J. comp. Physiol. 93, 203—235 (1974)

Electric Organ Discharge Interaction during Interspecific Agonistic Behaviour in Freely Swimming Mormyrid Fish

A Method to Evaluate Two (or More) Simultaneous Time Series of Events with a Digital Analyser

B. Kramer

Laboratoire de Physiologie Nerveuse,
Département de Neurophysiologie Sensorielle,
C. N. R. S. Gif-sur-Yvette, France

Received March 19, 1974

Summary. A data acquisition technique is described, which uses a digital analyser to measure off-line the lengths of intervals between events on two (or more) lines. The method compensates for cumulative flutter of tape recorders; thus the temporal relationships between series of events on different lines are maintained.

On the introduction of a *Mormyrus rume* into the tank of a resident *Gnathonemus petersii,* both fishes increase their mean electric organ discharge (EOD) frequencies. Range and relative proportion of interpulse intervals (Fig. 1) as well as the discharge rhythms (Fig. 3a, b) are different from that observed in isolated animals, at rest or while swimming (Figs. 4, 3c—f). During agonistic behaviour, the discharge rhythm of *G. petersii* exhibits a high degree of variation, whereas for *M. rume* the inverse is true. At rest and during swimming, however, an isolated *G. petersii* displays a marked tendency of at least eleven consecutive intervals to stay all above or below the mean value; at rest, there is a tendency for a long interval to be followed by a shorter one, the next two intervals being again long (or vice versa). With minimal delay, *G. petersii* tends to regulate the lengths of its discharge intervals inversely in response to concurrent *M. rume* intervals (Fig. 5). There is no regulation of *M. rume* intervals in response to *G. petersii* pulses. Furthermore, *G. petersii* (♂ ♂ and a ♀) tends to discharge with a latency of approx. 12 ms to the preceding *M. rume* pulse (Fig. 7). This effect is shown neither to be the result of a particular phase relationship (Fig. 6), nor to be due to the activity of the *M. rume* (Figs. 8, 9). In five out of six *G. petersii,* the observed latency distribution differs significantly from what would be expected if the two discharge trains were independent. *G. petersii* tends to produce "preferred" latencies in runs of up to twenty-one (Fig. 10). Animals which are less aggressive, display a greater number of preferred latencies (Fig. 11) and longer runs (Fig. 10). Runs of two or more preferred latencies never occur during attack associated burst activity. It is only during these bursts that EOD coincidence was observed. The significance of the preferred latency response is thought firstly to be avoidance of discharge coincidence in intraspecific social behaviour. Secondly, evidence is discussed which seems to indicate that it is a "hiding" behaviour.

Introduction

Ever since the first suggestion by Möhres (1957) that frequency variations of the electric organ discharge (EOD) are involved in social interaction, especially agonistic behaviour in the Mormyridae, it has been presumed that individuals "communicate" with each other by means of their EOD. Since the waveform of the EOD (i.e. pulse amplitude and duration) is nearly invariable in mormyrids and gymnotids, electric signalling may be accomplished by variations of the discharge rate solely.

Further preliminary evidence, supporting the hypothesis of the involvement of the EOD in electric signalling, has been given by Lissmann (1958) and Szabo (cited by Lissmann, 1961). Substantial support was furnished by Moller (1969, 1970), Bauer (1972), Moller and Bauer (1973), and Bauer and Kramer (1973) in mormyrids, and Black-Cleworth (1970), Box and Westby (1970), Westby and Box (1970), Valone (1970), Hopkins (1972) and Westby (1972) in gymnotids.

In this investigation, it is not the electric signalling of an individual in a certain behavioural situation, but interaction (action and reaction by means of the EOD) between two individuals, which is under study. Interaction thus is understood as the emission of a signal by one individual, its perception by another animal, which may utilise this information for its own signalling. This information in turn is received by the first individual and influences its further behaviour, and so on.

For this reason, findings, which consider the relationships between the pulse trains of two interacting fish, are of special interest in the context of this work. Valone (1970) notes that "fish (*Gymnotus*) interacting with one another appear to lock into a common frequency more often than fish that are not in physical contact with one another". Westby (1972) observed "EOD synchrony" during "orientating behaviour" in *Hypopomus* and, more rarely, in *Gymnotus*. Both observations refer to a regular alternation of the two fishes' pulses. Due to the technical difficulty of discriminating the EOD of two fish, there is no further information available about the relationships between the two trains of discharges.

In this study, two different species of mormyrids, *Gnathonemus petersii* and *Mormyrus rume*, were used. *G. petersii* is found in a large equatorial area of Central Africa, whereas *M. rume* lives in the tropical region of West Africa and also in the lower Congo (Poll, 1959; Gosse, 1963; Blache, 1964). The two species live sympatrically in the upper Tchad (Blache, 1964) and lower Niger basins (Belbenoit, personal communication), as well as the lower Congo river (Poll, 1959).

These two fishes were chosen, because the durations of their EODs are different. Electronic separation was therefore possible by means of a "window" circuit. The two discharge trains were analysed firstly for interdependence of interval lengths, and secondly for phase and latency relationships.

The existence of a latency relationship of the EODs of a resident *G. petersii* to the pulses of an intruder (*M. rume*) during agonistic behaviour has been reported in a short communication (Bauer and Kramer, 1974).

A latency relationship is also described in two short abstracts by Russell and Bell (1972, 1973), who performed stimulation experiments and observed intraspecific behaviour.

Methods

I. General Features

Six *Gnathonemus petersii* (15.5—20.5 cm) and two *Mormyrus rume* (15 and 20.5 cm) were used in this study. The fishes had been imported by tropical fish dealers from unknown locations in Central Africa. They were kept in the laboratory for long periods. Unfortunately, no other specimens of *M. rume* could be obtained. Normally, they were maintained in individual compartments of approx. 70 *l*, formed by dividing a large aquarium with plastic partitions. Water temperature of the experimental and the home tanks was maintained between 26 and 27° C, electrical resistivity ranged from 920 to 740 Ohm · cm. Both species were fed on live *Chironomus* larvae. A 12 h/12 h light-dark cycle was used both for the experimental and the home tanks. An air bubbler was provided per fish, and the water was filtered by activated carbon and glass-wool or synthetic fibre. Head to tail peak to peak EOD voltages, measured in water, ranged from 2.7 to 3.9 V in *G. petersii* (water conditions: 26.5° C, 840 Ohm · cm). The voltages measured in the same manner in *M. rume* were 6.0 V in the large specimen, 4.1 V in the smaller one.

The experimental tank measured 1.0 × 0.4 × 0.5 m (200 *l*). 120 fine silver wires, insulated except at the tips, were fixed on the walls, the bottom and onto a floating plastic cover, forming a regular array on each of the six surfaces. Each silver wire was connected, through a 47 kOhm resistor, to the other wires mounted on the same surface of the tank, which was then referred to as an electrode. A cage of coarse plastic mesh restricted the animals to more than 5 cm from the electrodes. The three pairs of opposite electrodes, orientated orthogonally, were connected to three differential amplifiers. The amplified potentials were rectified, summed, and displayed on an oscilloscope. An electronic window circuit separated the pulses of the two fishes; the discrimination criterion was the discharge duration (*G. petersii*: approx. 300 μs, *M. rume*: approx. 600 μs). Only the discharges of the bigger *M. rume* could be separated reliably from the concurrent *G. petersii* discharges by the circuit, because the pulse amplitude of the smaller *M. rume* was lower and hence the length of pulses shorter at the triggering level. An 800 address digital analyser (Didac, Intertechnique) was used to measure the length of intervals and to compute histograms. A peripheral teletype punched BCD paper tapes of 800 fish pulse intervals. The paper tapes were read and the data transferred to magnetic tape files in the Centre Inter-Régional de Calcul Electronique (C. N. R. S., 91 Orsay). From the magnetic tape, the sequence of times of occurrence of EODs was punched on IBM cards. These cards were used as the input to a programme written in FORTRAN IV for an IBM 370/168 computer. Interval vs. time of occurrence plots

(Figs. 2a and b, lower parts) were made by a plotter (Benson, France), connected to the 370/168 computer.

II. Experimental Procedure

Successive five days' series of one experiment per day were performed with six *G. petersii*, each of which had been habituated to the experimental tank prior to the first experiment for at least three days. An experiment consisted of three periods: a) the discharges of a *G. petersii* in the experimental tank, and of a *M. rume* in its home tank were amplified and recorded on magnetic tape (Uher Royal) on separate tracks for 3 min. b) Then the *M. rume* was carefully introduced into the experimental tank for 3 min, and the simultaneous activity of the two fishes was recorded. c) The *M. rume* was transferred back into its home tank, and another record of 3 min of the two fishes' discharges, on separate tracks, concluded the experiment.

III. A Method to Evaluate Two (or More) Simultaneous Time Series of Events with a Digital Analyser

In order to analyse the relationships between two trains of pulses, a complete list of the intervals of each series of events is necessary. A digital analyser (e.g. Didac), which measures the length of successive intervals, accepts only one series of pulses at a time. For this reason, the two pulse sequences must be registered on magnetic tape and processed off-line one after the other. The measured interval lengths, as determined by the number of computer clock pulses between two events, depend on the speed of the tape transport. When a pulse series is processed on-line, and then off-line from a record on magnetic tape, slight differences in the measured interval lengths in the order of one to several in 1000 will be noticed, depending on the tape speed used and the quality of the tape recorder. There is a systematic, long-term trend of most of the intervals of the sample (in this study: 800) to be more or less longer than the corresponding on-line analysed ones ("cumulative flutter"). This is true for the Uher Royal tape recorders (tape speed: 7.5 cm/s), and—although less pronounced—for the Ampex PR 500 machine used in this study. In the Ampex recorder tape speed (9.52 cm/s) is maintained much more constant by a servo system.

When the mean speed of a tape, on which 800 pulses, separated by intervals of 50.0 ms, are recorded, is smaller during play-back by three in 1000, the total length of the series is 40.1200 s instead of 40.0000 s. When interpulse interval histograms are computed from the data, these differences are normally negligible, since the appropriate class width usually is much greater. Care has to be taken, however, when an analysis of the temporal relationship between two series of pulses is desired. When two trains of pulses are analysed successively, the relationships between them are slightly at first, then more and more grossly distorted even by a very small difference in mean tape speed. When the tape speed variation is three in 1000, the two series are out of phase by 0.3 of a period after 100 cycles; after 800 cycles, one of the trains is lagging by 2.4 periods. Obviously, an analysis of the temporal relationship between the two pulse trains is not possible.

A solution to this problem was found as follows. The original records of the pulse trains of the two fishes (experimental period b), being separated by the window circuit, were simultaneously transferred to different tracks of a 1.27 cm Ampex tape. During this process, small speed variations of the tapes, being exactly the same for both of the two time series of pulses, do not break the temporal relationships between them. Then, on a third track of the Ampex tape, a series of equally spaced, quartz clock (Didac) generated timing pulses of a frequency of 10 kHz were recorded (direct recording for better frequency response). An interval between events of one of the experiment generated pulse trains is evaluated during playback by counting the recorded clock pulses (and not, as usually, the pulses of the free running clock) in the computer's accumulator. At the next event, the content of the accumulator is transferred to the computer's memory, the accumulator is cleared, and the process is repeated. In this manner, a complete list of all the intervals of each pulse train, analysed successively, is obtained.

