Distance, shape and more: recognition of object features during active electrolocation in a weakly electric fish

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Summary

In the absence of light, the weakly electric fish *Gnathonemus petersii* detects and distinguishes objects in the environment through active electrolocation. In order to test which features of an object the fish use under these conditions to discriminate between differently shaped objects, we trained eight individuals in a food-rewarded, two-alternative, forced-choice procedure. All fish learned to discriminate between two objects of different shapes and volumes. When new object combinations were offered in non-rewarded test trials, fish preferred those objects that resembled the one they had been trained to (S+) and avoided objects resembling the one that had not been rewarded (S–). For a decision, fish paid attention to the relative differences between the two objects they had to discriminate. For discrimination, fish used several object features, the most important ones being volume, material and shape. The importance of shape was demonstrated by reducing the objects to their 3-dimensional contours, which sufficed for the fish to distinguish differently shaped objects. Our results also showed that fish attended strongly to the feature 'volume', because all individuals tended to avoid the larger one of two objects. When confronted with metal *versus* plastic objects, all fish avoided metal and preferred plastic objects, irrespective of training. In addition to volume, material and shape, fish attended to additional parameters, such as corners or rounded edges. When confronted with two unknown objects, fish weighed up the positive and negative properties of these novel objects and based their decision on the outcome of this comparison. Our results suggest that fish are able to link and assemble local features of an electrolocation pattern to construct a representation of an object, suggesting that some form of a feature extraction mechanism enables them to solve a complex object recognition task.

Key words: environmental imaging, object recognition, shape perception, contour, volume, feature extraction.

Introduction

Object discrimination plays an important role in the life of animals. In visual perception of vertebrates, optical images of objects appear on the retinas of the two eyes, each of which is focused by the lens and cornea. Because the image is kept in focus, the geometrical relations of an object are preserved and the object's contour can be derived from analysing the metrics of the retinal image. Recognition of an object's size, distance, or its three-dimensional (3-D) shape requires more complicated computations by the visual system. Vision requires light and thus is only of limited use to nocturnal animals, which have to rely on other senses for orientation and object recognition. The lateral line system of fishes provides two non-contact alternatives for vision in dark habitats. One is the mechanosensory lateral line, which senses water motions and provides hydrodynamic information that can be used for object recognition (Bleckmann et al., 2003; Burt de Perera and Braithwaite, 2005). The second is the electrosensory lateral line system, which enables electrosensory fish to perceive their surroundings through their electric sense (Hopkins, 2005), and is especially well suited for detailed environmental imaging in weakly electric fishes.

Weakly electric fishes generate electrical fields around their bodies by emitting electric signals (electric organ discharges, EODs) with a specialized electric organ. The waveform and duration of single EODs are constant, while the EOD discharge rate depends on the behavioural context (Carlson, 2002; Moller, 1995; von der Emde, 1992). If an object is present near the fish, it causes distortions of the electrical field lines, which change the voltage patterns on the skin of the animal opposite the object. The changed pattern is detected by electroreceptors located all over the fish's skin. The detection and analysis of objects through this process is called 'active electrolocation' (Bastian, 1994; Lissmann and Machin, 1958; von der Emde, 2006). The local modulation of the electric field at an area of the skin caused by an object is called the 'electric image' of an object (Caputi et al., 1998; Migliaro et al., 2005; Rasnow and Bower, 1997; von der Emde et al., 1998).

Electric images have a centre-surround ('Mexican hat') spatial profile (Caputi et al., 1998). For example, a good conductor produces an electric image with a large centre region where the local EOD amplitude increases, surrounded by a small rim area where the amplitude decreases. The image of a non-conductor has an opposite appearance. Because there is no

focusing mechanism, electrical images are always blurred, or 'out of focus' and, in this respect, are fundamentally different from optical images that are projected onto the retina of a vertebrate eye. Electric images would be in focus only if the distance between object and skin was zero. In addition, there is no one-to-one relationship between spatial object properties and image shape: electrical images are always strongly distorted compared to an optical projection of a 3-D object onto a 2-D surface. Optical images are mainly determined by an object's geometrical features, such as shape and size. In addition, electric images depend on parameters such as electrical material properties, object depth, location along the fish's body, bending movements of the fish's body, and many more (Caputi and Budelli, 2006).

During active electrolocation, weakly electric fish analyse the electric images of objects and can thereby not only detect objects, but also perceive several object properties. For example, *G. petersii* can independently measure the resistive and capacitive components of an object's complex impedance (von der Emde, 1990; von der Emde and Ronacher, 1994). When trained to discriminate between two objects that differed only in their distance from the fish, *G. petersii* could determine object distance up to a maximum of about 10 cm (Schwarz and von der Emde, 2001).

Even though there is no focusing mechanism during active electrolocation, can weakly electric fish also perceive an object's 3-D shape? The results of several studies, all of which involved some sort of training experiments with *G. petersii,* suggest that this is indeed the case (Davis and von der Emde, 2003; Graff et al., 2004; Schwarz, 2000; von der Emde, 2004). For example, fish could recognize a free-standing object of a certain shape after it was moved within an arena (Schwarz, 2000; von der Emde, 2004). In another study, *G. petersii* preferred a metal cube rather than several other differently shaped objects after being trained to chose it in a two-alternative, forced-choice procedure (Davis and von der Emde, 2003; von der Emde, 2004). The fish can also learn to recognize a 3-D, 'virtual' electrical pattern and discriminate it from other patterns (Graff et al., 2004).

In the present study, we have investigated in more detail whether and how electric fish can distinguish between objects differing in shape, size and material during active electrolocation. By training several fishes in a complex object recognition task, we wanted to find out which object features the animals use when discriminating between real 3-D objects differing in several parameters.

Materials and methods
Animals
Eight *Gnathonemus petersii* Gunther 1832 (standard length: 12–15 cm) were used in the experiments. They lived individually in rectangular tanks (80 cm$\times$35 cm$\times$40 cm), which were also used for training. The light:dark cycle was 12 h:12 h, water temperature 26$\pm$1°C and water conductivity was 100$\pm$5 μS cm^{-1}.

Experimental set-up
Training tanks were similar to those described (Schwarz and von der Emde, 2001), and were divided into two compartments (areas: 50$\times$35 cm^2 and 30$\times$35 cm^2) by a widely perforated, plastic mesh screen, which contained two lockable gates (4$\times$4 cm^2). The bigger of the two compartments was used as the 'living area' for the fish, and contained water plants and a single hollow, water-filled cylinder as a shelter. The fish were trained in a food-rewarded, two-alternative, forced-choice procedure to pass through one of the gates in order to obtain a food reward on the other side. During training and testing sessions, an object was placed at a distance of 0.5 cm behind each of the two gates in such a way that the fish had to pass it to access the smaller compartment. The fish were trained to swim through the gate leading to the object defined as positive (S+), and to avoid the gate with the punished object (S–) behind. Most experiments were conducted with the aquarium lights on, because it has previously been shown that under these conditions *G. petersii* orients mainly electrically (for a review, see von der Emde, 2006). In addition, *G. petersii* is not able to perceive objects visually under conditions of bright light (>100 lx) (Schuster and Amtsfeld, 2002). Control experiments (see below) were also conducted in total darkness, however, in order to validate our assumption that the performance of the fish depended on the use of the electric sense rather than on vision.

The training procedure
The fish were trained to discriminate between two differently shaped metal objects placed at a distance of about 5 mm behind the gates. In later experiments, several other object combinations were tested. During each training trial the same object combination, consisting of a rewarded (S+) and a non-rewarded (S–) object, was used. Before each trial, the S+ and S– were first placed behind the left and right gates according to a pseudorandom schedule (Gellermann, 1933). A trial was started by opening both gates simultaneously. The fish swam to the dividing wall and, after inspecting both objects through the corresponding gates, decided which gate to pass through. Passage through the correct gate, behind which was positioned the S+, was rewarded with a small worm (chironomid larva). After eating the reward, the fish had to swim back into the living compartment. In the case of a wrong decision, the fish was mildly 'punished' by knocking against the aquarium glass and chasing it back to the living compartment, immediately. The gates closed again and a new trial was prepared by the experimenter. On average, 40 trials per session (one session per day, 5 days a week) could be conducted.

Test trials
Once fish were performing with at least 75% correct choices over 3 consecutive days, test trials using novel object combinations were interspersed between training trials during a session. During test trials, fish were neither rewarded nor punished in order to avoid further learning and to determine preferences of the fish for the test objects based on the learning experience obtained during the training trials. At the beginning of testing, single test trials were interspersed into a session only after 3–4 training trials. When a fish was more experienced with the procedures and learning was established more firmly, every second trial of a session was a test trial. This procedure avoided repeated frustrations without a reward at the beginning and maintained discrimination performance and motivation at a high

level. Between 40 and 100 test trials were conducted for each object combination tested.

Discrimination tests and transfer tests

Several objects of different shapes, sizes, and material (plastic or metal) were used for training and testing (Table 1). Each fish was trained to discriminate between a certain pair of objects and was then tested with novel object combinations.

