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Distance and shape: perception of the 3-dimensional world by weakly electric fish

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Abstract

Weakly electric fish orient at night in complete darkness by employing their active electrolocation system. They emit short electric signals and perceive the consequences of these emissions with epidermal electroreceptors. Objects are detected by analyzing the electric images which they project onto the animal's electroreceptive skin surface. This process corresponds to similar processes during vision, where visual images are cast onto the retinas of eyes. Behavioral experiments have shown that electric fish can measure the distance of objects during active electrolocation, thus possessing three-dimensional depth perception of their surroundings. The fundamental mechanism for distance determination differs from stereopsis used during vision by two-eyed animals, but resembles some supplementary mechanisms for distance deduction in humans. Weakly electric fish can also perceive the three-dimensional shape of objects. The fish can learn to identify certain objects and discriminate them from all other objects. In addition, they spontaneously categorize objects according to their shapes and not according to object size or material properties. There is good evidence that some fundamental types of perceptual invariances during visual object recognition in humans are also found in electric fish during active electrolocation. These include size invariance (maybe including size constancy), rotational invariance, and translational invariance. The mechanisms of shape detection during electrolocation are still unknown, and their discoveries require additional experiments.
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Keywords: Object detection; Active electrolocation; Depth perception; 3-d space; Identification; Categorization

1. Introduction

When animals move around in their environment they have to be able to detect, localize, and identify various kinds of objects such as food items, predators and conspecifics, obstacles and landmarks, and many others. Most diurnal vertebrates solve their orientation problems by using their eyes, i.e. by employing their visual sense, e.g. in [14,24,38,39,44,46]. Weakly electric fishes, however, are nocturnal, and during their active period their eyes provide no information for the perception of objects [20,30]. As an alternative means of orientation, these fish use an active electrosensory motor system, which is called 'active electrolocation' [1,19, 27,48,49]. For imaging their surroundings they produce weak electrical current pulses with a specialized electric organ in their tail. In the elephant nose fish, *Gnathonemus petersii*, each electric organ discharge (EOD) lasts for only about 400 μs, during which an electrical current flows through the water building up an electrical field around the fish [29]. The electrical current is channeled through hundreds of epidermal electroreceptor organs, which are distributed over almost the entire body surface of the fish. In *G. petersii*, each electroreceptor organ contains several electroreceptor cells, which are excited by the current passing through them and "measure" its amplitude and temporal pattern [54].

When a fish has produced an EOD, each electroreceptor organ provides information about the locally occurring EOD amplitude and waveform to the brain. The first station in the brain that receives input from all electroreceptor organs is the electrosensory lateral line lobe (ELL), where a 'map' of the electrosensory body surface of the fish is formed [2]. When the fish is swimming in the open water without any objects nearby, local field amplitudes have a medium value, which is

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'stored' in the neurons forming the map within the ELL [3]. However, when an object with an electrical resistance different from that of water (which are almost all objects in the natural habitat of these fish) approaches the fish, the electrical field produced by the EOD is distorted, which leads to an altered electrical current flow at those parts of the skin which are closest to the object [9,36]. Consequently, the electroreceptor organs located in this region report an alteration of the local electrical amplitude, which leads to a change of neural activity in the corresponding part of the map of the ELL.

Each object, which is present in the vicinity of the fish up to a distance of about a body length, projects an electrical 'shadow' or electrical 'image' onto the skin of the fish. The electric image is defined as that skin region, which experiences an alteration of amplitude or waveform of the local electric signal because of the presence of the object [52]. In order to get information about the object itself, the fish has to analyze the electric image, i.e. its representation on the electroreceptive maps within the brain. By doing so, it can detect, localize, and analyze many physical object properties.

Behavioral experiments have shown that weakly electric fish acquire a very precise and detailed perception of their surroundings and the objects within it [49]. Because the local EOD amplitude of the electric image depends directly on the electrical resistance of an object, fish can precisely measure resistive object properties. For example, they can easily discriminate between a nonconductor (isolator), such as most stones, and a low-resistive object, such as a water plant or a stone with metallic inclusions. In addition, they also can tell apart resistive values in between these extremes and thus can discriminate between differently conducting objects [51].

Some natural objects not only change the local EOD amplitude but, in addition, distort the local EOD waveform. These temporal EOD changes are caused by objects with a complex impedance, which includes a capacitive component. Especially living objects, such as water plants, other fishes, or insect larvae (food items) possess capacitive properties and therefore distort the local EOD waveform [19,40,48]. Some of the electroreceptor cells within each electroreceptor organ of Gnathonemus petersii respond to these waveform distortions, thereby enabling the fish to detect them. In behavioral training experiments G. petersii has proven its ability to detect even minute capacitive object properties, and thereby to discriminate between animate and non-living objects categorically [48,50,51].

These examples show that weakly electric fish can detect the electrical properties of objects during active electrolocation. However, they can do much more than this: they also can detect and localize an object in three-dimensional space, and can detect an object's shape and possibly its size independently of other object parameters, such as distance. In this paper, I want to review the current knowledge about 3-dimensional object localization and provide some new evidence about size- and distance-independent detection of object shape.

2. Distance perception during active electrolocation

An electric image projected onto the skin surface of a G. petersii during active electrolocation is not only dependent on the material of the object, but in addition on other object parameters such as size, shape, and distance. When an object moves away from an electric fish, the image it projects increases in size and decreases in modulation amplitude. For example, a spherical metal object at a close distance to the fish projects a relatively small electrical image with a large amplitude increase in its center. If the same object is located further away from the fish, the image gets larger while the amplitude increase in its center gets smaller (Fig. 1A and B).

However, an image very similar to the one produced by the far away object can also be obtained with an object close to the fish (Fig. 1C). Such an object would have to be larger than the objects shown in Fig. 1A and
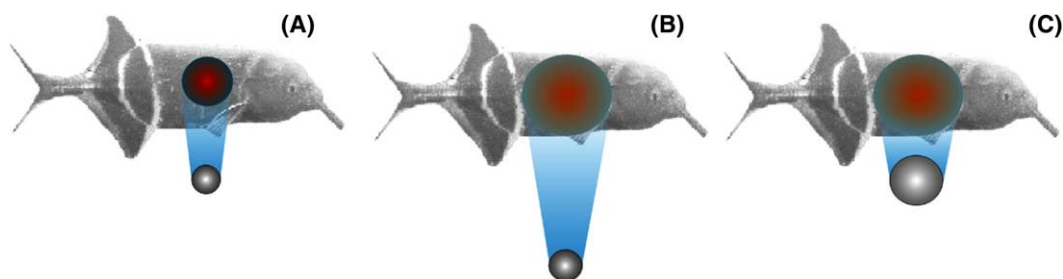

Fig. 1. Electric images of metal spheres of different sizes at different distances. The electric images are drawn as color coded circles on the fish's skin. Dark colors depict an increase of the locally occurring EOD amplitude, light colors an amplitude decrease. (A) A small sphere is located close to the fish, projecting a small electric image with strong amplitude modulations. (B) The small sphere is located farther away than in (A), which leads to an increase in image size and a decrease in amplitude modulation. (C) A large sphere of slightly higher electrical resistance is located at the same distance as in (A). Despite the shorter distance of the object, the image it projects is very similar to that in (B).

