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# Perception of electric properties of objects in electrolocating weakly electric fish: two-dimensional similarity scaling reveals a City-Block metric

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**Abstract** During electrolocation weakly electric fish monitor their self-emitted electric signals in order to detect and evaluate nearby objects. Individuals of the mormyrid species *Gnathonemus petersii* were trained to discriminate between resistive and capacitive objects that differed only in their electric properties. Capacitive properties are found almost exclusively among living objects, and are thus of special importance to the fish. Resistive and capacitive properties of objects influence the amplitude and waveform of the perceived electrolocation signals in different ways. Resistive objects change only signal amplitude, whereas capacitive objects affect both amplitude and waveform. The electro-perceptual system of weakly electric fish was investigated by systematic variation of amplitude and waveform using objects of various electric properties as electrolocation targets. After training with a particular stimulus set, the fish reacted in a graded manner to differences in both signal parameters. The perception of each stimulus dimension was found to be independent of the other one. In a kind of 'cross modality matching' experiment, amplitude and waveform parameters were tested against one another. For each amplitude value there was a corresponding waveform value that was judged by the fish to be equally different from the training stimuli. Because of these results, a two-dimensional "perceptual space" is postulated with the two stimulus dimensions waveform and amplitude as its axes. A scaling procedure, using Minkowski metrics, was applied to determine the fish's "perceptual metric". The City-Block metric, and not the Euclidean metric, provided the best description of the data. The two signal dimensions were found to be separable, i.e. to combine additively in complex stimuli. The results are discussed with regard to the discrimination of animate and inanimate objects in the natural environment of the fish.

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**Key words** Weakly electric fish · Electrolocation Stimulus perception · Multidimensional scaling Minkowski metric · Perceptual space

**Abbreviations** *EOD* electric organ discharge *CI* choice index · *S+* positive training stimulus *S–* negative training stimulus

## Introduction

Objects are detected by an animal's sensory system through the physical energies which they reflect or emit. An animal perceives some parameters of the physical energy and thereby gains information about the object. To allow for the classification of a great number of objects a sensory system should be able to assess the similarities between objects. A prerequisite for this is to evaluate quantitatively differences between objects. The amount of perceived differences, however, will often deviate from the actual physical differences.

Weakly electric fish have a perceptual world that is not shared with other animals. They detect and discriminate objects in total darkness using a unique electro-sensory modality. The process is called active electrolocation (Lissmann and Machin 1958). With an electric organ in their tail, the fish emit weak electric signals (electric organ discharges, EODs) that induce a three-dimensional electric field around the fish's body. This field is perceived by electroreceptors in the fish's skin that monitor the "local" EOD. An object that is close to the skin with electric properties different from the surrounding water distorts the electric field and thereby changes the locally perceived electric signals (Heiligenberg 1977).

Both amplitude and waveform of the local EOD can be altered by an object (Fig. 1): (1) The *local EOD amplitude* depends on the impedance of the object under investigation. If its impedance is higher than that of the surrounding water, the local EOD amplitude is decreased. If it is lower, i.e. the object is a better conductor than the water, the local amplitude is increased. Because

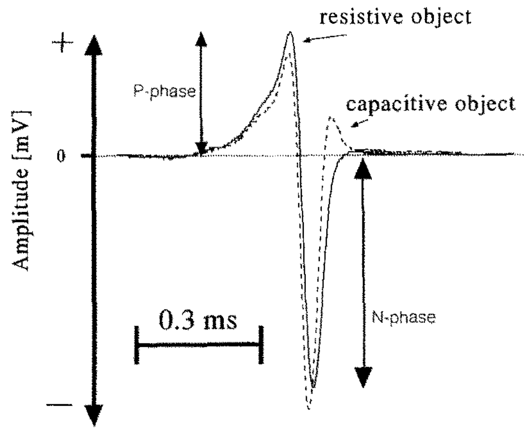


**Fig. 1** Waveforms of two local EODs recorded close to the skin of a discharging *G. petersii*. Peak-to-peak amplitudes are normalized to the same value. One EOD (*solid line*) was recorded in the presence of a resistive object that caused no waveform distortion. A capacitive object (*dashed line*) distorted the EOD waveform: The amplitude of the first, positive phase (*P-phase*) was reduced; the second, negative phase (*N-phase*) was increased, and a third, positive phase developed. Also the relative timing of the zero crossing of the rapid transient changed

