

## On the discrimination of spatial intervals by the blind cave fish (*Anoptichthys jordani*)

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**Summary.** The performance of the blind cave fish in discriminating spatial intervals was investigated. The fish had to discriminate between pairs of grids consisting of equidistant vertical bars. The intervals between the bars on the grid to be chosen were kept constant while the intervals between the bars on the other grid were altered in steps so as to become gradually closer to the interval between the bars on the grid to be chosen. It was found that the fish were still able to discriminate between the two grids when the difference between the bar intervals amounted to at least 1.5 mm. In interpreting the results it was concluded that the phase information in the stimulus on the skin of the fish must be significant for it.

### Introduction

The lateral line organ (LLO) of the fish has been characterized as a sense organ for 'distance-touch' ('Fernstastsinn') in the near field around the fish (Dijkraaf 1962). It responds to low frequency vibrations and water currents in its surroundings (Dijkraaf 1952; Görner 1961; Flock and Wersäll 1962; Kuiper 1967). Recent studies on the blind cave fish have shown that the fish can actively investigate its surroundings with the aid of its LLO. When investigating a new object '...the fish accelerates and then glides past the object in close proximity without moving the tail' (von Campenhausen et al. 1981; Weissert and von Campenhausen 1981). It has been supposed that the gliding fish produces a flow field around itself, which is modified by obstacles in the vicinity. Certain obstacles

produce well defined spatial and temporal distributions of the water current at the skin of the fish (Hassan 1985). The flow field and its alteration are supposed to act as a stimulus for the LLO, allowing the fish to gain information about its environment. Behavioral experiments with the blind cave fish have shown that it is able to discriminate between two different grid patterns (Weissert and von Campenhausen 1981). They proposed that the phase relationships between the signals of different sensory channels resulting from such a stimulus could be used to construct a three-dimensional percept of the surroundings of the moving fish. Similarly, the surface feeding fish was shown to detect the direction and distance to the origin of surface waves by using the differences in the arrival time, amplitude and frequency content of the surface wave at the neuromasts of the head within one stimulus wave (Schwartz 1965, 1971; Bleckmann 1980; Bleckmann et al. 1981; Bleckmann and Schwartz 1982; Hoin-Radkovski et al. 1984).

In the case of the gliding fish passing a certain grid it is to be expected that the alteration of the water current at a certain point on the surface of the fish will vary periodically in time. The periodicity of this alteration depends on the velocity of the fish and the spatial interval between the bars on the grid. At different points on the surface of the fish these alterations of the water current will occur with a certain phase relationship which depends on the spatial interval between the grid bars alone. In contrast, water motion in the near field of a vibrating body occurs with the same phase over the whole surface of the fish (Harris and Bergeijk 1962; Skudrzyk 1971). So, for the same temporal course of the water motion in the two cases, the stimulus to the LLO in the first case will include additional phase information. If the fish is able to use such phase information in the stimulus,

*Abbreviations:* LLO lateral line organ; SDP spatial discriminatory performance; SDPF spatial discriminatory performance factor; TDPF temporal discriminatory performance factor

then it could be expected that the performance of the fish in discriminating spatial intervals would be better than when based on the discrimination of temporal intervals alone. To confirm such an expectation, quantitative data are needed on the discriminatory performance of the fish for temporal and spatial intervals. The discriminatory performance of the blind cave fish for the frequencies of a vibrating ball in the water has been recently investigated (Frühbeis 1984; von Campenhausen, personal communication). The discriminatory performance of the fish for spatial interval has been qualitatively investigated (Weissert and von Campenhausen 1981) but no quantitative data are available on this topic yet.

In the present study the discriminatory performance of the blind cave fish for spatial intervals was quantitatively investigated. The fish had to discriminate between pairs of grids of equidistant vertical bars. The intervals between the bars on the one grid were kept constant while the intervals between the bars on the other one were made closer to these in successive experiments. This made it possible to determine the minimal difference between the two intervals still detectable by the fish.

Data from such investigation can aid in gaining insight and in outlining models for the processing mechanisms underlying the behavior of the fish based on the spatial distribution of the stimulus to the LLO.

## Materials and method

*The experimental animal.* Blind cave fish, *Anoptichthys jordani*, with body lengths of 5 to 7 cm were used for the experiments. Some of them were purchased from dealers, others had been bred in the laboratory.

*The experimental set-up.* The experimental tank (40 × 40 × 15 cm) was divided into two equal halves by a plexiglass plate (Fig. 1). The grids to be discriminated were fixed onto this plate, one grid on each surface of the left half and the others on each surface of the right half. The grids were constructed with nylon bars of 1 mm in diameter fixed directly onto the surfaces of the plate. In the middle of each half of the plate, there was an opening (2 × 2 cm) at the bottom to permit the fish to swim through. The fish's task was to associate the grid to be discriminated with the 'rewarded opening'; when the fish swam through this opening, it was rewarded for its correct choice with food. Swimming through the other opening, the 'unrewarded opening', was punished as a false choice.

