

## Detection of Stationary Objects by the Blind Cave Fish *Anoptichthys jordani* (Characidae)\*

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**Summary.** It was noticed that the blind Mexican Cave Fish repeatedly passes along objects new to it at a short distance. Observations and experiments are reported which support the hypothesis that water movements occurring between the stationary object and the fish as it passes by convey information about the location and possibly the shape of the object, which is detected by the lateral line organ of the fish. Water movements of the expected type were recorded with the help of a model fish equipped with a mechano-electric analogue of a free neuromast.

### Introduction

The behavior of a blind cave fish confronted with new objects placed in its aquarium supplied hints on how it, and possibly other fish, acquire information on stationary objects under water. When there are obstacles in an aquarium, blind cave fish swim about restlessly, avoiding collisions with and traversing narrow gaps between them. A new object placed in the water may be investigated by the cave fish with its snout, but it may also elicit the following behavior. On approaching the new object, the fish first accelerates and then glides past the object in close proximity without moving its tail. When repeating this performance, the fish may glide along different sides of the object. If the fish swims over the object, it may rotate sideways shortly before reaching the object so that one side of its body is directed towards the object while passing. Our experiments and observations were aimed at finding out whether the fish gains information on the objects via this behavior and whether water movements between the fish and the object convey this information.

Stationary objects can be detected and localized

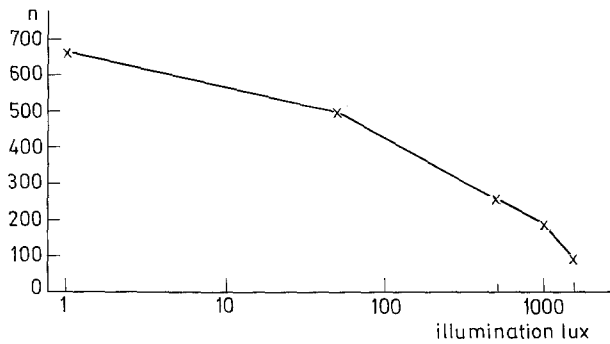
by blinded electric fish (review: Heiligenberg 1977), and, in certain cases, by non-electric fish which have electroreceptors (Kalmijn 1974). There is no evidence that the cave fish *Anoptichthys* can employ electroreceptors for this purpose. On the other hand, moving objects which cause water displacements can be detected and localized by the lateral line organ as shown by many investigations on amphibians and fish (review: Schwartz 1974). The ability of a blinded codfish to stop swimming in front of an obstacle before bumping into it has been tentatively explained as due to the detection of water currents caused by the swimming movements and deflected by the obstacle (Dijkgraaf 1967). In this case the postulated signal may be very weak. We repeated our experiments with a model fish equipped with a mechano-electric transducer simulating one free neuromast of the lateral line organ in order to show that water movements carrying information about the objects occur and can be recorded by the lateral line organ.

### Pilot Experiments and Observations

In order to analyse the fish's ability to detect and discriminate objects, conditions had to be found under which the cave fish would cooperate in the experiments and glide past objects as described above. The following observations turned out to be of importance for the design of the experiments.

1. In familiar surroundings, the cave fish swims through narrow holes, but it hesitates to enter enclosures such as tubes, even if lured towards the entrance by the smell of food. If the cave fish finds itself trapped in a confined area, it immediately starts to move about violently, often unable to find the exit. In open water, on the other hand, the fish swims calmly and apparently always knows its location. Therefore experiments have to be carried out in open water.

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**Fig. 1.** Ordinate: Counts of spontaneous swimmings through one of four tunnels in a wall dividing an aquarium into two equal halves. Abscissa: Illumination of the tank; each point on the curve gives the pooled data recorded during four hours from five fish

2. When swimming along the glass walls of its home aquarium, the fish usually tilts its back away from the wall so that its dorsoventral body axis forms an angle of about 30 degrees to the wall. When gliding along objects of interest, however, the fish orients itself so that its side is approximately parallel to the surface of the object.

