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Capacitance Discrimination in Electrolocating, Weakly Electric Pulse Fish

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Mormyrid, weakly electric fish emit and receive brief electric signals (electric organ discharges, EOD) for the purpose of active electrolocation [1] and electrocommunication [2]. During active electrolocation, a fish monitors its own signals with cutaneous electroreceptors in order to detect and evaluate nearby objects [1]. Electrolocating mormyrids are especially sensitive to capacitive object properties. Such capacitive attributes are found mainly in living objects [3–5]. Mormyrids can unequivocally distinguish capacitive objects from purely resistive objects [3, 6]. This surprising finding showed that mormyrids can sense both the resistive and the capacitive components for the complex impedance of an object. It is not known, however, whether they can also evaluate the magnitude of the capacitance and thus discriminate between objects of different capacitive values. Using a conditioned discrimination procedure, I tested the mormyrid fish *Gnathonemus petersii* for its ability to discriminate between two capacitive objects during electrocation. It turned out that *G. petersii* can do so only if the capacitive values of the objects are different from each other by a factor of about four.

An object with an impedance that is different from that of water alters the local EOD amplitude when placed near the skin of the fish. An object with capacitive properties also alters the local EOD waveform [3]. It has been hypothesized [3, 6, 8] that mormyrids detect capacitances by measuring these EOD waveform distortions. The hypothesis is supported by three findings: 1) Mormyrids can only detect capacitances that cause waveform distortions. If the same kind of objects as in this study are used, *G. petersii* can detect capacitances with values between about 0.3 and 300 nF [3].

2) All mormyrid species tested so far are able to discriminate between a capacitive and a resistive object even if both cause the same local amplitude change, but only the capacitive one causes waveform distortions [6]. 3) Electrophysiological recordings from primary electroreceptor afferents showed that one of the two classes of primary afferents from mormyromast electroreceptors [7] is extremely sensitive to waveform distortions [8].

The accuracy with which mormyrid fish of the species *G. petersii* can discriminate between different capacitive objects was tested in five fish. These fish were trained in a two-alternative forced-choice procedure to discriminate between two objects with different capacitive properties. The objects were identical except for the capacitive properties. Each of the two objects was placed in front of a gate. Their electrical properties could be changed quickly from outside the aquarium. The testing procedures and apparatus are described in detail elsewhere [3, 6]. Briefly: The fish had to choose the correct object by swimming through the corresponding gate. The fish were rewarded with a small food reward if they chose the object with the correct capacitance, as defined by the experimenter.

A single capacitive value was defined as correct (S+) for each fish. Different S+'s had values between 0.35 and 50 nF and thus covered well the detectable range of capacitances of *G. petersii*. A descending method of limits was used to determine the just noticeable difference (JND) in capacitance. Two thresholds were determined for each fish: the "upper" threshold, where the negative stimulus (S–) had a larger capacitance than the S+, and the "lower" threshold, where S– had a smaller capacitance than