Two kinds of tests were conducted. (1) 'Discrimination tests' tested whether (i) the initial choice for S+ was based on the properties of the rewarded object (S+), (ii) fish had learned to avoid S–, or (iii) both S+ and S– were relevant. In discrimination tests, one of either the positive or the negative training object was retained, and the other was exchanged for a novel object of different shape, material or size. (2) 'Transfer tests', in which two novel objects were presented to the fish, both of which differed from the training objects in at least one parameter. Like the discrimination test, transfer tests were non-rewarded and were interspersed between training trials, during which the original training objects of the particular fish were presented. Transfer tests without either the original S+ or S– present aimed to determine the object features used by the animals as the basis for their decision about a particular object.

A special series of transfer tests was conducted with fishes 1 and 2. In these experiments we used so-called 'wire objects', made out of 1 mm copper wire bent into the shape of a cube or a pyramid of the same outer dimensions as the solid S+ and S– that were initially used. The wires followed the outline of the objects and were fixed together by soldering (Fig. 7). The wires were covered with insulating tape on the vertical and horizontal sides. These wire objects were also modified to give so-called 'discontinuous wire objects'. Here, small parts of the four

Table 1. *Features of objects used for training and testing and their symbols*

Object shape	Dimensions (cm)	Volume (cm³)	Material	Symbol
Small cube	2, 2, 2 (l, w, h)	8	Metal	
Cube	3, 3, 3 (l, w, h)	27	Metal	
Large cube	4, 4, 4 (l, w, h)	64	Metal	
Cube	3, 3, 3 (l, w, h)	27	Plastic	
Small pyramid	2, 2, 2 (l, w, h)	2.66	Metal	
Pyramid	3, 3, 3 (l, w, h)	9	Metal	
Pyramid	3, 3, 3 (l, w, h)	9	Plastic	
Small cone	2, 2 (d, h)	2.09	Metal	
Cone	3, 3 (d, h)	7.07	Metal	
Large cone	4, 4 (d, h)	16.75	Metal	
Very large cone	5, 5 (d, h)	32.7	Metal	
Small sphere	2 (d)	4.18	Metal	
Sphere	3 (d)	14.14	Metal	
Half sphere	3, 1, 5 (d, h)	7.07	Metal	
Small cylinder	2, 2 (d, h)	6.28	Metal	
Cylinder	3, 3 (d, h)	21.2	Metal	
Cylinder	3, 3 (d, h)	21.2	Plastic	
Small hexagon	1.2, 2, 1	7.2	Metal	
Hexagon	2.2, 3, 1.5	29.7	Metal	
A	2.7, 1, 4 (l, w, h)	7.125	Metal	
Mushroom	4, 4 (d, h)	23.03	Metal	
Mushroom	4, 4 (d, h)	23.03	Plastic	
E	2.5, 1, 4 (l, w, h)	4.4	Metal	

l, length; w, width; h, height; d, diameter.

vertical (and also, in another case, of the horizontal) wires of these objects were cut out in such a way that the vertical (and horizontal) sides of the objects were interrupted. In order to keep the upper and lower parts of these objects in place, the whole object was moulded in a cube-shaped agar–agar block (Fig. 7). Following earlier studies by Heiligenberg (e.g. in Heiligenberg, 1973; Heiligenberg, 1975), the agar was prepared in such a way that it was electrically 'transparent', with the same electrical conductivity as the aquarium water.

Statistics

Significant differences ($P<0.05$) between the choice frequencies obtained in test experiments and the results expected under random choice conditions (50%) were determined using the χ^2 test.

Control experiments

In order to test whether vision played a role during object discrimination, experiments were conducted with all sources of visible light turned off. Under these conditions (light ≤1 lx), the fish could probably not see the objects and therefore would have to use alternative cues such as active electrolocation. In order to monitor the behaviour of the fish, the aquarium was illuminated by infrared light (>880 nm), which is invisible to *G. petersii* (Cialo et al., 1997). Each fish was observed using an infrared-sensitive video camera (DCR-Pc120E, Sony Corporation, Tokyo, Japan) and visualized on a TV screen. The experiments were performed in the same way as regular training trials except that the fish were neither rewarded for a correct nor punished for a wrong decision.

In order to evaluate the role of tactile senses in object discrimination, additional control experiments were conducted. To exclude all tactile and mechanosensory lateral line cues, two training objects (pyramid and cube) were each moulded in electrically 'transparent' agar (see above) that was also visually non-transparent, so the fish could not see the object inside. The two resulting agar blocks were both cube-shaped and of identical outer dimensions. The experiments were conducted in the same way as the visual control experiments described above.

Results

Training

At the beginning of training, fish had to learn to pass through either one of the gates in order to receive a worm as a food reward. Depending on the individual, it took the fish 1–2 weeks to learn this basic task. Next, an object was placed behind each gate, and the fish was only rewarded when it passed through the gate leading to the positive object (S+) and avoided the gate leading to the S–. Depending on the individual, fish needed 5–24 days of training to solve this task at a level of >75% correct choices. During the subsequent period of testing, fishes' performances remained >75%, increasing over time for most fishes.

All eight fish learned their particular tasks, and ultimately discriminated between their training objects with >85% correct choices (Fig. 1). Fishes 1 and 2 were trained to discriminate between pyramid and a cube of equal height and base area (Table 1). Starting at the choice performance level of 50% correct, these fishes needed 7 and 4 days, respectively, to reach
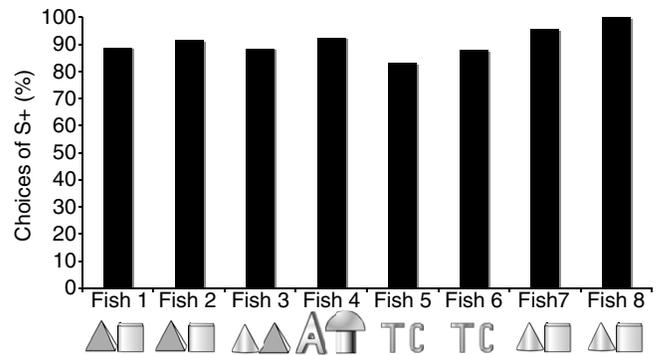

Fig. 1. Choice frequency for S+ of eight fishes trained to discriminate between two differently shaped objects, symbols of which (taken from Table 1) are shown below each bar along the abscissa. For each object pair, the object on the left depicts the S+ and that on the right the S–. In this and subsequent figures, choice frequency for the object on the left was determined in non-rewarded and non-punished test trials. The total number of choices recorded for each fish was always >100.

the 75% level of correct choices. Fish 3 was trained to discriminate between a cone and a pyramid of equal height and base diameter and similar volume (Table 1). This fish reached the criterion after 19 training days. Fish 4, trained to choose a letter A and avoid a 'mushroom' (Table 1), was the fastest individual to learn its task. From the first day of training its performance never fell below 78% correct choices. Fishes 5 and 6 were trained to discriminate between a metal T and a C. Both individuals started from a performance level of 50% correct choices and took relatively long (19 and 24 days of training, respectively) to reach a stable discrimination performance. Fishes 7 and 8 were trained to discriminate between a cone and a cube of equal height and base area (Table 1). Starting from the 50% correct choice level, these individuals reached the 75% level after 8 and 10 days of training, respectively.

Control experiments

The performance of fishes 1 and 2 during control tests was the same as for regular trials. When tested with objects moulded into agar-cubes (Fig. 2A), or in the absence of visible light (Fig. 2B) both fish still discriminated successfully between their training objects. Fish inspected the two objects for longer times when agar-objects were used. In contrast, when the visible lights were turned off, the behaviours of both fishes were indistinguishable from the usual testing situation with dim lights on. In both types of control experiments, fish could recognize the objects, even though they could not see and/or touch them. Thus the fish did not rely on visible, tactile or mechanosensory lateral line cues to discriminate between the objects and instead used electrolocation to do this.