3. Given the choice between a dark and an illuminated compartment in an aquarium, the cave fish were more often found in the dark half. Of two fish living for 40 weeks in such an aquarium, one was found in the illuminated half only in 10% of 2,501 inspections and the other in 20%. Except for the water, this aquarium was empty and the fish were transferred to another one for feeding to keep olfactory influences to a minimum (Hoch 1980). Despite this obvious negative phototaxis, light stimuli proved ineffective as punishment in conditioning experiments. However, the experimental tanks had to be provided with even illumination.

4. The cave fish did not actively cooperate in the experiments in bright illumination. In an aquarium divided into two equal halves by a wall with four holes, five fish crossed from one half to the other clearly more often under low illumination (Fig. 1). Therefore, illumination of the experimental tanks had to be kept as low as possible.

5. Cave fish can be conditioned to swim to a certain spot in the aquarium and wait there for food. The conditioning stimulus was switching on a lamp above the aquarium. This ability to remember and find the feeding place was demonstrated when a plastic dividing wall was put into the aquarium with the fish on one side and the feeding place on the other. When the lamp was switched on, the trained fish jumped out of the water and over the wall and swam to the feeding place. This was recorded repeatedly and documented photographically. Thus the training

experiments had to be designed so that the fish responded not to the location but to the shape of the objects.

6. Chemical orientation is very important for blind cave fish. If a glass rod, taken from a jar containing tubifex worms, is dipped into an aquarium at a certain spot and then removed, a cave fish will stop and search up and down at this spot if it happens to pass it by. In the training experiments, we did not try to avoid chemical stimuli, but rather provided the same smell everywhere. If a tubifex worm was used as a reward, we also provided one at the place of the wrong choice but screened it off so that the fish could only smell but not swallow it.

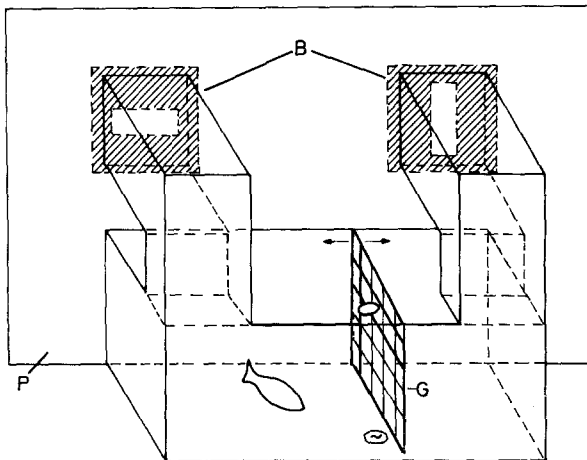
7. If more than one fish participated in an experiment, the largest fish ferociously defended the feeding location by biting at any other approaching fish. This constitutes an example of aggressive behavior, which has been considered of minor importance among cave dwelling fish (Parzefall 1974). Because of this, the experiments had to be carried out with single fish to avoid any influence from social interaction.

8. Electric shocks proved effective as punishing stimuli eliciting sudden movements and flight. When individual fish were tested in a particular aquarium, the minimal effective voltage of square wave pulses of 50 cps was found to vary considerably. The electric current was not recorded in these tests. There was no obvious correlation between shock threshold and body size, consequently the minimal effective voltage had to be adjusted individually for each fish at the beginning of the training experiments. If the punishing shocks were too strong, the fish no longer participated in conditioning experiments.

## Materials and Methods

*The Experimental Animal.* The Mexican cave fish, *Anoptichthys jordani* (Characidae) was first described in 1936 (Hubbs and Innes 1936) and has been intensively studied since then. Young hatchlings have eyes with differentiated retinas (Kuhn and Kähling 1954). The eyes degenerate during development in a genetically determined way but some optic fibers have been found innervating the optic tectum in adult cave fish (Voneida and Sligar 1976). The cave fish also responds to light stimuli after extirpation of the degenerated remains of the eyes (Thines and Kähling 1957; Kähling 1961). Cave fish of between 4 cm und 8 cm long were used in the experiments. Some were purchased on the market, some had been raised in the laboratory. We do not know which natural population they came from.