To prevent water disturbances due to ventilation and heating, the experimental tank was placed in a larger tank containing the facilities for heating (23–25 °C) and ventilating the water (Fig. 2).

There was a depression in which the reward was presented for the fish in the bottom of each half of the experimental tank (Fig. 1). This reward consisted of a food paste of flake food (Tetramin) mixed with water and thickened with powdered Tragacanth (von Campenhausen et al. 1981). It was pressed

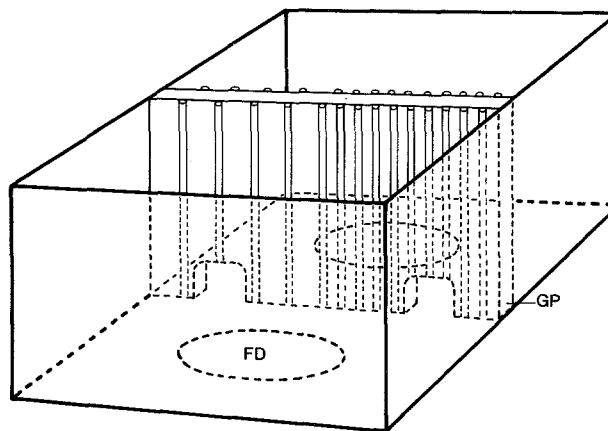


Fig. 1. Schematic diagram of the experimental tank. PG grid plate; FD food depression

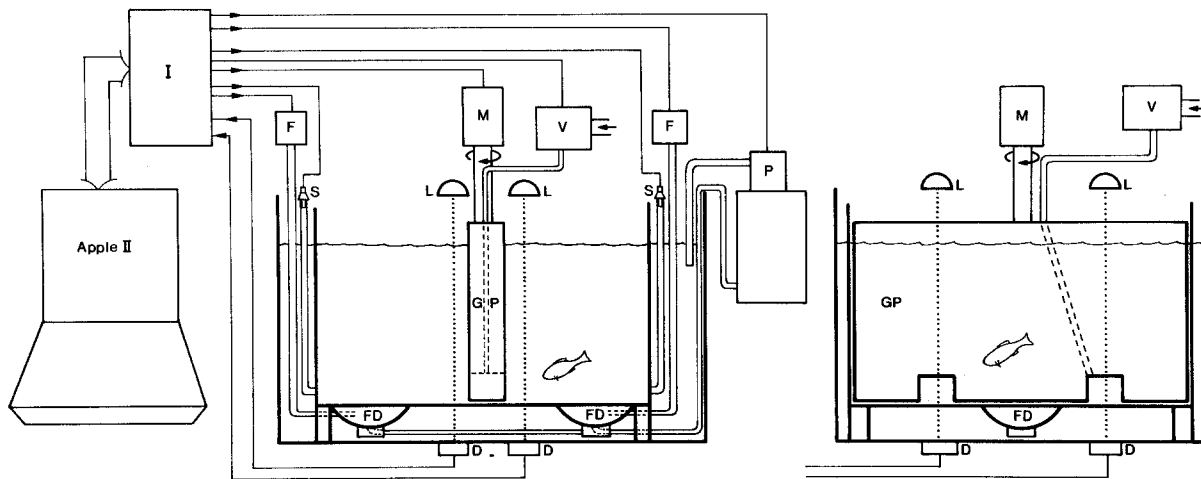
out onto a small circular piece of wire mesh in the middle of the depression through a tube by means of syringe compressed by an electric motor outside the water. Another tube fixed below the piece of wire mesh was used to suck off water continuously to prevent any chemical stimuli which may have been produced by the food from spreading in the water of the experimental tank. The punishment was a suddenly produced water jet at the unrewarded opening to alarm the fish. The water jet punishment was preferred to an electric shock which might have produced chemical compounds in the water which the fish could have used to recognize the unrewarded opening.

The set-up was automated with the aid of a microcomputer (Apple II) (Fig. 2). Four light detectors were placed under the large tank, one below either side of each opening in the grids. The four light detectors were illuminated from the top of the tank. The interruption of one light beam of any detector by the fish was signalled to the microcomputer, which determined the location of the fish at that moment. If the detector became free again, this was interpreted as the fish having swum past the door. If, however, the two light beams illuminating the two detectors of one opening were interrupted, it was interpreted as a choice of the fish to swim through the opening. Depending on which opening was chosen, the fish was rewarded or punished. On a correct choice the food paste was presented at the bottom of the depression. At the same time a tone of 1,000 Hz was emitted for 10 s to indicate the presence of its reward to the fish. For a period of 20 s, the water was not sucked away so as to give the fish a chance to find the food. On a false choice, a valve fixed to a water tap was opened for half a second to pass water under pressure through a tube whose other end was fixed in hole at the side of the unrewarded opening. This produced a sudden jet of water in the opening which alarmed the fish.

The computer recorded all choices, both correct and false, and the time of their occurrence. After ten choices the grid plate was rotated slowly through 180° to avoid place training. The automation of the experimental set-up made it possible to continue the experiment for 24 h a day for several weeks without interruption; so the fish could be left follow its own natural rhythm in cooperating in the experiment.