B in order to project a larger electric image. In addition, it would need to be higher in impedance than a metal object in order to produce smaller amplitude modulations. If these two conditions are met, the two electric images shown in Fig. 1B and C would be almost identical to a superficial observer. The question is, whether a fish would notice a difference between these two images, and thus would be able to discriminate between the two objects that produce them.

Because of these presumed ambiguities, it was assumed for a long time that it was impossible for a fish to measure exactly the distance of an unknown object during active electrolocation. It was suspected that the 2-dimensional electrical image on the skin does not provide unambiguous information about 3-dimensional parameters. However, neither behavioral experiments nor actual measurements of electric images projected by real objects were available to test this assumption. Therefore, we conducted both types of experiments by employing the African weakly electric mormyrid fish, *G. petersii*.

2.1. Experiments

Behavioral experiments were designed to measure the ability of *G. petersii* to discriminate between the distances of two objects. Two objects were offered to a fish, which differed in their distance to a gate in a dividing wall in the experimental tank (Fig. 2). Individual fish were trained in darkness to discriminate between these two objects by using distance cues only. In order to receive a food reward, the fish had to inspect both objects electrically by swimming towards (but not through) the gates from the other side. After comparing the distances of both objects towards their respective gates, the animal finally had to choose that object which was located further away from its gate than the other one. A correct choice resulted in the presentation of a little worm as a food reward. In contrast, if it swam through the gate with the closer object, the fish was chased back without receiving any reward. The location of the correct gate changed from left to right in a pseudorandom manner [17] from trail to trial.

For training the animals, we decided that the objects should be two identical metal cubes with a side length of 3 cm. At the beginning of training, the 'correct' object was placed far away (>6 cm) from its gate while the 'wrong' object almost touched the dividing wall. After the fish had learned the basic task, the distances of the two objects were changed gradually in such a way that the closer object moved away, while the far away object approached its gate. Finally, the close object was kept constant at a distance of 3 cm from its gate, while the further away object was at a distance of 5–6 cm. When the fish solved this task in more than 80% of the trails during three successive sessions, the threshold measurements began. Employing a method-of-constant-stimuli, the further away object was moved stepwise to closer and closer distances so that the distance difference between the two objects became smaller and smaller and finally approached zero cm. The distance of the closer object was kept constant. At each distance difference, the percentage of correct discrimination was measured. Distance discrimination thresholds were defined at a performance of the fish of 70% correct discriminations.

All fish tested learned the task to discriminate the distances of two identical metal cubes (Fig. 3A), and after basic training was completed, discriminated the distances of the two objects fast and efficiently. Distance discrimination thresholds were measured for several fixed distances of the closer object to its gate, called 'gate distance'. It turned out that threshold values increased from an average distance difference of less than 0.5 cm for a gate distance of 2 cm to more than 3 cm for a gate distance of greater than 5 cm (Fig. 3B) [42].

Even though the fish performed very efficiently in our experiments, these first results did not prove that they were actually measuring object distances. In order to solve the task mentioned so far, which involved comparing distances of two identical objects, actual distance measurements were not necessary. The fish could have solved the task just as well by only measuring and comparing the maximal amplitude changes each of the two objects evoked in the center of their respective electric images. The object further away would always cause a smaller amplitude change than the closer object, no matter which relative distance they were positioned at. Besides amplitude cues, also cues involving the size of the electric images would have worked: the further away object always caused a larger image than the closer object.

In order to prove that actual distance measurements were performed by the fish, additional experiments were
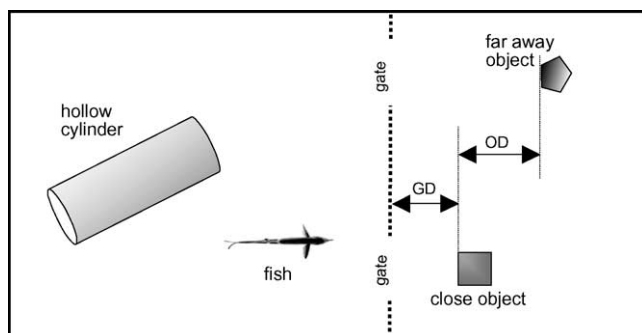

Fig. 2. Experimental set up seen from above, which was used for the training a fish to discriminate between the distances of two objects. A mesh wall (dotted line) containing two gates divided the tank into two compartments. Behind each gate an object was placed. The closer object had a fixed gate distance (GD). The distance difference (inter-object difference, OD) between the two objects was reduced in steps for threshold determination (see text). This figure was not drawn to scale.
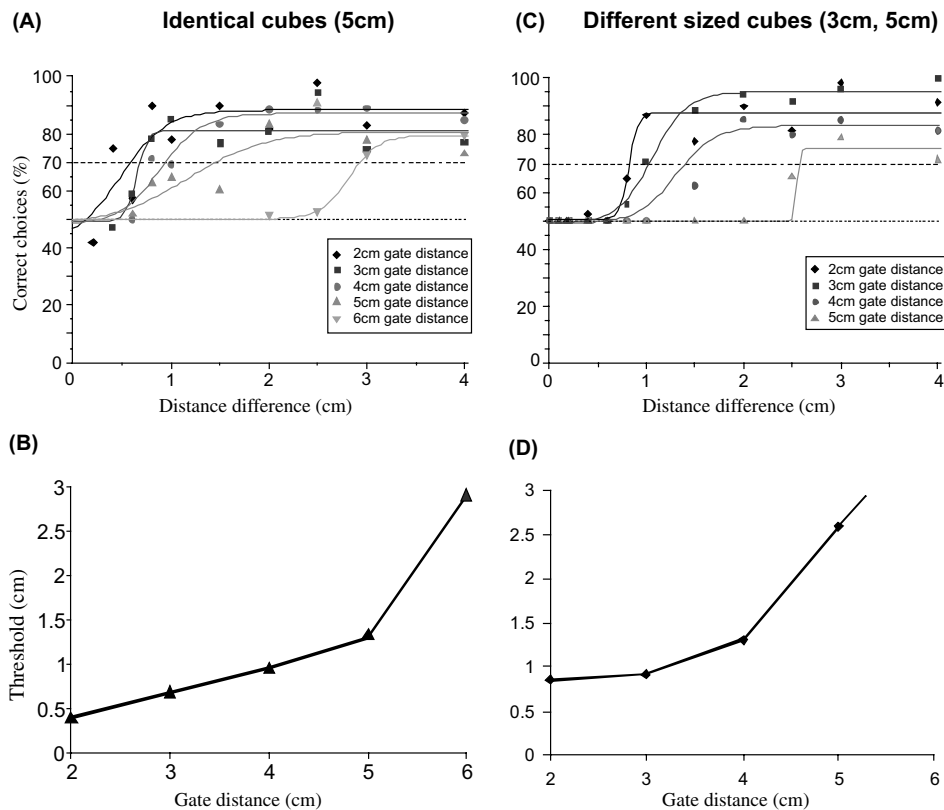
Fig. 3. (A,C) Psychometric functions of single *G. petersii* discriminating between the distances of two identical (A) or different-sized (side lengths 3 and 5 cm) (C) metal cubes. Each curve gives the results for a fixed gate distance. A sigmoid function was fitted to each data set. Threshold was defines as that distance difference where the fitted function crossed the 70% correct level (dashed lines). The dotted lines mark the chance level of 50% correct choices. Each data point represents at least 50 decisions by the fish. (B,D) Distance discrimination thresholds with two identical (B) or two different-sized (D) metal cubes of one animal plotted versus gate distance. Thresholds were determined from the psychometric functions shown in the diagrams above.

