \times 50 \times 50$ cm) where they were kept isolated for at least 24 h before recording. The aquarium was bare except for a porous pot shelter in its centre. The walls of the aquarium were fitted with electrodes which were fine silver wires, arranged in a matrix of 20–28 per aquarium wall surface, making only point contact with the water. Via 47-kΩ resistors the silver wires were connected to a single lead which was the output of one electrode matrix (see Kramer 1974). A plastic mesh cage kept the fish 5 cm away from the electrodes.

Opposite electrodes (i.e. two horizontal pairs normal to each other, in X and Y orientation) were connected to separate, differential pre-amplifiers (up to $1000 \times$; 10 Hz–33 kHz); the output of each was full-way rectified, summed and fed into a Schmitt trigger which generated a $+5$ V, 0·75 ms square-wave pulse for each EOD. This pulse was recorded on magnetic tape (Uher 4400 Report Monitor).

The Schmitt trigger level was continuously monitored by an oscilloscope. Before recording on magnetic tape, we made several test recordings using a Nicolet digital analyser (model 1074) in 'Time Interval Trend' mode which stored up to 4096 inter-discharge intervals; interfering noise impulses were detected by the occurrence of intervals <9 ms in the Nicolet display. The Schmitt trigger level was adjusted as low as possible in order to detect all EODs (independent of the amplitude fluctuations associated with a fish's orientation relative to the electrodes), but sufficiently high in order to reject noise impulses.

A fish's discharge sequence was recorded in total darkness, that is, during its activity phase. To ensure that only EOD activity accompanying active swimming was recorded, the fish's behaviour was continuously monitored by video equipment (consisting of two infra-red light sources mounted overhead; an infra-red-sensitive video-camera, Grundig model FA 70H; and a remote video monitor). The camera was positioned such that the aquarium was seen from its side and glass bottom (through a mirror below the aquarium inclined by 45°).

The taped sequences of discharges were analysed by the Nicolet analyser (with model SH-71 Time Frequency Analyzer module) in 'Time Interval Trend' mode with a resolution of 0·1 ms, or in 'Time Interval Distribution' mode with a resolution of 1 ms. The memory contents stored in the Nicolet analyser were transferred to disc and plotted under computer control.

Spontaneous Choice Experiments

The experimental aquarium (250-litre; 90 ± 10 µS/cm; 26 ± 0.5°C) was bare except for a central porous pot which served as a fish's shelter, and two electric fish dipole models symmetrically placed at the far ends of the aquarium, in parallel to and 5 cm from the smaller sides of the aquarium (a T-maze paradigm). The dipoles were made from 0·5 cm carbon rods, vertically inserted in a horizontally oriented, water-tight Perspex tube which carried the leads (electrode separation, 2·1 cm; electrode length, 0·9 cm). The Perspex tubes were 5 cm above the aquarium bottom, and 38 cm from the porous pot shelter.

Stimulus intensity was adjusted to the EOD amplitude of a medium-sized fish hiding in its porous pot, measured with a pair of carbon rod electrodes separated by 49 cm, symmetrically placed behind the fish's tail and in front of its head. At 90 µS/cm and 26·5°C the EOD peak-to-peak amplitude thus measured was 40 mV. For the stimulus pulse, a monopolar square wave of 180 µs and 40 mV amplitude (from baseline to peak; i.e. peak amplitude as measured under identical conditions) was chosen; the amplitude

Table I. Discharge activity ($\bar{X} \pm$ SE) during nocturnal swimming in isolated fish

	Discharge rate (Hz)	Measure of skewness of histograms (ms, see text)
C. rhynchophorus	25·88 ± 1·16	14·53 ± 1·634
N=4	N=9	N=9
C. tamandua	22·13 ± 0·57	30·53 ± 1·24
N=8	N=23	N=23
P*	0·003	<0·0001

Each sample comprises between 18 070 and 43 951 discharges. *C. tamandua*, 26·5 ± 0·5°C; *C. rhynchophorus*, 26 ± 0·5°C.
*Unpaired *t*-test, two-tailed, *df*=30.

was adjusted after the fish was replaced by a dipole.