*The conditioning procedure.* The fish was conditioned in three steps:

*Step 1.* The fish was put into the experimental tank without the grid plate in the middle of it. Food was presented in the depressions and left there until the fish noticed it. Each presen-



**Fig. 2.** Schematic diagram of the automated experimental setup, left: front view, right: side view. *I* the interface between the setup and the microcomputer; *F* food donor; *S* loudspeaker; *M* motor to rotate the grid plate, *GP* grid plate; *P* pump for sucking away the food remains; *V* water valve for producing a water jet; *L* lamp; *FD* food depression; *D* light detector

tation was accompanied by a tone of 1 kHz to condition the fish to associate the availability of food with the tone.

*Step 2.* The grid plate was mounted in the middle of the tank. Each time the fish swam along the half of the plate, on which the grid to be chosen (training grid) was fixed, a tone was emitted in the other half of the tank signalling the presentation of food at the other side of the plate. The fish then had to swim through the rewarded opening in the bottom of the training grid to get the food. If it swam through the other opening no food was presented and the water jet was released.

*Step 3.* After the fish had shown a clear preference for swimming through the opening in the training grid, the tone was no longer presented when the fish passed by this grid. Food and tone were presented at the same time but only when the fish was swimming through the rewarded opening, i.e. at the time when it had made its definite choice.

For most of the fish the association between the tone and the food presentation in the first step of the conditioning was a relatively simple task. In the second step, it was difficult for the fish to associate between the tone and the presentation of the food in the other half of the tank. At this stage, six fish were able to cooperate in the experiment. However, in the third step it was still more difficult for the fish to associate between the grid and the opening through which it had to swim to get the food. Three fish were able to cooperate at this stage and the experiment was continued with them.

The range of the intervals between the bars on the grids was limited both by the body length of the fish and by the diameter of the bars. In this study, the upper interval limit was 30 mm to ensure that, at any one time, the fish was alongside at least two bars. The lower limit was 5 mm to minimize the effect of unavoidable inaccuracies in the construction of the grids.

Two series of experiments were carried out. In one series the training grid had bars at an interval of 10 mm, in the other intervals of 20 mm. The interval between the bars on the other grid (comparison grid) was then made systematically closer to that of the training grid in each series. At the beginning, the interval between the bars on the comparison grid was twice that between the bars on the training grid. In the successive experiments the difference between the two grids was reduced to the half of the foregoing one until a difference of ca 1 mm

was reached. Experiments with the same interval between the bars on the comparison and training grids were not carried out. The experiment was then continued in the same way, beginning with the interval between the bars on the comparison grid at half that of the bars on the training grid. Each experiment was carried on until at least 400 choices had been made by the fish.

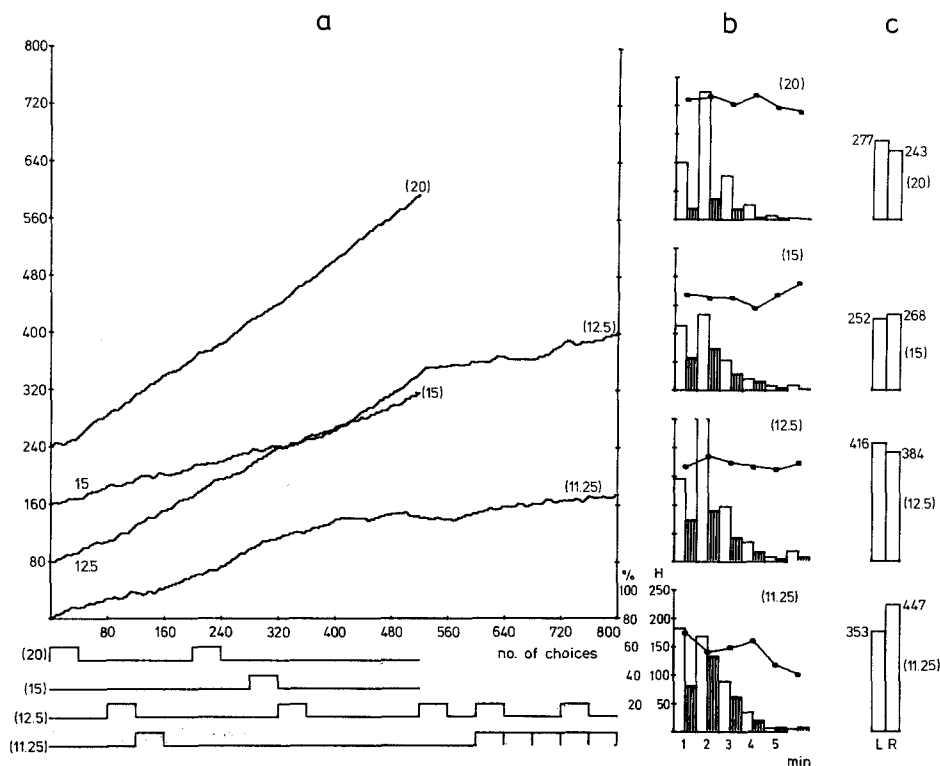
## Results

To determine the spatial discriminatory performance (SDP) of the fish, the data were analyzed in a specific way so as to take into account some peculiarities in the fish's behavior associated with the experimental set-up.

