EIN ZWERGWELS, DER NICHT KOMMT, WENN MAN IHM PFEIFT

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This work was part of the master" thesis of Erik van Wijland performed at Utrecht University in 1973, and tutored by Rob Peters. Most parts of the study were published by Peters & van Wijland in 1974. The unpublished introductory investigations however, based on studies of von Frisch (1923) and Lissmann & Machin (1958), led to the surprising finding that the electrosensitive catfish Ameiurus sp. can use its electric sense in the active mode (Peters & van Wijland 1993), thus making use not only of exafferent stimuli but also of reafferent stimuli (cf. von Holst, 1950).

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*Corresponding author at http://www.deTraditie.nl

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Materials & Methods, Results, Conclusions, References, Acknowledgements

1 Netherlands: ‘Onderzoekstage voor het Doctoraalexamen’.

Summary

Behavioural experiments revealed the ability of catfish, Ameiurus (Ictalurus) nebulosus, to use its electric sense in the active mode by sensing deformations of its own bioelectric dc-field, brought about by the presence of conductivity anomalies.

Keywords


Introduction

One of the leading questions of the research at Sven Dijkgraaf’s laboratory² was: what is the biologically adequate stimulus of a sensory system, or in other words, which components of stimuli that are detectable by a particular sensory system are actually used for survival. This question had troubled Dijkgraaf considerably during his efforts to understand the biological function of the ampullae of Lorenzini in cartilaginous fish. The ampullae of Lorenzini had been shown earlier to respond to various stimulus modalities, including electrical stimuli in the microvolt range (Murray 1962). But ever since Dijkgraaf observed in 1935 that dogfish reacted to the exposure of weak electrical stimuli, he hesitated to accept the possibility that electrical potential gradients were the biologically adequate stimuli for the ampullae of Lorenzini. Influenced by his corresponding with Hans Lissmann, the argument went: common sharks and dogfish have no electric organs to produce electricity, so why would they have electrosensory organs to detect electric stimuli. To what purpose?

2 1948-1974
In my view two events were vital for a breakthrough in Dijkgraaf’s understanding of the true nature of the ampullae. The first event was the electrophysiological demonstration of an extreme sensitivity to electrical currents by Murray (1962). The other event was the – forgotten or never mentioned – visit of Sir John Eccles to Dijkgraaf’s laboratory in 1969 (exact date to be verified). It was Eccles who suggested to look for dc-potentials in the pharynx of fishes instead of for muscle potentials as possible biologically relevant electrical stimuli. Ad Kalmijn, then a PhD student at Dijkgraaf’s lab, confirmed the presence of suprathreshold dc-stimuli in the marine environment (Kalmijn 1972), and also the possibility to locate prey by the detection of bioelectric prey fields (Kalmijn 1971). From that time on Lorenzian ampullae were recognized as a real sensory system, used for the detection of very weak electrical stimuli of very low frequencies.

It were these studies that served as landmarks when I started my PhD study on the function of the ‘small pit organs’ or microampullae of the freshwater catfish *Ameiurus (Ictalurus) nebulosus*. In February 1967, I was appointed at Dijkgraaf’s laboratory to assist Kalmijn in teaching electrophysiology and to start my research. Unfortunately I had to interrupt my study already in March, to fulfill my military service duties, and to leave my catfish to the care of my promotor Dijkgraaf (Dijkgraaf 1968). After leaving the army, I found my position still waiting for me, but also both Dijkgraaf’s (1968) and Roth’s (1968) publications on the electrosensitivity of the catfish’s ‘small pit organs’. Moreover Kalmijn was preparing his departure for Ted Bullock’s laboratory. However, there were enough unanswered questions regarding the biological significance of the small pit organs to continue my PhD track.

I received help from many people, among whom Rob Buwalda, who established catfish electrosensitivity by recording nerve activity in unrestrained fish (Peters & Buwalda 1972), and Frankiin Bretschneider, who measured dc-fields in fresh water, of both animate and inanimate origin (Peters & Bretschneider 1972). So two thirds of von Uexküll’s trinity (1909), stimulus – sensitivity – biological relevance, were already covered. Which left me the third question: what purpose does the electric sense serve in catfish? Orientation, feeding, communication? Erik van Wijland helped me to tackle the orientation question.