Behaviour during discrimination

In about 70% of the trials during a discrimination session, fish swam to both gates and inspected both objects before passing through one of the gates. However, in 30% of the trials a fish immediately passed through the first gate it encountered without checking on the alternative object. Comparison of the error rates of trials where only one of the two objects was
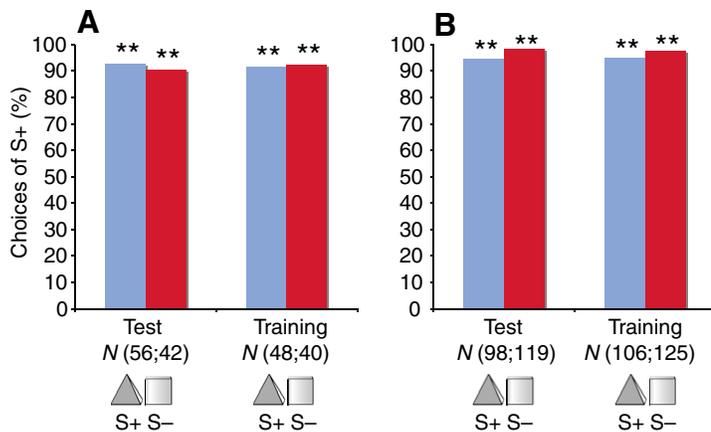
Fig. 2. In order to prove that fish used active electrolocation for object discrimination, control experiments were conducted with fish 1 (blue) and fish 2 (red), when they were prevented from using other senses. In (A), the training objects were concealed during test trials within electrically transparent agar to prevent their tactile (and visual) inspection. In (B), test trials were conducted under infrared light (invisible for the fish), which prevented vision. Both fish were trained to choose a pyramid (S+) and avoid a cube (S–). Choice performances during test conditions (Test) and during training conditions (Training) are compared. N denotes the total numbers of choices of fish 1 and fish 2, respectively. Asterisks above each graph indicate significant differences from random choice conditions; *$P<0.05$; **$P<0.01$.

inspected with those trials in which both objects were inspected revealed that the percentage of correct choices was higher in the latter cases.

During object inspection, fish performed so-called 'probing motor acts' close to the object under investigation (Toerring and Belbenoit, 1979; Toerring and Moller, 1984; von der Emde, 1992). At the beginning of training, most fish approached the gates by swimming tail first towards the object. At a distance of 1–3 cm they stopped and moved their tail left and right several times, a behaviour called 'tail-probing' (Toerring and Belbenoit, 1979). Some fish even swam past the object in this manner, i.e. passing the gates tail first. In addition to tail-probing, other probing motor acts were performed, in particular: 'head-probing' (approaching the object head first and stopping), 'lateral *va-et-viens*' (swimming forwards and backwards several times laterally to the object), and 'radial *va-et-viens*' (swimming backwards and forwards around the object). The more a fish became experienced with a particular discrimination task, the fewer tail-probing and more head-probing events were observed. However, when a novel object combination was presented to a fish, tail-probing often reappeared. During head-probing, fish stayed close to the object and often moved their chin appendix (the Schnauzenorgan) around the object. During this 'chin probing', some of the fish actually touched the object with their Schnauzenorgan. Control experiments showed, however, that tactile cues were not necessary for successful object discrimination (Fig. 2A).

Fish emitted a specific temporal rhythm of EODs at each stage of a trial when solving the electrolocation task. While probing or actively exploring an object, *Gnathonemus* transiently regularize and increase their EOD rate, sometimes to >70 Hz. At the instant of passing through the gate, EOD rate transiently increased to 80 Hz in most fish. In contrast, when swimming in the home compartment, EOD production was often extremely irregular and the average EOD rate was lower (data not shown).

Discrimination tests
Exchanging S–
In several discrimination tests involving fishes 1–4, 7 and 8, animals were offered combinations of objects with one of the original training objects exchanged for a novel object. When the original S+ was offered together with a new test object replacing

S–, the results depended strongly upon which object replaced the S–. Different fish also behaved differently (Fig. 3).

Fishes 1 and 2 (training: pyramid *vs* cube) still preferred their S+ when the alternative was a hexagon or a cylinder. However, preference for S+ decreased with a sphere acting as S–, and performance dropped to about 60% choices of S+, falling further below the significance level to 55% and 46% when S– was a cone (Fig. 3A). Very similar results were obtained with fishes 7 and 8, which were originally trained to discriminate between a cone and a cube. However, in these fish, choices of the cone remained over 60% even when S– was replaced by a pyramid (Fig. 3D). In all four fishes, the drop in performance appears to correlate with the size difference (expressed as a volume ratio) of S+ and the alternative object. The 'volume ratio' is the volume of S– divided by the volume of S+ (see ratio numbers below the columns). Fish tended to choose S+ as long as its volume was less than half as large as that of the other object. When ratio was <2, the performance of the fish also dropped.

Fish 3 (trained to cone *vs* pyramid) kept choosing its original S+ when the S– was replaced by a cylinder, a sphere or a cube (Fig. 3B). In all of these cases, the new S– had a larger volume than the S+ (cone), leading to volume ratio ≥2.

Fish 4, which was trained to discriminate between an **A** (S+) and a 'mushroom' (S–), kept choosing the **A**, when a sphere or a half-sphere was offered as the alternative. However, with a cylinder (lower part of the mushroom) or the letter **E** acting as a new S–, performance dropped near chance level to slightly under 50%. In these two cases, the S+ was larger than the new S–, resulting in volume ratios <1 (Fig. 3C).

Exchanging S+
In this series of experiments, the original S– was offered together with a new test object replacing S+. Again performance depended on the fish and the type of object used.

Fishes 1 and 2 accepted a cone, a sphere and a cylinder as replacements for the pyramid, while a hexagon was only chosen in 55% of the cases (Fig. 4A). These performances again followed the volume ratio of the two objects in a similar way as in Fig. 3. The results of fishes 7 and 8 were partially similar to those of fishes 1 and 2, although the hexagon was still chosen at the 79% level by fish 7 and 68% level by fish 8, even though the volume ratio was only 0.9 (Fig. 4D).
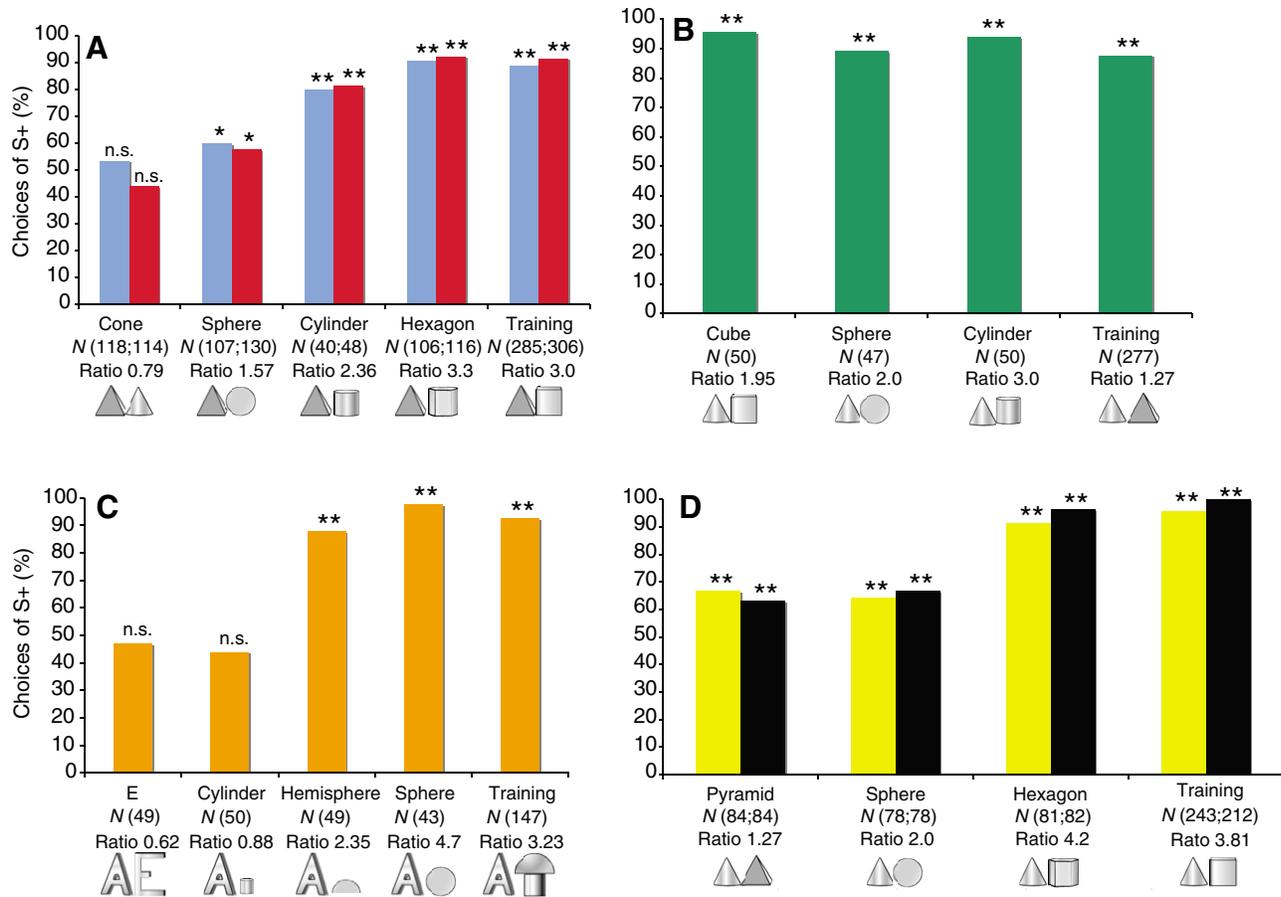
Fig. 3. Results of transfer tests, during which the S– used during training was replaced by a novel object. Each bar depicts the choice frequency for the left object (S+) of each pair. Below each bar, the object replacing S– is named. Numbers in parentheses are the total number of each fish's choices. 'Ratio' is the volume ratio of the two objects offered, i.e. volume of the right object (novel object, except for training conditions, shown in far right columns) divided by the volume of the left object (S+). (A) Fish 1 (blue) and fish 2 (red), both of which were trained to discriminate between a pyramid (S+) and a cube (S–). (B) Fish 3, trained with a cone (S+) and a pyramid (S–). (C) Fish 4, trained with an A (S+) and a mushroom (S–). (D) Fish 7 (yellow) and fish 8 (black), both trained with a cone (S+) and a cube (S–). Asterisks above each graph indicate significant differences from random choice conditions: *$P<0.05$; **$P<0.01$; n.s., non significant.

