INFLUENCE OF WATER TEMPERATURE ON THE ELECTRIC ORGAN DISCHARGE (EOD) OF THE WEAKLY ELECTRIC FISH MARCUSENIUS CYPRINOIDES (MORMYRIDAE)

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SUMMARY

1. The influence of different water temperatures on the electric organ discharge (EOD) of a mormyrid fish Marcusenius cyprinoides was studied. The range of the water temperatures was fixed according to the seasonal temperature variations of the rivers in Central Africa, the natural habitat of this species.

2. The EOD activity was characterized using the following parameters: mean EOD rate, EOD pattern in the form of Interpulse Interval Histograms (IIH), IIH range, and shortest pulse interval. These parameters remained constant during control experiments at constant temperature (27 °C) for 4 days.

3. The mean EOD rate increases with increasing water temperatures. The lowest mean EOD rate is always found at 17 °C, the highest between 26 and 33 °C. The characteristics of the IIH are modified by stepwise temperature increases. These IIH show during high temperatures (26–33 °C) similar patterns to those previously observed during high level motor activity and excitement. The IIH range diminishes with stepwise temperature increases. The shortest pulse interval has a negative, linear correlation with water temperature.

4. The possible role of water temperature in the reproduction of the mormyrids is discussed. The high discharge rate of M. cyprinoides produced by high water temperatures during the rainy season could serve to improve the resolution of the electroreceptors during this period.

INTRODUCTION

Many electric fish (such as the Mormyridormes and Gymnotoidei) have a weak electric organ discharge (EOD) of only a few volts at maximum. These so-called 'weakly electric fish' possess specific lateral line organs, the electroreceptors (Szabo & Fessard, 1963; Szabo, 1967; Derbin & Szabo, 1968), which respond to electric field gradients, produced either by their own EOD, or by the EOD of other electric fish. The combined function of the EOD and the electroperception allows the fish both to electrolocate nearby objects and to recognize other electric fish ('communication') (Lissmann, 1958; Lissmann & Machin, 1958; Hagiwara, Szabo & Enger, 1965; Belbenoit, 1970; Moller, 1970; Moller & Bauer, 1973; Westby, 1974, 1975a, b; Kramer, 1975, 1976).
Mormyrid fish display an irregular EOD pattern, strongly influenced by all kinds of exogenous factors: electrical, mechanical, chemical, optical, or thermal stimuli can effect the ongoing discharge activity (Moller, 1970; Moller & Bauer, 1973; Serrier, 1974, 1975; Kramer, 1975). The EOD pattern is equally influenced by various endogenous factors by the motor activity of the fish, or more generally, by its state of arousal or excitement (Lissmann, 1958; Dewsbury, 1964; Moller, 1970; Mortenson, 1970; Bauer, 1973; Westby, 1975a, b; Kramer, 1975, 1976). These factors produce variations in the mean discharge rate, cause sudden frequency accelerations ('bursts') and temporary cessations of EOD activity (Moller, 1970; Bauer, 1973; Serrier, 1974).

The importance of such variations is shown by the fact that a higher discharge rate probably improves the resolution of the electroreceptors (Lissmann, & Machin 1958; Schlegel, 1973). The rate of information input coming from the fish's environment is increased and might improve the electrolocation of objects and the electrical signalling in these fish.

It is well established that thermal changes influence the discharge rate of the regular discharging gymnotids (high- and low-frequency species) (Enger & Szabo, 1968; Boudinot, 1970; Feng, 1976). To find out how temperature changes alter the EOD patterns of the irregularly discharging mormyrids, we made a quantitative analysis of the relationship between water temperatures and the EOD patterns of a resting mormyrid fish.

*Marcusenius cyprinoides* were exposed to temperature changes of 17-33 °C, which is comparable to the range experienced in their natural habitat in tropical Africa (Blanc, Daget & D'Aubenton, 1955).

Our experiments showed that the EOD patterns are modified by temperature changes in a highly significant way. The higher electrical activity and improved resolution of the electroreceptors which is observed during high temperatures is probably of biological and ecological significance, since the breeding season of the mormyrids coincides with high water temperatures. This temperature effect plays an essential role in 'electrolocation' and 'electrosignalling' during the reproduction period.