conducted. Now we offered two different objects, e.g. a cube and a pyramid or two cubes of different sizes, some of which the fish had never experienced before. Again, the fish was rewarded when it choose the closer of the two objects. Quantitative threshold measurements were performed with various combinations of objects. It turned out that even at a first presentation of a new object combination, all our fish could solve the task immediately and at the same speed as before, when two identical cubes were used. None of our fish had any difficulty in detecting the distance difference, even when the objects were novel to the fish and were never used before in an experiment. The resulting threshold curves looked very similar to the ones obtained with two identical cubes (Fig. 3C and D) [42].

These results showed that *G. petersii* indeed measured the distances of the objects when solving the task, and probably had done so already when two identical objects were used. Now we could be sure that *G. petersii* can determine the distance of an object during active electrolocation, despite the assumed ambiguities mentioned above. Moreover, our results showed that the fish were able to form and learn abstract concepts. They had

learned to pick an object that was located further away than another object, irrespective of the absolute distance of the two objects involved. This formation of the concept ("choose the object located further away") goes far beyond pure stimulus-response learning and can therefore be called 'cognitive'.

2.2. A mechanism for distance measurement during active electrolocation

How do electric fish actually measure the distance of an object during active electrolocation, despite the fact that the electric images of some objects located at different distances look so similar? In order to answer this question we measured the electric images, which several different types of objects of different sizes and shapes projected onto the skin of an electrolocating *G. petersii*. All images were digitally stored and analyzed, in order to find those image parameters which only depended on object distance but not on other factors such as size, shape, or material. Several image parameters were determined, e.g. the maximal amplitude change in the image's center, the maximal amplitude slope (i.e. maxi-
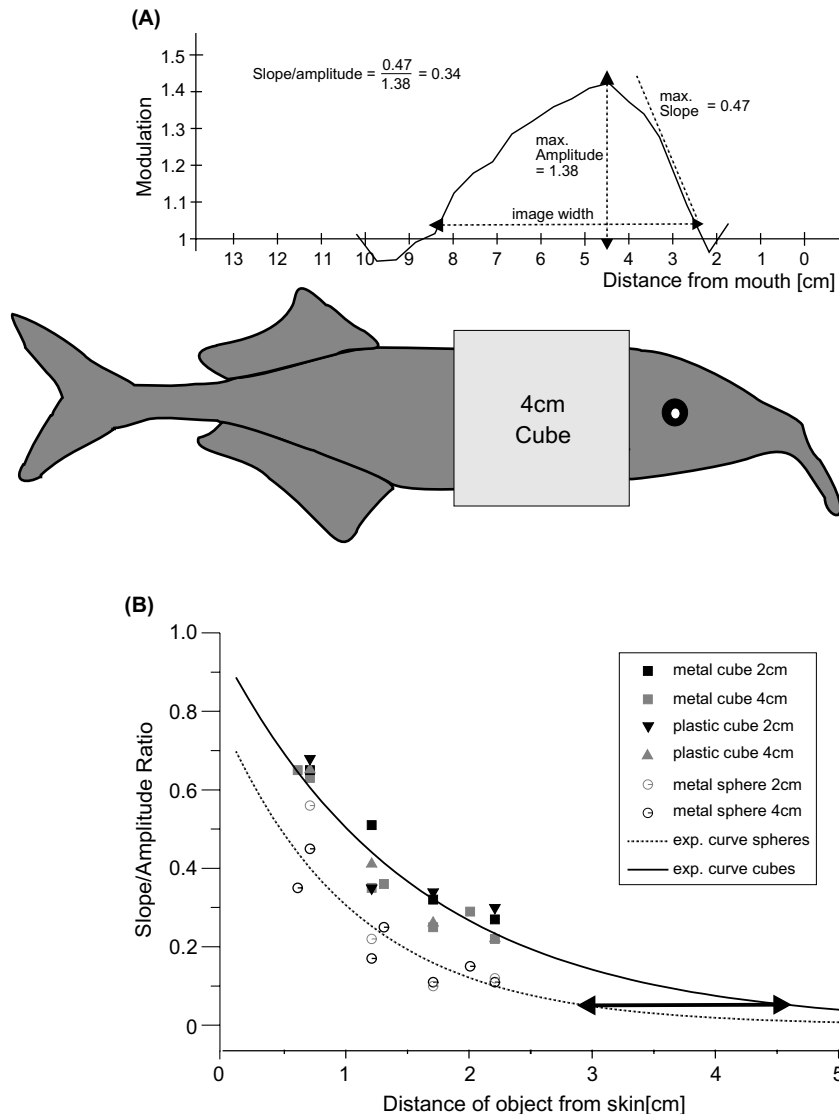
Fig. 4. (A) One-dimensional electric image (above) of a solid metal cube, which was placed at the side of a discharging *G. petersii* at a distance of 22 mm from the skin. The image is expressed as the modulation of the locally measured amplitude value in the presence of the object relative to the value measured when the object was not present. A value of 1 means that the object did not influence the local amplitude, while a value of 2 represents a doubling of the local amplitude value by the object. The dotted lines depict the maximal slope at the rostral side of the image, the maximally occurring amplitude value, and the width of the image, respectively. The ratio of the slope and amplitude values is a number that only depends on the distance of the object. (B) Slope/amplitude values of various objects plotted versus the distance of the object from the skin of the fish. Cube-shaped objects are plotted as squares and triangles, while spherical objects are plotted as circles. To each set of data an exponential function was fitted and extrapolated to object distances of up to 5 cm. Note that the curve for spheres runs below that for cubes. The double arrow depicts the distance difference of the SAR value of a sphere located 3 cm from the fish relative to the same SAR value of a cube. At the same SAR value, the cube would be located 4.5 cm from the fish's skin.

mal change in amplitude) at the rim area of the image, and the diameter of the image (Fig. 4A).