There was, however, a problem: how to condition a catfish to investigate its information processing potential? Because neither I, nor Erik had experience in psychophysics and the conditioning of fish at the time, we fell back on Karl von Frisch’s paper ‘Ein Zwergwels, der kommt wenn man ihm pfeilt’ (von Frisch 1923). Presenting food and whistling sounds simultaneously seemed the most sure way to evoke a conditioned response. However, we found out that we somehow did not have von Frisch’s persuasive powers. This is not the place to describe all the noises and sounds we made to try to control the catfish’s behaviour; it was fun, but not effective. Be it sufficient to mention that after several weeks, months even, we gave up and switched to photic stimulation.

One of my first observations namely, on my first catfish (10 cm), had been that whenever I wanted to have a proper look at the fish by switching on the lights, it fled to the most dark part of the tank. And the other way around, if the lights were switched off, it slowly left its dark shelter. This kind of behaviour, which we later called the skotokinetic response (Peters et al. 2010), allowed us to signal the fish the start of a trial to explore its electro-orientation potential more in depth. Since we also knew that catfish had a dc-field of their own (cf. Butsuk & Bessonov 1981, Kalmijn 1972, 1974; Peters 1973, Peters & Bretschneider 1972, Roth 1972), like a kind of aura, we also decided to investigate whether or not it could recognize deformations of its own electrical field by objects with a conductivity different from that of fresh water. We guessed that such deformations could give additional information to the catfish about the electrical fine structure of its habitat. If that would be the case, catfish thus would also use their electric sense in the active mode, just like electric fish. In the following I shall describe our efforts to imitate the study of Lissmann and Machin (1958), who demonstrated electrical object location in *Gymnarchus niloticus* by investigating its reactions towards insulators and conductors hidden in porous pots.
Materials and Methods

All tests took place in a full glass tank, 120 x 50 x 60 cm (l,w,h), from which all other electrical sources had been removed. We used 3 specimens of *Ameiurus* (*Ictalurus*) *nebulosus*, with body lengths of about 25 cm. They were housed and studied individually one after another in the same sink. During the tests the fish stayed in a dark shelter between trials, in an otherwise illuminated tank. Each trial was initiated by switching off the light; to the fish this was a signal to leave its shelter and to start roaming about, possibly in search for food (fig 1). The experiments were performed within a time window of 11 months.

We performed two different types of experiments. In *Experiment 1*, the fish was subjected to a two-alternative forced-choice regime; in *Experiment 2*, we observed the spontaneous reactions towards extraction thimbles hidden in the sandy bottom.

**Experiment 1.** In *Experiment 1* two porous glass fiber extraction thimbles (Tamson, Zoetermeer, The Netherlands) of 2.5 cm diameter were hung in the two entrances of the feeding compartments (fig 1) in such a way that there was just enough space underneath to let the fish pass. Inside one of the extraction thimbles a non-conducting body, *i.e.* a 2 cm thick PVC rod, was hung with the purpose to deform the bio-electric dc-field of the passing fish. The open end of the thimble was up, the closed round bottom down. In this way conductivity anomalies could be presented without additional visual or mechanical cues (fig 2).

**Experiment 2.** Feeding compartments with extraction thimbles, with and without non-conducting PVC rod, as seen through the eyes of the fish from the shelter point of view. In this particular situation the bottom of the thimbles is removed, and the PVC rod is protruding from the thimble cuffs. The fish was rewarded if it passed through the passage with the PVC rod.
The fish were trained to pass under one of the thimbles, diameter 25 mm, i.e. the one containing the PVC rod. We tried to condition it by creating an odor trail from the shelter to the extraction thimble containing the PVC rod. The odor source was a small piece of beef, later used as reward. Between the training trials the odor trail was removed by homogenizing the odorous water with an air stone, and by filtering the water with active coal. The thimbles were either presented intact, so that the insulator was invisible, or without a bottom, which let the insulator protrude from the cylinders (fig 2). Left or right presentation of the PVC rod was randomized. If the fish chose to enter the compartment with the PVC rod, it was rewarded with a very small piece of beef of about 2 mm diameter; if it chose the rodless compartment it did not receive a reward. The end of the trial was signaled by switching on the light after an arbitrary interval. For Experiment 1 we used 3 specimens of Ameiurus (Ictalurus) nebulosus. When conditioning with hidden PVC rods did not succeed, the lower end of the thimble was cut off, to add visual an mechanical cues to the electrical cues. The PVC rod protruded from the thimble cuffs by 1 to 4.5 cm (fig. 2). After having finished the trials where the PVC rod was presented dorsally, we developed a method to present the PVC rod, i.e. the conductivity anomaly, ventrally. However, it turned out that the fish did not consider the conductivity anomaly as a cue to choose between left and right, but apparently as a feeding target. The response, spontaneous digging, induced us to quit the 2AFC paradigm and to study this particular spontaneous behaviour, described in Experiment 2.