**MATERIAL AND METHODS**

Juvenile specimens of the weakly electric fish *Marcusenius cyprinoides* (Mormyridae, Teleostei) were obtained from a tributary of Lake Chad, the Elbeid river, during an expedition in Central Africa in December 1974. They were kept in the laboratory, either isolated or in groups of 5-8 individuals, at a water temperature of 26-28 °C. The water resistivity was kept constant at about 550 μS.cm⁻¹. A diurnal cycle (D: 12/12) with light on from 7 to 19 h was maintained by means of a diffuse 60 W tungsten source.

Six fish from 11.0 to 16.5 cm length were used for the experiments. The fish remained under observation in a 4 x 12 cm porcelain tube placed on the floor of the 30 l experimental tank. Water resistivity and diurnal cycle were held constant before, during and after experimentation.
Recording

The EOD was recorded by means of two carbon electrodes placed at each side of the tube, near the head and the tail of the fish (Moller, 1970). The biphasic EOD pulses were first differentially amplified (Tektronix, 3 A3) and displayed on the first channel of an oscilloscope (Tektronix 561 A) (Fig. 1).

The pulses were fed in parallel into a pulse-former (Tektronix 161; pulse duration: 0.1 ms). The trigger pulses were displayed on the second channel of the oscilloscope and sent simultaneously to the first channel of a tape recorder (Revox, A 77) and to an audio monitor (Uher, Royal de Luxe). The fish was observed by means of a closed-circuit video system (Sony, CVM-306 UMP/3-2100). The tape recordings were fed into a digital analyser (Didac 800, Intertechnique) programmed to display the EOD activity in the form of Interpulse Interval Histograms (IIH).

Temperature regulation

The temperature-regulation system had to satisfy the following conditions: (1) that the obtained water temperature should stay within constant limits, (2) that a rapid change in water temperature should be possible. The temperature was controlled by means of a thermostatic bath and water circulation was maintained by a rotary pump. The water from the tank was first cooled down to 0 °C in a refrigerating system then warmed by a heating system. The latter was controlled by an electronic thermostat in which the thermistor sensor placed near the fish gave a precision of ±0.2 °C. Such a set-up allows a rapid and accurate change of ±1 °C of the water temperature over the whole experimental tank within 20 min (Fig. 2).
Experimental procedure

The fish were allowed a 2- or 3-day period of habituation to the experimental tank. The series of EOD recordings were carried out in the 5-7 days which followed.

Each experiment consisted of a stepwise change of the water temperature from 17 to 33 °C and back again in steps of 1 deg. At each degree the EOD of the six individuals was recorded twice: firstly when the water reached the desired temperature and secondly 10 min later.

Statistical analysis of the EOD recordings

As the IIH do not show a Gaussian distribution form (see Figs. 3, 5, 6), the significance of the different IIH was first tested by means of the non-parametric Kolgomorov–Smirnov test. This statistical method, however, had to be abandoned because of its extremely high sensitivity: very small variations in the histograms accumulated under the same conditions (constant temperature) always gave significant differences. The test could therefore not be used to compare the IIH of EOD activity under different temperature conditions. The asymmetric histograms were therefore compared simply by calculating the medians of the distributions. A chi-square test was then used to test for significant differences.
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RESULTS

(A) EOD rate

The EOD activity of *M. cyprinoides* was analysed using Interpulse Interval Histograms (IIH).

The IIH represents a quantitative analysis of the pulse intervals in a fixed recording period. It gives a global representation of EOD activity, enabling comparison of preferred discharge frequencies. However, it should be noted that the IIH gives no information about the sequential order of these pulse intervals. This is of only minor importance in the following experiments, because the unstimulated, irregularly discharging mormyrid shows no regular variation in the sequential order of interval while resting.