Unfortunately, none of these parameters depended only on the distance of the object, but all were also influenced by the type of object used. Therefore, we started to look at parameter *combinations*, which might correct for the influence of single object properties (e.g. electrical resistance or size) and thus avoid ambiguities. This approach turned out to be successful, because we finally found one parameter combination that worked for most of the objects we had used for image measurements. This combination was the ratio of the maximal amplitude slope over the maximal amplitude of the image (Fig. 4A). For all the objects used in our behavioral experiments so far, the slope–amplitude ratio (SAR) depended only on object distance and not on any other cues (Fig. 4B). The smaller the SAR the further away an object was located from the fish's skin, no matter if the object was large or small, had a high or low electrical resistance, or what shape it had. We thus came

up with a hypothesis about how our fish measured the distance of objects during active electrolocation: fish determine the slope–amplitude ratio of the electric image which an object projects onto their skin and use this value to determine the distance of the object. This would allow them to measure object distance quickly from single electrical 'snapshots' of an object.

The SAR worked fine for all objects except for one type: metal spheres. This type of objects, made to perfection at the mechanical shop of the University of Bonn, always yielded smaller SAR than all other objects (Fig. 4B). Our initial disappointment about this failure turned into optimism when we realized that these results offered us a unique tool to test our hypothesis about the mechanisms of distance measurement during active electrolocation. We designed an experiment during which the fish had to discriminate the distances of two objects, one of which was a metal sphere and the other one was a metal cube. If our hypothesis was correct, the fish should judge the sphere to be further away than it actually was, because the SAR of spheres always yields smaller values compared to that of other objects. When the sphere and the cube are placed at equal distances form the fish, the sphere should appear to be further away than the cube. From the results of our image measurements we even could quantify this illusionary distance difference between a cube and a sphere: at an actual distance of three centimeters the sphere should appear to the fish to be at a distance of 4.5 cm (Fig. 4D).

The results of our experiments completely confirmed our prediction (Fig. 5A). The psychometric functions obtained during a sphere–cube distance comparison differed from all other functions obtained with different object combinations (Fig. 5C). Instead of reaching chance level at a distance difference of about 0.7 cm, the fish had problems comparing the distance of a sphere and cube at much greater distance differences. We found that when the fish electrolocated a sphere, an 'electrical illusion' occurred. This illusion became especially apparent when two different cases were plotted separately, as in Fig. 5: If the sphere was further away, and thus the choice of the sphere was correct (remember that the fish were trained to choose the object which was located further away than the other object), the fish always performed correctly (dashed line in Fig. 5A). Even when the sphere was exactly at the same distance as the cube, the fish continued to choose it, because it appeared to be further away than it actually was. However, when the cube was located further away than the sphere (solid line in Fig. 5A), fish made lots of mistakes when the distance difference was smaller that about 1.5 cm. In these cases, the illusionary greater distance of the sphere added to its actual distance and made the fish choose the sphere, even though the choice of the cube would have been correct. When we compared quantitatively the performance of the fish with and without spheres, our
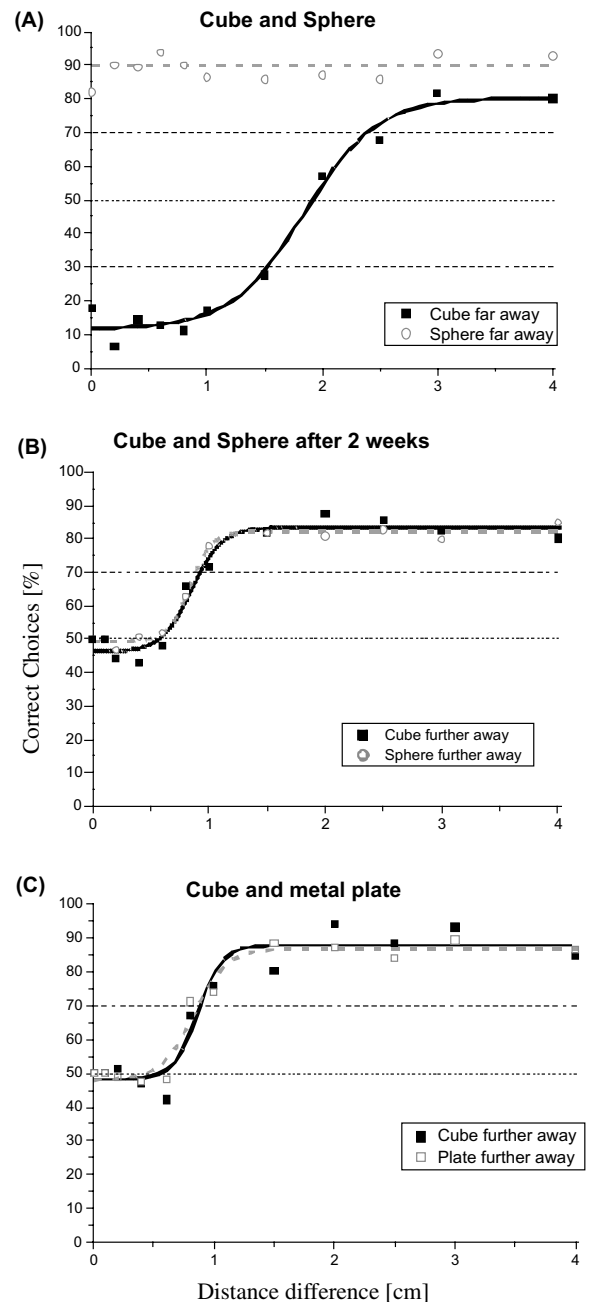

Fig. 5. Psychometric functions for one fish discriminating between the distances of a metal cube and a metal sphere (A,B) or a metal plate (C). In each graph, the results were split into two cases: filled symbols (solid black lines) depict the discrimination performance for those trials during which the cube was placed farther away from its gate than the alternative object. In these cases, the choice of the cube was correct. Open symbols (dashed grey lines) show the results obtained when the alternative objects (sphere = circles in A and B; plate = square in C) was placed farther away than the cube. Hence, choices of these objects were correct. Each data point consists of a minimum of 50 decisions by the fish. In (A), tests were performed before the fish had had any training experiences with spheres. (B) shows the results after training the fish for two weeks with a sphere/cube combination and rewarding correct choices only. In (C), tests were performed before the fish had had any training experience with a metal plate.

hypothesis was confirmed: at an actual distance of 3 cm, the sphere appeared to be at a distance of 4.5 cm, which is 1.5 cm further away than it actually was [53].