Each dipole was connected to its own custom-built, microprocessor-controlled stimulus generator with memory (described in Kramer & Weymann 1987). Before each trial, these devices received one of four inter-discharge interval lists (up to 2048 intervals) via a digital interface from a computer; the computer also started the stimulation on the operator's command and stopped it automatically after 7 min. Two of four interval lists (discharge sequences) were presented simultaneously: one *C. rhynchophorus* pattern was paired with one *C. tamandua* pattern. From both species the randomly selected discharge patterns from two individuals, recorded during their night-time swimming activity, were used in order not to depend so heavily on possible idiosyncrasies of an individual (Kroodsma 1989). There was only one individual of each 'stimulus' species in an earlier study and the EOD pulse sequences were stored on conventional magnetic tape instead of being encoded in digital form and stored on computer disc (earlier study, Kramer & Lücker 1990).

The sequence of trials followed a randomized blocks design (Cochran & Cox 1957); all possible pattern pairings were used except those opposing the two patterns from the same species; the sequence of the remaining four pattern combinations was randomized using Table 15.5 of random permutations of nine from Cochran & Cox (1957). Any possible side preferences of the fish were balanced by presenting all patterns equally often on the right and on the left dipole (on a random sequence).

There were up to 12 trials per day with a minimum of 15 min between trials. Half of all trials were performed during the dark phase. The operator started a trial only when the experimental fish was hiding in its porous pot shelter.

Using two stopwatches we measured a fish's preference for a stimulus pattern as the time it spent within 20 cm of a dipole. Fish were observed by an overhead mirror inclined by 45°; direct vision was obscured by isolation material covering all sides of the aquarium. Attack intention movements directed at the dipole were recorded by two mechanical counters; characteristic attack sequences were videotaped (Panasonic, model AG7330) for subsequent analysis.

On the completion of a set of four trials that represented a permutation of all four pattern pairings the computer calculated a mean value for each measure; these data represented a sample size of *N*=1. After *N* had sufficiently increased by repeating the experiments the data were analysed using Sachs (1984), Neave & Worthington (1988) and Siegel & Castellan (1988), as well as the statistical package 'InStat' (version 2·0, 1993).

RESULTS

Inter-discharge Interval Patterns

During their nocturnal swimming activity the mean discharge rates of both *Campylomormyrus* species were rather high compared with those of other mormyrid species: from 17·3 to 26·7 pulses/s (Hz) in *C. tamandua*, and from 20·3 to 31 pulses/s in *C. rhynchophorus* (for other species, see review in Kramer 1990b). The grand mean discharge rate of the *C. rhynchophorus*, 25·9 pulses/s, was significantly higher than that of the *C. tamandua*, 22·1 pulses/s (Table I).
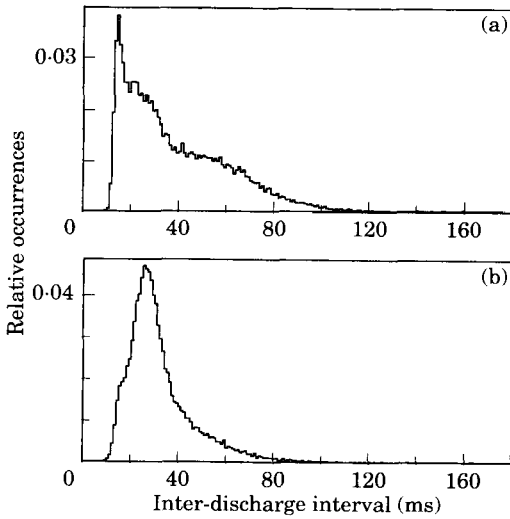
The two species displayed similar ranges of inter-discharge intervals, as best seen in statistical distributions or histograms, from 9 to 16 ms as the lower and from 80 to 140 ms as the upper boundary, not taking into account isolated 'stray' intervals on the right side of the histograms (for examples, see Fig. 2). The histograms of both species had only one clear, prominent peak (or mode, which is the interval of most frequent occurrence), but those of *C. tamandua* had their modes (15–16 ms) very close to the shortest interval of a distribution. Therefore, the *C. tamandua* histograms had a long tail of longer intervals and were heavily skewed to the right; quite often there were small secondary peaks or broad 'shoulder' regions. By contrast, the *C. rhynchophorus* histograms had their modes (26–28 ms) nearer to the centre of a histogram, although they never quite reached it. Therefore, they were more bell-shaped: both long and short intervals were rare.