The advantage of this method is that the maximum error in each interval evaluated is equal to the interval between one clock pulse pair ($= 100\,\mu s$ in the present study); the worst possible ratio is 1:60. Of special importance is the fact that these errors do not represent a trend. Thus the maximum error of an estimation of the length of a whole pulse series (regardless of the number of intervals it consists of) is the same as for one interval: the interval between one clock pulse pair.

Owing to the relatively high frequency of the clock generated timing pulses, the shape of these, when reproduced from magnetic tape, is distorted, and a pulse shape restoration circuit was required. It consisted of a gated type 162 Tektronix waveform generator triggering a type 161 Tektronix pulse generator. These could be regulated to reproduce exactly the fast edged pulses of the computer's clock.

Results

Reactions of one fish to the pulse train emitted by another may be observable firstly in terms of mean discharge frequency, range and relative proportion of intervals, discharge rhythm, and interdependence of the lengths of concurrent intervals. Secondly, a preference for certain phase or latency relationships may exist. Following this classification, these problems will be dealt with in the following two sections.

I. Frequency Analyses

Fig. 1 gives two examples of the concurrent discharge activities of a *M. rume* and a resident *G. petersii*. *G. petersii* H did not butt the *M. rume* during the whole experimental period of 3 min, only seven head butt intentions were observed. A histogram representing the discharge activity of *G. petersii* H is shown in Fig. 1a—2, the concurrent EOD activity of the *M. rume* in Fig. 1a—1. The histograms of the two animals both exhibit a single mode. These modes are nearly identical. This suggests that there might exist periods when the two fishes lock into a common discharge frequency. However, the mean discharge frequency of the *G. petersii* (15 Hz) is considerably lower than the one displayed by the *M. rume* (22.5 Hz).

Fig. 1b—2 shows the electrical activity of the highly agressive *G. petersii* Q (fourty-four head butts and twenty-three head butt intentions in 3 min). There are two distinct modes of 7.5 and 15.5 ms. Variation of interval length is still large but less than in the animal H (Fig. 1a—2). Neither of the two modes in Fig. 1b—2 coincides with the mode displayed concurrently by the *M. rume* (32.5 ms, Fig. 1b—1); in this case,

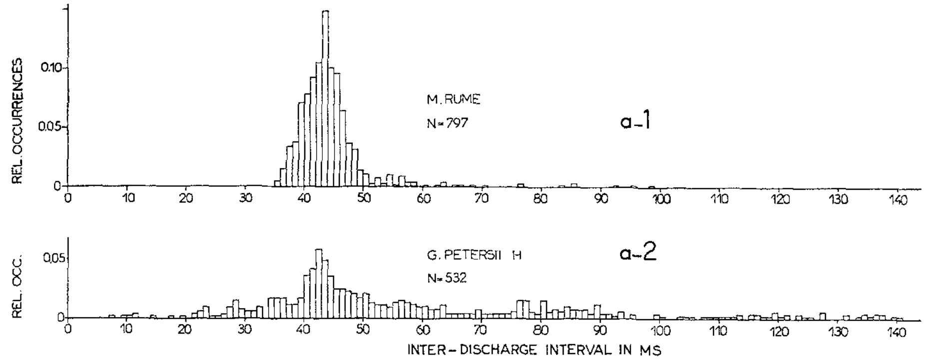


Fig. 1a

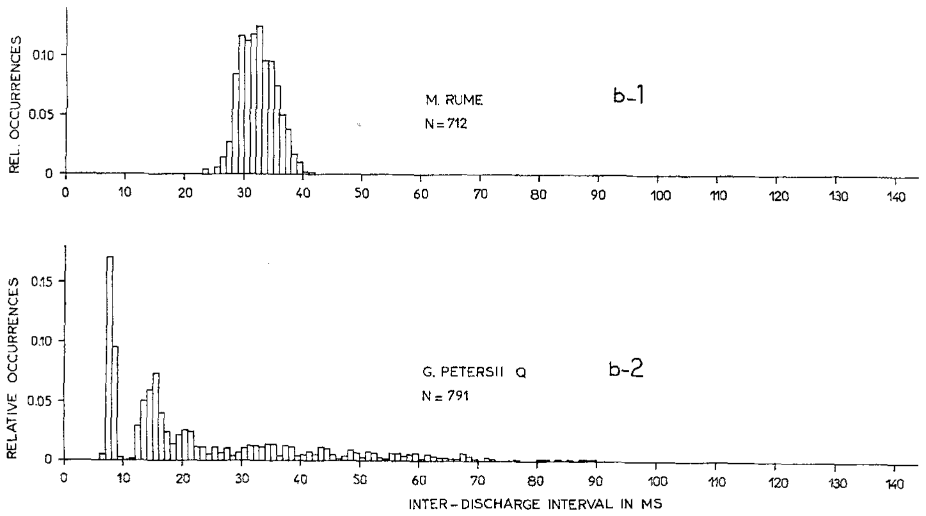


Fig. 1 a and b. Interpulse interval histograms of the concurrent discharge activities of a resident *Gnathonemus petersii* and an intruding *Mormyrus rume*. a *M. rume* in the tank of the non-attacking *G. petersii* H (total length of records: 35.38 s). b *M. rume* in the tank of the very aggressive *G. petersii* Q (total length of records: 23.23 s). Note higher discharge frequency for both fishes in Fig. 1b. *N* total number of intervals analysed

each fish seems to regulate its discharge frequency independently of the other. The mean discharge frequencies, however, are only slightly different: 34 Hz in *G. petersii*, and 31 Hz in *M. rume*. In general, the modes of the *M. rume* histograms, which are in the range of 62 to 32 ms in these experiments, tend to be smaller the higher the mean discharge rate of the *G. petersii* is.

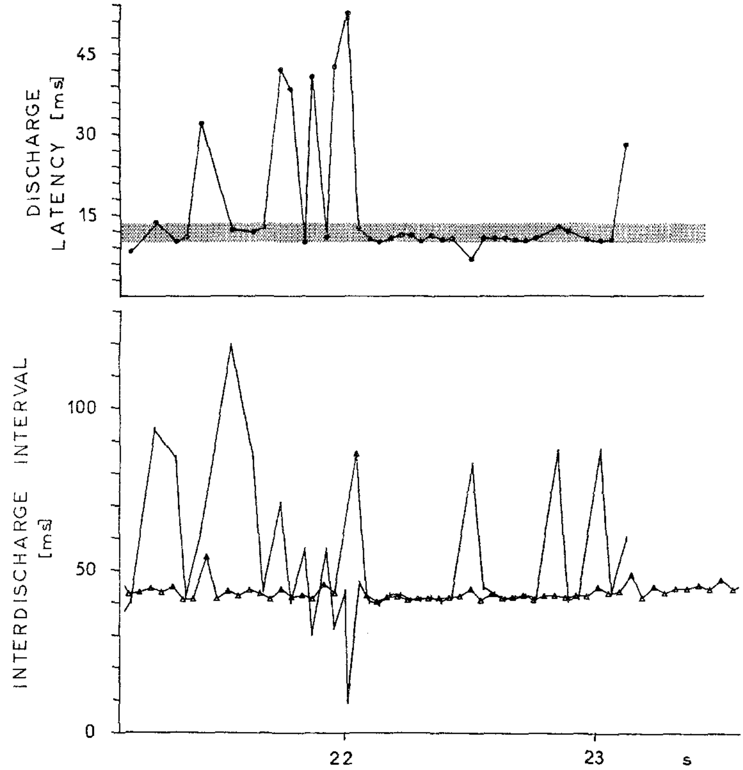


Fig. 2a and b. Sequential representation of the concurrent discharge activities of a *G. petersii* and a *M. rume* during agonistic behaviour. Below: Interdischarge interval vs. time of occurrence for *M. rume* (triangles) and *G. petersii* (small vertical bars). The abscissa of each point is the time of occurrence (in s) of each discharge, and the ordinate is the interval (in ms) from the previous discharge. Above: The latency of each *G. petersii* pulse to the preceding *M. rume* pulse vs. the time of occurrence of the *G. petersii* pulse. The abscissa of each point is the time of occurrence (in s) of each *G. petersii* discharge, and the ordinate is the latency (in ms) from the preceding *M. rume* pulse. Hatched zone (10.0 to 13.5 ms): approximate range of the "preferred" latency (cf. text). In a, *M. rume* is together with the non-aggressive *G. petersii* H; b (see p. 210) shows the same, but for the very aggressive *G. petersii* Q. Note instances of close frequency following and long runs of preferred latencies in (a) as compared with (b). Horizontal bars under lower abscissa: periods of attack associated frequency acceleration and subsequent high frequency bursts emitted by *G. petersii*

In order to show the sequence of intervals emitted concurrently by each fish, small sections of the two fishes' discharge trains are presented by an interpulse interval vs. time of occurrence plot in the lower halves of Figs. 2a and b. In both records, *M. rume* (triangles) displays a rather

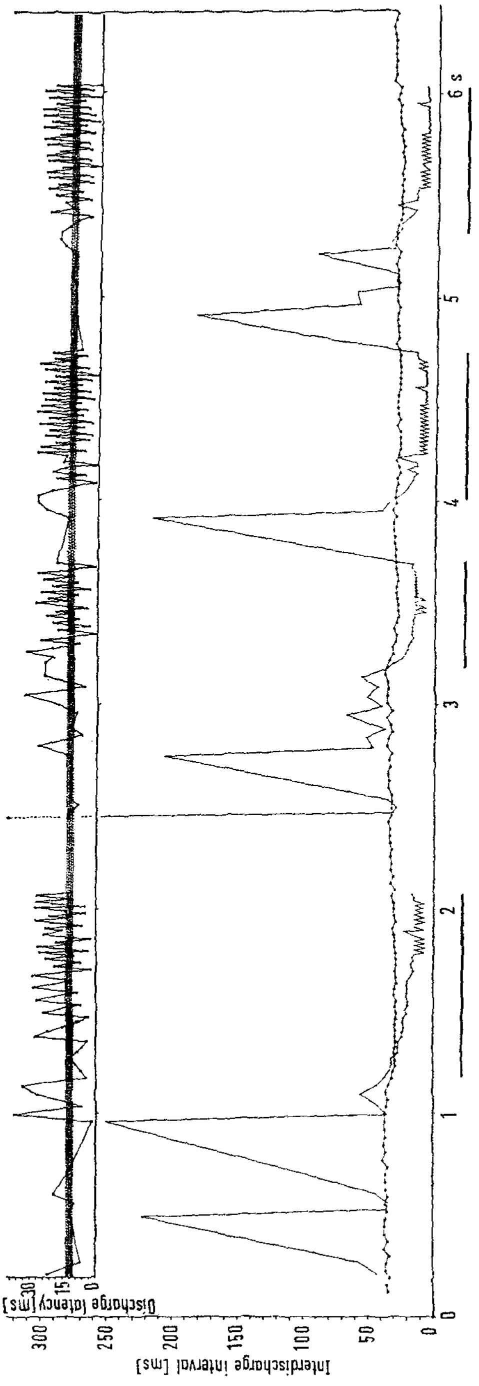

Interdischarge interval [ms]
0
50
100
150
200
250
300
Discharge latency [ms]
0
15
30
0
1
2
3
4
5
6 s

Fig. 2b

steady discharge rate, i.e. there seems to be a tendency of adjacent intervals to be similar in length. In contrast, in *G. petersii* Q (Fig. 2b) adjacent intervals may differ in length by a factor of 46, and also in *G. petersii* H (Fig. 2a) the variation is considerable. During high frequency bursts of an aggressive *G. petersii* (Bauer, 1972), shown in Fig. 2b (horizontal bars), a regular alternation of very short and somewhat longer intervals and/or a series of equally spaced, short intervals can be observed. These bursts are associated with lateral display, immediately following a head butt, which occurs during a regular frequency acceleration (Bauer and Kramer, 1973). These bursts are elicited by an intruder; however, the highly regular discharge rhythm must be controlled by internal factors (see discussion). For this reason, an interaction of the two fishes' discharges seems possible only during interburst periods.