The electrical distance illusion occurring with spheres showed that in our experiments fish indeed used the SAR to judge the distance of objects during active electrolocation. This mechanism is unique in the animal kingdom. The fish only need a few (in some cases just a single EOD) 'snapshots' of an object in order to determine its distance. They use a single 2-dimensional array of receptors, upon which an electrical image of the three dimensional world is projected and calculate the third dimension from this projection. All sensory mechanisms found so far to be used by animals (including humans) for distance determination work differently: Often, two receptor surfaces are used (e.g. the two retinae in our eyes), which perceive slightly different images of an object. During stereopsis, the brain compares the two images and uses the differences between the images to derive object distance, e.g. in [21,33,45,47]. Other animals might suffice with only one receptor array (or two very close-by surfaces), but in this case these arrays have to be moved. The praying mantis, for example, moves its head in a lateral motion in front of its prey to derive distance information [35]. In contrast, toads and chameleons focus an object with the lenses of their eyes and derive distance information from this 'movement' [11,12,18].

Distance information can also be acquired from movement of the whole animal, or movement of the object to be measured. Many animals, including humans and flies, can derive distance information from optic flow, i.e. from the dynamics of the change of the object image on their retina, e.g. in [4,8,15,22,23,25,37,55]. Electric fish also might exploit such dynamic cues for depth perception. However, they do not have to: in our experiments they first and foremost used the slope–amplitude ratio of the electric image to judge distance. There are two arguments supporting this: (1) Electrical distance illusions should not occur when motion cues are used. Therefore, the fact that illusions occurred in all the fish trained argues for the use of the SAR and against optic flow cues. (2) The fish did not always approach the objects in a stereotyped manner. Sometimes, they swam directly head first towards the object, while equally often they swam along the object with their lateral body side. Very often they remained motionless just in front of the object for a few seconds while emitting electrolocation pulses at a high rate. In these situations no motion cues were available. However, when the fish live in their home streams, motion cues might play some role during distance determination.

When deriving object distance from the slope–amplitude ratio, the fish note the 'focus' of the electrical image. The more 'blurred' the image is, the smaller is the SAR and the farther away the object appears. The

advantage of using this mechanism might be speed. Theoretically, only a single 'snapshot' of an object is enough to determine its distance. When using motion cues at least two, but better several images of the object are required. Because active electrolocation is a near field orientation system, which works only up to a distance of about one fish length [32,42], speed is a crucial factor. A fish is already quite close to an object when it appears on its 'radar screen' and there may not be much time for object inspection before making a decision. A quick retreat in the right direction from a dangerous object could be life saving, and a fast estimation of the distance of such an object by employing the SAR certainly will help. When watching electric fish with an infrared camera swimming around in complete darkness in a complex environment, one is awed by the swiftness of their movements and the apparent ease and rapidity of detecting and avoiding obstacles or catching a prey item. Their depth perception must be fast to allow for these movements and the SAR mechanism might be the basis for this speed.

Judging distance from the blurriness of the image of an object might have a parallel during vision in some animals, e.g. in humans [26]. Under normal conditions, our visual system combines the information from both eyes to accurately determine an object's distance. Under different viewing conditions, however, other visual cues for judging distance can play more important roles. For example, it is well known that both visual contrast and image blur provide monocular cues for visual distance perception [28,34]. Lower contrast and increased blur generally suggest an increased viewing distance. Indeed, painters commonly use these effects to create 3-dimensional images on a 2-dimensional surface.

Using a psychophysical approach, Lewis and Mahler [26] compared quantitatively the effects of visual blur in human distance judgment and electrical blur during active electrolocation in electric fish. The psychophysical functions obtained from humans and those obtained from fish look remarkably similar: In both cases the functions obtained with blurred images were significantly shifted towards greater distances (to the right when the solid lines in Fig. 5A and C are compared). Thus, visual blur had the same effect on human distance judgment as that described in electric fish, where the more blurred electric image of a sphere results in it appearing farther away than a cube at the same distance. The human experiments showed that the visual and the electrosensory systems share analogous cues, namely contrast and blur, and that these cues also interact in similar ways.

There may be even more sensory systems that use similar cues. In auditory distance perception, both the amplitude and the spectral content of a sound can provide distance cues [31]. Decreased amplitude and less high frequency content are usually associated with a

sound source being farther away. These cues are analogous to visual contrast and blur: contrast can be considered to be the amplitude of the signal relative to the background noise and blurring is a decrease in high spatial frequencies [26]. When in acoustical psychophysical experiments subjects are presented with a sound that is low-pass filtered (blurred) it is judged to be coming from a source farther away than a sound of the same amplitude which was not filtered [7]. The observation that there is a shift in estimated distance towards more distant values strongly suggests that the psychometric curve is shifted with auditory blur in a way that is analogous to that caused by visual and electrosensory blur.

3. Object shape perception during active electrolocation

A first hint that *G. petersii* might be able to perceive the 3-dimensional shape of objects during active electrolocation came from our distance experiments (see above). We had tested whether the fish can detect a distance difference between a sphere and a cube. During these experiments an electrical illusion occurred: spheres appeared to the fish to be farther away than they actually were (Fig. 5A). In consecutive experiments, we continued to train the fish to perform the same discrimination task. In contrast to the previous tests, however, we now rewarded the fish for correct choices and 'punished' them (by not giving any food reward) for incorrect ones. To our surprise the electrical illusion started to disappear in the course of this training. After about two weeks, the fish could tell the distance of a sphere correctly, indicated by the fact that the psychometric functions obtained with a sphere–cube combination (Fig. 5B) looked identical to those obtained with other object combinations, e.g. a cube versus a metal plate (Fig. 5C).

How can the disappearance of the illusion be explained? According to our hypothesis, the fish started to learn to recognize the sphere during training and took this knowledge into account when performing distance estimations. When a sphere was identified, the fish now knew that it appeared to be further away then it actually was and corrected for this perceptional error, thus arriving at a correct distance estimate. This hypothesis implies that the fish are able to detect the shape of an object during active electrolocation.

3.1. Experiments

Experiments were performed that tested directly whether fish can recognize the shape of an object. We designed a new behavioral set-up (Fig. 6) that allowed us to test a fish in a 3 h experimental session for shape recognition: two objects of different shapes were placed in a rectangular experimental tank. No visible light was present, except for an infrared illumination from below, which was invisible for the fish [10]. An infrared-sensitive video camera was mounted above the tank, which recorded the fish and the objects as dark shadows over a bright background. The video signal was fed into a computer which calculated the position of the fish relative to the objects at a rate of 2 Hz. Two stimulus electrodes, one of which was positioned around each object, allowed us to present electric communication signals (EODs of another fish) to the animals in certain situations. The play back of these signals was controlled by a computer depending on the position of the fish in the tank (Fig. 6).

An experiment started by putting a fish into the experimental arena. After 30 min of getting used to the new environment, the position of the fish relative to the two objects was determined every half second. We especially recorded how much time the animal spent close to each object. It turned out that a fish usually swam between 10% and 20% of its time close to each of the objects (Fig. 7). During a one hour period of observation, a baseline of 'interest' for each object was established. In the following 'training' phase, the playback of social signals started: One of the objects was defined as 'positive', which meant that every time the fish was close (<5 cm) to this object, an EOD of another fish was played back through the corresponding stimulus electrode. *G. petersii* is very interested in the EODs of other individuals, and the playback of EODs caused the fish to spend more and more of its time close to the positive object. Finally, the fish stayed more than 50% of the time near the 'rewarded' object and only rarely near the negative object. After about one hour of 'training' the fish, another observation phase of the experiment followed. The positions of both objects within the arena were changed. In Fig. 7A, for example, the locations of the two objects were exchanged. Now, the animal was no longer rewarded by playback, but only its position relative to the objects was determined.

