

Electroreception in the Catfish, *Amiurus nebulosus*

Catfish and other silurids are known to be remarkably sensitive to local electrical stimulation^{1,2}. Blindfolded catfish usually responded to a current of about 1 μ A or more by swimming away, whereas weaker currents caused approach and nibbling¹. No attempt was made to establish experimentally which receptors were stimulated by these weak currents. On general indications, however, it was considered very probable that the external taste buds were the sense organs involved¹. In the light of more recent knowledge³⁻⁵, however, it seemed a priori much more likely that the so-called small pit organs⁶ – typical ampullary lateral-line organs^{4,7} – would have acted as electroreceptors, and not the external taste buds which are known to be used as gustatory sense organs^{8,9}. The following experiments were performed to clear up this question.

Four big catfish, each about 24 cm long, were blinded by removal of their eyes in 1% urethane narcosis. The animals were kept single in plastic aquaria. The stimulating device accorded with that used by the earlier investigators¹ and consisted of 2 insulated copper wires connected to the poles of a 1.5 V dry battery. The tips of the wires from which the insulating covering was removed and which were used as stimulating electrodes in the aquarium were kept about 2 cm apart. The preceding parts of the wires were mounted in a long glass tube as a waterproof handle. Between the battery and the aquarium both wires were interrupted by a double switch. To reduce the current and to regulate its strength, a resistance was inserted on the line of each wire between the switch and the handle tube. This was made by cutting the wire and inserting between the 2 cut ends a U-shaped tube filled with distilled water. The cut ends could be moved within the glass tube in order to vary the length of the column of distilled water between them, thus varying the resistance.

When the fish rested motionless on the bottom, or at least remained at a constant position within the aquarium, with its dorsal and caudal fins rhythmically waving to and fro, the electrodes were cautiously brought near the skin at a distance of about 2 cm. Without current, this caused no response. On closing the circuit with the switch, however, the animals usually responded. Responses occurred always instantly; in this respect there was no difference whether the electrodes were kept at 2 cm or, say, at 12 cm from the skin. When the head was stimulated, sometimes responses like those described above were observed: either the head was turned away or drawn back from the current area, or the fish turned towards the electrodes, followed them if they were drawn back and sometimes bit at them. Clear avoidance reactions were evoked by currents of about 1 μ A (corresponding to a potential gradient of about 75 μ V/cm at a distance of 2 cm from the electrodes¹⁰) or more; clear feeding behaviour was released by currents of about 0.4 μ A (potential gradient 30 μ V/cm) or less.

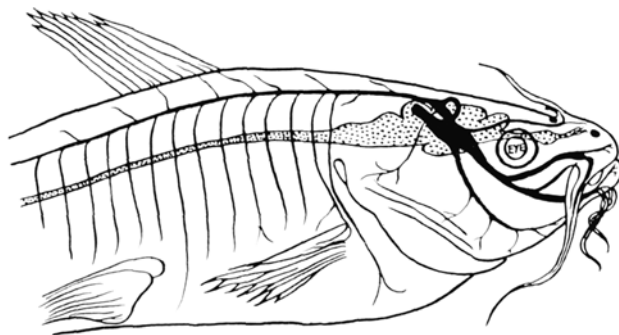
On lateral stimulation of the trunk, other responses prevailed of which particularly the following were used: (1) bending of the trunk, the stimulated side becoming concave (incidentally followed by swimming); (2) a lasting deflection of the dorsal fin towards the stimulated side. After a number of trials showing that stimulation of both sides of each fish was equally effective, the following operations were performed (urethane narcosis):

(1) In fish No. 1 the ramus lateralis accessorius facialis was cut at its anterior end at the left side only. This nerve supplies all external taste buds of the trunk (Figure⁸). The operation had no influence whatsoever on the electric

sensitivity of the fish. Stimulation of both sides remained equally effective.