Fish 3 (trained to a cone *vs* a pyramid) did not accept a sphere, a cylinder or a cube as replacements for its S+. In all these cases, the fish was undecided, choosing the novel objects in only about 50% of the trials. When a hexagon was offered together with the trained S–, choice behaviour of fish 3 changed. The fish now preferred the pyramid, which had been the original S–, in 75% of the trials, and clearly avoided the hexagon (Fig. 4B).

When an E, a hemisphere, or a cylinder was offered together with the mushroom (S–), fish 4 preferred the new objects and continued rejecting its original S–. Choice behaviour changed, however, when a sphere was offered with the mushroom; the fish rejected the sphere and chose the mushroom (S–) in 74% of the cases (Fig. 4C).

The relationship between choice performance and volume ratio was less clear in these experiments than in the discrimination tests shown in Fig. 3. Although there was a tendency to choose the smaller object of a pair, fish were often undecided even when one object was clearly smaller the other one.

Transfer tests
Smaller and larger objects

Fish 1 and 2 were tested in transfer tests using pairs of objects that were both smaller proportionally than the original objects used during training. Both objects were reduced in volume by 70% compared to the training objects (height reduced from 3 cm to 2 cm). The volume ratio of the two small objects of a given pair was identical to that of the original objects as shown in Fig. 3 (Table 1). Experiments were conducted in the same way as during the 'exchanging S–' experiments, i.e. the smaller version of S– was exchanged for differently shaped objects of the same height.

Fig. 5 shows that the choice behaviours of both fishes 1 and 2 were almost identical to those observed during the tests with larger objects. When both objects were smaller, exchanging the S– resulted in the same choice frequencies as when the original S– was exchanged (Fig. 5, original objects). This shows that the fish paid attention to the *relative ratio* between the two objects and did not remember the absolute geometries of the training objects.
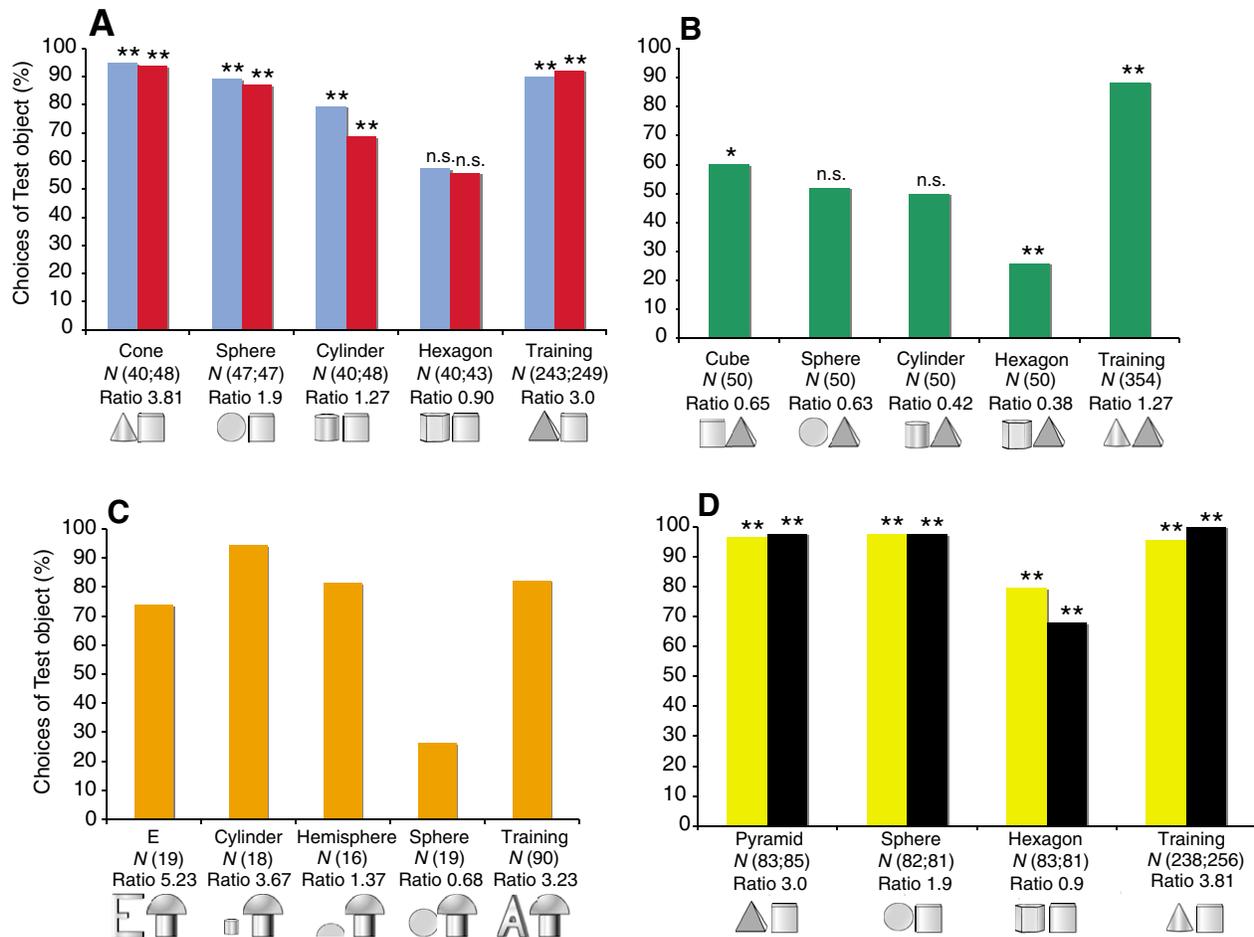
Fig. 4. (A–D) Choice frequencies of six fishes in transfer tests, during which the S+ used during training was replaced by a novel object. Each bar depicts the choice frequency for the left object (novel object or S+) of each pair. Below each bar, the object replacing S+ is named. 'Ratio' is the volume ratio of the two objects offered, with the volume of the right object (S–) divided by the volume of the left object (novel object, except for training conditions, far right columns). Other details as in Fig. 3.

In order to further study the influence of object volume on choice behaviour, objects were exchanged for larger versions of the original objects in transfer tests. Fishes 1 and 2, originally trained to discriminate between a pyramid (S+) and a cube (S–), were now tested with different sized cones replacing the pyramid. When a cone of similar dimensions to the pyramid (S+) was used, both fish chose the cone over the cube in >93% of the trials (Fig. 6, pair 4). The volume ratio between the cube and the cone was 3.81, which is similar to the initial training paradigm where S– (cube) was three times more voluminous than S+ (pyramid). Again this indicates that the volume ratios of S+ and S– were used as a cue by these fishes for object discrimination.

Increasing the volume of the cone such that the volume ratio dropped to 1.62 left the fish undecided (Fig. 6, pair 1). Decreasing the ratio further (0.82; pair 3) led to rejection of the even larger cone and choice of the cube in 70% of the cases by the single fish tested (Fig. 6, pair 3). However, this preference for the cube was surprisingly strong, considering the fact that the cube:cone volume ratio was 1.22 (inverse of 0.82). As just mentioned, the same fish was completely undecided at a ratio of 1.62, when the cone was smaller than the cube.

Another interesting result was obtained when the big cone (which was still smaller than the cube – volume ratio 1.62) was moved 3 cm away from the gate, and was thus a greater distance away from the fish than the alternatively presented cube. Under these conditions, the choice behaviour of fish 1 was the same as when the distances of both objects were equal. In contrast, fish 2 noticeably began to avoid the far away cone and instead, in 87% of the cases, chose the cube (Fig. 6, pair 2).

Wire objects

While the results obtained with fishes 1 and 2 as well as fishes 7 and 8 indicate that the objects' volume/size ratio plays an important role in choice behaviour, the results with fishes 3 and 4 as well as some of the results of the transfer tests indicate that 'shape' is also important. To investigate this further, we conducted experiments with fishes 1 and 2 using so-called 'wire-objects'. Copper wires were bent in such a way that they followed the contours of the original objects, thus forming the 3-D outline of a cube or a pyramid (Fig. 7).