Therefore, an analysis of the discharge rhythm displayed by *G. petersii* only during interburst periods was undertaken. Considering these periods, it is not clear from visual inspection whether or not adjacent intervals tend to be similar in length. A statistical correlation study of the order in which intervals of different length occur gives an answer to this question. A method by which each interval is compared with the L$^{\text{th}}$ preceding interval (scattergram or "joint interval histogram"), is given by Wyman (1965).

According to this method, the L^{th} order serial correlation coefficient of N interpulse intervals $(a_1 \dots a_N)$ is computed by formula

$$R_L = \frac{1}{N-L} \sum_{i=1}^{N-L} \left[\frac{a_i - \mu_s}{\sigma_S}\right] \left[\frac{a_{i+L} - \mu_L}{\sigma_L}\right]$$

where

$$\mu_s = \frac{1}{N-L} \sum_{i=1}^{N-L} a_i\,; \qquad \sigma_S = \left[\frac{1}{N-L} \sum_{i=1}^{N-L} (a_i - \mu_s)^2\right]^{\frac{1}{2}};$$

and

$$\mu_L = \frac{1}{N-L} \sum_{i=L+1}^{N} a_i\,; \qquad \sigma_L = \left[\frac{1}{N-L} \sum_{i=L+1}^{N} (a_i - \mu_L)^2\right]^{\frac{1}{2}}.$$

These coefficients have the range -1 to $+1$. The first order coefficient indicates the degree of similarity between adjacent intervals; the second order coefficient gives the same information but compares each interval with the interval that follows one after the next, and so on.

Since the interpulse interval histograms do not seem Gaussian (Fig. 1a), confidence levels of the coefficients have been computed according to a "nonparametric" method given by Wald and Wolfowitz (1943). For a large N, a normalized variable t, valid for a time series with any cumulative distribution function is computed as:

$$C_L = \sum_{i=1}^{N-L} (a_i - \mu)(a_{i+L} - \mu) \quad \text{where} \quad \mu = \frac{1}{N} \sum_{i=1}^{N} a_i.$$

The mean of CL is $E(C_L) = -S_2/N - 1$ and the variance is

$$\sigma^2(C_L) = \frac{S_2^2 - S_4}{N-1} + \frac{S_2^2 - 2\,S_4}{(N-1)(N-2)} - \frac{S_2^2}{(N-1)^2}$$

where

$$S_2 = \sum_{i=1}^{N} (a_i - \mu)^2 \quad \text{and} \quad S_4 = \sum_{i=1}^{N} (a_i - \mu).$$

Several orders of t are obtained as

$$t_L = \frac{C_L - E(C_L)}{\sigma(C_L)}.$$

Fig. 3a shows the first ten orders of serial correlation coefficients for a *G. petersii* discharge interval sequence, emitted during the presence of a *M. rume*.

The coefficients are all positive, but three of them (of the fifth, the sixth and the tenth order) are not significantly different from zero. That the first coefficient is the largest indicates that adjacent intervals are kept closer in size than are intervals ten cycles apart; the relatively high fourth and ninth coefficients show that there is a tendency of intervals, separated by three and eight intervals, to be more similar in length than intervals separated by one, two, four, five, six, seven and nine intervals. Between intervals separated by four, five and nine intervals, there does not seem to exist a regulation of interval length, because the associated correlation coefficients are insignificant; i.e. the variance is due to random jitter. In summary, in a run of eleven intervals, the first five tend to be all above or below the mean value; the lengths of the sixth and seventh intervals are not regulated (randomly distributed), the eighth, ninth, and tenth interval show the same trend as the first five intervals, and the eleventh interval again is not regulated with respect to the first.

Fig. 3b presents a similar analysis for the concurrent discharge activity of *M. rume*. All coefficients are significantly positive, demonstrating that runs of at least eleven intervals tend to stay above or below the mean value. That the first coefficient is smaller than the second indicates that long intervals are compensated by being followed by shorter ones, the following interval is again long. A comparison of the two correlograms (Fig. 3a and b) shows that the regulation of discharge rate in agonistic behaviour is very different in both species. In contrast to *G. petersii*, *M. rume* displays a discharge rhythm with a high degree of regularity, since runs of at least eleven intervals tend to stay above or

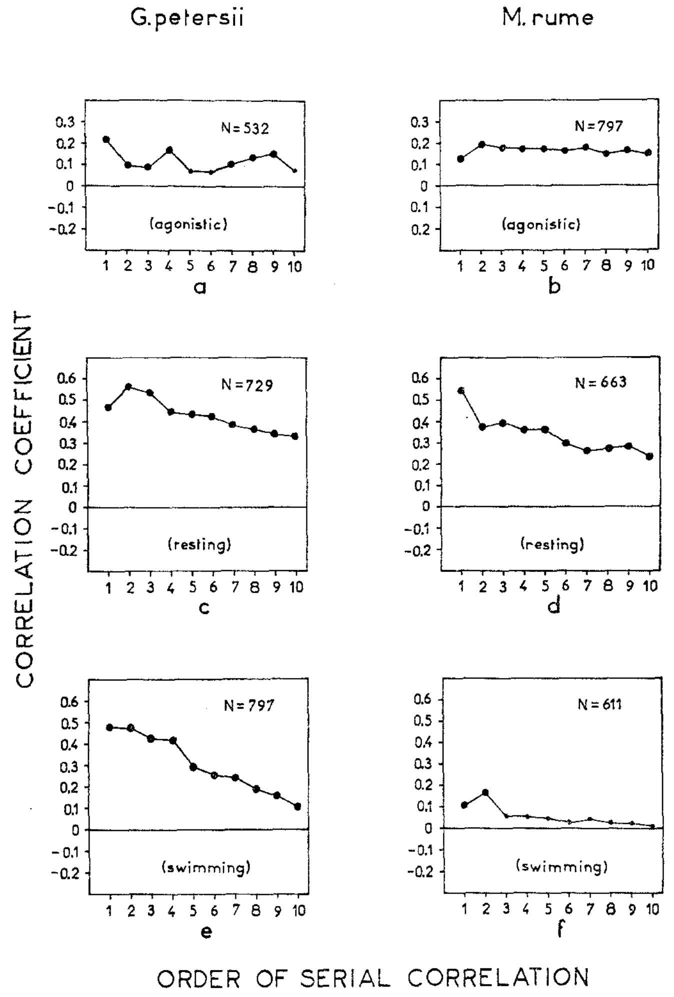


Fig. 3a—f. Serial correlograms of interpulse interval sequences of *G. petersii* and *M. rume* emitted during three different behavioural situations. *N* total number of intervals analysed. Large dots are significant correlation coefficients ($p < 0.05$), small dots are not ($p > 0.05$). In detail, non-parametric Wald-Wolfowitz confidence levels are in (a) $p < 0.001$ for the 1^{st}, 4^{th}, and 9^{th} order coefficients (o.c.); $p < 0.002$ (8^{th} o.c.); $p < 0.02$ (7^{th} o.c.); $p < 0.05$ (2^{nd} and 3^{rd} o.c.); $p > 0.10$ (5^{th}, 6^{th} 10^{th} o.c.). In (b) $p < 0.001$ (1^{st} to 10^{th} o.c.). In (c) $p < 0.001$ (1^{st} to 10^{th} o.c.). In (d) $p < 0.001$ (1^{st} to 10^{th} o.c.). In (e) $p < 0.001$ (1^{st} to 9^{th} o.c.); $p < 0.002$ (10^{th} o.c.). In (f) $p < 0.001$ (2^{nd} o.c.); $p < 0.01$ (1^{st} o.c.); $p > 0.05$ (3^{rd} to 10^{th} o.c.)

below the mean value, compared with only four in *G. petersii*. A further important difference is the regulation of the lengths of adjacent intervals, as indicated above.

In order to know whether or not the observed discharge regulations are specifically associated with agonistic behaviour, it is necessary to analyse also the discharge activity of the two fishes i) at rest, ii) during swimming of isolated animals.

i) Contrary to the agonistic situation, a *G. petersii* at rest (Fig. 3c) exhibits runs of at least eleven intervals above or below the mean value (all coefficients are significantly positive). Long intervals are compensated for by being followed by shorter ones, as indicated by the second coefficient which is the highest. Intervals separated by one and two intervals are more similar to each other than are adjacent intervals (the third coefficient is also higher than the first; no such regulation was found in the agonistic situation). Beyond this, the degree of similarity gradually diminishes, but is still high at the tenth following interval; this was not found during agonistic behaviour. Thus, the discharge rhythm displayed at rest (Fig. 3c), resulting in a trimodal interpulse interval histogram (Fig. 4a), differs fundamentally from the one displayed during agonistic behaviour (Figs. 3a, 1a—2).

The same is true in *M. rume*. For data obtained from a resting animal, all the coefficients are significantly positive (Fig. 3d), as in *G. petersii*. However, in *M. rume* the discharge pattern is characterised by a high degree of similarity between adjacent intervals (the first coefficient is the highest), whereas in the agonistic situation, it is the next interval but one which is the most similar to the first. The next interval but one compensates two preceding long intervals by being shorter (or vice versa), as is indicated by the great difference between the first and the second coefficient, and by the fact that the third coefficient is higher than the second. In contrast to this, a compensation mechanism was found during agonistic behaviour involving adjacent intervals. A run of intervals above or below the mean consists of at least eleven intervals. The interpulse interval histogram (Fig. 4b) displays a very great range of interval lengths, as compared with a resting *G. petersii*.

When *G. petersii* is swimming, runs of intervals above or below the mean consist of at least eleven intervals (Fig. 3e), similarly to a resting animal (Fig. 3c). However, there is no short term frequency compensation, since adjacent intervals are kept closer in size than any other two intervals. The degree of similarity between two intervals diminishes gradually as more intervals separate them. The decline is steeper than in a resting *G. petersii*. The discharge rhythm displayed by a swimming *G. petersii* neither resembles the one found in a resting nor the one found in an agonistic animal. In addition, the three interval histograms associated with the three different behavioural situations (Figs. 1b—2, and 4a) are very dissimilar.