*Conditioning Procedure.* The set-up for a conditioning experiment is sketched in Fig. 2. A plexiglass wall (P) with two square openings divided the aquarium into two halves. Two small pieces of plexiglass (B), each with a rectangular hole in the middle covered these openings. One of the rectangular holes was oriented vertically, the other horizontally. The position of the two holes was changed about during the experiments. A fish swimming through one of



**Fig. 2.** Training set-up for discrimination between vertical and horizontal rectangular openings. Detailed description in text

these holes entered a wide tunnel leading to a large enclosure where a tubifex worm was presented by means of a pipette as a reward for the correct choice. In the case of a wrong choice, a grid wall (G), which could be moved sideways, stopped the fish before it reached the worm. This set-up provided equal distribution of the chemical stimuli from the prey. After the fish had entered the rewarding compartment, it was transferred back to the other side of the dividing wall for the next test. The rectangular openings measured  $4.3 \text{ cm} \times 2.3 \text{ cm}$ . The rest of the set-up is drawn in approximately the same scale. It turned out that the fish learnt faster when, in addition to the reward, they were punished for wrong decisions by a train of electric shocks administered upon entering the wrong tunnel. They stopped swimming when shocked and learnt to escape from the tunnel back through the rectangular hole.

Only one fish at a time was in the experimental apparatus in each test. It was transferred from another aquarium in a net. Individuals which participated in the experiments, i.e., which entered the holes, found the worm and responded to the electric shocks, were selected.

**Spontaneous Discrimination.** An experimental tank was divided into two equal halves by a wall with four tunnels. The frequency of swimming through each of these tunnels was recorded on a pen recorder by means of photoelectric devices mounted within the tunnels (Weissert 1979). In the first experiment the tunnels had entrance doors of different widths, one of which was equipped with a vertical bar in the middle (Fig. 4a). In the second experiment, four entrance doors of equal width equipped with rods of different diameters were used. In the last experiment, the doors were equipped with different rods and the width of the openings on both sides of the rods was kept constant. The positions of the different entrance doors were changed once an hour during the experimental sessions, each of which lasted 12 h. All recordings were repeated five times with different fish.

**The Model Fish.** A model fish equipped with a mechanoelectric transducer was constructed to record water currents in its vicinity when passing a stationary object. The plastic model is only a crude approximation of the cave fish.

The model is 130 mm long, the longest vertical and horizontal axes measure 70 mm and 40 mm respectively. It was fixed to a roundabout above the water by means of a stiff tube containing the electric connexions. Driven by an electric motor, the model

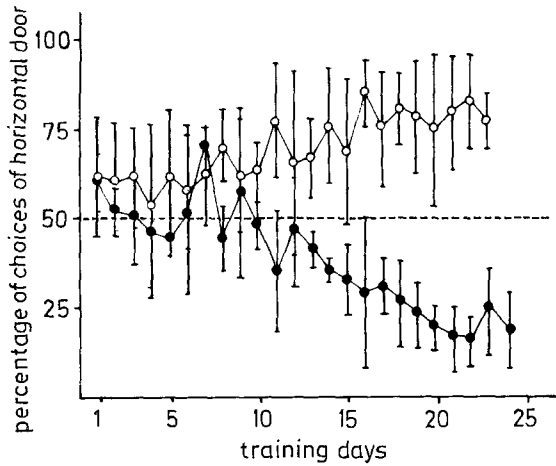
moved along a circular path (Fig. 5b) in the water in a large tank ( $120 \text{ cm} \times 200 \text{ cm} \times 40 \text{ cm}$ ). A 5 mm wide hole was drilled into one side of the chamber containing the transducer (Fig. 5a). This hole was sealed with a fine rubber membrane (M), through the center of which a fine needle (N) was inserted. A soft plastic blade (C) was attached to the outside end of this needle and a piece of black paper (P), which partly intersected a beam of light from a small lamp on a photoelement, was fixed to the inside end. When the blade outside is moved by a water current, the photoelectric output of the system changes due to the paper passing through the light beam. The blade outside was oriented so that the system was sensitive to movements in its plane only, as has been shown to be the case for the cupula of a free neuromast in the lateral line organ (Görner 1963). The output of this system was recorded on an oscilloscope and photographed.