The skewness of a histogram was characterized by the difference between the pulse interval of the mean discharge rate (for that specific histogram) and the mode (Fig. 3). The average
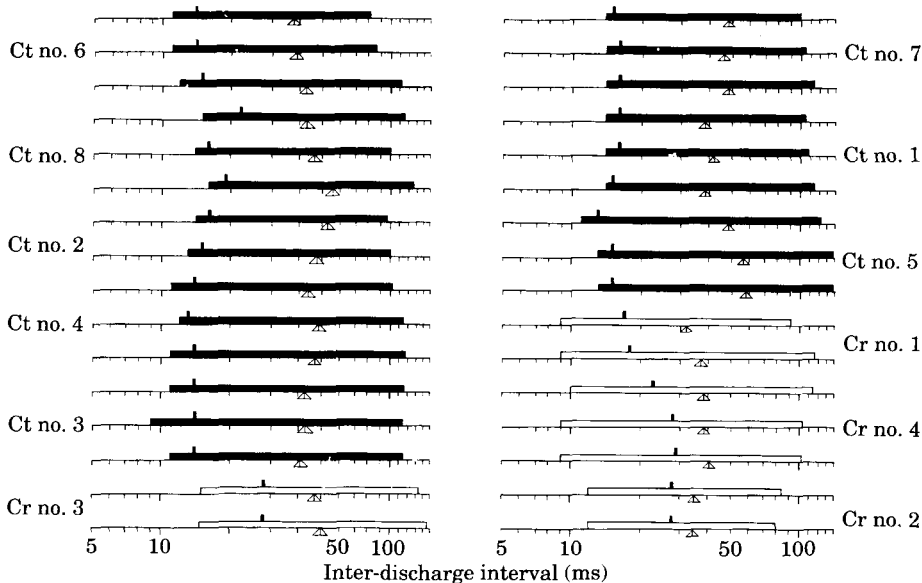
Figure 2. Histograms of inter-discharge interval distributions during nocturnal swimming in (a) *C. tamandua* number 1 and (b) *C. rhynchophorus* number 2. Number of EODs analysed: 29 413 in (a) and 27 276 in (b). The mean pulse rates were 25·6 and 28·8 pulses/s in (a) and (b), respectively.