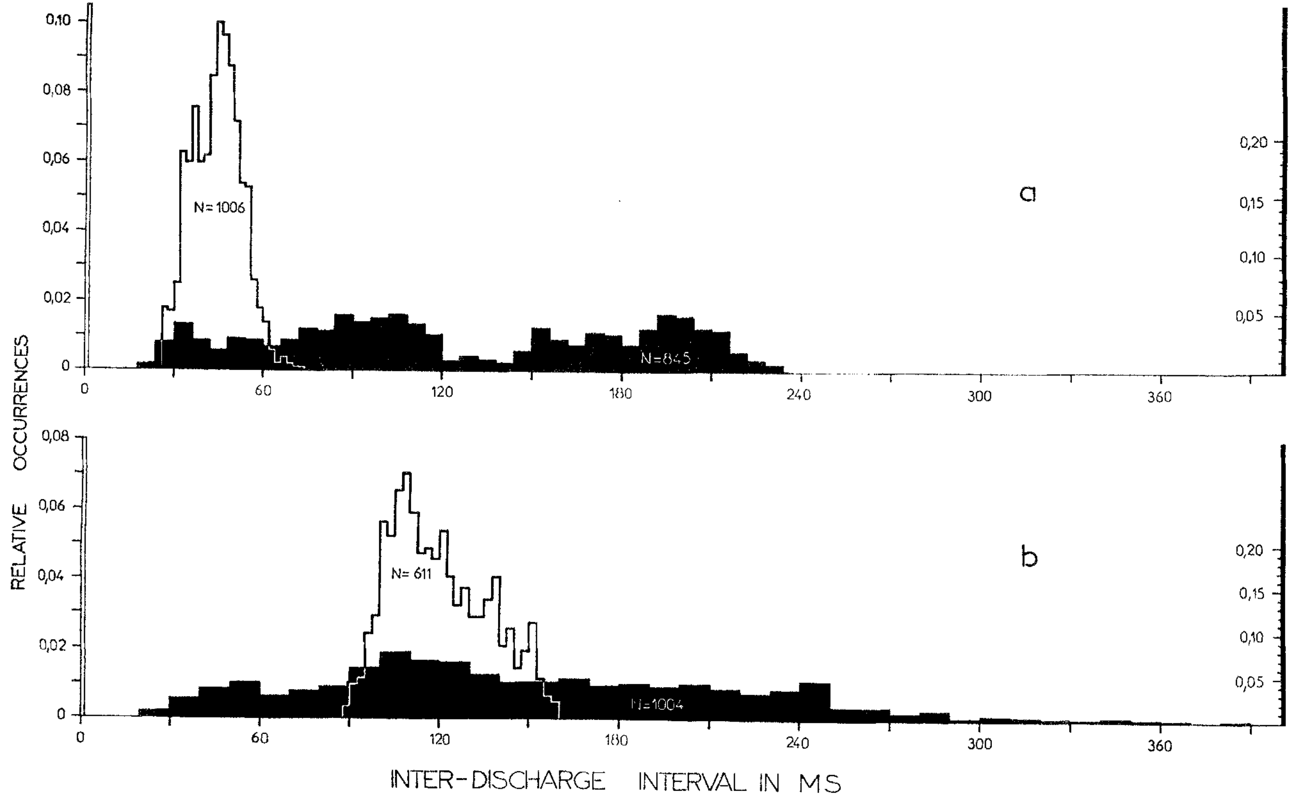


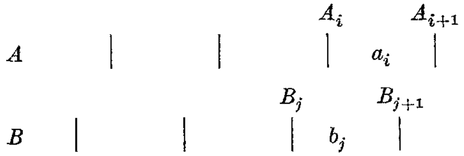
Fig. 4a and b. Interpulse interval histograms of a resting (black) and a swimming (white) *Gnathonemus petersii* (a) and a *Mormyrus rume* (b). White ordinates indicate relative occurrences in white histograms, black ordinates in black histograms. The two histograms of each system are normalized to cover the same area, i.e. equal areas are the same densities of probability. Note high variation of interval lengths in resting fishes (showing up clearly as three modes in *G. petersii*), as compared with swimming fishes. *N* total number of intervals analysed

In an analysis of data obtained from a swimming *M. rume* (Fig. 3f), only the first and the second order coefficients are found to be significantly different from zero, i.e. a regulation mechanism exists only for three consecutive intervals. Together, these three intervals are either longer or shorter than the mean. However, the third of these intervals resembles the first more closely than does the second, which compensates a long first interval by being shorter (or vice versa). Thus, the discharge rhythms displayed by *M. rume* in three different behavioural situations (Figs. 3b, c and f) are very dissimilar, as in *G. petersii*. Likewise, there is no resemblance between the three associated interval histograms (Figs. 1a—1, and 4b).

Having established that both fishes display a discharge rhythm characteristic of the agonistic situation, it has not yet been shown, however, that there is a detailed interaction of EODs. From the interval vs. time of occurrence plot of Fig. 2b, showing the concurrent discharge activities of the very aggressive *G. petersii* Q, and of a *M. rume*, being attacked, it is clear that in general the interpulse intervals of the two fishes do not parallel each other. During interburst activity, however, there are a few instances when the *G. petersii* assumes a discharge frequency very close to the one displayed by the *M. rume* (for three cycles at best). Fig. 2a shows the same as Fig. 2b but for *G. petersii* H not daring to butt the *M. rume* put into its tank. In this example, there are two periods where locking into a common discharge frequency occurs during eight and five cycles.

A correlation of *G. petersii* pulse intervals with concurrent *M. rume* pulse intervals (cross correlation) would allow us to state more precisely whether the two fishes tend to have their periods of high and low instant discharge frequencies together or not. Because such an effect might be delayed by one or several intervals, lagged correlation coefficients were also calculated.

For zeroth order (or unlagged) cross correlation, each interval a_i[1] on one line (A) was correlated with the interval b_j[2] on the other line (B), which is in part concurrent but starts earlier:



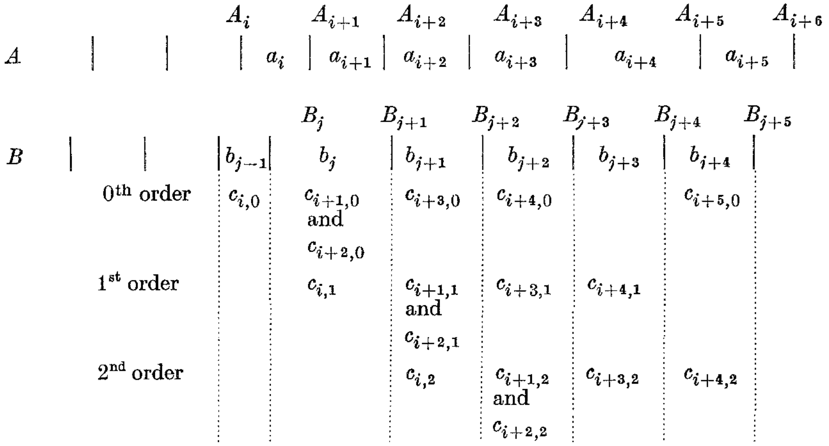
B_j is the largest B still smaller than A_i. To denote the interval b_j it is inserted into a third list of intervals as $c_{i,o}$[3]. Thus a complete list of b intervals of zeroth order can be established:

---

[1] i is an integer.

[2] j is an integer.

[3] Zero stands for zeroth order cross correlation.



A b interval of L^{th} order with respect to an interval a_i is the L^{th} b interval after the one which has been determined to be of zeroth order. It is denoted as $c_{i,L}$; e.g. the second order b interval with respect to a_{i+1} is $c_{i+1\,2}$ in this notation. Note that for any L a b-interval can be on the c list more than once (for zeroth order, it is b_j in the above example); on the other hand, a b-interval may be omitted (for zeroth order, it is the interval b_{j+3}).

Having established these c lists, L^{th} order cross correlation coefficients can be computed according to a method adapted from Wyman (1965):

$$r(L) = \frac{1}{N-L} \sum_{i=1}^{N-L} \frac{(a_i - \mu_a)(c_{i,L} - \mu_c)}{\sigma_a \sigma_c}$$

where

$$\mu_a = \frac{1}{N-L} \sum_{i=1}^{N-L} a_i; \qquad \mu_c = \frac{1}{N-L} \sum_{i=1}^{N-L} c_{i,L}$$

and

$$\sigma_a = \left[\frac{1}{N-L} \sum_{i=1}^{N-L} (a_i - \mu_a)^2\right]^{\frac{1}{2}}; \qquad \sigma_c = \left[\frac{1}{N-L} \sum_{i=1}^{N-L} (c_{i,L} - \mu_c)^2\right]^{\frac{1}{2}}.$$

In Fig. 5, the zeroth order coefficient is significantly negative ($p < 0.01$), showing that a short *M. rume* interval is immediately "compensated" for by a long *G. petersii* interval. The first order coefficient does not differ significantly from zero, indicating that there is no regulation of *M. rume* interval length in response to *G. petersii* intervals. This does not change when the lag of *M. rume* intervals is increased up to ten intervals.

No significant results are obtained when the analysis is reversed. Only when a *M. rume* interval precedes a *G. petersii* interval (zeroth order

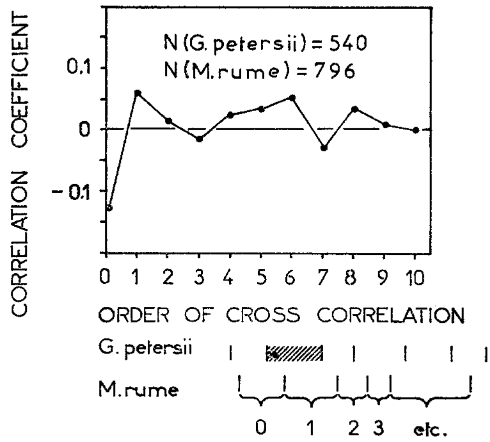


Fig. 5. *G. petersii*—*M. rume* interval cross correlation. The lower scheme indicates the system of comparison. A particular interval (hatched) on one line is compared to the overlapping but preceding interval on the other line for zeroth order correlation, and then with later intervals for higher orders. Only when a *M. rume* interval starts earlier than a *G. petersii* interval (zeroth order cross correlation), is a significant negative coefficient ($p < 0.01$) found. *N* total number of intervals analysed during 36.85 s

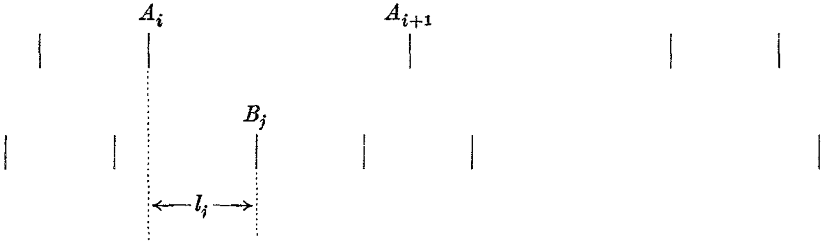
in Fig. 5), a regulation of discharge frequencies, as described above, can be detected.

In the analysis presented up to now, it has been shown that during agonistic behaviour, each fish changes its mean discharge frequency, rhythm, and the range and relative proportion of intervals (i.e. shape of interpulse interval histograms). Furthermore, *G. petersii* tends to regulate its discharge activity inversely to that of the *M. rume* with minimal delay. There is still one type of response which might not have been detected by the above analysis—this will be dealt with in the following chapter.

II. Phase and Latency Analyses

When analysing the relationships between two trains of pulses the possibility should be considered that one fish might discharge with a certain "preferred" latency or phase relationship with respect to the pulses of the other. In a preliminary communication (Bauer and Kramer, 1974), a preferred latency of about 11 ms of the *G. petersii* pulses to the preceding *M. rume* pulses was reported. However, in our analysis, executed on the fixed programme Didac computer, only the latency of the earliest (if there were more than one) *G. petersii* pulse occuring during any *M. rume* interval could be considered; in addition, it was not possible to measure latencies in order of occurrence (Figs. 2a and b, upper parts). Furthermore, it was impossible to calculate phase relationships. The FORTRAN-programme used in the present study was devised to solve these problems.

The latency of each B pulse to the preceding A pulse



is computed as:

$$l_j = B_j - A_i.$$

A_i is the largest A pulse still smaller than B_j. The phase of a B pulse to the concurrent interval a_i is

$$\varphi_j = \frac{l_j}{A_{i+1} - A_i}$$

φ_j therefore varies between 0 and 1.