(2) In fish No. 2 the main branch of the ramus lateralis vagi as well as its ventral branch⁶ were cut anteriorly, shortly posterior of the point where they join, again only at the left side. These nerves supply (a) all ordinary lateral-line organs of the trunk (both canal organs and free neuromasts, called here large pit organs) and (b) all small pit organs of the trunk. After this operation, the sensitivity of the operated side for weak electric currents was abolished, whereas the intact side was as sensitive as it had been before. With relatively strong currents (5–10 μ A) 'reversed' responses on stimulation near the operated side could occur; for instance, strong stimulation of the left side made the dorsal fin deflect to the right side. Thus, evidently sense organs of the intact side were reached by these currents and released the response.

(3) In fish No. 3 the ventral branch only of the ramus lateralis vagi was cut at the left side. This branch innervates only small pit organs and supplies the ventral part of the trunk. Since of all lateral sense organs only the small pit organs exhibit structurally the electroreceptive ampullary type, they might be expected to represent the electroreceptors involved. Indeed there was a slight difference in responsiveness between both sides of the fish on stimulation of the ventral trunk areas, the left side being somewhat less sensitive, but the results were not clear enough to draw a definite conclusion. Evidently the stimulating current was not sufficiently localized and may have reached intact small pit organs, either of the operated side (dorsal area) or of the intact side of the fish. The following experiment was designed to overcome this difficulty.



Innervation of taste buds in *Amiurus melas* by branches of the facial nerve (black). The recurrent ramus lateralis accessorius facialis supplies external taste buds on the trunk. After HERRICK, 1904.

¹ G. H. PARKER and A. P. VAN HEUSEN, *Am. J. Physiol.* 44, 405 (1917).

² H. W. LISSMANN and K. E. MACHIN, *Nature* 199, 88 (1963).

³ H. W. LISSMANN, *J. exp. Biol.* 35, 156 (1958).

⁴ S. DIJKGRAAF, *Biol. Rev.* 38, 51 (1963).

⁵ S. DIJKGRAAF and A. J. KALMIJN, *Z. vergl. Physiol.* 47, 438 (1963); 53, 187 (1966).

⁶ C. J. HERRICK, *J. comp. Neurol.* 11, 177 (1901).

⁷ A. M. MULLINGER, *Proc. R. Soc. [B]* 160, 345 (1964).

⁸ C. J. HERRICK, *Bull. U.S. Fish Comm.* 22, 237 (1904).

⁹ G. H. PARKER, *Science* 27, 453 (1908).

¹⁰ I am indebted to Mr A. J. KALMIJN for determination of current strengths and potential gradients.

(4) In fish No. 4 the main branch of the ramus lateralis vagi was cut anteriorly on both sides; the ventral branch of this nerve, however, was cut only at the left side. So, of all trunk lateralis sense organs, only the small pit organs at the ventral part of the right side were still innervated. A number of clear and oriented reactions were observed on stimulation of the tail region at the right side, though only with relatively strong currents. In a few cases a 'reversed' response occurred on stimulation of the left side; again (see above) intact electroreceptors of the right side were evidently involved.

The following conclusions can be drawn: (a) From 1 and 2: the external taste buds are not at all involved in electroreception. (b) From 2: electroreception resides in lateral sense organs. (c) From 3 and 4: the small pit organs are electroreceptors.

The experiments are to be continued.

Zusammenfassung. Zwergwelse (*Amiurus nebulosus*) sind elektrisch sehr empfindlich. Geblendete Tiere sprechen, je nach der Stromstärke, auf schwache Ströme ohne Dressur mit biologisch bedeutsamen Reaktionen an: Ausweichen oder Annähern und gegebenenfalls Schnappen. Auf Grund einseitiger Denervierungsversuche konnte festgestellt werden, dass die sehr zahlreichen äusseren Geschmacksknospen mit dem Empfang schwach-elektrischer Reize nichts zu tun haben. Als Elektrozep-toren erweisen sich vielmehr die anatomisch zur Gruppe der ampullären Seitensinnesorgane gehörigen, ebenfalls in weiter Verbreitung am Körper vorkommenden «small pit organs».