Remarkably, the preference for S+ (pyramid) was not changed when wire objects of the same dimensions as the original objects
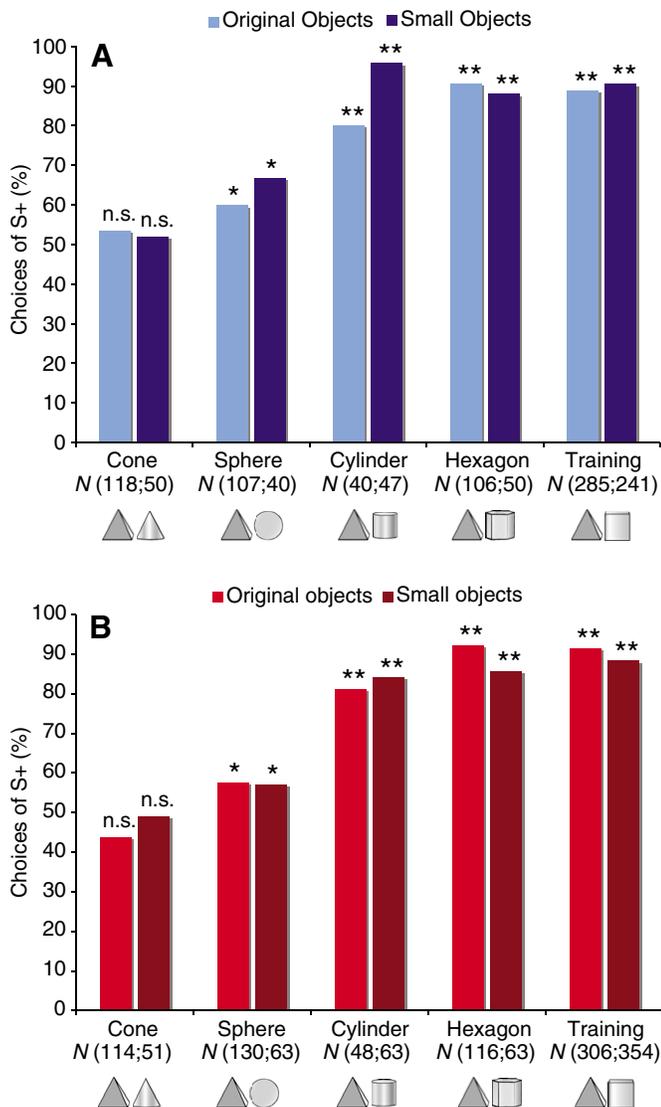
Fig. 5. Results of transfer tests with fish 1 (A) and fish 2 (B), in which the original objects were replaced by smaller but otherwise identical versions of them. The left lighter coloured bar of each pair gives the results with the small objects, the right darker coloured bar gives results with original sized objects. Same conditions as in Fig. 3, i.e. S–, which was used during training, was replaced by a novel object. Each bar depicts the choice frequency for the left object (S+) of each pair.
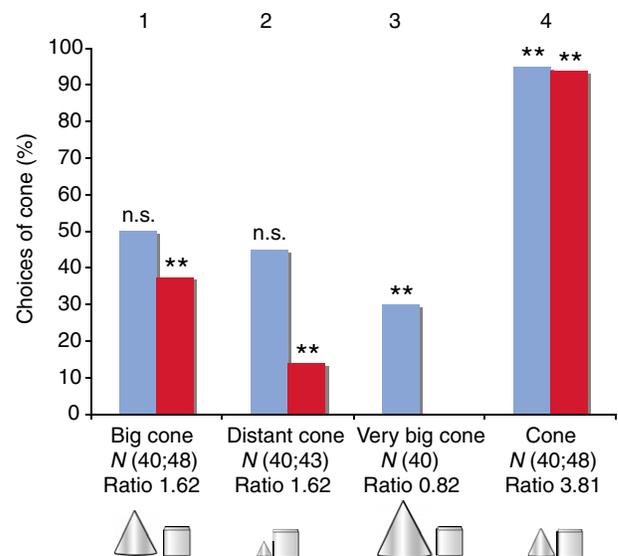

Fig. 6. Results of transfer tests with fish 1 (blue) and fish 2 (red), during which the size of the S+ (cone) was varied. In pair 2, the big cone was moved further away from the gate (3 cm instead of 0.5 cm) than during all other trials. Each bar depicts the choice frequency for the cone (S+). 'Ratio' gives the volume ratios of the cube (S–) divided by the respective cone. Asterisks above each graph indicate significant differences from random choice conditions: **P<0.01; n.s., non significant.

were used (Fig. 7A). These wire objects are basically volume-free, suggesting that the shapes of the objects must indeed have been evaluated by the fish. When the contours of the wire objects were interrupted by removing all vertical (in the case of the pyramid almost vertical) parts of the wire objects (Fig. 7), both fish still preferred (although at a somewhat lower percentage level, ~81 and ~72%) the disconnected outline of the pyramid over that of the cube (Fig. 7B). The fish could apparently complete the interrupted outlines, perceiving something similar to an illusionary contour (Nieder, 2002). When the horizontal wires of the objects were also interrupted in addition to the vertical wires, however, the performance of both fishes dropped close to chance level (Fig. 7C); leaving only the corners of the

objects was not enough for the fish to complete the shapes of the objects and to perceive illusionary contours.

Object material

In addition to volume/size and shape, object material played an important role in determining choice behaviour of the animals. When both the S+ and the S– were exchanged for plastic objects of the same dimensions as those used during training, fish continued to choose their old S+, now made out of plastic (Fig. 8A). Similarly, when S+ was changed into a plastic version (S– remaining metal), both fish tested still chose this object over the metal S– (Fig. 8A). However, when S– was turned into plastic and S+ remained metal, choice behaviour changed. While fish 2 still preferred its original metal S+ (pyramid), fish 1 was now undecided, preferring neither the plastic cube nor the metal pyramid (Fig. 8A). Apparently, the S– cube had lost some of its negative properties through being plastic instead of metal.

When two objects of identical shape and dimensions but made out of different material were offered to fishes 1 and 2, the influence of object material on choice behaviour again became apparent. When the fishes were offered two cubes (shape of the original S–), both animals preferred the plastic cube over the metal cube, rejecting their trained S– (Fig. 8B). In the case of two pyramids made out of different material, the two fish again behaved differently. Fish 2 still preferred the metal pyramid (its original S+) over the plastic pyramid (in 70% of the choices compared to >90% during training). Fish 1, in contrast, rejected the metal pyramid and preferred the plastic version (Fig. 8B).

Fish 4 (trained to choose a metal A and reject a metal mushroom) was also influenced by the material of the test objects. When two cylinders were offered, one made out of plastic and the other out of metal, it preferred the plastic object (Fig. 8C). When the metal mushroom was replaced by a plastic version, it lost a lot of its negative properties. In this case, the

fish was undecided whether to choose it or its original metal S+ (Fig. 8C). Similarly, the fish was undecided when a plastic mushroom was offered together with a metal cube of equal height (Fig. 8C).

Discussion

Our experiments showed that during active electrolocation, weakly electric fish can do much more than just detect objects and determine their electrical resistance (Lissmann and Machin, 1958). Instead, even in complete darkness, they can perceive parameters such as the volume, size, 3-D shape, contour, material and possibly the orientation of an object. The fish might use these parameters to discriminate between different objects in their habitat. In addition to finding food (von der Emde and Bleckmann, 1998), this might enable them to localize and recognize environmental landmarks even in complete darkness and thus be able to navigate through their surroundings during their nightly activity period. Even though *Gnathonemus* can also use vision to perceive the outline of objects (Schuster and Amtsfeld, 2002), they mainly use their electric sense even in the presence of light (Schwarz and von der Emde, 2001) (M. Landsberger and G.v.d.E., unpublished observation). In fact turning off the lights during control experiments had no effect at all on the behaviour of the fish (Fig. 2B).

Learning to discriminate objects through active electrolocation

In this study, all fish learned to discriminate between the objects they were offered as S+ and S–. However, there were differences in the speed that the different learning tasks were acquired.

Fish 4 was the fastest individual to learn its task. The objects that this fish was trained to discriminate (an A and a 'mushroom' of very different sizes) were so different from each other that it was easy for the fish to distinguish them, resulting in fast learning. Later it turned out that this fish had used a different strategy for object discrimination than most of the other fishes: for discrimination, fish 4 attended mainly to the S– (mushroom) and did not pay much attention to the S+. S+ could be exchanged for almost any other object and the fish kept choosing it as long as the S– remained the same (Fig. 4C). Apparently, the fish more or less ignored the S+ and mainly used just one feature to recognize the S–: the half-spherical shape of the mushroom's head. All other fishes that were trained in this study paid attention to both the S+ and the S– and their choice behaviours were based on a more complicated comparison of positive and negative object parameters (see below).

Two individuals (fishes 5 and 6) were trained to discriminate between a T and a C. They needed the longest time to learn their tasks (19 and 24 days of training). The objects used were almost identical in volume, and both objects were letters of the alphabet, i.e. they were relatively thin and basically consisted of a 'wire' bended into a shape. Because these objects differed only in detail, it took the fish some time to learn to discriminate between them. The fact that discrimination was eventually possible shows that the fish was receptive to subtle differences in object shape.