In the upper parts of Figs. 2a and b, the latencies of *G. petersii* pulses to *M. rume* pulses, calculated in the manner indicated above, are represented vs. their times of occurrence. There are instances, when latencies in the range of 10.0 to 13.5 ms occur in runs of various lengths. Runs of ten and eleven, separated by one shorter latency, are shown in Fig. 2a. The longest run observed is twenty-one. From this evidence it may be inferred that *G. petersii* prefers to discharge with a delay of about 10 to 13.5 ms to *M. rume* pulses, i.e. latencies within this range seem to occur more frequently than would be expected from two pulse trains which are unrelated. In order to express this statement more precisely, the following considerations are useful.

If the sequences of two series of pulses are not related, then any phase should be as likely as any other, i.e. the histogram of phases should be flat over its distribution from 0 to 1. When EOD sequences, which had not been recorded simultaneously, are used as an input to the computer programme (Fig. 6a), there should be no phase preference. As shown by a two-tailed Kolmogorov-Smirnov test (cf. Siegel, 1956), a random sample drawn from a flat population would give a no better fit than the results shown in Fig. 6a ($p \gg 0.20$). On the contrary, when two concurrent sequences of pulses are analysed, this probability is $\ll 0.01$ for *G. petersii* H (Fig. 6b). There is a marked phase preference of about 0.26

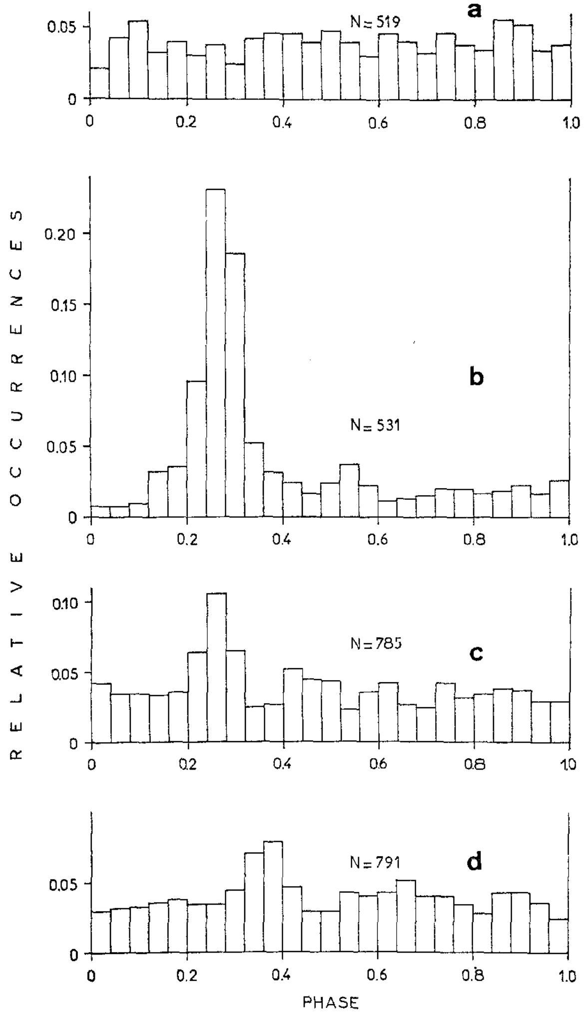


Fig. 6a—d. Histograms of the phases of *G. petersii* pulses as a fraction of the concurrent *M. rume* intervals. a A Kolmogorov-Smirnov test shows that the distribution obtained from two records made at different times (or simultaneous records from isolated fishes) does not differ significantly from random ($p \gg 0.20$). The theoretical random distribution (not represented) is a straight line at 0.04 from phase 0 to 1. The length of the records is 35.38 s. b Shows the same as (a), but for the concurrent discharge trains of *G. petersii* H and *M. rume* ($p \ll 0.01$). The length of the records is 35.38 s. c Shows the same as (b), but for *G. petersii* F ($p < 0.01$). The length of the records is 34.17 s. d Shows the same as (b), but for *G. petersii* Q ($0.05 < p < 0.10$). The length of the records is 23.23 s. *N* total number of discharges emitted by *G. petersii*

of a period. *G. petersii* F prefers the same phase ($p < 0.01$, Fig. 6c). However, *G. petersii* Q exhibits a mode of 0.38 (Fig. 6d, $0.05 < p < 0.10$). Two other *G. petersii* display modes of 0.18 and 0.30, respectively ($p < 0.01$). In a sixth animal (mode at 0.22), the two-tailed Kolmogorov-Smirnov *p*, as in *G. petersii* Q, is not significant ($0.05 < p < 0.10$). In summary, in four out of six *G. petersii*, a significant phase preference has been found; it ranges between 0.18 and 0.30 of a period.

The strength of this phase preference seems to be inversely related to the aggressivity of *G. petersii*. *G. petersii* H (Fig. 6b) did not butt the *M. rume* even once during 3 min, only seven head butt intentions were observed; *G. petersii* F (Fig. 6c) performed twenty-seven head butts and nine head butt intentions, and *G. petersii* Q (Fig. 6d) butted *M. rume* fourty-four times (twenty-three head butt intentions).

As in phases, there should be no preferred latencies when two pulse series, which had not been recorded simultaneously, are used as an input to the computer programme (Fig. 7a). The distribution of latencies in Fig. 7a is not flat, as is the distribution of phases in Fig. 6a. A decline of occurrences is observed for long latencies, since a *G. petersii* latency cannot, of course, be longer than the concurrent *M. rume* interval. While short *G. petersii* latencies can occur either during long or short *M. rume* intervals, long *G. petersii* latencies can occur only during long *M. rume* intervals. This means that the shape of the latency histogram of pulses of a series *B* to the pulses of a second, unrelated series *A* depends on the distribution of *A* intervals, as has been pointed out by Wyman (1965). A pulse train, which shows no preferred latencies with respect to another must be one in which a) a *G. petersii* pulse is as likely to occur during one fraction of a *M. rume* interval as during any other equal fraction, and b) the phase of a *G. petersii* pulse is independent of the length of the concurrent *M. rume* interval.

Under these assumptions, a distribution of expected latencies of *B* pulses to *A* pulses is computed according to Wyman (1965)

$$f(l) = \int_{l}^{\infty} \frac{1}{a} h(a)\, da$$

where $f(l)$ = the probability density function of the latencies of *B* pulses to the *A* pulses which immediately precede them, and
$h(a)$ = the probability density function of the concurrent *A* intervals.

For Fig. 7a, the probability is $p \gg 0.20$ that a random sample drawn from the calculated distribution of expected latencies (indicated by crosses) would give a no better fit than the results shown. In Figs. 7b—c, the results of analyses of two concurrent sequences of pulses are shown. There is a marked preference for *G. petersii* H (Fig. 7b) to discharge

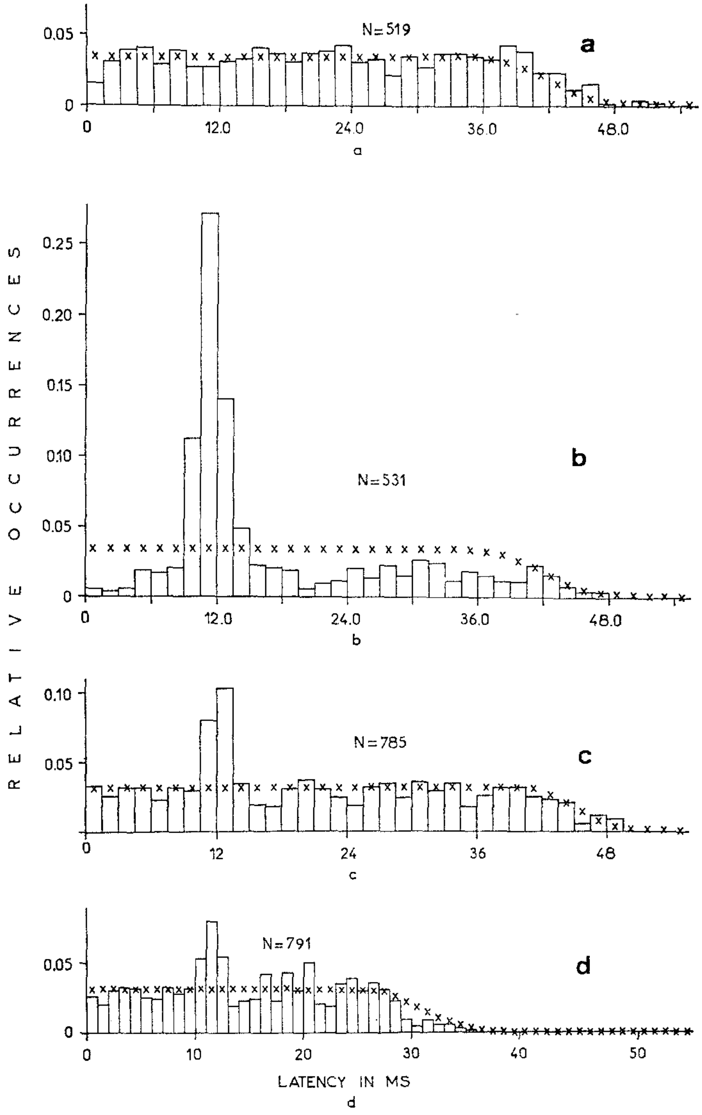


Fig. 7a—d. Histograms of the latencies of *G. petersii* pulses to *M. rume* pulses. a A Kolmogorov-Smirnov test shows that the distribution obtained from two recordings made at different times (or simultaneous records of isolated fishes) does not differ significantly from random ($p \gg 0.20$), indicated by crosses. The length of the records is 35.40 s. b Shows the same as (a), but for the concurrent discharge activities of *G. petersii* H and *M. rume* ($p \ll 0.01$). The length of the records is 35.39 s. c Shows the same as (b), but for *G. petersii* F ($p < 0.01$). The length of the records is 34.17 s. d Shows the same as (b), but for *G. petersii* Q ($0.05 < p < 0.10$). The length of the records is 23.23 s. N total number of discharges emitted by *G. petersii*

with a latency of about 11.5 ms with respect to the *M. rume* pulses. The probability that this distribution might have been drawn from a random sample of the distribution of expected latencies is $\leqslant 0.01$.

G. petersii F (Fig. 7c) displays a mode very close to the one found in *G. petersii* H (about 12 ms, $p < 0.01$). In three other animals (not represented), a significant latency preference of 11.5 ms was found. The sixth animal (*G. petersii* Q, Fig. 7d) displays the same mode, but the associated two-tailed Kolmogorov-Smirnov p is slightly below the confidence level of 5%. Thus, five out of six *G. petersii* showed a significant latency preference of 11.5–12 ms with respect to *M. rume* discharges. One of these animals was a female (determined post mortem).

As has been noted for phases (p. 221), the strength of the latency preference seems to be inversely related to the aggressivity of *G. petersii*. As can be seen in Fig. 11, the ratio of observed to expected "preferred" latencies (i.e. latencies within 10.0 to 13.5 ms) tends to approach unity in the most aggressive animals. In contrast, the least aggressive *G. petersii* produces 6.5 times more preferred latencies than what would be expected, if the two discharge trains were independent.