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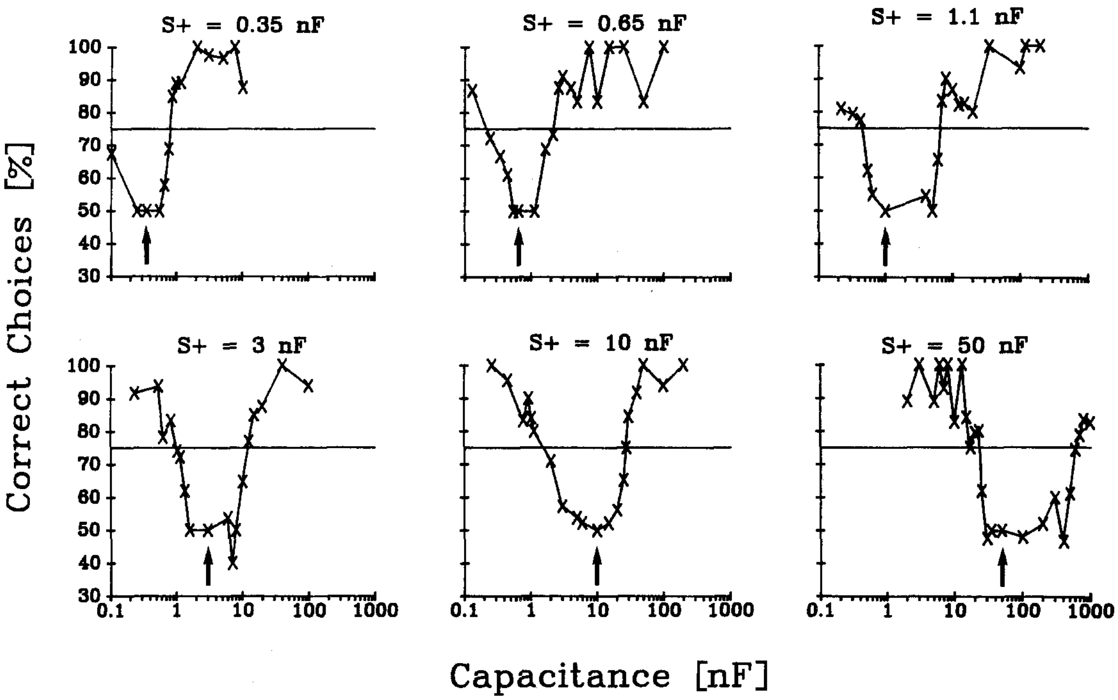

Fig. 1. Each diagram shows the psychometric function of one *Gnathonemus petersii* discriminating between two capacitive objects. The *arrows* indicate the point where the two objects had the same capacitance. The abscissa represents the capacitive values of the negative stimuli (S–) that had to be discriminated from the positive stimulus (S+), which was an object with the capacitive value under the arrow. All curves are U-shaped, i.e., fish could discriminate well between the two objects if their capacitive values were different, but not if they were similar. In the latter case, performance dropped to chance level (= 50 % correct choices). Thresholds were defined at the X-values where the curves crossed the horizontal 75 % line. Each point consists of at least 50 decisions by a fish

S+. Thresholds were defined as the capacitance of the S– where the fish made 75 % correct choices. This value was interpolated from the psychophysical functions (Fig. 1). The difference between the capacitance of S+ and the upper or lower threshold was termed the upper and lower JND.

The fish learned the discrimination task after about 3 weeks of daily training. They could easily discriminate between the two objects if the difference in capacitance was large. However, fish performance started to deteriorate as the value of the S– approached that of the S+ and finally reached chance level (50 % correct choices) (Fig. 1).

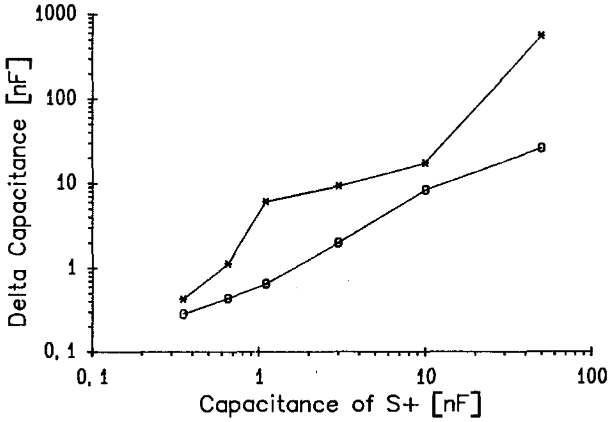

Fig. 2. Just noticeable difference (JND) in capacitance as a function of the capacitance of the positive stimulus (S+). The JND is expressed as the difference between S+ and the threshold value (Delta Capacitance) as revealed in Fig. 1. *Circles* give JNDs towards smaller capacitances (= lower thresholds), *stars* towards larger values (= upper thresholds) relative to the S+

Both the lower and the upper JND increase logarithmically with the value of the corresponding S+ (Fig. 2). The ratio between S+ and the upper or lower JND is almost constant. At the highest S+ used (50 nF), however, the value of the upper JND shows disproportional increase (Fig. 2).