Fishes 1 and 2 were trained to discriminate between a pyramid (S+) and a cube (S–). When S– was exchanged for a
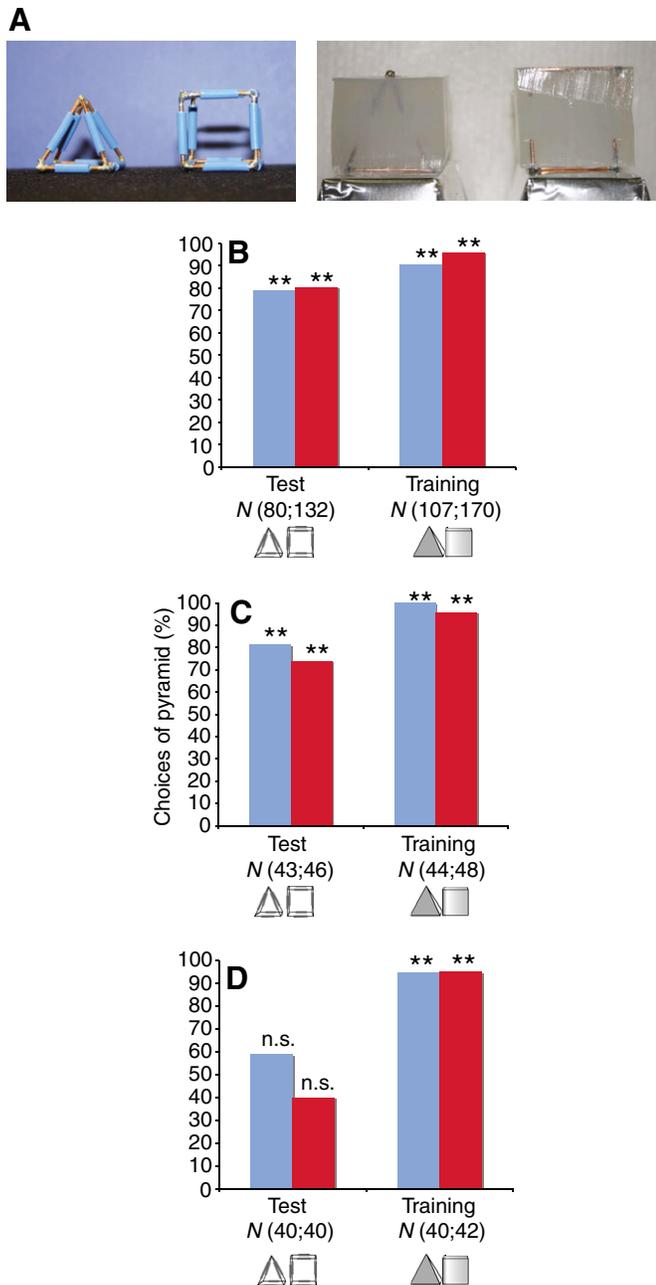

Fig. 7. Results of transfer tests with fish 1 (blue) and fish 2 (red), during which the training objects (pyramid, S+; cube, S–) were replaced by so-called wire objects of the same outline as the training objects (see text). (A) Photos of the wire objects (left) and of the wire objects embedded in electrically transparent agar with interrupted vertical parts (right). (B–D) Choice frequencies for the pyramid (S+) by fish 1 (blue) and fish 2 (red). Right bars, original training objects; left bars, wire objects (B), vertically interrupted wire objects (C) and vertically and horizontally interrupted wire objects (D). Asterisks above each graph indicate significant differences from random choice conditions: **P<0.01; n.s., non significant.
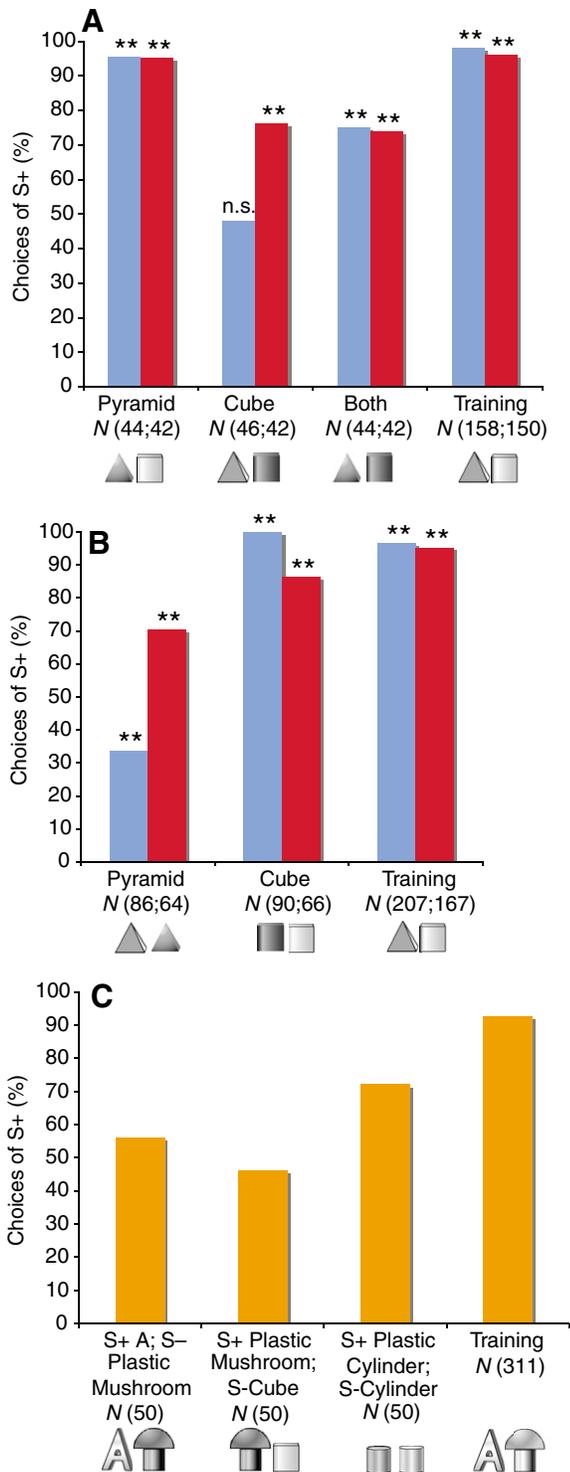
Fig. 8. Results of transfer tests with fish 1 (blue) and fish 2 (red) (A,B) and fish 4 (C), during which one or two objects were replaced by plastic objects. In (A), object shapes remained unchanged, while S+ (pyramid), S– (cube) or both objects were replaced by otherwise identical plastic versions. In (B), two identically shaped objects (either two S+ or two S–) were offered, one of which was made of metal and the other one of plastic. In (C), several combinations of S+ (**A**) and S– (mushroom) made out of plastic or metal, respectively, were offered. Numbers in parentheses are the total number of each fish's choices. Asterisks above each graph indicate significant differences from random choice conditions: **$P<0.01$; n.s., non significant.

cone, which resembled the pyramid in many ways and also had a similar volume (Table 1), performance dropped to chance level (Fig. 3A). In order to decide whether electric fish are unable to discriminate between a cone and a pyramid or whether the particular training conditions made fishes 1 and 2 judge these objects to be undistinguishable, a cone and a pyramid were used as training objects with another fish (fish 3). It turned out that after training this fish was able to discriminate between these objects very well (Fig. 1), but it needed a longer training time to reach a stable discrimination level compared to fishes 1 or 2 (19 days for fish 3 compared to 10 and 11 days for fishes 1 and 2, respectively). As for fishes 5 and 6, clearly it takes the fish longer to learn the subtle differences between similar objects (Fig. 1).

A discrimination performance of 50% in a test experiment does not necessarily mean that a fish cannot discriminate between the two objects offered. Instead, it means that for the fish the two objects are equally similar to the original S+ (or equally dissimilar to the original S–), and that given the criteria it uses, it cannot judge which of the two objects it should choose. When a fish is especially trained to discriminate between the objects, however, it might then find enough distinguishable parameters to discriminate between the two. The same phenomenon is regularly seen in multidimensional scaling experiments with *G. petersii* (von der Emde and Ronacher, 1994) and with other animals, including humans, employing other senses (e.g. Shepard, 1987; Werner and Rehkämper, 2001).