Comparing Figs. 6 and 7, the question arises whether it is the latencies or the phases which are kept constant within a narrow range. Since *M. rume* discharges very regularly (cf., for example, Figs. 2a and b), the preference of a certain latency to *M. rume* pulses by *G. petersii* must bring about a peak in the distribution of phases also. The phase of this peak depends on the length of the concurrent *M. rume* intervals. When these are short (Fig. 1b—1), the phase of the mode is large (Fig. 6d). For this reason, it must be concluded that *G. petersii* tends to keep the latencies, and not the phases within a narrow range.

Up to now, the reactions of *G. petersii* to the discharges emitted by *M. rume* have been analysed. However, there might also be a tendency of *M. rume* to maintain a certain phase or latency relationship to the pulses of the discharge train of *G. petersii*. An analysis designed to look at this possibility is described in the following paragraphs.

Figs. 8b—d show the phases of *M. rume* pulses in concurrent *G. petersii* intervals. *M. rume* exhibits a preference of the phase 0.74 when in the tanks of *G. petersii* H and F ($p < 0.01$; Figs. 8b and c, respectively), in the presence of *G. petersii* Q, no particular phase seems to be preferred. Phase relationships to the EOD-trains of three other *G. petersii* differ significantly from random ($p < 0.01$). In these cases, however, two or three modes show up in each distribution. They range from phase 0.06 to 0.82. In summary, the same *M. rume* maintains certain phase relationships of its EOD activity with respect to the discharge trains of five out of six different specimens of *G. petersii*; the range of modes, however, is extremely great.

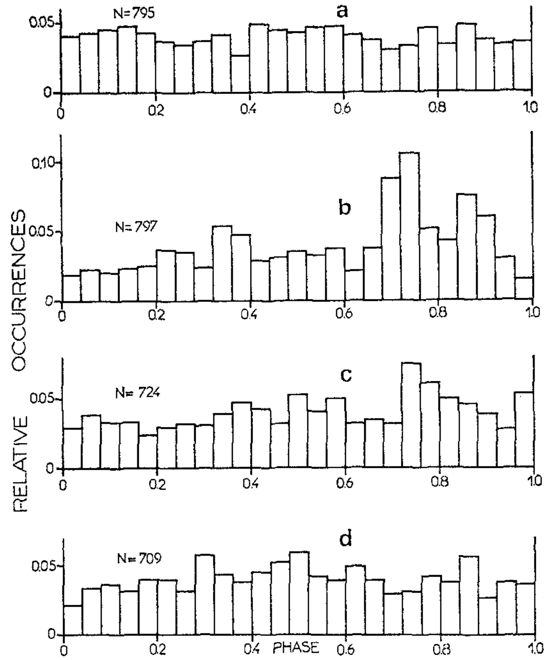


Fig. 8a—d. Histograms of the phases of *M. rume* pulses as a fraction of the concurrent *G. petersii* intervals (i.e. the inverse of the analysis in Fig. 6). a A Kolmogorov-Smirnov test shows that the distribution obtained from two records made at different times (or simultaneous records from isolated fishes) does not differ significantly from random ($p \gg 0.20$). The theoretical random distribution (not represented) is a straight line at 0.04 from phase 0 to 1. The length of the records is 35.40 s. b Shows the same as (a), but for the concurrent discharge trains of *M. rume* and *G. petersii* H ($p \ll 0.01$). The length of the records is 35.39 s. c Shows the same as (b), but for *M. rume* in the tank of *G. petersii* F ($p < 0.01$). The length of the records is 34.17 s. d Shows the same as (b), but for *M. rume* in the tank of *G. petersii* Q ($0.05 < p < 0.10$). The length of the records is 23.23 s. *N* total number of discharges emitted by *M. rume*

Figs. 9b—d show the latencies of *M. rume* pulses to the preceding *G. petersii* discharges. In the presence of *G. petersii* H (Fig. 9b), *M. rume* prefers to discharge about 28 ms after a *G. petersii* pulse; when *M. rume* is put into the tank of *G. petersii* F (Fig. 9c), this latency is about 33 ms. The preferred latency to the pulses of *G. petersii* Q (Fig. 9d) is about 21 ms, as judged by the greatest positive difference between experimental and expected latencies. The distributions of latencies of *M. rume* pulses to the discharges of three other specimens of *G. petersii* also differ from random ($p < 0.01$). The modes found in these examples range from

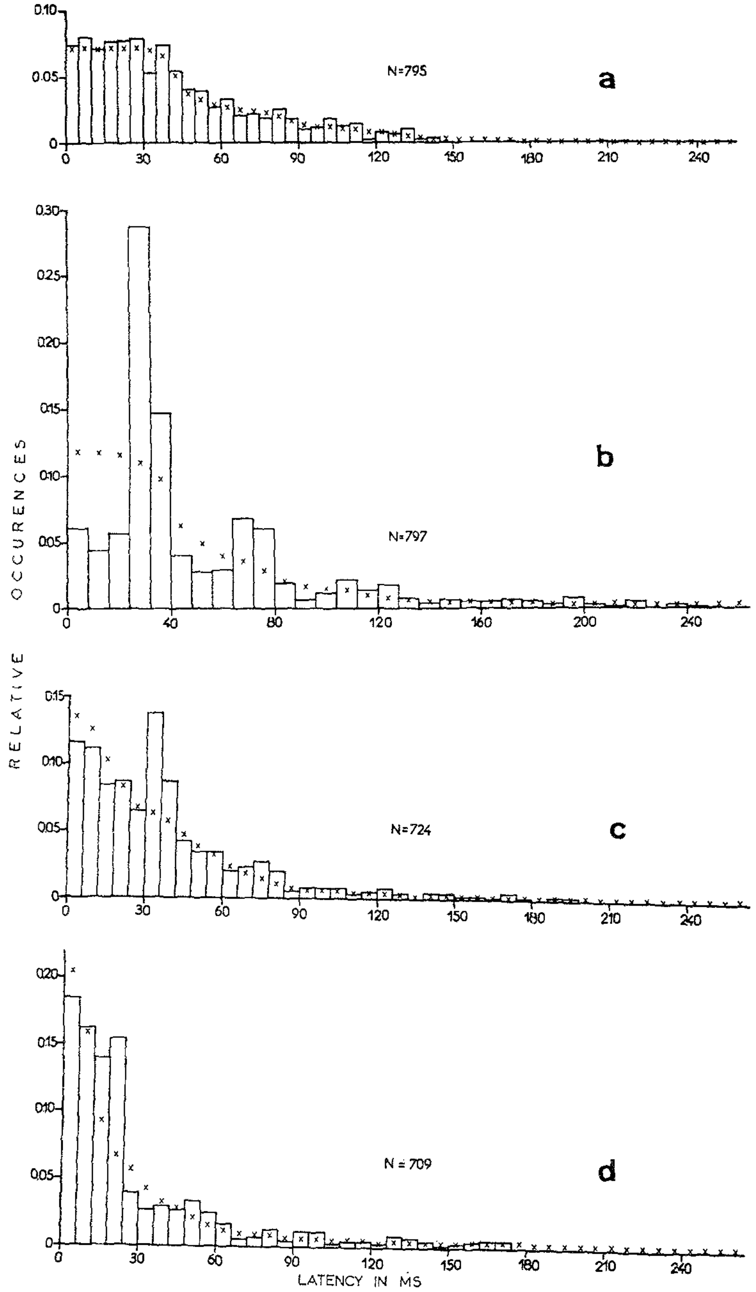


Fig. 9a—d
(for legend see p. 226)

30 to 38 ms. Thus the same *M. rume* exhibits quite variable latency preferences (from 21 to 38 ms) to the discharges of six different *G. petersii*.

In summary, consistent results are not obtained when the reaction of *M. rume* to *G. petersii* pulses is studied. Of all the phase and latency analyses presented, the tendency of *G. petersii* to discharge with a delay of about 12 ms with respect to *M. rume* pulses is the only consistent observation. Since within an experiment the discharge frequency of *M. rume* varies only in a narrow range, the latency of *M. rume* pulses to those *G. petersii* discharges, which are delayed by 12 ms to the preceding *M. rume* pulse, vary only slightly too. However, *M. rume* phases and latencies differ considerably in different experiments. The latencies of *M. rume* pulses to *G. petersii* pulses are short (Fig. 9d), when the mean discharge frequency of *M. rume* is high (Fig. 1b—1). *M. rume* pulses display short phases when *G. petersii* discharges only every second, third or n^{th} *M. rume* interval, as may be seen during interburst activity in Fig. 2a and in Fig. 2b. The reverse is true for the modes of the latency distributions of *G. petersii* pulses to *M. rume* pulses which are independent of the mean discharge frequency of *G. petersii*, although the variations are more extreme than in *M. rume*:

G. petersii H: 15 Hz; *M. rume* in H's presence: 22.5 Hz
G. petersii Q: 34 Hz; *M. rume* in Q's presence: 32.5 Hz

(Figs. 1, 7, 9). Thus it is concluded that the observed latency and phase relationships (Figs. 6 to 9) are due to the tendency of *G. petersii* to maintain a discharge latency of about 12 ms to the pulses of *M. rume*.

As has been mentioned earlier, these latencies may occur in runs, i.e. the lengths of several latencies are within 10.0 to 13.5 ms in uninterrupted succession (Figs. 2a and b, upper halves). Fig. 10 shows a histogram of the distribution of runs of different lengths for *G. petersii* Q and *G. petersii* H. A "run" of one preferred latency (i.e. the lengths of the preceding and the following latency are *not* within 10.0 to 13.5 ms) occurs in 88% of all runs observed in the highly aggressive *G. petersii* Q. In the animal

Fig. 9a—d. Histograms of the latencies of *M. rume* pulses to *G. petersii* pulses (i.e. the inverse of the analysis in Fig. 7). a A Kolmogorov-Smirnov test shows that the distribution obtained from two recordings made at different times (or simultaneous records of isolated fishes) does not differ significantly from random ($p \gg 0.20$), indicated by crosses. The length of the records is 35.38 s. b Shows the same as (a), but for the concurrent discharge activities of *M. rume* and *G. petersii* H ($p \ll 0.01$). The length of the records is 35.38 s. c Shows the same as (b), but for *M. rume* in the tank of *G. petersii* F ($p < 0.01$). The length of the records is 34.17 s. d Shows the same as (b), but for *M. rume* in the tank of *G. petersii* Q ($p < 0.01$). The length of the records is 23.23 s. Note the steeper decline of expected latencies when there are many short concurrent *G. petersii* intervals, as in (c) and especially in (d). *N* total number of discharges emitted by *M. rume*

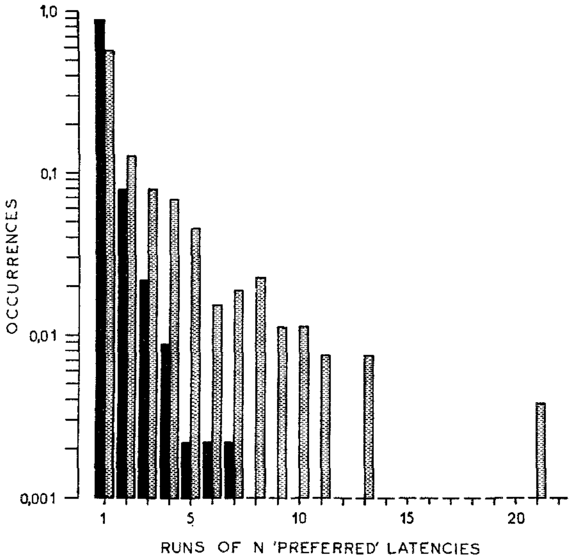


Fig. 10. Histograms of the lengths of runs of the "preferred" discharge latency (i.e. a latency within 10.0 to 13.5 ms) to the pulses of a *Mormyrus rume*, performed by *Gnathonemus petersii* Q (black) and H (grey). Black histogram: $N=456$; the total number of preferred latencies $= 467$. A total of 2973 discharges, emitted during 93.48 s, were evaluated. Grey histogram: $N=263$; the total number of preferred latencies $= 648$. A total of 1717 discharges, emitted during 109.93 s, were evaluated

H, which did not overtly attack the *M. rume*, this value is 58%. The longest run performed by the animal Q is seven, whereas in the animal H, it is twenty-one. The two distributions of runs are significantly different ($p \ll 0.01$, two-tailed Kolmogorov-Smirnov test). Thus it may be concluded that a highly aggressive *G. petersii* produces less preferred latencies (cf. Figs. 7b—d), and smaller runs of preferred latencies than a less aggressive animal.