All fish that had been attracted to the rewarded object during training continued to swim close to this object after relocation during the second observation phase (Fig. 7A). Most fish inspected the object closely for many minutes, clearly indicating that they remembered the object and the fact that social signals had been radiated from it just before. The fish chose the positive object no matter at what location within the arena it was placed or where the negative object was located. None of the fish searched at the location from which the playback signals had originated during training. We trained the fish to various kinds of objects: cubes, spheres, pyramids, plates, cones, hexagons, natural stones, and many other shapes. Independently of which alternative object was used (or whether the negative object was exchanged for a different object), the fish
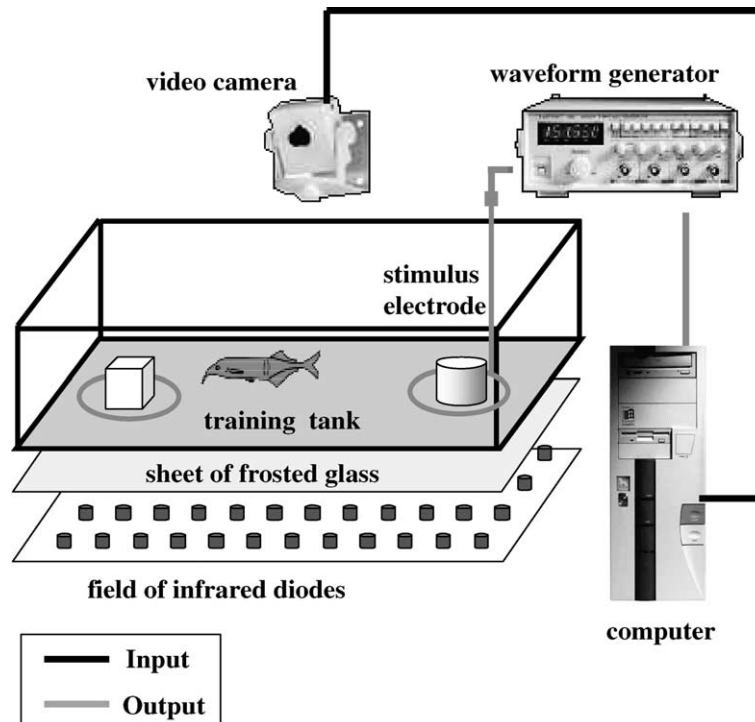
Fig. 6. Experimental set-up used for conducting 'social reward' experiments. A fish was placed in an experimental arena which contained two objects, in this case a cube and a cylinder of equal height. A circular stimulus electrode was fitted around each object. The only illumination present was infra-red light (which is invisible to the fish) provided by an array of diodes below the tank. An infra-red sensitive video camera above the tank was connected to a computer, which localized the fish silhouette within the arena. Social signals (EODs of another fish), stored in a waveform generator, were played-back into the tank when the computer determined that the fish was close to one of the objects.

would recognize all types of objects and could associate them equally well with a social reward. These results show that electric fish can learn to recognize objects of different shapes and identify them independently of their location in space.

In additional experiments, we started to alter the positive (or the negative) object during testing. During the second observation phase of the experiment, we not only changed the location of the objects but additionally exchanged one (or both) of them with different objects. First, we varied the material of the object: For example, during training a metal cube was used as the positive object. In the following observation period this cube was exchanged with a plastic cube of identical size and dimensions. To our surprise, all fish continued to choose the cube during testing, even though it was made of plastic (Fig. 7B). Obviously, the fish preferred to associate the cube-shape of the object with the reward and not its material. This is especially interesting, because metal and plastic objects project images of opposite polarities onto the electroreceptive skin surface of the fish [41].

In a next series of experiments, we changed the size of the previously rewarded object. For example, a fish was trained to a metal cube with a side length of 3 cm and later tested with a metal cube of 5 cm. It turned out that

the fish continued to chose the cube-sized object as long as the change in size was not too large (Fig. 7C). For example, when trained to a 4 cm sphere, a 3 or 5 cm sphere was still preferred, while a 2 cm sphere was not. When the fish no longer recognized an object, because the change of size was too large, it started to search at the *location* where the reward had occurred previously, even when there was no longer an object present (Fig. 7D) [41].

Our experiments show that *G. petersii* can recognize the shape of an object during active electrolocation. Moreover, fish appear to use shape as an important object parameter for object classification. Shape appears to be more important than material or size, as long as the size differences are not too large. In our experiments, fish spontaneously categorized objects according to their shapes and not according to their material or size [41,43].

