Agonistic Behaviour in Mormyrid Fish: Latency – Relationship Between the Electric Discharges of *Gnathonemus petersii* and *Mormyrus rume*

Gnathonemus petersii exhibits rapid frequency rises of its electric organ discharge (EOD), and sterotyped, regular pulse patterns of high frequency, when a *Mormyrus rume* is introduced into its aquarium[1]. These phenomena are strictly associated with certain components of aggressive behaviour[2], which are identical with those observed in intraspecific agonistic behaviour[3]. In this paper, a latency relationship of the pulses of a territorial *G. petersii* to those of an intruding *M. rume* will be described, this being of interest in order to assess the role which the EOD might play in 'communication' between individuals.

The experimental tank measured $1.0 \times 0.4 \times 0.5$ m. 120 fine silver wires, making only point contact, were fixed on the walls, the bottom, and onto a floating plastic cover, forming a regular array on each of the 6 surfaces. Each silver wire was connected, through a 47 kΩ 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 3 pairs of opposite electrodes, orientated orthogonally, were differentially connected to 3 separate 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 their duration (*G. petersii*: approx. 300 µsec; *M. rume*: approx. 600 µsec). A data acquisition system (Intertechnique) was used to measure the length of intervals and latencies, and to compute histograms.

A 12 h/12 h light – dark cycle was used throughout the experiments, temperature varied from 26 to 27 °C. Successive 5 day series of experiments were performed with 6 *G. petersii* (15.5–20.5 cm), each of which had been habituated to the experimental tank prior to the first experiment for at least 3 days.

A *M. rume* (20.5 cm) was put into the experimental tank, where a *G. petersii* was hiding in a tube of plastic mesh, for 3 min a day. During this experimental period, *M. rume* discharged very regularly at about 25 Hz (Figure 1a), abrupt frequency rises never occurred and 'breaks' were very rare; when changing frequency, it slowly shifted up or down. *G. petersii*, however, in most cases stopped its discharge for some seconds on the introduction of *M. rume*; when the latter came near its hiding place, it vigorously attacked *M. rume*, while displaying a sharp increase of EOD frequency and eventually a regular, high frequency pulse pattern[1]. A sequence of many attacks and pursuits of the *M. rume* by the *G. petersii* during the rest of the 180 sec experimental period followed. The pulse interval histograms of *G. petersii* show peaks at about 140 and 70 Hz (Figure 1b), which correspond to the regular high frequency discharge pattern displayed during a particular agonistic behaviour[2]. In these histograms, a definite minimum, observed in each experiment, is found at about 100 Hz (or 9 to 11 msec interval length).

When evaluating the time elapsing between the occurrence of a *M. rume* discharge, and the immediately following *G. petersii* pulse, and representing the results statistically, a latency relationship is found (Figure 1c). In this latency distribution of *G. petersii* pulses to *M. rume* pulses, a peak in the class of 10–11 msec, distinct in

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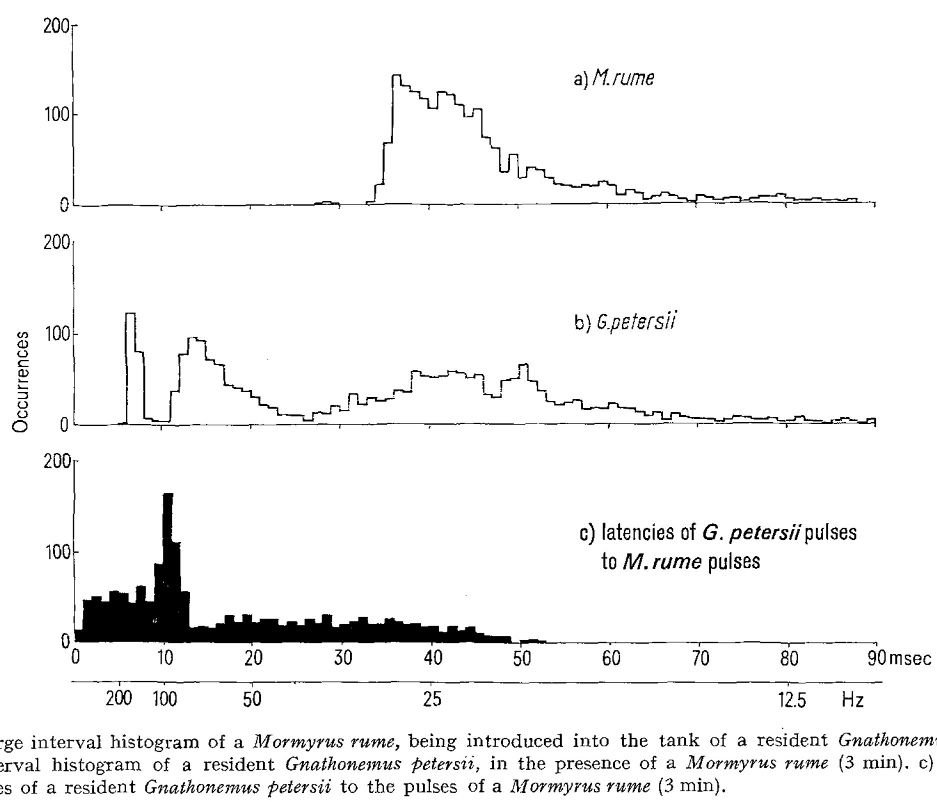