In the five *M. cyprinoides* examined, the IIH are characterized by an asymmetric distribution which can be uni-, bi- or trimodal, varying individually. The position of the modes in the IIH indicates the preferred EOD frequencies (Bauer, 1973). The first modes (10–35 ms, i.e. 100–29 Hz) are always due to spontaneous EOD rate accelerations, called 'bursts' (Moller, 1970). The second mode corresponds to an interval population situated in a lower frequency range (50–120 ms, i.e. 20–8 Hz), and seems to be very sensitive to endo- and exo-genous factors. In a few cases, a third mode (200–550 ms, i.e. 5–1.8 Hz) appeared.

Table 1. Shortest pulse-intervals (ms) of the IIH of the individuals *F₂, F₃* and *F₄* submitted to constant temperatures of 27.0 °C

<table>
<thead>
<tr>
<th>Days</th>
<th><em>F₂</em></th>
<th><em>F₃</em></th>
<th><em>F₄</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(\bar{x} \pm \sigma)</td>
<td>(\bar{x} \pm \sigma)</td>
<td>(\bar{x} \pm \sigma)</td>
</tr>
<tr>
<td>1</td>
<td>10.8 ± 0.71</td>
<td>16.0 ± 0.66</td>
<td>14.4 ± 1.85</td>
</tr>
<tr>
<td>2</td>
<td>10.5 ± 0.54</td>
<td>15.8 ± 2.25</td>
<td>13.9 ± 1.73</td>
</tr>
<tr>
<td>3</td>
<td>11.1 ± 0.36</td>
<td>16.3 ± 1.58</td>
<td>15.0 ± 1.60</td>
</tr>
<tr>
<td>4</td>
<td>10.5 ± 0.53</td>
<td>16.5 ± 1.00</td>
<td>13.8 ± 1.17</td>
</tr>
</tbody>
</table>

The IIH show a range that fluctuates under natural conditions between 10 and 350 ms (≈ 100–2.8 Hz). The left extremity (shortest pulse interval) is constant for the same individual, whereas the right one (largest pulse interval) shows large variations, mainly due to temporary cessations of EOD activity.

To study the variations of EOD activity due to the modification of a single external parameter (temperature), the limits of EOD variations of *M. cyprinoides* under constant conditions must first be described.

(B) EOD rate under constant conditions (fixed temperature).

The temperature in the control experiments was fixed at 27.0 °C. As in the experimental phase, the stability of the following parameters was considered: (a) the distribution of the pulse intervals (IIH), (b) the range of the IIH, and (c) the mean EOD rate.

(a) The distribution form of the EOD activity of *M. cyprinoides* remains stable over 4 consecutive days (Fig. 3). First a statistical test for constancy was used by comparison of the IIH medians (Table 3A). The medians of the IIH are situated in
individually different positions (differing for fish 2, fish 3, fish 4), whereas the single values are significantly constant for the same individual. Secondly, the form of the distribution of the IIH remains stable (Fig. 3). F₃ and F₄ display a constant unimodal IIH, in contrast to F₂ which always presented a bimodal distribution. Modal population values stay constant. The unimodal population (F₃ and F₄) lies between 15 and 120 ms, i.e. 67–8 Hz.

Both populations of the bimodal IIH of F₂, the one at 11–25 ms, i.e. 90–40 Hz, representing ‘burst’ activity, and the one at 35–90 ms, i.e. 29–11 Hz, lie within that of the unimodal distribution range of F₃ and F₄. However, the second population seems to be less constant than the first ‘burst’-like frequency population (Fig. 3).

(b) The range of the IIH of the individuals F₂, F₃ and F₄ shows only slight variations during the 4 successive days of recordings. These variations are exclusively due to the high variability of the longest pulse intervals (right IIH extremity) (Fig. 4). In contrast, the shortest pulse intervals remain strictly constant (see Table 1).

(c) The mean values and standard deviations of the EOD rate of each irregularly discharging *M. cyprinoides* remains fairly constant – in spite of sudden accelerations as well as temporary cessations – during the 4 following control days (Table 2). The
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Fig. 4. Schematic representation of IIH ranges over 4 successive days (horizontal bars) for three *M. cyprinoides*. Constant temperature conditions of 27 °C. Mean EOD rate in Hz for each fish over the total recording period is given. Figures at each end of IIH ranges express the total variation in shortest and longest interval.