### Data analysis

Figures 3 and 4 show typical raw data from two fish obtained in two series of experiments with a training grid bar interval of 10 mm. In the series in Fig. 3 for fish no. 1, the interval of the comparison grid bars was varied successively in four experiments beginning with an interval of 20 mm and continuing with the intervals 15 mm, 12.5 mm and 11.25 mm. In the series in Fig. 4 for fish no. 2, the interval between the comparison grid bars in the first experiment was 5 mm then 7.5 and 8.75 mm in the subsequent ones.

The choices the fish made in each experiment are plotted sequentially as step curves (Figs. 3a and 4a). The curves are displaced vertically from each other to avoid intersections between them. Two successive correct choices are represented in these curves by an upward step, and two successive false choices are represented by a downward step. For one correct and one false choice the curve remains constant.



**Fig. 3a-c.** Raw data from fish no. 1 obtained in a series of experiments with a training grid interval of 10 mm. **a** step curves representing the sequence of the fish's choices in each experiment. The ordinate has the same scale as the abscissa: an upward step represents two correct choices and a downward step two false choices. Step curves are plotted displaced from each other to avoid intersection between them. Each curve is labelled with the bar interval length of the comparison grid. Lines under the curves, which are also labelled with the comparison grid bar interval, indicate the place oriented period in the experiments with an upward step. **b** interval histograms of the time interval between the choices of the fish. The numbers of correct (open) and false (hatched) choices are represented separately in each bin (bin width=1 min). Percentages of correct choices for each bin are also plotted and connected with a line. Each histogram is labelled with the length of the comparison grid bar intervals. **c** number of choices made by the fish at the left (L) and at the right (R) side of the tank

The step curves were divided into segments of 40 choices so as to be able to compare how the fish performed at various times in the experiment. On examining these segments individually, it became apparent that the fish had sometimes chosen according to the side of the tank and not according to the type of grid. This 'place orientation' disclosed itself as follows: the fish preferred the opening at one side of the tank as long as it received its reward there (result achieved=ca. 100% correct choices) but, after the grid plate was rotated, it began to choose the openings on either side alternately (result=ca 50% correct choices) until the grid plate was again rotated back to the former position whereupon the fish reverted to choosing the rewarded side (result=ca. 100% correct choices). This meant that the total of correct choices for the whole segment was ca 75%, which, though quite good, was not attained by discriminating between the grids. To check whether the fish was place oriented or not, each segment was examined to ascertain the number of choices made

by the fish to swim through the opening in the plate on the left and on the right side of the experimental tank. If the percentage of decisions for one side exceeded 62.5, i.e. the difference between the number of choices at each side amounted to more than a quarter of the whole number of choices in a particular segment, it was assumed that the fish was more place oriented than 'grid oriented'. These segments are marked by steps in lines under the plot of the step curves. For each experiment the whole number of choices made at each side of the experimental tank are represented as bars (Figs. 3c and 4c). Fish no. 2 had more place oriented periods in the experiments where the difference between the bar intervals of the two grids was large (Fig. 4). This behavior was observed in many experiments whose raw data are not presented here. Periods of place orientation were not included in the further evaluation of the data. Figures 5 and 6 show the same data for the two fish after omitting these periods