Fig. 1. a) Discharge interval histogram of a *Mormyrus rume*, being introduced into the tank of a resident *Gnathonemus petersii* (3 min). b) Discharge interval histogram of a resident *Gnathonemus petersii*, in the presence of a *Mormyrus rume* (3 min). c) Histogram of the discharge latencies of a resident *Gnathonemus petersii* to the pulses of a *Mormyrus rume* (3 min).

each experiment, is particularly noticeable. This means that *G. petersii* prefers to respond to an exteroceptive electric stimulus, perceived through its electroreceptors, by an electric organ discharge within about 11 msec.

As pointed out by electrophysiological work, 7–8 msec are required to conduct the command signal from the medulla oblongata to the electric organ in mormyrids[4]. Hence less than 4 msec remain for the transmission of the coded receptor signal to the medulla oblongata, via 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, are capable of such a rapid signal transmission[5–7]. This pathway comprises neurons with axons of large diametre, and probably electrical synapses between them[8].

Although a latency of about 11 msec 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 Figure 1c. Shorter latencies than the 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.

The observation reported in this paper demonstrates a hitherto unknown interaction between the discharges of 2 electric fish at the interval level, indicating the existence of an extremely rapid reflex arc. This reflex arc seems to be specifically involved in the perception of, and in responding to, the electric signals of congeners because of 2 reasons: 1. The threshold to short electric stimuli is low in tuberous receptors, compared with the other electroreceptor types[5], enabling the fish to detect a conspecific, when the distance between them is ca. 30 cm or less[9]; 2. When responding to the fish's proper discharge, tuberous receptor evoked activity in ganglion cells of the lobus lateralis was found to be inhibited[10]. This excludes the possibility of a significance of tuberous receptors, and their cerebral connections, in electrolocation, and suggests their importance in 'communication'.

Zusammenfassung. Während des agonistischen Verhaltens beantwortet *G. petersii* elektrische Organentladungen eines *M. rume* statistisch bevorzugt nach einer Latenzzeit von nur ca. 11 msec. Dies deutet auf die Existenz einer besonders raschen Reflexbahn hin, deren spezifische Aufgabe offenbar die Wahrnehmung und Beantwortung elektrischer Fremdsignale ist.

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The Effects of Reticular Stimulation on Digastric Reflex Activity During Sleep and Wakefulness

The spontaneous variations in digastric reflex (jaw-opening) activity during the course of sleep and wakefulness have been extensively investigated[1]. The orbital cortical control of this reflex during sleep and wakefulness in freely moving cats has also been described[2,3]. In immobilized cats, which presumably are awake, electrical stimulation of the reticular formation can modify digastric reflex activity[4,5]. We were therefore interested in determining whether stimulation of the reticular formation, in freely moving unanesthetized cats, would influence this reflex not only during wakefulness but also during sleep. In this paper we present data which indicate that electrical stimulation of the reticular formation exerts a consistent pattern of digastric reflex inhibition throughout quiet sleep and active sleep as well as during wakefulness.

The details of the experimental preparation for stimulation and recording with permanently placed electrodes in the freely moving cat have been previously described[1]. 6 adult cats were used in this experiment. Bipolar stimulating electrodes were placed in the pontomesencephalic reticular tegmentum. The digastric reflex was induced by electrical stimulation of the inferior dental nerve with a pair of stainless steel screws embedded in the mandibular canal. The reflex was monitored electromyographically by a pair of bipolar electrodes placed around the anterior belly of the digastric muscle. Other bipolar electrodes were used to record the frontal cortical EEG, eye movements (EOG) and neck EMG. The digastric reflex was monitored oscilloscopically and was recorded on a polygraph by utilizing a peak-amplitude, time-expanding electronic circuit.

Experimental sessions, which were started at least week after electrode implantation, were conducted in an environmental chamber where the animal was able to move about freely. The behavior of the animal was observed through a one-way window. Each experimental session lasted approximately 3 h, during which time continuous recordings of consecutive cycles of sleep and wakefulness were obtained. The digastric reflex was induced continuously throughout each session at rates of 0.5 to 1 per sec. The amplitude of the digastric reflex which followed short pulse train reticular stimulation (1–4 pulses; conditioning-test latency 0–20 msec) was compared with the amplitude of immediately preceding control reflexes during the states of wakefulness, quiet sleep and active sleep. The intensity of the reticular

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