Table 2. Mean EOD rates of *M. cyprinoides* at constant temperature of 27-0 °C
(Same conditions as in Table 1.)

<table>
<thead>
<tr>
<th>Days</th>
<th>F2</th>
<th>F3</th>
<th>F4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(8.6 \pm 3.41)</td>
<td>(11.7 \pm 6.63)</td>
<td>(25.4 \pm 4.24)</td>
</tr>
<tr>
<td>2</td>
<td>(8.2 \pm 0.86)</td>
<td>(10.8 \pm 5.87)</td>
<td>(19.8 \pm 9.77)</td>
</tr>
<tr>
<td>3</td>
<td>(7.9 \pm 1.33)</td>
<td>(10.1 \pm 5.43)</td>
<td>(13.4 \pm 6.38)</td>
</tr>
<tr>
<td>4</td>
<td>(8.8 \pm 1.15)</td>
<td>(10.2 \pm 5.34)</td>
<td>(16.8 \pm 2.58)</td>
</tr>
</tbody>
</table>

Mean EOD rates are different according to individual range (F2: 8 Hz; F3: 11 Hz; F4: 18 Hz). The greatest variation in mean EOD rate is observed for the individuals discharging in the highest frequency range (F4: 18 Hz) (see Table 2).

II. Effects of different water temperatures on the EOD of *M. cyprinoides*

To determine the influence of the temperature on the EOD rate, a range between 17 and 33 °C was chosen. Such a range corresponds to the temperature variations of the waters in the tropical areas of Central Africa, the natural environment of these mormyrids (Blanc *et al.* 1955).

The specimens used were caught during the ‘winter’ in waters ranging from 18 to 22 °C. During the ‘summer’ in this area the deep water in ponds can reach 32 °C.
Fig. 5. IIH of the EOD activity of a resting _M. cyprinoltes_, F3, submitted to temperature changes from 17 to 33 °C. Abscissa, interval length in milliseconds; ordinate, number of intervals per 1 ms bin. Note progressive modification of the interval distribution towards higher frequencies with increasing water temperatures.

(A) Effect on the distribution form of the IIH.

(1) Modification of the IIH of EOD activity over the whole temperature range. Fig. 5 gives an example of the IIH modification of the EOD activity of F3, submitted to increasing temperatures (17–33 °C). The IIH show a fairly regular distribution for low temperatures (17–19 °C) with two pulse interval populations clearly distinguishable.

At 19 °C the second mode is condensed to its maximum. From 20 °C upwards its relative percentage decreases and the centre shifts towards higher frequencies. Between 22 and 24 °C the distribution becomes asymmetric and the mode shifts towards still higher frequencies with a considerable increase in size (relative percentage of _N_i). The IIH range is reduced to half the size of that at low temperatures. The second mode disappears, but a short ‘tail’ remains up to higher temperatures.

From 25 to 28 °C the main pulse interval population still grows in percentage and
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shifts to the left. Although there are slight differences in form, it can be noted that the distribution of the population remains the same. The IIH range is reduced by another 50–100 ms.

At 29°C the population of the pulse interval reaches its maximum of relative percentage of \( N_i \), simultaneously the IIH range is reduced to its minimum.

From 29 to 33°C there are no further notable changes in the IIH. Fig. 5 shows the important influence of temperature on EOD activity of *M. cyprinoides*.

(2) *IIH of the EOD activity at three different temperatures (17, 25, 33°C)*. A more detailed and quantitative analysis was made for three given temperatures (17, 25, 33°C) and was carried out on five individuals. These fish showed two different types of IIH: tri/bimodal (F2, F5, F6) and bi/unimodal (F3, F4). Two representative examples are given in Fig. 6.