Figure 3. Diagrammatic representations of inter-discharge interval histograms, as shown in Fig. 2, in *C. tamandua* (Ct, ■) and *C. rhynchophorus* (Cr, □). A horizontal bar shows the range of each histogram and its mode as a 'spike' on top of it (on a logarithmic scale in ms). Note difference between a histogram mode and the interval corresponding to the mean pulse rate (arrow-heads below abscissae). Two or three samples per fish as observed on different nights. The average number of inter-discharge intervals sampled per distribution was 28 463·5 ± SE 980·4 pulses ($N=32$).
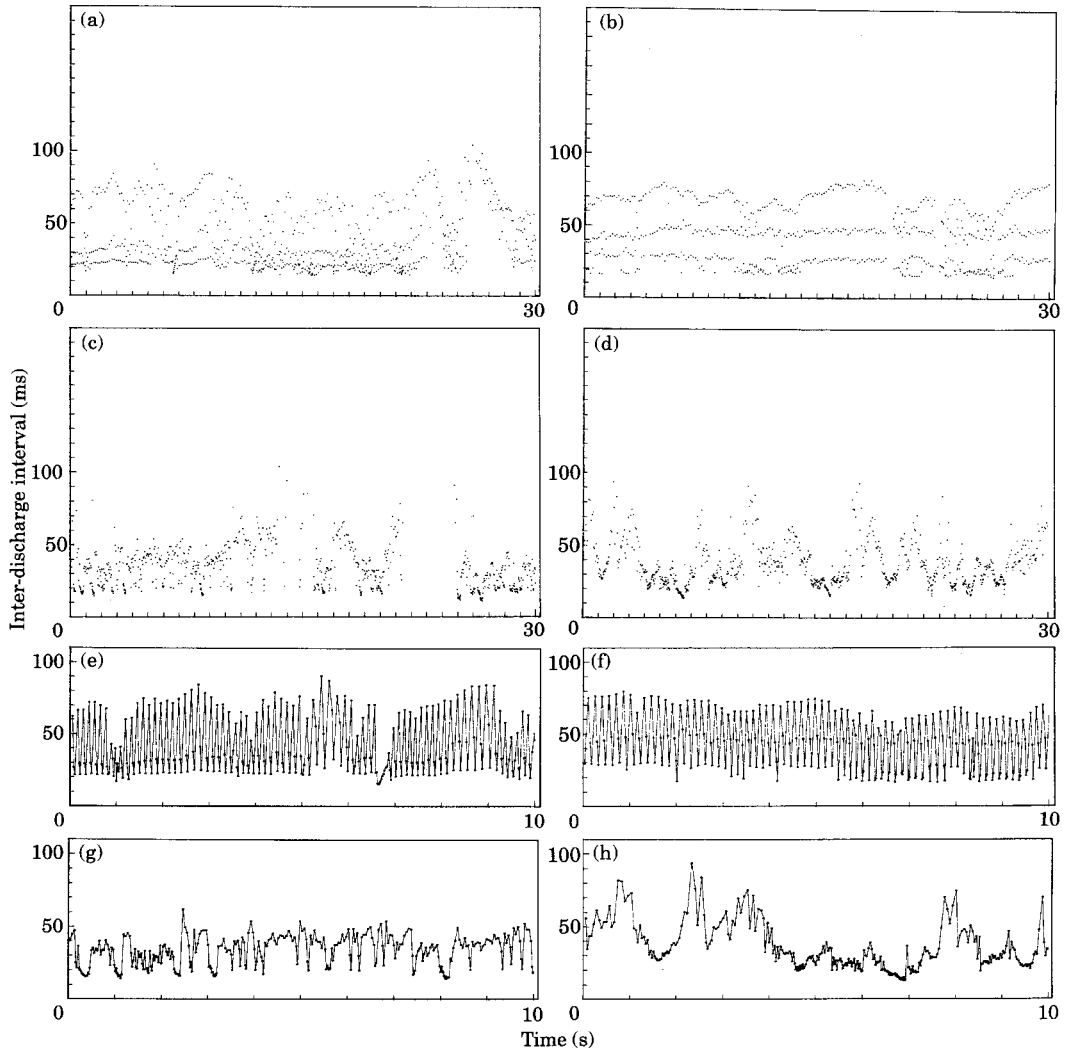
Figure 4. Sequences of inter-discharge intervals in (a) and (e) *C. tamandua* number 1, (b) and (f) *C. tamandua* number 8, (c) and (g) *C. rhynchophorus* number 1, and (d) and (h) *C. rhynchophorus* number 2, during their nocturnal activity phase. Each set of four plots shows sections of the four stimulus patterns used for playback in preference tests. Each point is one interval. (a–d) Note the broad range of intervals displayed at almost any time in the two *C. tamandua*, while the interval durations in the *C. rhynchophorus* records follow trends with a fairly strong tendency for bursts. (e–h) Finer time resolution plots to show sequences of adjacent intervals which are connected by lines; otherwise like (a–d).

difference was significantly greater (by a factor of 2) in *C. tamandua* than in *C. rhynchophorus* histograms: 30·5 versus 14·5 ms, respectively (Table I).

The sequences of inter-discharge intervals, although quite variable, differed in a characteristic way between the two species (Fig. 4). In all

C. tamandua there was a strong tendency to step through a sequence of three intervals of strongly contrasting durations: a long interval of 60–80 ms was followed by an intermediate one (40–50 ms) which was followed by a short one (15–30 ms); this three-interval sequence was sometimes repeated for many seconds without

Table II. Individual preference scores ($\bar{X} \pm$ SE; time, in s, spent within 20 cm of the dipole) for four *C. rhynchophorus* as experimental subjects, simultaneously stimulated with two pulse interval patterns, one conspecific ($N=2$), the other from *C. tamandua* ($N=2$)

Experimental subject: C. rhynchophorus	C. tamandua	C. rhynchophorus	P*	No. of replications
No. 1	8·315 ± 2·210	18·728 ± 4·230	0·0012 df=22	23
No. 2	27·568 ± 7·204	45·182 ± 10·100	0·0022 df=21	22
No. 3	47·861 ± 12·778	62·500 ± 11·378	0·0030 df=8	9
No. 4	83·273 ± 4·597	95·727 ± 4·480	0·0329 df=10	11

*One-tailed paired *t*-test.

interruption. As can be seen from Fig. 4, in different fish the intermediate interval may also be closer to the short interval than given in the above example.

The discharge interval sequences of *C. rhynchophorus* are more difficult to describe. Sometimes there was also a tendency for interval duration to alternate, but this concerned long or intermediate intervals rather than short ones, while the magnitude of the steps was also smaller. In general, the discharge intervals followed a trend of either increasing or decreasing duration for several seconds, rather often interrupted by brief bursts.