## Results

### Conditioning Experiment

One group of seven fish, which were individually recognizable, was trained to prefer the horizontal rectangular door (Fig. 2), another group of four was trained for the vertical one. On the first day the plates with the rectangular holes were removed. A worm was presented each time a fish reached the rewarding chamber, regardless of the route it followed. On the second day, the plates with the squares were introduced but not switched about between the learning trials. A reward was provided when the fish swam through the correct opening. The final test began on the third day. The upright and the horizontal openings were switched about at random, but at least once after three trials. Each fish stayed in the training apparatus until it had made between eight and ten choices. Only five choices could be recorded in a few cases. At the beginning, the fish waited for up to half an hour before entering one of the holes, later sometimes less than one minute.

Figure 3 shows the pooled results of all the fish tested. The ordinate gives the choices of the horizontally oriented opening in percentage of all choices of the day, the abscissa the day of the test. The vertical bars are the standard deviation of the results of all fish in the group. The upper curve belongs to the group trained to prefer the horizontal door, the lower curve to the group trained to prefer the vertical one. It can be seen that at the beginning of the training period the fish in both groups went through the horizontal door slightly more often. This spontaneous preference for wider openings was used in the experiment described in the next paragraph. After about the tenth day of training, the curves clearly separate and reach levels indicating that more than 75% of the choices were correctly made in both groups. The fish thus appear to discriminate between the vertical and the horizontal rectangular openings.



**Fig. 3.** Pooled results from seven cave fish trained to prefer the horizontal opening (empty dots) and from four cave fish trained to swim through the vertical opening (filled dots). Ordinate: Number of choices of horizontal opening, Abscissa: Number of training days. Vertical bars: Standard deviation of the results of all fish in the group tested

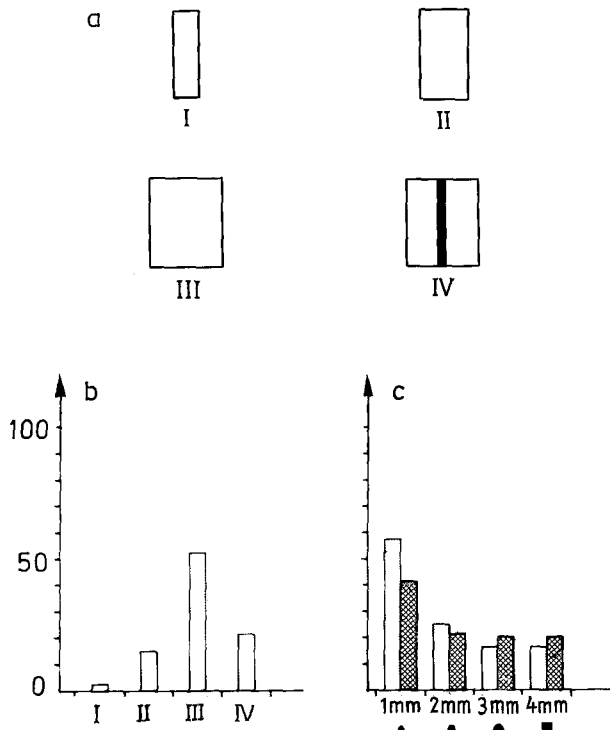
The electric shock punishment was not introduced until the eighth day for the group trained to prefer the horizontal door. The upper curve in Fig. 3 shows that the number of correct choices increased only thereafter. The fish in the group trained to prefer the vertical door were punished for wrong choices from the very beginning. On the sixth and seventh day their results became worse. Inspection of the apparatus revealed that there was a defect in the electric connexion so that no punishment had taken place. After the apparatus had been repaired, the results improved again, as the lower curve in Fig. 3 shows. The fish made most of their mistakes at the beginning of each experimental session throughout the whole experimental period, which means that retention of the conditioned state from one session to the next is poor. Unfortunately, no more than nine tests per fish could be carried out on one day because the fish did not cooperate very well after having been rewarded so often.