17°C. At this temperature the pulse intervals fluctuate from 24 to 800 ms (i.e. 42 to 1.3 Hz). For F5, the lower frequency range (200–800 ms, i.e. 7.3–5 Hz) contains a population of pulse intervals that represents 60% of the whole IIH. At higher frequencies (24–200 ms, i.e. 42–5 Hz) two populations can clearly be distinguished. The first one, with its peak at 26 ms, i.e. 38.5 Hz, represents the high-frequency accelerations (‘bursts’) and is about 16% of \( N_t \) (total number of pulse intervals). The ‘main’ mode (20% of \( N_t \)) is centred at 90 ms, i.e. 11.1 Hz. For F3, the IIH range is narrower (60–600 ms, i.e. 16.6–1.6 Hz). In F5, except in the ‘burst’ population which is not present at 17°C, two widely spread populations constitute the IIH. A population is grouped around 114 ms, i.e. 8.7 Hz, representing 35% of \( N_t \), the population in the lower frequency range is centred at 460 ms, i.e. 2.2 Hz, and consists of 60% of \( N_t \).

25°C. An 8°C increase of the temperature from 17 to 25°C induces various modifications in the IIH: in all cases a reduction of the IIH range to half of the values at 17°C (Fig. 7), associated with more than double the number of pulse intervals (\( N_i \)) (Table 3B and Fig. 6). In F5 both upper populations are present, although they tend to overlap. The ‘burst’ mode focuses at 17 ms, i.e. 58.8 Hz, the second around 45 ms, i.e. 22.2 Hz. The relative percentage of each population increases slightly, but the size of the ‘burst’ population around the main mode stays relatively constant (about 25% of \( N_t \)). There is also a peak around 180 ms, i.e. 5.5 Hz, in a population representing about 50% of \( N_t \), spread from about 100 to 360 ms.

In F3, the upper, ‘main’ mode also moves towards higher frequencies and lies at 82 ms, i.e. 12.2 Hz. The frequency shift of this mode is relatively smaller than for that of F5 (from 114 to 82 ms, i.e. 8.7–12.2 Hz), but the size of the peak increases up to 18% of \( N_t \), and the associated population accounts for more than 80% of \( N_t \).

The second mode, observed at 17°C near 400 ms, i.e. 7.7–3.1 Hz) contain less than 20% of the IIH distribution, with no precise accumulation.

33°C. The IIH range undergoes a further decrease. The modes shift towards still higher frequencies and their size increases.

In F5 the two modes can still just be distinguished. The ‘burst’ activity mode is constituted of two close peaks, at 10 and 13 ms, i.e. 100 and 77 Hz. The size of the population grouped around the main mode has not varied constituting less than 20% of \( N_t \).
The peak of the ‘main’ population moves up to 38 ms, i.e. 26.3 Hz, with a relative increase of 3.5%. This population exceeds 50% of $N_i$. Beyond 100 ms the rest of the distribution is fairly regular, and declines at about 300 ms.

In F3 the single population now peaks at 51.0 ms, i.e. 19.6 Hz. At this temperature it represents almost the entire population, only a few pulse intervals are distributed beyond 140 ms.
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Fig. 7. Schematic representation of IIH ranges (mean values) of five *M. cyprinoides* at three temperatures: 17, 25 and 33 °C. Note the decrease of the IIH range and the shift towards higher frequencies.

Fig. 8. Mean EOD rate of four *M. cyprinoides* submitted to increasing (● ... ●) and decreasing (■ — ■) water temperatures. Ordinate, mean EOD rate expressed as percentage of total number of pulse intervals (N).
(B) The range of the IIH

As described above, increasing water temperatures cause a shift of the population of pulse intervals towards higher frequencies (Fig. 6). In Fig. 7 the mean values of all experiments with five individuals are given. It shows the modification of the limits of the IIH range with the different water temperatures (17, 25, 33 °C). Although the temperature step is the same (8 °C), the modification of the IIH range is more important between 17 and 25 °C than between 25 and 33 °C.