The reason for the skewed histograms in *C. tamandua* was the strong tendency for interval duration to alternate: the shortest category of intervals clearly occurred most often. The absence of a clear second mode in the interval histogram of *C. tamandua* was due to the 'smear' of the long intervals in an alternating sequence: their variation was enormous (unlike that observed in *Gnathonemus petersii* during agonistic behaviour where two peaks do occur in the interval histogram; Kramer & Bauer 1976). In contrast to *C. tamandua*, the shortest category of intervals was much rarer in *C. rhynchophorus*, intermediate intervals occurring most frequently, resulting in almost symmetrical histograms.

Playback Experiments

Campylomormyrus rhynchophorus

On the onset of the simultaneous playback of two pulse interval patterns presented via two dipoles, one pattern previously recorded from a conspecific *C. rhynchophorus* and the other from a *C. tamandua*, fish often hesitated to leave their central porous pot for a considerable time during a trial. In most cases the fish finally swam to one of the two dipoles positioned at opposite ends of the experimental aquarium, and occasionally changed sides. They either kept in close contact with the dipole, attacked it with their mouths, or gave the dipole strong, lateral tail beats.

The times fish stayed in the vicinity (20 cm) of a dipole differed between the playback patterns: as expected, the attraction from conspecific playback patterns was significantly greater than that of *C. tamandua* patterns in all fish (Table II). Even fish number 3 with the extremely long EOD made no exception; this is additional support for its classification as a *C. rhynchophorus* on anatomical grounds (see Methods).

Campylomormyrus tamandua

The behaviour of the *C. tamandua* was very similar to that of the *C. rhynchophorus* except for three specimens which did not leave their central shelters and thus were excluded from the study. However, the expectation that the remaining five *C. tamandua* might prefer conspecific playback patterns rather than heterospecific ones, similar to the behaviour observed in *C. rhynchophorus*, was clearly not borne out by the results; therefore, one-tailed significance tests were inappropriate (and two-tailed tests used instead). The results were inconclusive in four out of the five *C. tamandua* (Table III); fish number 2 even appeared to discriminate against its own species'

Table III. Individual preference scores ($\bar{X} \pm$ SE; time, in s, spent within 20 cm of the dipole) for five *C. tamandua* as experimental subjects, simultaneously stimulated with two pulse interval patterns, one conspecific ($N=2$), the other from *C. rhynchophorus* ($N=2$)

Experimental subject: *C. tamandua*	*C. rhynchophorus*	*C. tamandua*	P^*	No. of replications
No. 1	77·989 ± 4·611	78·065 ± 8·790	0·9926 *df*=22	23
No. 2	101·83 ± 11·791	80·567 ± 6·116	0·0213 *df*=14	15
No. 3	87·583 ± 7·244	95·389 ± 7·545	0·4105 *df*=17	18
No. 4	117·161 ± 18·860	112·857 ± 12·480	0·8795 *df*=13	14
No. 5	117·08 ± 21·039	123·44 ± 15·402	0·8222 *df*=12	13

*Two-tailed paired *t*-test.

playback patterns because the preference score for the *C. rhynchophorus* patterns was significantly higher ($P<0·05$).

This paradoxical result might, however, be due to the very weak response (perhaps a kind of 'dislike'?) of this fish regarding one conspecific playback pattern; there was very little difference between the scores for the alternative pattern and the *C. rhynchophorus* patterns. Therefore, fish number 2 appeared to discriminate between conspecific patterns rather than between the playback patterns from its own species and those from *C. rhynchophorus*. Neither conspecific pattern had been recorded from fish number 2.

DISCUSSION

The waveform of an EOD is species-characteristic (Lissmann 1958; Hopkins 1981) and individually variable (for reviews see Hopkins 1986; Kramer 1990b, 1994). Some authors consider sexually dimorphic differences in a species' EOD waveform rather than in its sequence of pulse intervals as the basis for mate recognition (Hopkins & Bass 1981); others consider the sequence of pulse intervals to be of prime importance in mormyrid communication, and regard the EOD waveform variability as the sensory basis for individual rather than mate recognition (Graff & Kramer 1989, 1992). Some of these discrepancies may be due to species differences within the large family of Mormyridae (almost 200 species).

In the species studied best in this regard, *Pollimyrus isidori*, initial mate recognition occurs via the male's sound production (Crawford et al. 1986; Bratton & Kramer 1989), while the sequence of pulse intervals is important during subsequent courtship and spawning (Bratton & Kramer 1989; Crawford 1991). The two latter studies also showed that the EOD waveform was not a factor in mate recognition and pair formation.