Experiment 2. In Experiment 2 the fish was still fed in one of the two feeding compartments, but had to pass a single extraction thimble buried halfway in the sandy bottom, under about 3 mm of sand. The thimble was either filled with sand or with water only, and we observed the spontaneous, non-conditioned, reactions when the fish passed over the buried thimble. The diameters of the thimbles were either 10, 16, or 25 mm. Experiment 2 was repeated less than four times a day, 44 times in all.

Fig. 3. Schematic view of the porous extraction thimble (Filter) hidden in the sandy bottom. The thimble was either filled with sand, or with water. Results see table 1.
Results

Experiment 1. During the whole experimental period of 11 months we did not succeed to condition any of the three fish. Apparently they could not be trained to detect and recognize conduction anomalies in their dorsal space under the present conditions. On the other hand, it proved possible to train the fish to discriminate between compartments with and without a PVC rod. If no extraction thimbles were used, and only the PVC rod was hung in the entrance of the feeding compartment, one of the catfish for instance, made only 2 mistakes in a test series of 35 trials, after 245 conditioning trials spread over 14 days. Conditioning proved also possible if extraction thimbles were used where the closed end was cut off (fig 2). If more than 1.5 cm of the insulator was protruding from the thimble cuff, the fish performed extremely well: 100% correct choices (n = 25). If 1½ cm of the PVC rod was protruding from the thimble cuff, the fish made 70% correct choices (n = 30); if less than 1.5 cm of the PVC rod was protruding, the number of correct choices leveled out at 50%.

Experiment 2.

In Experiment 2 the electrosensitivity in the ventral space was investigated. In each trial, after switching off the lights, the fish left its shelter and, when it passed over the thimbles buried under 3 mm of sand, it reacted spontaneously with feeding movements to the presence of thimbles when they were not filled with sand. More specifically the reactions consisted of a slight interruption of the swimming movements, sometimes followed by backwards swimming, and even digging up the thimble. Thimbles containing sand as well as other buried insulators like marbles or solid PVC rods were neglected in most cases. The fish showed such reactions almost exclusively when they swam over water filled thimbles with a diameter of 16 mm (table 1). If these test were done more than 2 or 3 times a day, the fish no longer reacted to the water filled thimbles.

<table>
<thead>
<tr>
<th>thimble diameter mm</th>
<th>thimbles containing sand</th>
<th>thimbles containing water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No reaction</td>
<td>Reaction</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>16</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>25</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Totals:</td>
<td>18</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 1. Spontaneous reactions of a single fish to buried extraction thimbles of different sizes, filled with water or sand. Note that thimbles with a diameter of 16 mm were most effective in evoking reactions (yellow background, bold print).

After these introductory experiments, and after having been convinced that conditioning per se was easier than expected, we decided to continue our investigations with the 2AFC orientation tests described elsewhere (Peters & van Wijland 1974). A side effect of our efforts to condition catfish was silent admiration for the man who wrote the paper about 'Ein Zwergwels der kommt wenn man ihm pfeift' (von Frisch 1923).

Conclusions

The brown bullhead, *Ameiurus (Ictalurus) nebulosus*, is able to detect distortions of its own bioelectric dc-field, brought about by the presence of objects with an electrical conductivity differing from that of water. Distortions of the ventral part of the bioelectric dc-field are apparently effective, whereas those of the dorsal region are not. Moreover, distortions of the ventral part of the bioelectric dc-field cause feeding responses. According to van Holst's 'Reafferenzpinzip' (von Holst 1950) this particular way of stimulating a sensory system is reafferent stimulation: stimulation caused by motion of the fish itself. Apparently, the non-electric catfish *Ameiurus (Ictalurus) nebulosus* can use its electric sense in the active mode, in a way similar...
to the way of electric fish. Whereas electric fish probe their environment by Electric Organ Discharges of several volts strength, the non-electric catfish *Ameiurus nebulosus* can use its bioelectric dc-field of a few mV only. How relevant this is with respect to other features of the electric sense remains to be investigated.

**References**


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