capacitive and resistive objects have an electric impedance, they both affect the local EOD amplitude. (2) *EOD waveform distortions* are caused only by capacitive objects. Both EOD waveform and EOD amplitude are changed depending on the capacitive value of the object (von der Emde 1990). EOD waveform distortions can be perceived by electric fish and are used to identify capacitive objects (von der Emde 1990, 1993a; von der Emde and Bleckmann 1992). The fish can also discriminate between objects of different capacitive values (von der Emde 1993b). Objects with capacitive properties are of special importance to the fish because such properties are chiefly found in animate objects, such as other fishes, plants, and insect larvae (food).

If objects do not differ in other parameters like size and shape, fish will use the two physical parameters amplitude and waveform distortions in categorizing objects. Thus, the electrolocation system of weakly electric fish can be used to investigate a perceptual system that receives only two physical parameters which are also easily manipulated by the experimenter.

Weakly electric fish can be trained to choose objects that cause a particular amplitude change and amount of waveform distortions of the local EOD (von der Emde 1992, 1993b). By using so called "dipole-objects" (von der Emde 1990), whose electric properties can be changed quickly without affecting other stimulus parameters, numerous combinations of resistive and capacitive object properties can be realized. These dipole objects in turn alter the local EOD at a given electroreceptor in almost any desired way. Thus, this method allows one to present stimuli of defined amplitude and waveform and to vary the two stimulus parameters independently.

For other sensory systems, an abstract perceptual space has been postulated into which the physical parameter space is mapped by a psychophysical function, and similarities between objects can be represented as distances between points (Garner 1974; Ronacher 1979b; Shepard 1964, 1980, 1987; Stevens 1957; Torgerson 1958). Therefore, it is of special interest to investigate whether the perception in a completely different sensory system can be described by similar rules.

The axes of the perceptual space are the perceptual components (perceptual parameters) that are extracted by the CNS from the physical parameters available for the sense organs. It is important to note that these perceptual axes do not necessarily coincide with physical parameters. An example is color vision where colors can be described by lightness, hue, and saturation; a different concept has been used by Hering (1875) who classified colors by their red/green, blue/yellow, and black/white components. In other animals, other dimensions can be taken as perceptual axes, for example "blue/greenness" and "UV/blue-greenness" in the honeybee (Backhaus et al. 1987).

Multidimensional scaling (MDS) experiments (Backhaus et al. 1987; Ronacher 1979b, 1992b; Ronacher and Bautz 1985; Shepard 1980; Torgerson 1958) can be used to identify the number of dimensions and also the type of "metric" that best describe a perceptual space. The metric of the perceptual space defines the geometrical rules according to which distances in the space (i.e. object dissimilarities) can be determined. At least two different types of metrics (Garner 1974; Shepard 1964) have been found in MDS experiments: (i) the familiar Euclidean metric, which is mainly present with so called "unitary" or "integral" stimuli such as in human color vision and some aspects of hearing, and (ii) the City-Block metric, so called because distances between points in an orthogonal grid of streets conform with this metric. A City-Block metric is often found for "analyzable" stimuli, such as shapes differing in the perceptually separable attributes of size and orientation (Shepard 1987). Color vision in honey bees can best be described by a City-Block metric (Backhaus et al. 1987), while in humans colors are rated according to the Euclidean metric.

In this paper, we want to address the following questions concerning the quantitative perception of the two physical parameters during electrolocation: How are the physical parameters mapped into the perceptual space? Are the physical parameters perceived independently and how are they weighted? Does a variation of one parameter affect the perception of the other? Which metric describes best the distances in perceptual space?