The motivation to discriminate between the two doors increased the fishes' tendency to glide past both doors before going through one of them. It was observed that the trained fish swam along the plexiglass wall with the doors nearly all the time. This supports the view that discrimination between the shape of the doors was achieved through this behavior.

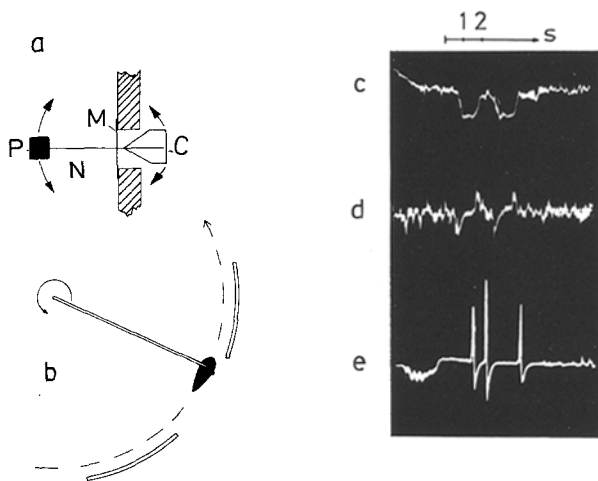
*Spontaneous Discrimination*

The frequency distribution of five fish spontaneously swimming through each of the tunnels I to IV (Fig. 4a) is shown in Fig. 4b. The fish passed through the dividing wall between 44 and 94 times during each 12 h experiment. They obviously preferred the widest opening, and chose the tunnel with the bar less often.

Detection of the vertical bar was investigated with four entrance doors of equal size (30 mm × 35 mm) equipped with bars of different widths, three of which had a circular cross section and the fourth a square cross section. The fish passed through the wall between 75 and 150 times during 12 h. The frequency distribution (Fig. 4c, light columns) shows that the fish used the door with the finest bar most often. The reason may be that, in searching for the largest hole, the fish failed to detect the finest bar more often. The alternative interpretation, i.e., that what matters is not the width of the rod, but the width of the openings on either side of it, is less likely as shown by a third experiment carried out in the same way with five fish. This time the width of the openings on both sides of the bars was kept constant at 13.5 mm regardless of the widths of the bars. The



**Fig. 4.** a Shape of four holes in a plastic wall dividing the experimental tank into two equal halves. Height of the opening 35 mm, width 10 mm, 20 mm, 30 mm, and 30 mm respectively. b Frequency distribution for the spontaneous choices of the different holes. Pooled data from five fish separately tested, duration of each test: 12 h. c Frequency distribution of choices between four holes equipped with bars of different diameters as indicated along the abscissa. Light columns: All openings measure 30 mm × 35 mm. Dark columns: The width of the opening is adjusted so that the distance between the bar and the vertical rim measures 13.5 mm in all cases



**Fig. 5.** a Construction of the mechano-electric transducer simulating a free neuromast in the model fish. Description in the text. b Circular path of a model fish when guided along obstacles. c Recording of the mechano-electric signal on an oscilloscope when the model fish was guided along the two metal sheets (b), D.C. recording. d The same as c in A.C. recording. e Mechano-electric signal when the model fish passed three metal bars positioned at unequal distances from each other, A.C. recording; depression at the beginning indicates the start of movement of the model fish. Radius of the circular path 45 cm. Difference between the recordings c, b and e is due to changes of shape and orientation of the blade C and the stiffness of the membrane M

frequencies for passing through holes were not significantly altered (Fig. 4c, dark columns).