Exchanging S– or S+

In discrimination tests, the fishes in this study did not always choose their S+, even when they discriminated perfectly between the S+ and the original S–. This shows that none of our fish had learned to pick a particular S+ regardless of the alternative object. Instead, fish had learned to pay attention to the *relative* differences between the two objects they had to discriminate. When the S– was exchanged, choice behaviour depended very much on the type of object that replaced it (Fig. 3A–D). Similarly, the fish did not always avoid their original S–. When a novel object was paired with the S–, choice behaviour depended on the properties of this novel object (Fig. 3E–H). So the fish had learned to attend to both the S+ and the S– during training and their decision was based on a positive response to the features of S+ and a negative response to the features of S–. Attendance to S– might reflect the training method used: because the fish were mildly punished when they swam through the gate with the negative object, they paid attention to the S– and learned about its properties. This is in contrast to an earlier study, in which a *G. petersii*, in a similar set-up to this study, was trained to discriminate electrically between a cone and a cube. After about 1 year of training, this fish kept choosing the cone no matter which alternative object was offered (Davis and von der Emde, 2003). Ignoring S– by this fish might have been due to the extra long training period, which allowed it to pay attention to only the positive object.

Several object features influenced the choice behaviour of our fish when a novel object combination was presented in discrimination or transfer experiments. (1) Relative volume of

the two objects; all fish tended to avoid the larger and prefer the smaller object of a pair (Figs 3, 4, 6; Table 1). (2) Object material; all fish tended to avoid metal (a good conductor) and to prefer plastic (an electrical insulator) objects (Fig. 8). Thus, fishes avoided object parameters that led to an increase in local stimulus amplitude: low resistances and large volumes. (3) Object shape; fish tended to choose an object of the same shape as S+ and to avoid the shape of S– (Fig. 7).

In addition to these three most important parameters, other object features evidently played a role, but for a human observer it is not easy to identify those features that were given negative or positive attributes by the fish. For example, object height might have played a role (higher objects were avoided). We never varied object height and volume independently, however, and therefore cannot make a clear statement regarding height. Some fish, especially fish 4, which was trained with a mushroom as the S–, tended to avoid round objects (spheres and half spheres). In contrast, other fish avoided corners, especially those fish whose S– was a cube (Figs 3, 4). During training, each fish acquired certain knowledge about its particular S+ and S– and then applied this knowledge during discrimination and transfer tests when judging new objects.

Influence of object volume on choice behaviour

The sensory stimulus encoding object volume is the local electrical amplitude in the centre of the electric image, which the object projects onto the electroreceptive skin surface (Bastian, 1994). Local amplitude correlates with object volume: the larger a metal object the higher the amplitude change it evokes. The reverse is true for a plastic object: local amplitude decreases with volume of a non-conducting object. However, local amplitude change is also inversely correlated with object distance.

As mentioned above, there was a general tendency with all fishes to reject the larger object of a pair, regardless of the material of the object. Even fishes that were trained to discriminate between two objects of similar volume tended to avoid larger objects in transfer tests. In discrimination tests, when S– was exchanged and the original S+ was maintained, the fish tended to keep choosing their S+ as long as it was smaller in volume than the substitute S–. Similarly, when S+ was exchanged, fish kept rejecting their original S– as long as it had a larger volume than the alternative object. This can be seen in Fig. 3, where columns are arranged according to the size of the object replacing S–, with objects getting larger from left to right. The percentage of choices for S+ tend to increase with size of the S–. In contrast, Fig. 4 shows the results of experiments where S+ was exchanged. Here, column heights decrease from left to right because the new S+ increases in volume from left to right. However, both figures also show that there are exceptions to this rule. Choice behaviour of different fish appears to be influenced not only by volume but also by additional parameters.

The tendency to choose the object of smaller volume is further analysed in Fig. 9, which is based on data shown in Table 2. Here, the percentage choices of the smaller object are plotted *versus* the volume ratio of the two objects (volume of S+ divided by volume of S–). A small volume ratio means that the chosen object was relatively small compared to the
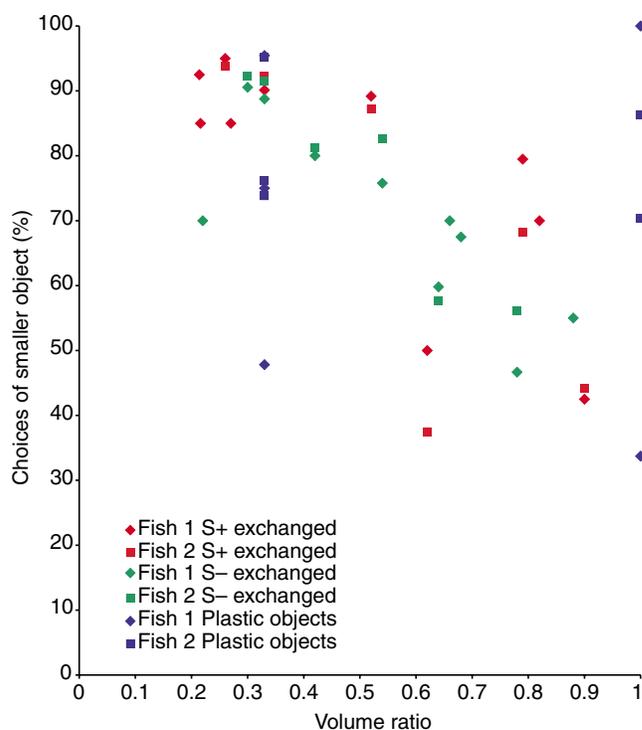

Fig. 9. Summary of the results of a variety of transfer tests conducted with fish 1 (diamonds) and fish 2 (squares) deciding between objects of different volumes. The choice frequencies for the smaller object of each combination are plotted *versus* the volume ratio of the two objects used, with the volume of the smaller object divided by the volume of the larger object. Colours depict the type of transfer experiment: red, exchange of S+ for a novel object (see Fig. 4); green, exchange of S– (see Fig. 3); blue, transfer tests with at least one plastic object (see Fig. 8).

alternative object; a ratio of 1 corresponds to two objects having the same volume. The data show that small volume ratios resulted in high choice frequency for the smaller object. When objects became more similar in volume, the preference for the smaller object decreased. However, Fig. 9 and Table 2 also show that there is quite a large scatter of data points at a given volume ratio, so it was not only volume ratio that determined choice behaviour, but other object features also played a role. Even at small volume ratios, choice frequencies can vary from near 50% to >95%. In these cases, other object features such as material strongly influenced the decision of the fish in addition to volume.

Fig. 6 also emphasizes the importance of volume for object recognition. When the S+ (cone) became larger (compare the choices for the three cones of different sizes), fish tended to more and more avoid it. At a volume ratio of 1.62, when the cube was still larger than the cone, fishes 1 and 2 already showed no preference for any of the objects. By contrast, when the cube was only slightly smaller than the cone (cube:cone ratio 0.83, corresponding to a cone:cube ratio of 1.22), it was chosen by fish 1 in 70% of the cases. Thus it is not only the relative size of the objects that determines choice behaviour.

Fish 2 was influenced in its choice behaviour by the distance of an object away from it (Fig. 6). A far away cone was strongly

Table 2. *Choice frequency of the smaller object in three different experiments with fishes 1 and 2*

Experiment	Object combination S+ / S−	Volume (cm^3) S+ / S−	Volume ratio	Choice of smaller object (%)	
				Fish 1	Fish 2
S+ replaced	**Cube** / Big hexagon	27.0 / 126.1	0.214	92.5	
	Cube / Big cube	27.0 / 125.0	0.216	85	
	Cone / **Cube**	7.07 / 27.0	0.26	95	93.75
	Cube / Big cylinder	27.0 / 98.1	0.27	85	
	Pyramid / Cube	**9.0 / 27.0**	**0.33**	**90.12**	**92.27**
	Sphere / **Cube**	14.14 / 27.0	0.52	89.18	87.23
	Big cone / **Cube**	16.75 / 27.0	0.62	50	37.5
	Cylinder / **Cube**	21.20 / 27.0	0.79	79.48	68.23
	Cube / Extra big cone	27.0 / 32.7	0.831.21	70	
	Cube / Hexagon	27.0 / 29.7	0.9	42.5	44.19
S− replaced	Small cone / **Pyramid**	2.0 / 9.0	0.22	70	
	Pyramid / Hexagon	9.0 / 29.7	0.3	90.56	92.24
	Pyramid / Cube	**9.0 / 27.0**	**0.33**	**88.77**	**91.5**
	Pyramid / Cylinder	9.0 / 21.20	0.42	80	81.25
	Pyramid / Big Cone	9.0 / 16.75	0.54	75.78	82.6
	Pyramid / Sphere	9.0 / 14.14	0.64	59.81	57.69
	Small Hexagon / **Pyramid**	6.0 / 9.0	0.66	70	
	Small Cylinder / **Pyramid**	6.2 / 9.0	0.68	67.5	
	Cone / **Pyramid**	7.07 / 9.0	0.78	46.67	56.15
	Small cube / **Pyramid**	8.0 / 9.0	0.88	55	
Plastic objects	Plastic pyramid / **Cube**	9.0 / 27.0	0.33	95.45	95.24
	Pyramid / Plastic cube	9.0 / 27.0	0.33	47.82	76.2
	Plastic pyramid / Plastic cube	9.0 / 27.0	0.33	75	73.81
	Pyramid / Plastic pyramid	9.0 / 9.0	1	33.72	70.32
	Plastic cube / **Cube**	27.0 / 27.0	1	100	86.36

Training combinations are underlined; training objects are printed in bold type.

avoided, which was not the case when the same object was close by. It could be that this fish paid attention to the size of the electric image of the cone, which increases in size when an object moves away from the fish (von der Emde et al., 1998). Maybe fish 2 judged the far away object to be bigger because of the increased image size. If this were true, it would mean that this fish did not measure the distance of the object and thus had no size constancy (Douglas et al., 1988; Leibowitz, 1971). It is important to note that the other fish (fish 1) was not influenced by object distance and thus might have taken object distance into account when judging object size. We are currently conducting experiments in our lab in order to test specifically for size constancy during active electrolocation in weakly electric fishes.