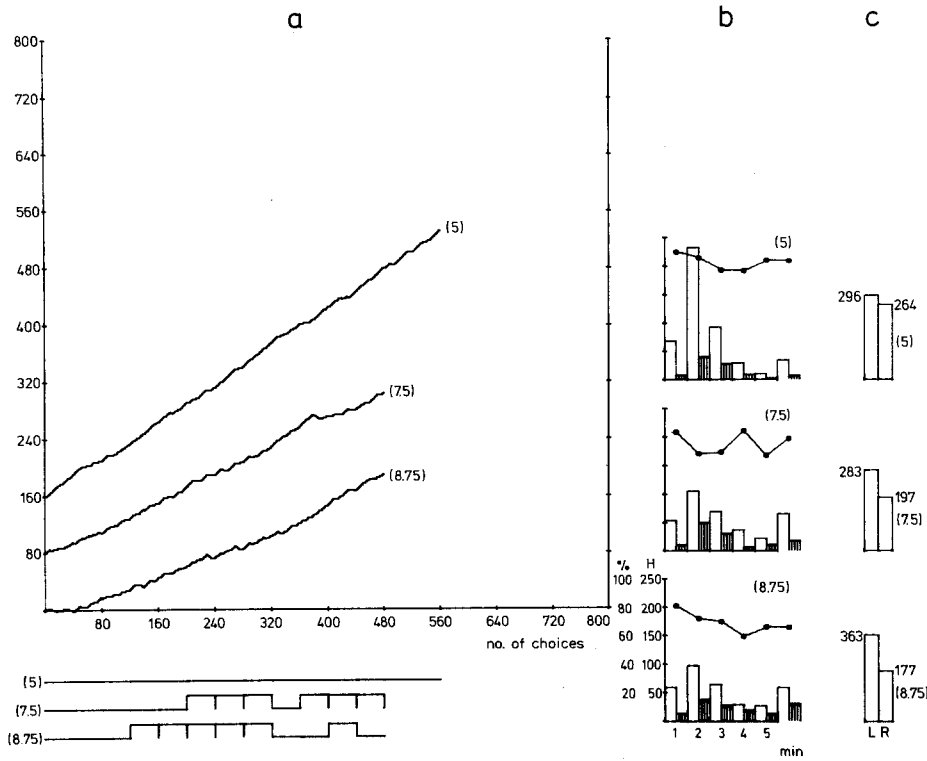


Fig. 4a-c. Raw data from fish no. 2 obtained in a series of experiments with a training grid bar interval of 10 mm. a, b and c as in Fig. 3

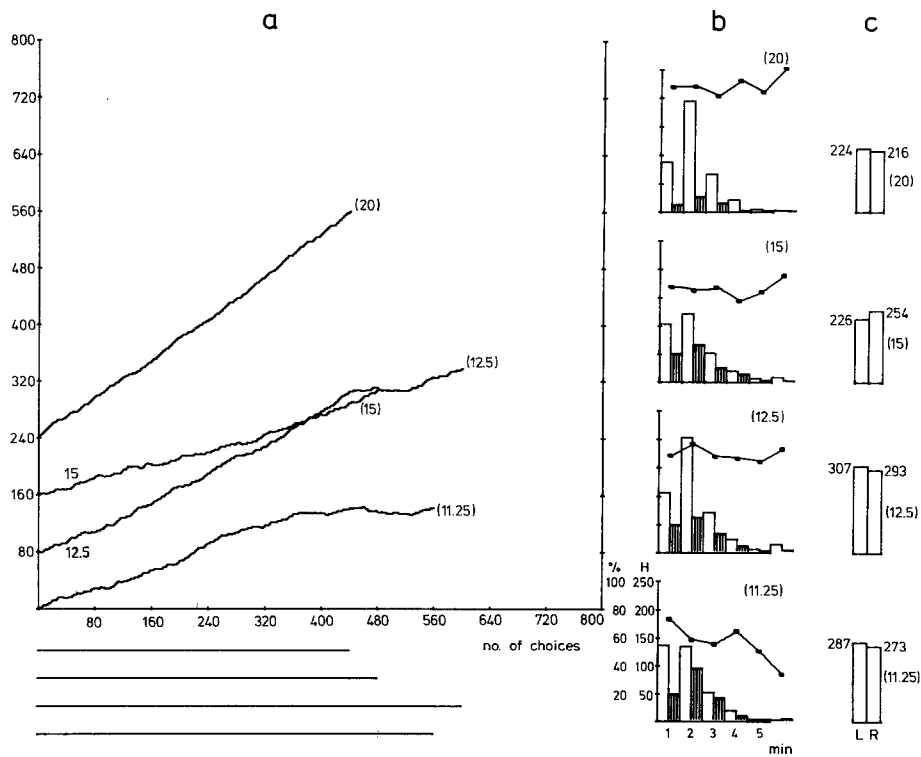


Fig. 5a-c. Same data as in Fig. 3 after omitting periods when the fish was place oriented, a, b and c as in Fig. 3

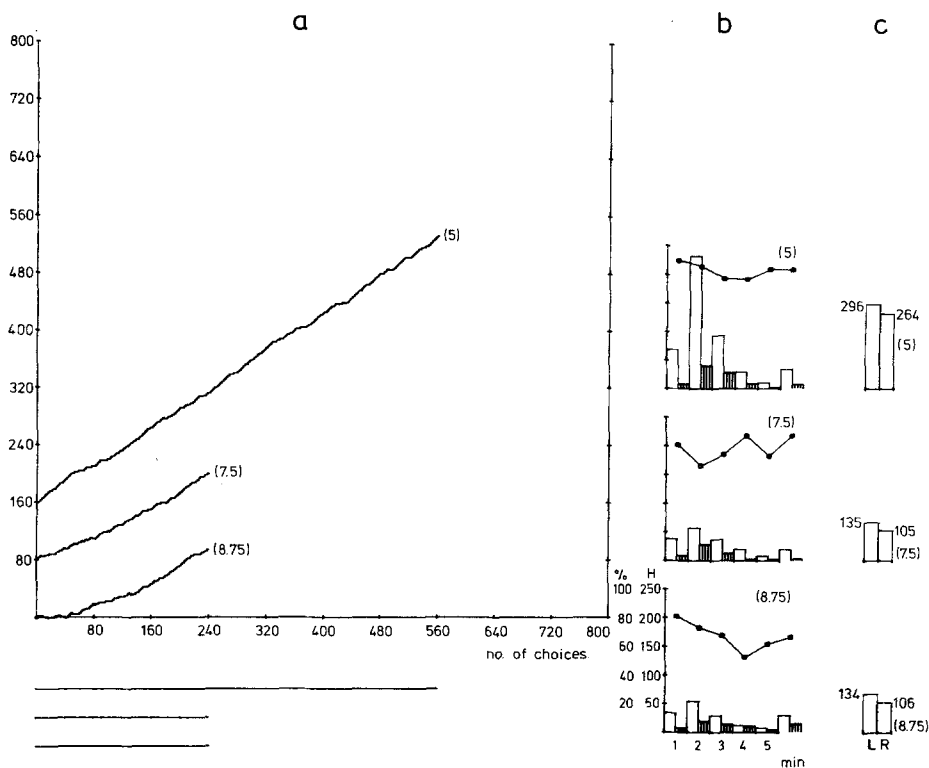


Fig. 6a-c. Same data as in Fig. 4 after omitting period when the fish was place oriented. a, b and c as in Fig. 3