This observation indicates that the fish can detect bars with diameters down to at least 2 mm when they pass by at a distance of a few millimeters. This result is more reliable than earlier attempts to find the finest detectable bar by showing that the blind cave fish does not swim around, but bumps at it (Hahn 1960), because whether a bar is actually touched or only nearly touched by the fish is hard to observe. It is also hard to decide whether an obstacle is touched accidentally or intentionally.

#### *Experiments with the Model Fish*

Figure 5c gives a recording from the model fish moving along a circular path with a radius of 45 cm at a velocity of 34 cm/s. Two curved metal sheaths (31 cm × 23 cm × 0.3 cm) were mounted alongside this path (Fig. 5b) to simulate the stimulus situations of Fig. 2. The distance of the tip of the artificial cupula from the metal sheaths was about 2 mm. The recording shows that the artificial cupula is deflected backwards when passing the curved wall (Fig. 5d, the same recorded with A.C. coupling). To simulate the experiments of Fig. 4, three metal rods with diameters of

12 mm each were mounted along the path of the model fish. The result recorded with A.C. coupling is given in Fig. 5e. The model correctly recorded the unequal distances between the rods. In this case, the artificial cupula was deflected forward on passing the rods as one can see from the first deviation of the recording e, which shows the deflection at the start of the movement. This difference cannot be explained at the moment, but may well be a matter of the shape and angular orientation of the artificial cupula. Since the model was only roughly adapted to the real situation, and since the true water currents were not recorded, the only conclusions to be drawn from this experiment are that water movements conveying information on the position and shape of stationary objects occur when a fish passes close by them, and that these signals are of a type which can be detected by the lateral line organ. Results of a more detailed investigation of water currents around a fish gliding past stationary objects will be reported elsewhere.

#### **Discussion**

Various observations have been compiled in this communication to corroborate the hypothesis that water movements occurring between a stationary object and a fish passing by may be detected by the lateral line organ and inform the fish about the location and possibly also about the shape of the object. This kind of perception would be of greater importance for the blind cave fish than for visually competent species. This might be the reason why the blind cave fish clearly displays the striking behavior of swimming along objects new to it. In still water, the appropriate water movements can occur only if the fish swims along the stationary objects. It therefore appears consistent that, in a water tank, the cave fish avoids any situation which restricts its possibility of free movement, that it hesitates to enter enclosures and that it fights desperately to free itself if trapped. It may be seen struggling close to the exit of an enclosure for many minutes without being able to find its way out. Water currents of the kind observed with the model fish are also produced if an object moves with respect to the fish in still water, and in running water when both the fish and the object are stationary. The case of the fish swimming in still water may be different from the others with respect to the kind of water currents produced. There may also be a difference between a moving and a stationary fish in the processing of sensory excitation in the nervous system.

In the clawed toad *Xenopus* efferent neural activity has been observed in the lateral line nerve when the

toad intends to move (Görner 1967). This efferent activity, which can also be elicited by electrical stimulation of descending reticular motor axons in the spinal cord, inhibits the afferent activity of the lateral line organ (Russel 1970). Since Weber (1846) it has repeatedly been demonstrated that stimuli acting on the human skin lead to different perceptions according to whether the person or the object actively moves (v. Campenhausen 1981). The possibility therefore has to be considered that sensory stimuli caused by active swimming movements by the fish will produce other sensory perceptions than passively received stimuli. Greguss (1975) suggested that swimming fish use excitations arising in their brain together with the motor excitation as reference signals to process the afferent excitation of the lateral line organ in a bio-holographic way. According to this hypothesis, the phase relationships between the signals from different sensory channels could be used to construct a three-dimensional perception of the surroundings of the swimming fish.