Influence of object material on choice behaviour

The electrical properties of the object, i.e. its complex impedance, determine the stimulus properties within the electric image (Caputi et al., 1998). Pure metal and pure plastic objects have negligible capacitive components (von der Emde, 1990) and thus do not change stimulus waveform, only its amplitude. The metal objects used in our study strongly increased stimulus amplitude, while plastic objects caused the opposite effect, strongly decreasing amplitude.

All fish tested preferred plastic objects over metal objects (Fig. 8), even though only metal objects were used during training. Apparently, even though the S+ was made out of metal, metal was not given positive attributes during training. When a plastic version of the S− was paired with the original metal S+, all but one fish chose this plastic S− and rejected S+ (Fig. 8).

Only fish 2 still preferred its S+ (Fig. 8A). In all other cases, the S− lost its negative properties when it was replaced by an otherwise identical plastic version. However, when both objects of a pair were exchanged for plastic versions, the preference for the trained shapes (and volume ratios etc.) returned (Fig. 8). This suggests that the fish can generalize what they have learned to novel object combinations.

Gnathonemus spontaneously judge metal objects as having negative qualities. Even without any training, fish spontaneously preferred plastic and avoided metal objects. Metal objects have a very low electrical resistance and are absent in the natural environment of the fish. Natural low-resistive objects never have as low resistances as pure metal objects. In the presence of metal, local amplitudes at the skin of the fish become extremely high, causing the electroreceptors to fire vigorously (Bell, 1990). Compared to other senses, metal objects might appear to electric fishes as being very bright or very hot and are thus perceived as being potentially dangerous.

Influence of object shape on choice behaviour

So far it is not known which sensory stimulus encodes an object's shape during active electrolocation. Because of the lack of focussing mechanisms and the non-symmetric electrical field during electrolocation, electrical images are always distorted and there is no one-to-one geometrical relationship between object shape and image shape like in visual images (Caputi and Budelli, 2006). Fish probably have to carry out some complex neural computations in order to acquire information about object shape.

So far there has been no detailed study on differences in electric

images of differently shaped objects. Schwarz (Schwarz, 2000) measured one-dimensional cross sections of electric images of objects of different shapes (cubes, spheres, and pyramids), but found no unambiguous cues that coded for object shape. By contrast, electric images measured in this way were much more influenced by object volume rather than shape. A similar result was obtained by Pusch (Pusch, 2006), who found that electric images of spheres and cubes differed mainly in the amplitude of the image, with cubes generating stronger images than spheres of equal volume. It may be necessary to measure complete electric images of objects, not just cross sections, however, in order to find shape-related cues. Maybe single electric images may not be sufficient to detect object shape, even for the fish. When discriminating between differently shaped objects, fish perform probing motor acts (see above) that provide multiple images of an object from different angles, and this might be essential for the extraction of shape information.

Despite this complex relationship between sensory stimuli and object shape, the choice behaviour of the fishes in our study depended on object shape in addition to object volume and material. This becomes especially apparent in the experiments involving the 'wire objects' (Fig. 7). When objects were reduced to just the outline of the original training objects, fish still preferred the object whose contours (or fragments of contours) resembled those of the positive training object. We conclude from the results that the cue used by the fishes to discriminate between objects of different shapes is located at the circumference of the shape. Contours, however, contain several sub-features, all of which contribute to the appearance of the shape, such as the number, length, the relative orientation of edges, the presence or absence of corners, etc. The choice of particular parameters by the fish for object identification probably depended on training conditions and on individual preferences.

The results using wire objects are very similar to those obtained with honey bees, which were trained to discriminate visually between different pairs of complex convex shapes (Lehrer and Campan, 2005). Like our fishes, when stimuli were reduced to just contours of the shapes, bees kept choosing those contours that corresponded to the positive training shape. In addition, in transfer tests bees based their decision for novel objects on several object features, which they extracted from the complex stimuli and compared them to those of the training objects. One of these features was the contour of the objects (Lehrer and Campan, 2005).

In our fish, and also in the bees of the above-mentioned study, the contour of an object can be perceived even when the outline is interrupted (Fig. 7B). Fish can apparently complete the breaches in the contour and mentally reconstruct the full shape of the object. This is similar to what humans and several animals, such as primates, cats and owls, can do visually when seeing so called illusionary contours (Nieder, 2002). Our study is the first to demonstrate the electrical perception of illusionary contours in weakly electric fishes.

Perception of 3-D objects during active electrolocation

Our experiments revealed that the fishes learned to pay attention to the relative differences between the two objects they had to discriminate. This again became apparent when both S+ and S– were replaced by smaller versions of the same objects in such a way that the volume ratio between them was unchanged. In these cases, fishes' choice behaviour did not change compared to when larger objects were used (Fig. 5). So for a decision, the fish investigated both objects, compared them and then decided according to the outcome of this comparison. When the relationship between the two objects did not change, i.e. when both objects changed by the same amount and into the same direction, choice behaviour did not change either. Apparently, fish were able to quantitatively determine several object features, such as shape, volume, material and others, and to place each object into a multidimensional perceptual space. Choice behaviour was determined by the overall perceptual distance of each object from the stored representation of S+ and S– in this space (Davison, 1983; von der Emde and Ronacher, 1994). When object features were determined, some were given more weight (volume, material) than others (shape). In addition, some parameters were counted as negative (large volume, metal) by the fish, i.e. objects with these parameters were rejected. In contrast, other parameters were counted as positive (plastic, shape of S+) and the fish tended to chose objects with them. Positive or negative assignments depended on training, but also on existing, maybe inborn, preferences and aversions. Interestingly, even though metal was a property of both the S+ and the S–, it was only given negative attributes. For a decision between two objects, fish added up positive and negative properties separately for S+ and S– and then chose that object with the most positive features. Choice frequency for S+ depended on the difference of these sums of features between S+ and S–.

These results are similar to those obtained in an earlier multidimensional scaling study with *G. petersii*, during which animals were trained to discriminate between electrolocation targets that differed in only two stimulus dimensions: local EOD amplitude and EOD waveform (von der Emde and Ronacher, 1994). These two dimensions proved to be analyzable separately for the fish and the overall dissimilarity between two different objects was derived additively from the component differences. Accordingly, the perceptual metric that best described the perceptual space of electrolocating *G. petersii* in this study was a so-called City-Block metric (Shepard, 1987; von der Emde and Ronacher, 1994). In the present study, we offered multidimensional stimuli, which made the choice behaviour of the fishes more complicated.

Feature extraction or template matching?

When *G. petersii* learn to recognize an object during active electrolocation, do they pay attention to local features, such as edges or certain parts of an object, or do they learn to recognize the object as a whole? This is a general question of sensory perception that has been addressed in the literature for various animal models, in most cases using vision for object recognition (e.g. in Dyer et al., 2005). According to one theory (termed 'feature extraction model'), the animal extracts and memorizes particular cues out of several possible ones that are present in the learned stimulus (Palmeri and Gauthier, 2004; Srinivasan, 1994). Similar to some insects orienting visually, our fishes would recognize rewarded or non-rewarded stimuli by the presence of learned cues in a novel object, even if other cues disagree with those of the trained object (Lehrer and Campan, 2005).

As an alternative to object recognition by feature extraction, fish

could have behaved according to a 'template theory' or 'image-matching hypothesis', for example as formulated for insect vision (Wehner, 1967). *G. petersii* recognizes visual patterns according to a 'template theory', forming and learning a visual snapshot of its environment, which is compared and matched to a stored template for recognition (Schuster and Amtsfeld, 2002). Template matching during active electrolocation could mean that the fish matches the electric image that a novel object projects onto its electroreceptive skin surface to a stored template of an electric snapshot of the learned objects.

Even though our experiments were not designed to ultimately decide which mechanisms governed electrical object recognition, our results best comply with a feature-extraction model. As mentioned above, our results suggest that fish are able to link and assemble local features of an electrolocation pattern to construct a representation of an object, suggesting that some form of a feature-extraction model may enable them to solve the complex object recognition task. Fish 'added up' certain object properties and chose according to how many of those parameters the novel object had in common with the objects they had learned during training. When calculating this 'sum', some features counted as negative, and were either learned features of the S– or innate aversions for certain object properties. It is hard to conceive how such a behaviour can be consistent with a template-matching model.

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