(C) Mean EOD rate and IIH medians

The mean EOD rate of *M. cyprinoides* shows slight variations, even in a resting animal (compare § I, B, c). Various external factors, such as mechanical vibrations in the building, and the internal state of arousal related to circadian rhythms, may interfere. Moreover, interruptions of a few days in the recording sessions in most cases probably caused the variation in the mean EOD rate. In spite of these factors a relationship between temperature and mean EOD rate could be established (Fig. 8). The four individuals (F1, F2, F3, F5) examined in this respect show an increase of their mean EOD rate related to the temperature level.

### Table 3. Medians of IIH in experimental fish F2, F3, F5, F6

<table>
<thead>
<tr>
<th>°C</th>
<th>N</th>
<th>M</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Control experiments (Fig. 3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F2</td>
<td>27</td>
<td>1486</td>
<td>11611</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>1503</td>
<td>10247</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>1502</td>
<td>10721</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>1713</td>
<td>11392</td>
</tr>
<tr>
<td>F3</td>
<td>27</td>
<td>1562</td>
<td>1872</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>2092</td>
<td>5983</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>1827</td>
<td>7620</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>1948</td>
<td>5899</td>
</tr>
<tr>
<td>F4</td>
<td>27</td>
<td>2027</td>
<td>4589</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>2378</td>
<td>5822</td>
</tr>
<tr>
<td></td>
<td>27</td>
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</tr>
<tr>
<td></td>
<td>27</td>
<td>1730</td>
<td>4890</td>
</tr>
<tr>
<td>(B) Effect of different temperatures</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F2</td>
<td>17</td>
<td>724</td>
<td>15540</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>1363</td>
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</tr>
<tr>
<td></td>
<td>33</td>
<td>3009</td>
<td>4597</td>
</tr>
<tr>
<td>F3*</td>
<td>17</td>
<td>353</td>
<td>19507</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>1681</td>
<td>8038</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>2698</td>
<td>5537</td>
</tr>
<tr>
<td>F5*</td>
<td>17</td>
<td>610</td>
<td>15508</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>1034</td>
<td>10412</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>1942</td>
<td>5516</td>
</tr>
<tr>
<td>F6</td>
<td>17</td>
<td>661</td>
<td>14557</td>
</tr>
<tr>
<td></td>
<td>25</td>
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<td>8591</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>2689</td>
<td>4505</td>
</tr>
</tbody>
</table>

* See also Fig. 6.
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Linearity and correlation cannot be tested because of the modification in the modalities of IIH distribution, even in unimodal IIH that are not stable (bimodality at low temperatures). For this reason significant changes in IIH from 17 to 33 °C were tested by calculating the medians of the histograms. In contrast to the medians of the control experiments, which showed that the IIH belonged to the same population (Table 3A), the medians here are highly significantly different at the various temperature levels (Table 3B).

These quantitative results confirm that temperature has a significant influence on the IIH and the mean EOD rate.

Fig. 9. Temperature-dependent modification of the shortest pulse interval of four *M. cyprinoides* submitted to increasing (●) and decreasing (▼) water temperatures. Triangle with dot, single value at 33 °C. Ordinate, duration of shortest pulse interval in milliseconds and corresponding value in Hz.
Table 4. Regression coefficients \((a, b)\) and correlation \((r)\) of the shortest pulse-intervals during increasing \((°)\) and decreasing \((\nabla)\) temperatures (see Fig. 9)

\[
\begin{array}{|c|c|c|c|c|}
\hline
\text{Time (min)} & a & b & r & P \\
\hline
F_1 & 0 & \text{0.36} & 26.13 & 0.6355 & 0.010 \\
& 10 & \text{0.39} & 25.74 & 0.6147 & 0.010 \\
& \nabla & \text{-1.32} & 51.44 & 0.8347 & 0.001 \\
& 10 & \text{-0.52} & 28.11 & 0.6627 & 0.010 \\
F_2 & 0 & \text{0.88} & 34.71 & 0.9328 & 0.001 \\
& 10 & \text{0.83} & 33.25 & 0.9389 & 0.001 \\
& \nabla & \text{-0.84} & 34.84 & 0.9559 & 0.001 \\
& 10 & \text{-0.77} & 32.94 & 0.8758 & 0.001 \\
F_3 & 0 & \text{-0.94} & 36.53 & 0.8306 & 0.001 \\
& 10 & \text{-0.75} & 30.93 & 0.8013 & 0.002 \\
& \nabla & \text{-1.33} & 47.63 & 0.8402 & 0.001 \\
& 10 & \text{-0.95} & 37.83 & 0.9232 & 0.001 \\
F_6 & 0 & \text{-1.23} & 44.94 & 0.8708 & 0.001 \\
& 10 & \text{-0.96} & 37.78 & 0.8687 & 0.001 \\
& \nabla & \text{-0.95} & 38.30 & 0.8711 & 0.001 \\
& 10 & \text{-1.10} & 41.92 & 0.8529 & 0.001 \\
\hline
\end{array}
\]