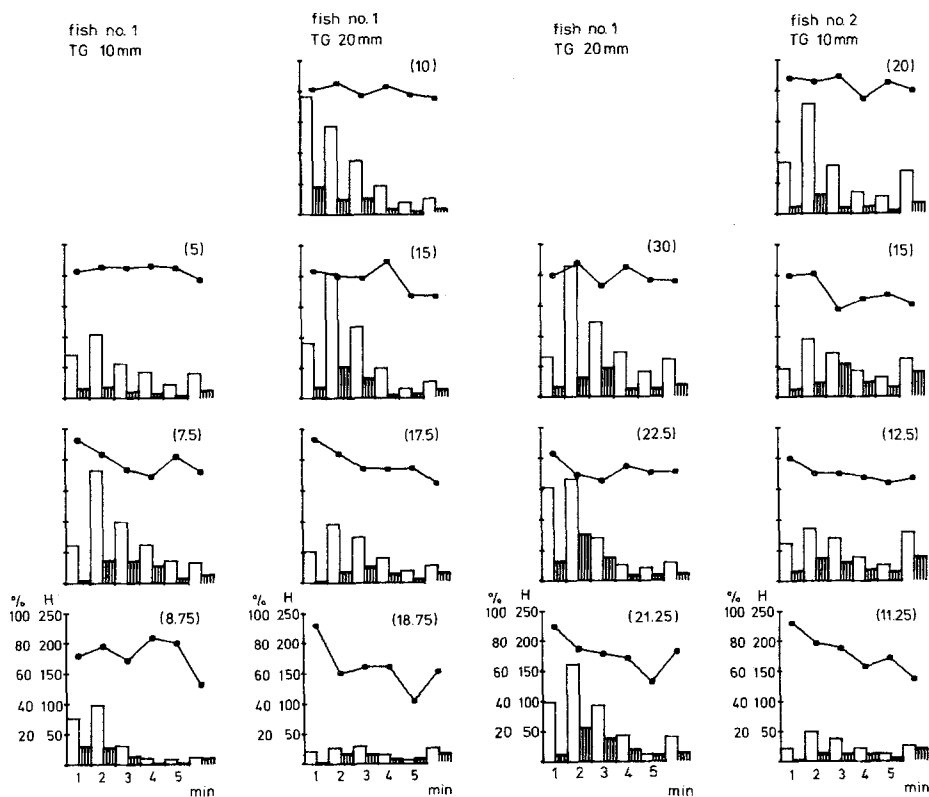


Fig. 7. Interval histograms of the time interval between the choices of the fish. Each bin represents the numbers of correct (open) and false (shaded) choices (bin width=1 min). Each histogram of each series is labelled with the comparison grid bar interval length

As can be seen from these figures, the step curves for the experiments with the largest difference between the bar intervals of the training and the comparison grids are uniform and have the steepest slopes. In contrast, the curves from the experiments with smaller bar interval differences between the two grids are not uniform and not so steep as the former one. However, in some segments the steepness of these curves is comparable to that of the first one.

As described above, the fish was left to follow its natural rhythm in cooperating in the experiment so the activity level of the fish varied during the experiments. This shows in the variation of the time interval between the choices. Short intervals were interpreted as an indication for high activity and long intervals for low activity. It is to be expected that the performance of the fish was correlated in some way with its activity. To investigate such a correlation, the time durations between the choices are represented as interval histograms. In each bin of this histogram the number of correct (open) and false (hatched) choices were plotted separately (Figs. 3b, 4b, 5b, 6b). As can be seen from these histograms, the fish made most of their decisions after a period of one to two minutes. In the same diagram the percentage of the correct choices for each bin is also plotted. The percentage of correct choices tends to decrease as the time interval between the fish's choices increases when the differences between the bar intervals on the two grids become smaller. In the experiments with large differences the percentage remains relatively constant. This tendency can be seen in Fig. 7 where the interval histograms of the rest of the experiments are plotted.