On different nights certain individuals differed in their mean discharge rates by up to 5 pulses/s. This is because we rarely observed uniform, moderate swimming in our fish; sequences of slow or more rapid swimming, sudden accelerations and stops, probing, hovering, etc. were usual. In *Pollimyrus isidori* these different types of swimming behaviour were also accompanied by markedly different discharge patterns (Bratton & Kramer 1989). Because of the rather great variability of discharge activity (even in the same fish), the discharge sequences from two individuals of each species were randomly chosen for the stimulation experiments.

To study the significance of pulse interval sequences for species recognition, the natural EOD waveform was replaced by a square-wave pulse in the present experiments. The sequences of discharge intervals accompanying nocturnal locomotory activity were clearly different for the two *Campylomormyrus* species: *C. tamandua* displayed long sequences of a rhythmic three-interval pattern marked by strong contrasts in interval duration, while in *C. rhynchophorus* there were

trends comprising longer sequences of intervals more similar in duration, often interrupted by brief bursts. There were also statistically significant differences in mean discharge rate and in the skewness of interval histograms. The *C. tamandua* discharge activity showed clear 'micro-patterns' as suggested by Kramer & Lücker (1990): interval sequences that were both short and characteristic. *Pollimyrus isidori* which discriminates a pulse rate change as small as 2% is the only species tested for its time interval resolution (Kramer & Heinrich 1990).

It is tempting to speculate that during sympatric evolution character displacement has acted on the two species' discharge interval patterns which are so markedly different, while their EOD waveforms are so surprisingly similar (except the EOD of *C. rhynchophorus* number 3 which was exceedingly long). Whether the two discharge durations in *C. rhynchophorus* represent a sexual dimorphism or a polymorphism (Moller & Brown 1990) is impossible to ascertain at present.

In the playback experiments the four *C. rhynchophorus* showed a significant preference for their conspecific patterns while this could not be demonstrated in the *C. tamandua* (Tables II and III). The behaviour of the *C. rhynchophorus* corresponded well to that shown by *Petrocephalus bovei* in similar preference experiments involving a choice between two pulse patterns, recorded from members of their own species and from those of other mormyrid genera (Lücker 1983; Kramer & Lücker 1990). Even though totally unnatural pulse waveforms were used for playback in both studies, conspecific pulse interval patterns were discriminated from other species' patterns. These patterns evoked association behaviour and also various forms of agonistic behaviour in the present study. It is possible that in our experiments the differences would have been still more pronounced had the natural EOD waveforms been used instead of a square-wave pulse. Mutual discrimination of the two species' EOD waveforms may be assumed because of *P. isidori*'s exceedingly high sensitivity to small differences in conspecific EOD waveforms (Graff & Kramer 1992).

The non-discriminating behaviour of the *C. tamandua* is difficult to explain given the pronounced differences in interval patterns which the *C. rhynchophorus* clearly noticed. Rather than being unable to detect the difference we believe the *C. tamandua* might not have shown discriminating

behaviour because of a propensity to join mixed-species groups. Such groups have been reported several times from the field (for reviews see Hopkins 1986; Kramer 1990b), and are especially likely in juveniles. Although our *C. tamandua* and *C. rhynchophorus* were of similar size, the *C. tamandua* were clearly juveniles while the *C. rhynchophorus* were not (see Methods). The maximum size of *C. tamandua* is more than twice that reported for *C. rhynchophorus*; in addition, even our biggest specimen of *C. tamandua* still had the characteristic juvenile coloration. In contrast to the *C. tamandua*, our *C. rhynchophorus* of about half maximal size were probably sexually mature or close to sexual maturity. This is suggested by a study on *Hippopotamyrus pictus* which were sexually mature at somewhat less than half maximum size (12 cm length versus 26 cm; Blake 1977).

Sexually mature fish are much more likely to discriminate against members of other species than are immatures. Therefore, we believe the present study supports the notion that one of the functions of the inter-discharge interval code of communication in mormyrids is species recognition, although fish may not show their sensory capabilities during all stages of their lives (especially when immature). The relatively more mature *C. rhynchophorus* were discriminating pulse interval patterns recorded during the fish's nocturnal active phase when species recognition is especially important for group cohesion or finding a mate.

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