(D) Relation between the temperature and the shortest pulse interval.

As mentioned in §11, the temperature and the upper limit of the IIH range are related. This relationship was analysed in four fishes for each degree from 17 to 33 °C – both ascending and descending (Fig. 9). The shortest pulse interval diminishes regularly with step-wise increasing temperatures, changing gradually from 22-27 ms, i.e. 45-37 Hz, to 7-9 ms, i.e. 143-111 Hz. This relationship is linear and has a negative slope with values ranging from \(a = -0.36\) to \(-1.32\). The correlation coefficients vary between \(0.61\) and \(0.96\), showing for the four individuals a highly significant linearity of the relationship and a probability of non-linearity less than \(0.001\), except for individual \(F_1\) (see Table 4). This animal's burst-activity was very irregular, probably due to its unusual restlessness.

**DISCUSSION**

Temperature influences on the mean EOD rate of the regularly discharging gymnotids and gymnarchids have been described by several authors (Lissmann, 1958; Enger & Szabo, 1968; Boudinot, 1970; Feng, 1976). Our results show that in the mormyrid fish *Marcusenius cyprinoïdes*, the very irregular EOD activity is also dependent on the water temperature. The bulk of this work consists of a quantitative analysis of the different EOD parameters and their dependency on water temperature.

It was demonstrated that:

1. Under constant temperature conditions the IIH are easily reproducible (Fig. 3A);
2. The water temperature has an influence on the mean EOD rate (Fig. 8) and a highly significant influence on the medians of the IIH (Table 3B);
3. Increasing the water temperature \((17-33 \, ^\circ C)\) shifts the pulse-interval population gradually towards shorter intervals (higher frequencies) and its size simultaneously
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increases (Fig. 5, 6). At the same time the range of the IIH decreases (Fig. 7) and the shortest pulse-interval diminishes (Fig. 9) in a highly significantly linear manner.

The mean EOD rate has a strict relationship with the water temperature, independent of the individual differences in the frequency range. The linear relationship in the regular discharging gymnotids reported by Enger & Szabo (1968) and Boudinot (1970) could not be demonstrated in mormyrids. This is due to the irregular distribution of pulse-intervals in ‘patterns’ and the presence of ‘burst’ activity (see below). Moreover, spontaneous variations in frequency were encouraged by external disturbance and were specially marked after pauses of more than 1 day (see arrows in Fig. 8). These variations are also seen in the control experiments: indeed the level of the mean EOD rate of each individual shifts from day to day according to factors that are not clearly distinguishable.

All these variations were too great for the detection of the very small variations of the mean EOD rate, described as a hysteresis in gymnotids by Boudinot (1970). This author demonstrated that the frequency values for a given temperature reached by an increase in temperature are less than those obtained by a decrease.