#### *Discriminatory performance curves*

In evaluating the whole percentage of correct choices in one experiment only those periods when the fish was not place oriented as discussed above were taken into consideration. The percentages evaluated in this way for all the experiments of one series in which the interval between the training grid bars was the same are plotted in Fig. 8a–d. With the aid of the Mann-Whitney statistical test, the choices of the fish in discriminating the largest and smallest differences between the training and the comparison grid intervals in each experiment were compared. The test gives as a significance level the probability that the data compared derive from the same distribution. The particular significance levels of the data for each experiment are given in Table 1. The diagrams in Fig. 8a and b represent results from experiments on fish no. 1,

**Table 1.** Significance level values of the choices of the fish in discriminating the largest and smallest differences between the training and the comparison grid intervals in each experiment

|            | Comparison grid intervals (mm) | Training grid intervals (mm) | Significance level |
|------------|--------------------------------|------------------------------|--------------------|
| Fish no. 1 | 20 and 11.25                   | 10                           | 0.001              |
|            | 5 and 8.75                     | 10                           | 0.01               |
|            | 30 and 21.25                   | 20                           | 0.05               |
|            | 10 and 18.75                   | 20                           | 0.025              |
| Fish no. 2 | 20 and 11.25                   | 10                           | 0.01               |
|            | 5 and 8.75                     | 10                           | 0.01               |
| Fish no. 3 | 30 and 21.25                   | 20                           | 0.001              |
|            | 10 and 18.75                   | 20                           | 0.001              |

Fig. 8c is for fish no. 2 and Fig. 8d for fish no. 3. As Fig. 8a–d shows the fish can detect a difference of 2.5 mm between the bar intervals of the two grids with over 70% certainty. For smaller differences, however, the percentage of correct choices is smaller on the average and varies strongly from one period to another. For these smaller differences, the fish also made more place oriented choices than for large differences. An average value of 1.5 mm can be calculated as the smallest difference between the bar intervals of the two grids which can be discriminated by the fish with 70% certainty.

The results of the third fish (Fig. 8d) show relatively poor discriminatory performance in comparison with the other two. It was also impossible to train the fish to avoid grids with bar intervals larger than that of the grid to be preferred after the first series of experiments, where the fish had to do the opposite. In the second series, the fish was still preferring the larger intervals (Fig. 8d).

#### **Discussion**

The results presented in this study show that the blind cave fish is able to discriminate between grids with bars set at different intervals. The fish can discriminate between large differences well whether its activity level is high or low. If the differences are small, however, the discriminatory performance of the fish is lower and falls off when it is less active. In the experiment with 15 mm comparison grid bar interval, the performances of fish nos. 1 and 2 were surprisingly low (Fig. 8a, d). On examining the grid it was found that the bars were not fixed directly onto the surface of the plate so that there was a small space between the plate and the bars. The exact interpretation for this result cannot be ascertained without examining the physics of the stimulus for the LLO in such a case. However, it can be expected that the modification to the flow current of the gliding fish will be