Both Fig. 1 and Fig. 2 show that *G. petersii* cannot discriminate very accurately between capacitances of similar values. To be discriminated the capacitance of an object has to be increased (upper threshold) or decreased (lower threshold) by a rather large amount: On average, the upper threshold is about four times larger and the lower threshold is about four times smaller than the S+. In contrast to the rather poor discrimination performance shown here, weakly electric fish have proved to be very capable of accurate evaluation of electric signals in other tasks. For example, some mormyrids can recognize the very small differences between foreign EODs and thus discriminate between EODs emitted by members of their own and other mormyrid species. They also can discriminate the slight differences between female and male EOD of their own species [9]. It is possible, however, that the fish may have used another class of electroreceptors, the "Knollenorgane", during these discrimination tasks rather than the "mormyromas" class of electroreceptors which are almost certainly responsible for the active electrolocation behavior described in this paper. The second group of weakly electric fish, the gymnotiform fish from South America, can also evaluate electric signals very accurately. They can notice very small frequency and intensity differences. For example, *Eigenmannia lineata*, a gymnotiform wavefish, was shown to discriminate a frequency change of only 0.11 % [10].

The rather poor ability of *G. petersii* to discriminate between different capacitive objects came as a surprise because these fish had proved to the highly sensitive to the presence of a capacitive object. Even objects that caused only minor waveform distortions could be detected [3]. Also, electrophysiological experiments revealed that one class of afferents from mormyromast electroreceptors was sensitive to very small waveform distortions such as those caused by capacitive objects: A phase shift of only 1 °, corresponding to a change in temporal cues of less than 700 ns, was sufficient to elicit a significant decrease in spike latencies in this class of afferents [8].

In the experiments reported here, the fish could have used either waveform or amplitude cues to discriminate between the two capacitances. Capacitive objects cause changes in both parameters. Which of these two parameters was actually used by the fish is not known.

The results of previous studies [3, 6, 8] showed that the electrosensory system of mormyrids is well suited to the detection of capacitive properties of objects. The present study demonstrates, however, that the system is not able to measure the capacitive properties very accurately. Capacitance detection appears to be more of a qualitative than a quantitative ability. Fish might use it to discriminate animate from inanimate objects, because the latter do not usually posses capacitive components [3, 5, 6]. The ecological context in which capacitive detection takes place, however, is not known.

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Spectral Responses, Including a UV-Sensitive Cell Type, in the Eye of the Isopod *Ligia exotica*

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In bees and other insects the detection of polarized lights is often mediated by UV receptors [1, 2]. In recent years ultraviolet sensitivity has also been shown to exist in vertebrate groups such as birds [3] and fish [4]. In crustaceans, however, despite numerous investigations [5–9], the definitive proof of a UV receptor by intracellular identification has until now been missing.

Ligia exotica Roux (Crustacea) is a largely diurnally active [10] beach isopod, whose terrestrial habitat is well lit by light of a broad spectrum. The ommatidial structure of the eye of *Ligia* is of the apposition type. In each ommatidium there are seven retinula cells with their corresponding rhabdomeres. An eccentric cell occupies a central position and possesses a dendrite that extends into the interrhabdomal space where it is surrounded by the rhabdomeres of retinula cells R1–7. Retinula cells R4 and R5 are somewhat smaller than the others [10]. Evidence was obtained earlier that one of the major peaks of the eye's spectral sensitivity curve was in the UV and that a minor peak was present in the green [10]. In this paper the spectral sensitivities of the photoreceptors in the compound eye of *L. exotica* were determined through conventional intracellular recordings (for details of the method, see [11]). In order to define the relationship between a cell and its spectral property, we injected Lucifer yellow intracellularly following a successful recording run. The relationships between the observed spectral types and the retinula