If we examine the relationship between temperature and shortest pulse interval rather than mean EOD rate (Fig. 9), a hysteresis can be shown. The values of the shortest pulse interval in *M. cyprinoides* are in fact significantly higher ($P=0.010$) during increasing than during decreasing temperatures. Thus, a hysteresis phenomenon may also exist in mormyrid fish, but for the shortest pulse interval it is the inverse of that observed by Boudinot (1970) concerning the mean EOD rates of the gymnotid fish *Eigenmannia*. These opposite effects in the two fish families may possibly be due to the different control mechanisms of the EOD. Higher water temperatures modify the IIH of the individuals, in spite of a lack of change in their motor activity, i.e. they remain in resting position in their tubes. However, the two discernible modes of the EOD patterns of the resting *M. cyprinoides* are not modified in the same way:

(a) The high-frequency mode (Fig. 6, F5), in individuals where it is present, is only slightly modified (position, size) by the different temperatures. Similar observations were reported by Moller (1970) in response to diurnal changes in motor activity, the high-frequency mode remaining largely constant at about 30 Hz.

In addition, this mode does not appear at higher temperature in fish which fail to show high-frequency ‘bursts’ at control temperature (see Fig. 3, F3, F4; Figs. 5, 6).

It should be noted that the individuals of this second group of fish had been kept isolated for several months before the experiment. The lack of ‘burst’ activity in these individuals could perhaps have resulted from the absence of social contact.

(b) In contrast, the second ‘main’ mode, lying in a slightly lower frequency range and appearing regularly in all individuals, is the interval population whose position and size depends very much on the different temperatures (Figs. 5, 6) and affects the mean EOD rate (see Fig. 8). The effect of the higher water temperatures on this ‘main’ mode is in fact comparable with that of increased motor activity, as described by Moller (1970) and Serrier (1974), even though the fish remain in resting position: both result in an increase of size and a simultaneous shift of the second mode towards higher frequencies.
Possible physiological mechanisms concerning the action of temperature on the EOD activity

Two facts, firstly that only the temperature of the head and not of the fish's body region is responsible for a modification of the EOD activity, and secondly, that the latency between the change of the temperature and the modification of the EOD activity lasts 5–12 s, led Enger & Szabo (1964, 1968) to the conclusion that for the temperature effect in gymnotids, no sensory pathways between the cutaneous thermoreceptors and the pacemaker centres are involved. It is likely that temperature acts directly on the EOD command centre by means of a change in metabolic rate. The latter leads to an increase of impulse activity of this part of the brain, modifying finally the EOD activity.

Besides a direct temperature action, other possibilities cannot be excluded. An indirect temperature action on the pacemaker centre via the hypothalamus can be suggested: in fact, special vascular receptive structure as well as surface thermoreceptors (Kahn, 1904) are localized in the supra- and preoptic regions of the hypothalamus (Magoun et al. 1938; Boulant, 1976). The environmental temperature changes being transmitted to these areas via the blood stream are detected by the hypothalamic thermoreceptive structures and then transferred, via neuronal interconnections, to the mesencephalic or bulbar command centre.

Similarly, the temperature actions in the hypothalamus could induce a modification of hormonal processes. In cyprinids (Teleostei) it has been shown that high temperatures have a significant effect on triggering gametogenesis (Breton, Billard & Gillet, 1976). Thus, it seems possible that in mormyrids the reproduction cycle as well as the aggressive behaviour during this period is influenced by temperature in a similar way. Indeed, maximum discharge frequencies (≈ 143 Hz) of M. cyprinoides observed at high temperatures are comparable with the discharge frequencies (≈ 140 Hz) of the mormyrid fish Gnathonemus petersii emitted during agonistic interactions (Bauer, 1972).

The temperature of the water surface of a subtropical river, which is inhabited by M. cyprinoides, varies over the year between 19 and 31 °C. These temperatures lie during the rainy period (May–October) between 28 and 31 °C, and in the dry season between 19 and 22 °C (Blanc et al. 1955).

Just as in the experiments described above, the different river temperatures should be able to modify the EOD activity of M. cyprinoides in similar way. Due to the high temperature-dependent increase of EOD activity, the resolution of the electroreceptors should be improved. This, in turn, should improve electrolocation and electric signalling.

As the period of the high water temperatures (rainy season) coincides with the breeding season of these fishes, the reported effect of high temperatures will improve the resolution of the electroreceptors and automatically the electrolocation and electric signalling of the mormyrids during their reproductive period. Possibly, this effect of temperature is an essential factor for the survival of this and other species.

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