These runs may be performed during a regular alternation of the pulses of *G. petersii* and *M. rume* (as can be seen over several cycles in Fig. 2a); in many cases, however, *G. petersii* omits one or two, or even more *M. rume* intervals between each discharge, which is nevertheless precisely delayed by approx. 12 ms to the preceding *M. rume* discharge.

Runs of two or more preferred latencies never occur during high frequency bursts (cf. Fig. 2b). Furthermore, coincidence (zero latency) of discharges occurs exclusively during high frequency bursts. *G. petersii* seems to be carefully avoiding coincidence during interburst activity (see discussion).

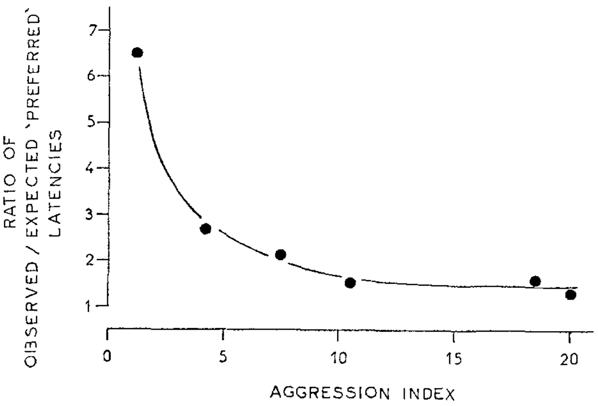


Fig. 11. Ratio of observed to expected "preferred" latencies (i.e. latencies within 10.0 to 13.5 ms) of *G. petersii* to *M. rume* pulses, as a function of the aggressivity of *G. petersii*. Each point represents one individual. The ordinate shows how many times more often than expected, preferred latencies occurred. The abscissa is the number of head butts (each tallied as 1) plus the number of approaches (each tallied as 0.5) per min (Fiedler, 1967; Kramer, 1971)

Discussion

A resting *G. petersii* increases its discharge frequency when a *M. rume* is introduced into its tank. *G. petersii* H, for example, exhibits a mean discharge frequency of 8.4 Hz at rest (Fig. 4a, black histogram); in the presence of *M. rume* (Fig. 1a—2), its frequency changes to a mean 15 Hz (34 Hz in the aggressive *G. petersii* Q, Fig. 1b—2). Likewise, *M. rume* displays mean EOD frequencies of 6.7 Hz at rest in its home tank (Fig. 4b, black histogram), and 22.5 Hz (31 Hz), when put into the tank of *G. petersii* H (Q) (Figs. 1a—1 and 1b—1, respectively). These increases in mean discharge frequency may in part be explained by the fact that the two fishes are rarely at rest—even for a few seconds—when together in one tank. As has been shown for *G. petersii* and *M. zanclirostris* (Belbenoit, 1972), the rate of the EOD is strongly correlated with motor behaviour. In fact, the discharge frequency of an isolated, swimming *G. petersii* (16 Hz, Fig. 4a) is approx. twice the frequency found during rest. However, an isolated *M. rume*, when swimming in its home tank, displays an EOD rate (8.7 Hz; Fig. 4b, black histogram), which is only slightly higher than at rest. In both species the ranges of interval lengths diminish dramatically during swimming (Fig. 4).

An increased motor activity is found generally, when two isolated fish are put together in one tank (cf., for example, Kramer, 1971). In most cases, the principal cues seem to be optical ones (cf., for example, Leong, 1971); in other species, they may be of acoustic, chemical, mechanical, or electric nature. Vision in *G. petersii* is excellent, the animals instantly hide in their tubes at the least movement in front of their aquarium, even several m away. They attack electrically silent (operated) *G. petersii*, and other, non-electric species of fish (Kramer and Bauer, in preparation). Thus, increased motor activity of *G. petersii* on the introduction of a *M. rume* must be thought to be brought about by visual cues; additional electric cues have a reinforcing action (Kramer and Bauer, in preparation). The increased motor activity is accompanied by a higher discharge frequency.

Weak electric, artificial stimuli alone also cause the discharge frequency to increase (Moller, 1969, 1970; Serrier, 1972a, b; 1973). In addition, there is a "regularisation" of the lengths of pulse intervals. These effects are thought to be of importance for the fish's electrolocating system (Moller, 1970). When *G. petersii* receives electric stimuli emitted by a *M. rume*, pulse interval variation is extremely great; no regularisation can be observed (Figs. 1, 2a and b). Therefore, it is unlikely that *G. petersii* uses its EOD principally for electrolocation in the agonistic situation.

Thus it seems that it is primarily the command centre for motor activity, which simultaneously influences the control of the electric organ of *G. petersii*, when a *M. rume* is put into its tank. This cannot be true, since interpulse interval length variation in an isolated swimming *G. petersii* (Fig. 4a, white histogram) is considerably less than during the presence of a *M. rume* (Figs. 1a—2, 1b—2). The results of serial correlation studies of the discharge rhythms displayed during rest, swimming and in the agonistic situation, shown in Fig. 3, highlight further principal differences between the EOD activities during the three behavioural situations. Thus it must be concluded that on the introduction of *M. rume* endogenous factors, "triggered" by exogenous stimuli, influence strongly the command centre of the electric organ of *G. petersii*. That EOD rate and motor activity are not coupled absolutely is also shown by the fact that *M. rume* and *G. petersii* are able to swim, even very rapidly, without discharging (Kramer and Bauer, in preparation; Kramer, unpublished).

The further analyses presented in this paper endeavoured to find out whether there are detailed reactions by the EODs of one fish to the pulses of the other. Moller and Bauer (1973) passively approached a *G. petersii*, resting in a ceramic tube, to a conspecific hiding in another tube. After having crossed a "communication threshold distance" of about 30 cm, they found a negative correlation of the two fishes' discharge rates, as determined by counting the number of EODs per successive 400 ms intervals. In the present study, it was possible to correlate interpulse intervals of one fish with those of the other (cross correlation, Fig. 5). A significant negative correlation coefficient is found between a *G. petersii* interval and the concurrent *M. rume* interval, which starts earlier. This means that *G. petersii* tends to react immediately to a long (short) *M. rume* interval by a short (long) interval. These results support the hypothesis of Moller and Bauer (1973) that a high discharge frequency might function as a threat signal causing the other fish to reduce its discharge activity. In fact, in experiments with two freely moving mormyrids, attack associated rapid EOD frequency increases could be demonstrated (Bauer, 1972; Bauer and Kramer, 1973; Kramer and Bauer, in preparation). On the other hand, a fleeing *G. petersii*, pursued by an aggressive mormyrid, stops discharging after having been bitten several times (Kramer, unpublished). In this context, it may be interesting to note that *G. petersii* H, which did not dare to butt the *M. rume*, displayed the lower mean discharge frequency. This is in contrast to *G. petersii* Q, and the other more aggressive individuals, which exceeded the *M. rume*'s mean discharge frequency.

As shown in the previous section, *G. petersii* prefers to delay its discharges by approx. 11.5 ms to the *M. rume* pulses. It could be excluded that this finding might be due to the preference of a certain phase, or that it might only be the result of a phase or latency relationship of *M. rume* discharges to *G. petersii* pulses. The ratio of observed to expected preferred latencies, displayed by an individual, is higher the less aggressive it is.

Valone (1970) obtained a record from two specimens of *Gymnotus carapo*, which were together in one tank, in which the pulses emitted by the two fishes alternate over five cycles. Latency and phase relationships, however, change considerably in this short record. In a similar record made by Box and Westby (1970), a drift of phases of the pulses of one fish from 0 to 1 during only seven concurrent intervals of the other can be observed.

In the present study it is always the preferred latency of approx. 11.5 ms, which is found when pulse alternation occurs. There is a tendency of preferred latencies to occur in runs of various lengths. The longest run observed is twenty-one. Of all preferred latencies emitted by *G. petersii* H, 76.5% constitute runs of two or more; 23.5% are "runs" of one. Runs of two or more never occur during high frequency bursts. It is during these high frequency bursts that coincidence of discharges of the two fishes occurs. High frequency bursts, triggered by exogenous stimuli, are presumably performed according to an endogenous programme (Kramer and Bauer, in preparation); during interburst activity, however, when runs of two or more "preferred" latencies occur, sensory input must have access to the pulse making decision.

The small value of the preferred latency indicates the existence of an extremely rapid reflex arc. As pointed out by electrophysiological work, 7—8 ms are required to conduct the command signal from the medulla oblongata to the electric organ in mormyrids (Bennett *et al.*, 1967). Hence less than 4 ms remain for the transmission of the coded receptor signal to the medulla oblongata, via the lateral nerve, lobus lateralis, and mesencephalon. Among the different electrosensory receptor types (mormyromasts, tuberous (Knollen-), and ampullary organs), and their connections to the brain, found in mormyrids, only the tuberous receptors and their "fast" junctions, and cerebral connections appear to be capable of such a rapid signal transmission (Bennett, 1965; Szabo, 1967; Bennett and Steinbach, 1969). In Gymnotids, this pathway comprises neurons with axons of large diameter, and probably electrical synapses between them (Szabo, 1967; in press). However, Russell and Bell (1973) conclude from their stimulation experiments that the mormyromasts (medium receptors) are involved. That runs of preferred latencies occur only during interburst activity, when the fishes are not in close contact, appears to argue against this possibility, since threshold in mormyromasts is considerably higher than that of tuberous receptors (Bennett, 1967). Both tuberous receptors and mormyromasts are phasic (Bennett, 1967; Kramer-Feil, in preparation).

Although a latency of about 11.5 ms seems to be the minimal reaction time of *G. petersii* to an external electric stimulus, the fish is free to respond after a longer time as well, as seen in Fig. 7. Shorter latencies than this minimal time were also observed, beginning at zero latency. In this case, it must be assumed that the pulse-making decision had already taken place before the *M. rume* pulse occurred and thus could not have been altered by sensory input.

In order to interpret the significance of these findings for intraspecific behaviour, the histogram of interpulse intervals of an aggressive *G. petersii* (Fig. 1b—2) was examined. It is particularly noticeable that the minimum of occurrences (9—12 ms) is of the order of magnitude of the preferred latency. This means that by delaying its discharges by the preferred latency, a *G. petersii B* can avoid coincidence with the pulses of a conspecific *A*, even when *A* performs a high frequency burst. Coincidence of discharges seems to be unfavourable to the power of the fish's electrolocating system (cf. also Moller, 1970). Furthermore, when the discharge of an individual *A* coincides with the discharge of a fish *B*, the pulse of the latter can possibly not be perceived by *A* because of an inhibition of tuberous receptor evoked activity in ganglion cells of the lobus lateralis found by Zipser (1971). Thus a *G. petersii*'s response by preferred latencies to the pulses of other individuals might justly be called a "jamming avoidance response" (Bullock, Hamstra and Scheich, 1972), although this term refers to *Eigenmannia*, where it signifies that individuals try to "escape" from stimulating frequencies close to their own, by lowering or increasing their discharge frequency. Responding by preferred latencies to the pulses of a conspecific, *G. petersii* can avoid "jamming" (i.e. coincidence of pulses) during high frequency bursts of the partner fish, i.e. during a period, when it is very probable that coincidence will occur.