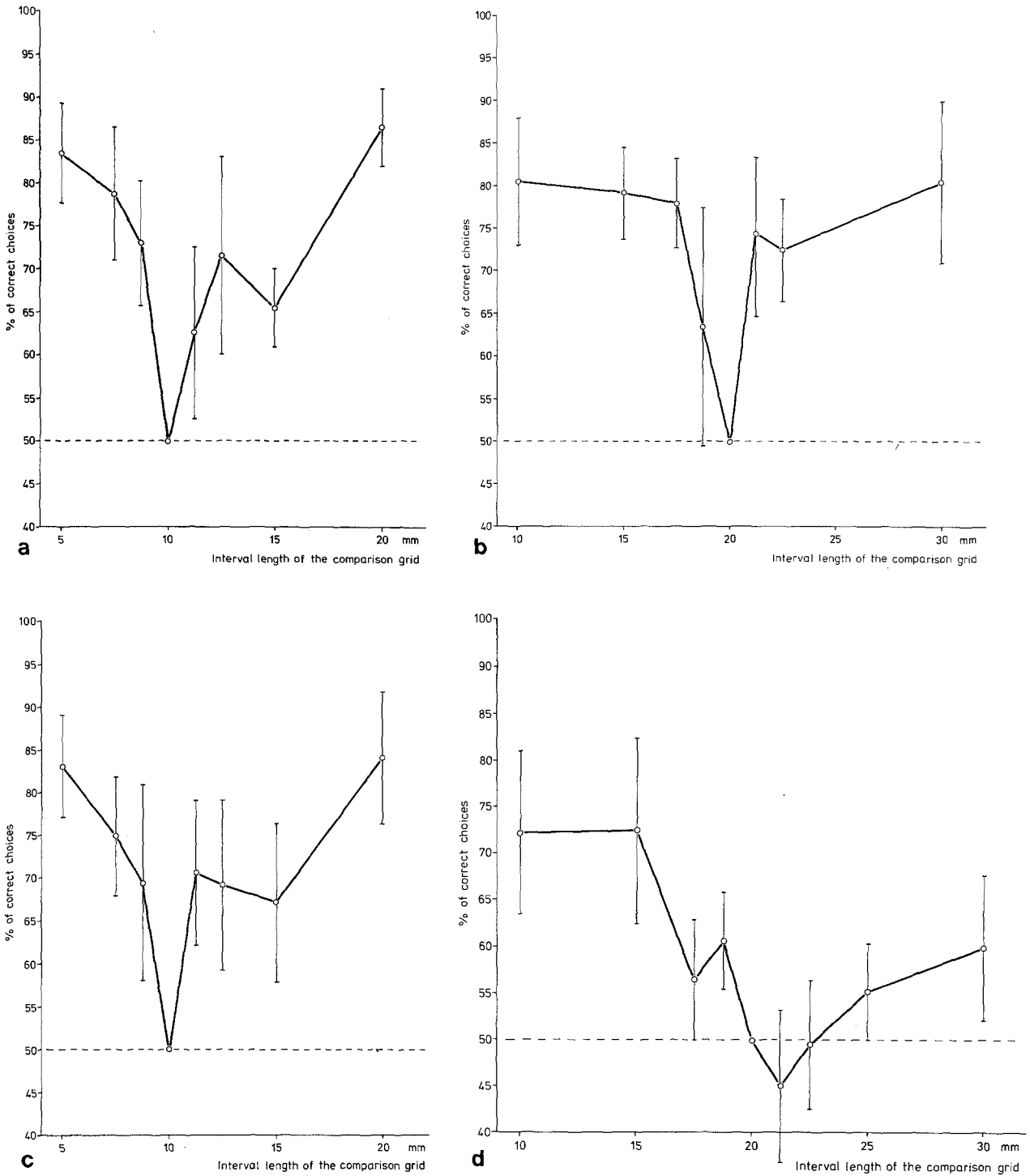


Fig. 8A-D. Discriminatory performance of fish no. 1 (A, B), fish no. 2 (C), fish no. 3 (D). Grid interval: A, C 10 mm; B, D 20 mm

smaller and consequently the stimulus to the LLO will be lower when there is a space between the bars and the surface of the plate than when there is no space in between. The results for the range of differences between the grid bar intervals tested in this study indicate that the fish can detect differ-

ences as low as 1.5 mm with a certainty of 70%. On normalizing this difference on the interval length of the training grid bars, one gets a factor, the spatial discriminatory performance factor (SDPF), between 0.15 and 0.075 for the intervals 10 and 20 mm, respectively.



It is of interest, as discussed before, to compare this performance of the fish with its performance in discriminating frequencies of vibrations in the water. Experiments on this topic with the blind cave fish (Frühbeis 1984) have shown that the corresponding temporal discriminatory performance factor (TDPF) (i.e. the difference between the training and the comparison frequencies at 70% correct choices normalized on the training frequency) has a value between 0.4 at 10 Hz and 0.11 at 110 Hz. In these experiments the vibration in the water was produced by two simultaneously vibrating balls. New experiments with non-simultaneously vibrating balls have shown that the TDPF tends to be larger (von Campenhausen, personal communication).

Assuming that only the temporal course of the stimulus to the LLO is relevant for the fish to gain information about its environment, it must be claimed that the temporal course should be the same for equal TDPF and SDPF values. Assuming further that the SDPF at the 20 mm training interval is equal to that of TDPF at the 110 Hz training frequency, the fish would have to glide past the grid at a velocity of 220 cm/s for the stimulus to the LLO to have the same frequency as that of the vibrating ball. This velocity is too high and cannot be achieved by the blind cave fish. Measurements of the fish's velocity resulted in a maximum value of 25 cm/s (Weissert and von Campenhausen 1981; Teyke 1985). Consequently, it can be argued that the fish is able to use the phase relationship of the stimulus to the LLO.

The comparison of the result obtained here with that obtained from behavioral experiments on the surface feeding fish *Aplocheilus lineatus* in discriminating frequencies of surface waves (Bleckmann et al. 1981) yields a good agreement between the SDPF values obtained here and those of the corresponding quantity, the Weber fraction, obtained there. In this study the average Weber fraction was  $0.1 \pm 0.03$  for the frequency range between 20 and 120 Hz. Deriving the difference between the wavelength of the surface waves which can be discriminated at 20 Hz yields a difference of about 1.4 mm (the surface wave velocity at 20 Hz has a value of about 25 cm/s (Schwartz 1965)). This value for the difference between the wavelengths agrees very well with that obtained here for the difference between the bar intervals on the grids. This agreement indicates that the processing mechanism in the two cases may be the same.

The analysis of the phase relationship in the stimulus over the skin of the fish requires the comparison of the temporal course of the stimulus at

different points. The precision of this analysis increases in proportion to the number of points compared. This may explain why a large number of neuromasts are found in the skin of the blind cave fish (Schemmel 1967). The comparing mechanism itself would have to use both the convergence of the signals from the different points to be compared as well as the divergence of the signal from each point to be compared from the signal from every other point. A similar branching plan seems to exist in the branching of primary afferents in the medulla of *Xenopus laevis* (Plassmann 1980) and in general in the medulla of bony fish (Münz and Claas 1983; Maler et al. 1973, 1974), where the primary afferents have a widespread arborization in the lateral line nucleus. However, to confirm that fish use the phase relationship to evaluate stimuli in the way described, stimuli with well-defined spatial distribution will have to be applied to the LLO to obtain electrophysiological recordings from the lateral line nucleus.

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