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## References

- Campenhausen C von (1981) Die Sinne des Menschen, Bd I: Einführung in die Psychophysik der Wahrnehmung, Bd II: Anleitungen zu Beobachtungen und Experimenten. Thieme, Stuttgart
- Dijkgraaf S (1967) Biological significance of the lateral line organs. In: Cahn PH (ed) Lateral line detectors. Indiana Univ Press, Bloomington, pp 83–95
- Görner P (1963) Untersuchungen zur Morphologie und Elektrophysiologie des Seitenlinienorgans vom Krallenfrosch (*Xenopus laevis* Daudin). Z Vergl Physiol 47:316–338
- Görner P (1967) Independence of afferent activity from efferent activity in the lateral line organ of *Xenopus laevis* Daudin. In: Cahn P (ed) Lateral line detectors. Indiana Univ Press, Bloomington, pp 199–214
- Greguss P (1975) Holographic concept in nature. In: Greguss P (ed) Holography in medicine. Proc Int Symp Holography Biomed Sci. IPC Science and Technology Press, Guildford, pp 97–100
- Hahn G (1960) Ferntastsinn und Strömungssinn beim augenlosen Höhlenfisch *Anoptichthys jordani* im Vergleich zu anderen Teleostiern. Naturwissenschaften 47:611
- Heiligenberg W (1977) Principles of electrolocation and jamming avoidance in electric fish. A neuroethological approach. Studies of brain function, vol 1. Springer, Berlin Heidelberg New York
- Hoch W (1981) Der lichtscheue Höhlenfisch. (personal communication)
- Hubbs CL, Innes WT (1936) The first known blind fish of the family Characidae: a new genus from Mexico. Occas Pap Mus Zool Univ Mich 342:1–7
- Kähling J (1961) Untersuchungen über den Lichtsinn und dessen Lokalisation bei dem Höhlenfisch *Anoptichthys jordani* Hubbs et Innes (Characidae). Biol Zentralbl 80:439–451
- Kalmijn J (1974) The detection of electric fields from inanimate and animate sources other than the electric organs. In: Fessard A (ed) Electroreceptors and other specialized receptors in lower vertebrates. Springer, Berlin Heidelberg New York (Handbook of sensory physiology, vol III/3. pp 147–200)
- Kuhn O, Kähling J (1954) Augenrückbildung und Lichtsinn bei *Anoptichthys jordani* Hubbs et Innes. Experientia 10:385–388
- Parzefall J (1974) Rückbildung aggressiver Verhaltensweisen bei einer Höhlenform von *Poecilia sphenops* (Pisces, Poeciliidae). Z Tierpsychol 35:66–84
- Russell IJ (1971) The role of the lateral-line efferent system in *Xenopus laevis*. J Exp Biol 54:621–641
- Schwartz E (1974) Lateral line mechano-receptors in fishes and amphibians. In: Fessard A (ed) Electroreceptors and other specialized receptors in lower vertebrates. Springer, Berlin Heidelberg New York (Handbook of sensory physiology, vol III/3, pp 257–278)
- Thines G, Kähling J (1957) Untersuchungen über die Farbempfindlichkeit des Höhlenfisches *Anoptichthys jordani* Hubbs et Innes (Characidae). Z Biol 109:150–160
- Voneida TJ, Sligar CM (1976) A comparative neuroanatomic study of retinal projections in two fishes: *Astyanax hubbsi* (the Blind Cave Fish), and *Astyanax mexicanus*. J Comp Neurol 165:89–106
- Weber EH (1905) Tastsinn und Gemeingefühl. In: Ostwald's Klassiker der exakten Wissenschaften, Bd 149. Engelmann, Leipzig
- Weissert R (1979) Dressurexperimente und Verhaltensbeobachtungen zum Formunterscheidungsvermögen des blinden Höhlenfisches *Anoptichthys jordani* (Hubbs et Innes). Dissertation, Mainz