These considerations do not explain, however, why less aggressive *G. petersii* display a higher preferred latency response than vigorously attacking animals. To account for these differences, estimations of a fish's threshold to EOD triggered, electrical stimuli should be considered.

In low-frequency gymnotids, Larimer and Macdonald (1968), Bullock (1969), Macdonald and Larimer (1970) and Westby (in preparation) found that stimulus thresholds depend very much on the latency relationship to the fish's own discharge. In mormyrids, the available information is less complete. Moller (1970) investigated thresholds at delay times of up to 4 ms, of 15 and 30 ms, i.e. the range of the preferred latency response (10 to 13.5 ms) is not covered. These experiments indicated a relatively high threshold within and shortly after a discharge. In further experiments with discharge triggered, single electrical stimuli, Serrier (personal communication) found evidence for a relatively high threshold around 10 ms. In the light of these observations, the preferred latency response might be interpreted as a "hiding" behaviour, because by delaying its pulse by the preferred latency to that of a conspecific, a *G. petersii* discharges at a time when the partner's sensitivity to electrical stimuli is presumably low. This would explain why the animals which attacked *M. rume* least, displayed a much higher preferred latency response than those which vigorously attacked it.

It remains doubtful whether the described electrical interaction between the two species of fish means that there is some sort of interspecific "communication". Since the two fishes are found together in a large area of Africa, naturally occurring aggressive or other encounters between *M. rume* and *G. petersii* cannot be excluded. The mean discharge frequency seems to be involved in the establishment of dominance in both species, as discussed above. Furthermore, transient discharge frequency increases in *M. rume* are probably aggressive signals as in *G. petersii* (Kramer, unpublished) and might mutually be "understood". However, the detailed, fast reaction to the other fish's discharge, as demonstrated by the cross correlation (Fig. 5) and the latency analyses (Fig. 7), is specific for *G. petersii*. It is therefore very likely that these reactions are important in *intra*specific behaviour of *G. petersii* only.

The experiments were made together with Dr. R. Bauer. The author was sponsored by a DFG (Deutsche Forschungsgemeinschaft) fellowship. I am deeply indepted to Dr. T. Szabo for his invitation to work in his laboratory, for his constant support and critical discussions. I wish to thank also Dr. M. Westby, who read the manuscript and corrected the English.

References

Bauer, R.: High electrical discharge frequency during aggressive behaviour in a mormyrid fish, *Gnathonemus petersii*. Experientia (Basel) **28**, 669 (1972)

Bauer, R., Kramer, B.: Relations entre le comportement agressif du Mormyridé *Gnathonemus petersii* et sa décharge électrique. J. Physiol. (Paris) **67** (2), 240–241 A (1973)

Bauer, R., Kramer, B.: Agonistic behaviour in mormyrid fish: latency—relationship between the electric discharges of *Gnathonemus petersii* and *Mormyrus rume*. Experientia (Basel) **30**, 51–52 (1974)

Belbenoit, P.: Relations entre la motricité et la décharge électrique chez les Mormyridae (Teleostei). J. Physiol. (Paris) **65** (2), 197 A (1972)

Bennett, M.V. L.: Electroreceptors in mormyrids. Cold Spring Harbor Symp. Quant. Biol. **30**, 245–262 (1965)

Bennett, M. V. L.: Mechanisms of electroreception. In: Lateral line detectors, p. 313–393 (Cahn, P., ed.). Bloomington: Indiana Univ. Press 1967

Bennett, M. V. L., Pappas, G. D., Aljure, E., Nakajima, Y.: Physiology and ultrastructure of electrotonic junctions. II. Spinal and medullary electromotor nuclei in mormyrid fish. J. Neurophysiol. **30**, 180–208 (1967)

Bennett, M. V. L., Steinbach, A. B.: Influence of electric organ control system on electrosensory afferent pathways in mormyrids. In: Neurobiology of cerebellar evolution and development, p. 207–214 (Llinas, E. R., ed), Chikago: American Medical Assoc. 1969

Blache, J.: Les poisson du bassin du Tchad et du bassin adjacent du Mayo Kebbi. Etude systématique et biologique. Paris: Orstom 1964

Black-Cleworth, P.: The role of electrical discharges in the non-reproductive social behaviour of *Gymnotus carapo* (Gymnotidae, Pisces). Anim. Behav. Monogr. **3**, 1–77 (1970)

Box, H. O., Westby, G. W. M.: Behavior of electric fish (*Gymnotus carapo*) in a group membership experiment. Psychon. Sci. **21**, 27–28 (1970)

Bullock, T. H.: Species differences in effect of electroreceptor input on electric organ pacemakers and other aspects of behaviour in gymnotid fish. Brain, Behav. Evol. **2**, 85–118 (1969)

Bullock, T. H., Hamstra, R. H., Scheich, H.: The jamming avoidance response of high frequency electric fish. J. comp. Physiol. **77**, 1–48 (1972)

Fiedler, K.: Ethologische und neuroanatomische Auswirkungen von Vorderhirnexstirpationen bei Meerbrassen (*Diplodus*) und Lippfischen (*Crenilabrus*, Perciformes, Teleostei). J. Hirnforsch. **9**, 481–563 (1967)

Gosse, J. P.: Le milieu aquatique et l'écologie des poissons dans la région de Yangambi. Annales du Musée Royale de l'Afrique Centrale—Tervuren, Belgique, série in — 8°—Sciences Zoologiques–no. **116**, 113–271 (1963)

Hopkins, C. D.: Sex differences in electric signalling in an electric fish. Science **176**, 1035–1037 (1972)

Kramer, B.: Zur hormonalen Steuerung von Verhaltensweisen der Fortpflanzung beim Sonnenbarsch *Lepomis gibbosus* (L.) (Centrarchidae, Teleostei). Z. Tierpsychol. 28, 351–386 (1971)

Larimer, J. L., Macdonald, J. A.: Sensory feedback from electroreceptors to electromotor pacemaker centers in gymnotids. Amer. J. Physiol. **214**, 1253–1261 (1968)

Leong, C. Y.: The quantitative effect of releasers on the attack readiness of the fish *Haplochromis burtoni* (Cichlidae, Pisces). Z. vergl. Physiol. **65**, 29–50 (1969)

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

Lissmann, H. W.: Ecological studies on gymnotids. In: Bioelectrogenesis, p. 215–226 (Chagas, C., Paes de Carvalho, A., eds.). Amsterdam: Elsevier 1961

Macdonald, J. A., Larimer, J. L.: Phase sensitivity of *Gymnotus carapo* to low-amplitude electrical stimuli. Z. vergl. Physiol. **70**, 322–334 (1970)

Möhres, F. P.: Elektrische Entladung im Dienste der Revierabgrenzung bei Fischen. Naturwissenschaften **44**, 431–432 (1957)

Moller, P.: Ein Beitrag zur Frage nach der Kommunikation unter schwach elektrischen Fischen (*Gnathonemus moori*, Mormyridae). Verh. Dtsch. Zool. Ges. (Würzburg) **33**, 482–489 (1969)

Moller, P.: "Communication" in weakly electric fish, *Gnathonemus niger* (Mormyridae). Variation of electric organ discharg e(EOD) frequency elicited by controlled electric stimuli. Anim. Behav. **18**, 768–786 (1970)

Moller, P., Bauer, R.: "Communication" in weakly electric fish, *Gnathonemus petersii* (Mormyridae). Anim. Behav. **21**, 501–512 (1973)

Poll, M.: Recherches sur la faune ichthyologique de la région du Stanley-Pool. Ann. Mus. Congo, sér. in — 8°, Zool., vol. **71** (1959)

Russell, C. J., Bell, C. C.: Short distance electrical interaction in a mormyrid fish. Soc. for Neuroscience, Second Annual Meeting (1972)

Russell, C. J., Bell, C. C.: Medium receptor mediation of the echo response, an electrical interaction between mormyrid fish. Soc. for Neuroscience, Third Annual Meeting (1973)

Serrier, J.: Comportement électrique de *Gnathonemus petersii:* modifications caractéristiques provoquées par un choc électrique unique. J. Physiol. (Paris) **65** (2), 302–303 (1972a)

Serrier, J.: Comportement électrique de *Gnathonemus petersii:* influence des paramètres intensité et durée d'une stimulation électrique artificielle. J. Physiol. (Paris) **65** (3), 503A (1972b)

Serrier, J.: Modifications instantanées du rythme de l'activité électrique d'un Mormyre, *Gnathonemus petersii*, provoquées par la stimulation électrique artificielle de ses électrorécepteurs. J. Physiol. (Paris) **66**, 713–728 (1973)

Siegel, S.: Nonparametric statistics for the behavioral sciences. New York: McGraw Hill Book Company, Inc. 1956

Szabo, T.: Activity of peripheral and central neurons involved in electroreception. In: Lateral line detectors, p. 295–311 (Cahn, P., ed.). Bloomington: Indiana Univ. Press 1967.

Szabo, T.: Central processing of messages from tuberous electroreceptors in teleosts. In: Electroreceptors and other specialized receptors in lower vertebrates. Handbook of Sensory Physiology, vol. III. Berlin-Heidelberg-New York: Springer 1974

Valone, Jr., J. A.: Electrical emissions in *Gymnotus carapo* and their relation to social behavior. Behaviour **37**, 1–14 (1970)

Wald, A., Wolfowitz, J.: An exact test for randomness in the non-parametric case based on serial correlation. Ann. Math. Stat. **14**, 378–388 (1943)

Westby, G. W. M.: Electric signalling and social behaviour in gymnotid fish. PhD Thesis, University of Reading, England 1972

Westby, G. W. M.: Comparative studies of the aggressive behaviour of two gymnotid fish. Anim. Behav. **22**, in press (1974)

Westby, G. W. M., Box, H. O.: Prediction of dominance in social groups of the electric fish, *Gymnotus carapo*. Psychonom. Sci. **21**, 181–183 (1970)

Wyman, R.: Probabilistic characterization of simultaneous nerve impulse sequences controlling dipteran flight. Biophys. J. **5**, 447–471 (1965)

Zipser, B.: The electrosensory system of Mormyrids. PhD Thesis, Albert Einstein College of Medicine, Yeshiva Univ., New York 1971

Dr. B. Kramer
Universität Konstanz
Fachbereich Biologie
D-7750 Konstanz
Postfach 733
Federal Republic of Germany

Note Added in Proof: The work of Russell and Bell (1972, 1973) has now appeared in a more detailed and accessible form:

Russell, C. J., Myers, J. P., Bell, C. C.: The echo response in *Gnathonemus petersii* (Mormyridae). J. comp. Physiol. **92**, 181–200 (1974)

Bell, C. C., Myers, J. P., Russell, C. J.: Electric organ discharge patterns during dominance related behavioral displays in *Gnathonemus petersii* (Mormyridae). J. comp. Physiol. **92**, 201–228 (1974)