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Protection against Hyperbaric Oxygen Toxicity after Feeding *N,N*-diphenyl-*p*-phenylene diamine

JAMIESON and VAN DEN BRENK¹ have shown that intra-peritoneal injections of *N,N*-diphenyl-*p*-phenylene diamine (DPPD) protects rats and Walker and Eliza strain mice against toxic effects of later exposure to 100% oxygen at 5 atmospheres. These effects included convulsions, lung damage and eventual death. We have obtained similar results in C₃H mice after feeding DPPD. The degree of protection is linked to the number of feedings and presumably to tissue accumulation of DPPD.

Methods. A 2% solution of DPPD² in sesame oil was fed by stomach tube to groups of adult C₃H mice (some obtained from Jackson Memorial Laboratory, Bar Harbor, Maine and some from Cumberland View Farms, Cumberland, Virginia). Dose was adjusted to body weight: in the first 2 experiments a total of 0.56 g of DPPD/kg mouse was divided evenly among 7 daily feedings. Previous experience showed this to be near the lethal limit; 8 feedings (0.64 g/kg) usually kills a large percentage.

In subsequent experiments 6, 4, and 3 daily feedings of the same solution were used. Control animals were fed sesame oil in the same proportion to weight as animals receiving DPPD in sesame oil.

In each experiment 5 DPPD and 5 sesame oil fed mice were used. They were placed in a high-pressure chamber³ on opposite sides of a dividing partition that permitted free passage of gas but not mingling of mice. The chamber was vented with 100% oxygen at 5 l/min until a pure oxygen atmosphere was attained to the end of each experiment. The oxygen concentration was determined by sampling and testing vented gas with a PO₂ electrode⁴. Pure oxygen was compressed at 1 atmosphere/min to 60 p.s.i.g. (5 atm. abs.) and maintained to the end of the experiment.

The time in oxygen at 5 atmospheres at which the mice died was recorded: the sign used was complete cessation of respiratory movements.

Dead animals were dissected, the lungs grossly and microscopically examined.

Results. Within 2–5 min after arriving at 5 atmospheres, distress, followed by full tetanic seizures, was observed in all animals regardless of treatment. Such seizures lasted approximately 15 sec and the animals appeared to fully recover. Within 5–10 min seizures reappeared. They

recurred thereafter with increasing frequency alternating with ever-shortening recovery periods. Finally, after 45 min to 1 h, the mice lay on their sides, breathing with gasping movements, having occasional seizures but little organized voluntary movement until death. The Table gives the survival data.

An analysis of the variance in survival time between DPPD and sesame oil fed animals shows highly significant differences ($P < 0.001$ in all cases except 3 feedings where $P < 0.01$ but > 0.001).

The difference between the 2 experiments with 7 feedings was not significant.

At autopsy, the lungs of treated animals had fewer hemorrhagic and collapsed areas than those of untreated animals. Histological sections bore out this observation.

No. of feedings of DPPD	No. of animals	Mean survival time (min)	Range of survival time (min)	Protection factor
7	5	661.4	319–950	4.17
0 ^a	5	158.6	148–170	
7	5	723.4	574–962	4.50
0 ^a	5	161.6	149–169	
6	5	561.8	470–641	3.17
0 ^a	5	177.5	160–192	
4	5	424.6	368–478	2.26
0 ^a	5	187.4	168–203	
3	5	376.6	266–587	2.06
0 ^a	5	167.8	147–180	

^a These received sesame oil in the same number of feedings as DPPD above.

¹ D. JAMIESON and H. A. S. VAN DEN BRENK, *Biochem. Pharmac.* 73, 159 (1964).

² Obtained through the courtesy of the U.S. Rubber Company.

³ Bethlehem Corporation, Table Top Hyperbaric Chamber Model No. 614, Bethlehem, Pennsylvania.

⁴ Instrumentation Laboratory Inc. II-113-51 Ultra Micro PO₂ electrode.