The experiments described above took advantage of the fact that *G. petersii* spontaneously associates an object with a social stimulus. During the experiments, the fish were free to explore the objects from all sides and could arbitrarily choose their distance to the object. Therefore it was not possible to present objects at a defined distance or in a certain orientation relative to the fish. To overcome these problems, we used an
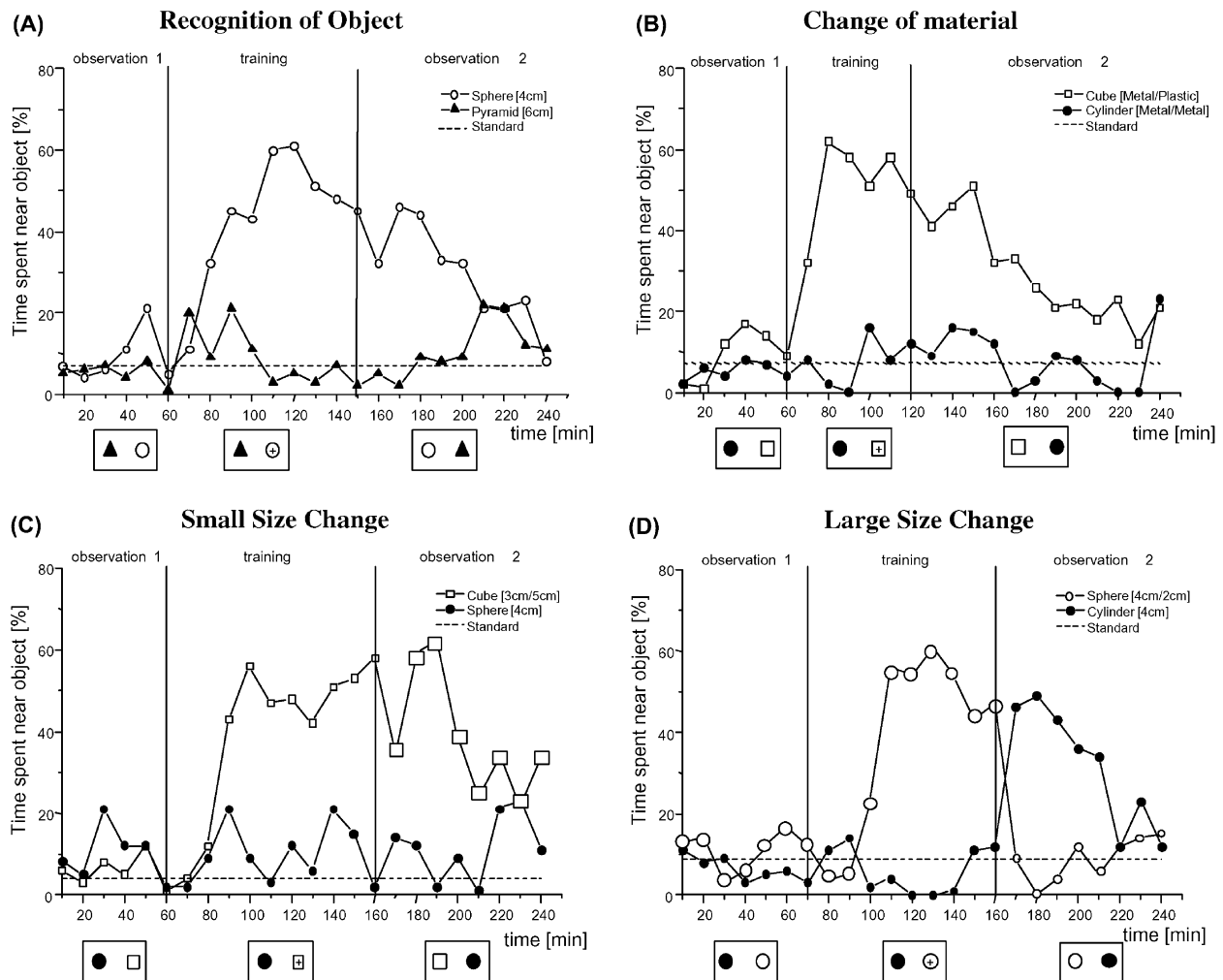
Fig. 7. Object shape detection during social training. (A) *G. petersii* was placed in a tank with two objects, and the time it spent close to each of the objects was observed (ordinate). In a first observation period, spontaneous interest in both objects was determines (observation 1). During a training period (training), the fish was 'rewarded' when staying close to one of the objects (light symbols) by play back of social signals, which attracted the fish to stay close to this object most of the time. In the following observation period (observation 2), the objects were rearranged and sometimes modified, and the fish was observed again without a social reward (observation 2). In (A), objects were rearranged but not modified. In (B), the metal cube used during the first two phases was exchanged for a plastic cube of equal size. In (C), a cube with a side length of 3 cm was exchanged for a 5 cm cube during observation period 2. In (D), a large sphere (diameter 4 cm) was exchanged for a small sphere (diameter 2 cm) during observation 2.

alternative behavioral technique in additional series of experiments. In a two-alternative forced-choice procedure, individual fish were trained to discriminate between two real objects using active electrolocation. The experimental set-up consisted of a training tank that was divided into two compartments by a mesh wall which contained two gates. Behind each of the gates an object was positioned, one of which was defined as 'positive'. During training, the positive object was a metal cube, while the negative object was a metal cylinder. The experimental fish had to learn to swim from their living compartment through one of the gates to the other side in order to receive a food reward. When the fish swam through the gate with the positive object they were rewarded. In contrast, when the gate with the negative

object was chosen, the fish was chased back immediately without receiving any reward.

Within about two weeks of training, the fish had learned to only swim through that gate behind which the metal cube had been placed (Fig. 8A). They could do so equally well under dim light conditions, which prevailed during training, and in complete darkness, indicating that they indeed used active electrolocation to discriminate between the two objects. If the negative object was exchanged for a differently shaped object such as a pyramid, a sphere, or a cone, the fish still preferred the cube (Fig. 8B). These results confirm our previous results obtained with the social training method (see above). They again demonstrate that *G. petersii* can learn to identify certain objects and discriminate be-
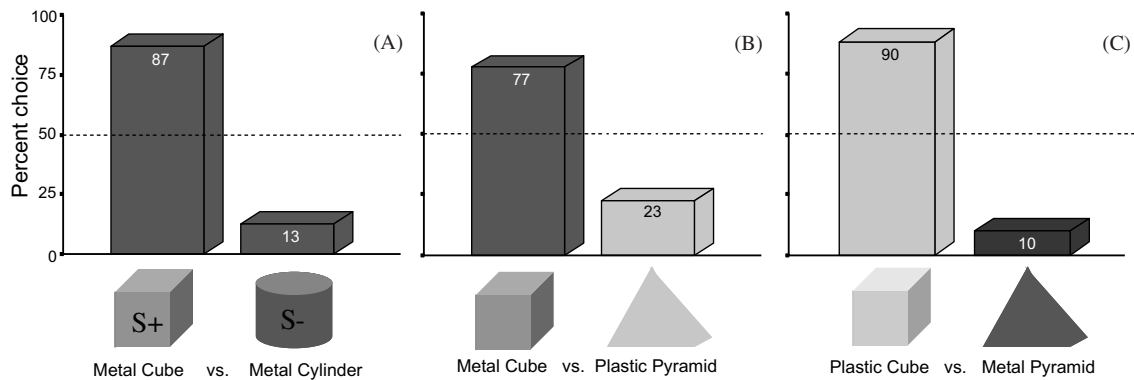
Fig. 8. Results of training a fish to discriminate between a metal cube (S+) and a metal cylinder (S−) of equal height in a food rewarded forced-choice procedure. In each column, the percentage of choices for the particular object is given. The left graph shows the performance (percent choices) of the fish when discriminating between the two training objects. In the middle graph, discrimination performance between a metal cube (S+) and a novel object (plastic pyramid) is given. The right graph depicts the choice behavior when discriminating between two novel objects: a plastic cube and a metal pyramid. In all cases, the fish preferred cubes over all other objects.

tween objects of different shapes using only active electrolocation [13].

When the fish could reliably discriminate between the training objects, test trails involving novel objects were interspersed with regular training trials. During a test trail, the fish was neither rewarded nor punished (chased back), but only its choice behavior was noted. When instead of the metal cube (the original S+) a plastic cube was paired with a differently shaped object, the fish clearly preferred this cube over all alternatives (Fig. 8C). Thus, the fish had remembered the shape and not the material of the object whose choice was rewarded [13]. These results confirmed our pervious findings obtained in the social training experiments (Fig. 7B).

Can the fish identify an object in nature, even when they experience it from a new angular position or another distance? Placing a cube at another distance from its gate will produced subjective changes in object size. For example, the size of the electric image on the fish's skin will increase when the object is placed farther away. According to the principle of size constancy, an object is still recognized as being of a certain size no matter from what distance it is viewed. Thus, an object is still identified even though it might appear to be larger or smaller in size caused by differences in distance from the viewer. We tested whether this also applies to our fish during active electrolocation. Would they still be able to identify a cube when it was placed farther away than during training?

So far, all object had been placed close (1 cm) to their gates. When this distance was increased to 3 or 5 cm, the fish still recognized the S+, but their performance decreased to 70% correct choices at 5 cm distance. At 7 cm, however, performance dropped to chance level (Fig. 9A) [13]. Apparently, this distance was too large to correctly identify the object. Active electrolocation is a near field orientation system and only functions up to a distance

of about one fish length [49]. The fish used in our experiments were about 10–12 cm long, and one can thus expect that they could detect objects up to this distance. However, object identification is a more difficult task than detection and might require a shorter distance between the fish and its target. Our experiments show that object identification is independently of distance as long as the distance is not too large. Thus, the principle of size constancy might apply during active electrolocation within a certain working range.

The experiments just mentioned indicate that the fish can learn to identify objects independently of their distance. This might work because the fish are able to measure their distance from an object first and then correct for the distance-induced size changes. What about object size? Would the fish also prefer a cube over an alternative object even if it was smaller or larger than the original S+, but was placed at the same distance? In additional experiments it turned out that when the size of the metal cube was decreased, our fish still preferred it, as long as the change in size was not too large. The original S+ had a side length of 3 cm, which corresponds to a volume of 27 cm^3. An 8 cm^3 object (side length = 2 cm) was still preferred over alternative objects, while a 1 cm^3 object (side length = 1 cm) was not (Fig. 9B). As was the case with distance changes, the fish tolerated a change in size up to a certain limit, beyond which the object was no longer recognized [13].

3.2. A mechanism for shape detection during active electrolocation

We have used two different behavioral techniques to show that *G. petersii* can detect object shape during active electrolocation: (i) a spontaneous 'social training method', during which the fish associated an object and a played back social signal, and (ii) a two-alternative
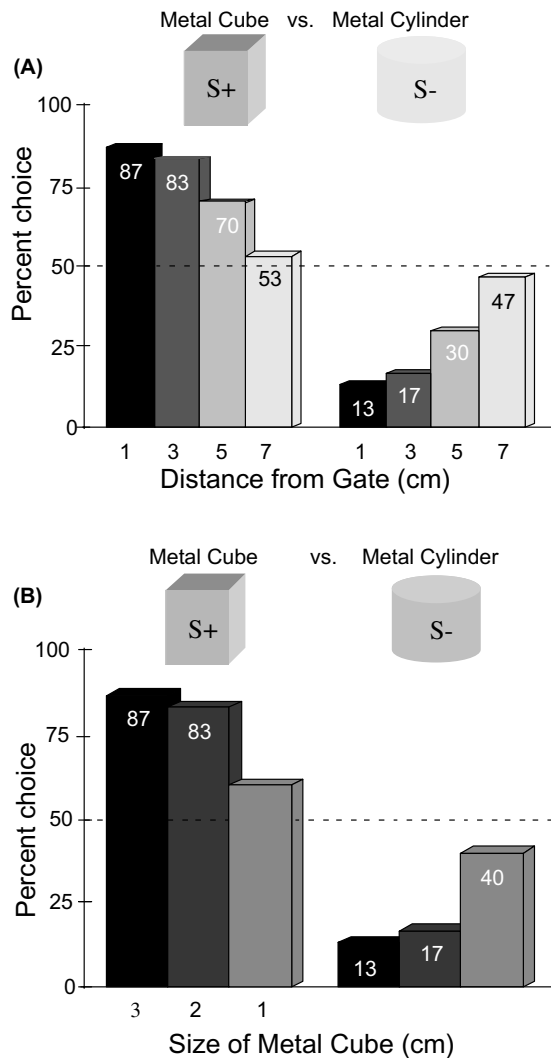
Fig. 9. Choice behavior of a fish that was trained to discriminated between a metal cube (S+) and a metal cylinder (see Fig. 8). The percentage of choosing the cube is given in the left columns of each graph. Corresponding columns have same colors. In (A), the distance of the objects from the fish during discrimination was varied (see text). The training distance was 1 cm. The cube was preferred up to a distance of 5 cm. In (B), the size of the S+ (cube) was varied. During training, the cube had a side length of 3 cm (darkest columns).

forced-choice training method that rewarded the choice of a certain object. Both methods showed that fish can detect an object's shape and can identify an object independently of its distance or size. This ability forms the basis for several cognitive concepts of object recognition, such as size constancy and perceptional invariance.

Visual object identification in humans has a lot in common with object recognition of weakly electric fish during active electrolocation. During vision, object recognition is largely invariant to changes in size, position, or viewpoint. The visual information falling onto the retina when an object is viewed varies drastically depen-

ding on the distance from the object (which affects the retinal size of the image), the vantage point from which the object is viewed, and the location of the object relative to the viewer (which affects the part of the retina that is stimulated). One fundamental and essential property of the visual system is the ability to recognize a particular object, despite these great variations in the images that impose on the retina. There are several types of invariances during visual object recognition in humans, e.g. size invariance (objects can be recognized despite variations in actual or apparent size [16]), rotational invariance (capability of recognizing objects from many different vantage points, even views that have never be seen before [6]), and translational invariance (when an object is moved to a new position in the environment, object recognition is not disrupted [5]). There is good evidence that these three fundamental types of invariances also apply to electric fish during active electrolocation.

The similarities in object recognition in electric fish and humans suggest that similar mechanisms may be employed. But how can an electrolocating fish recognize the shape of an object, and which mechanisms are actually used? These questions are very difficult to answer because no simple algorithm, like the slope–amplitude ratio for distance determination, could be found so far. From observing our animals during the experiments we conclude that shape is not detected as fast as object distance. Instead, when confronted with a novel object fish might have to inspect it more carefully and for a longer time period than during distance measurements before arriving at a conclusion about object shape. It cannot be decided at present whether this means that several 'views' of an object have to be stored in memory which than serve as templates for object recognition. Additional experiments have to be done before drawing any conclusions in this matter.

4. Conclusions

During active electrolocation, weakly electric fish perceive a three-dimensional image of their surroundings. They possess a true sense of 'depth perception' allowing them to get information about three-dimensional space. In addition, electric fish are able to perceive and remember the shape of an object and recognize this shape when encountering the object under novel circumstances. These abilities appear to be very similar to the abilities of visually orientated animals during object recognition using their eyes. During evolution, weakly electric fish developed a true alternative to vision, which allows them to acquire all relevant information about objects in their environment in complete darkness. As a consequence, their ability to recognize objects does not seem to differ fundamentally from visually oriented

animals. The evolutionary success of weakly electric fish in African and South American tropical freshwaters, which resulted in their proliferation and evolution of several hundred different species living in diverse ecological niches, may be attributed to a high degree to their efficient sensory abilities in perceiving their 3-dimensional nocturnal world.

Acknowledgements

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