The perceptual strategy used by the weakly electric fish *Gnathonemus petersii* during electrolocation was investigated by training the fish to choose an object that yielded a particular EOD amplitude and waveform, and to avoid an alternative one. When a fish had learned this task, new objects were used and tested either together with the old training stimuli or with other, new test stimuli. The observed choice frequencies were interpreted as measures of perceptual dissimilarity between the test stimuli relative to the trained stimuli. The choice frequencies thus represent distances in perceptual space. In addition, the best fitting metric of the presumed two-dimensional perceptual space was determined.

## Methods

### Experimental animals

Several individuals of the weakly electric fish *Gnathonemus petersii* (Mormyridae) were used in these experiments. They were obtained from a local dealer who had imported them from Nigeria. Their lengths (head to fork of tail) were between 12 and 14 cm. Single fish were kept in 100 l tanks that were also used for training. The temperature was held constant at 27±1°C, water conductivity at 50±10 μS/cm. The light/dark cycle was set at 12/12 h.

To determine the physical features of the electric signals the fish emitted, EODs of each fish hiding in a ceramic tube were recorded head-to-tail with two carbon electrodes. Single EODs of individual fish were extremely constant (von der Emde 1992). For training and recording experiments, only those fish were selected that had very similar EODs with regard to three signal parameters: peak-to-peak amplitude (which was a function of the size of the fish), peak power spectral frequency, and pulse duration. To determine the frequency composition of a single EOD the discharges were A/D converted (DSO 3335, Krenz Electronics) at a rate of 180 kHz for fast Fourier transformation (FFT). The peak power spectral frequency of single EODs was calculated by computer using a Pascal version of the subroutine FFT842 of the package FAST (Bergland and Doland 1979). At least 10 EODs were sampled for each fish and the measurements were averaged to obtain mean values.

### Experimental set-up

The set-up used is described in detail elsewhere (von der Emde 1990). Briefly: The experimental tank was divided into two compartments of about 60 l and about 40 l. The fish usually was hiding in a shelter in the bigger compartment that also contained heater and filter equipment. The dividing wall consisted of a 1 cm thick plastic frame covered with a plastic mesh. The wall had two gates (6×6 cm) that could be opened and closed by the experimenter by pulling a thin plastic thread.

Mounted directly behind each gate, in the smaller compartment, was an electrolocation object ("dipole-object"; von der Emde 1990). Each was made from plexiglass tubing (diameter 6.5 mm) in the form of an inverted T. The longitudinal axis of the horizontal part of the T was oriented perpendicular to the opening of the gate. Into the horizontal part of the T (length: 2.5 cm), a small carbon rod (diameter 6 mm) was inserted at each end. The carbon rod was inserted into the tube so that one end, which had contact with the aquarium water, fitted the end of the tube and sealed it water-tight. Wires were connected inside the tubing to each carbon electrode. The two wires left the water inside the vertical part of the T. By introducing resistors or capacitors into the circuit formed by wires, carbon rods, and aquarium water, the passive electric properties of the objects could be changed without affecting their geometry. For example, by simply connecting the two wires, the dipole object was rendered a conducting object. After introducing a resistor or a capacitor into the circuit the dipole object was turned into a resistive or capacitive object of a defined value. Several resistors or capacitors could be placed in the circuit at the same time, either in parallel and/or in series with each other. By varying the value or arrangement of the elements, a dipole object of any desired electrical property could be presented to a fish. For a discussion of the differences between the effects of natural objects and the dipole objects see von der Emde (1990).

In this study the capacitive and resistive properties of a dipole object are indicated in the following way: In parentheses, the capacitive value is given first followed by the resistive value. Two numbers separated by '=' indicate that the two elements are connected in parallel. For example, (0.95 nF=60 kΩ) represents a 0.95 nF capacitor and a 60 kΩ resistor connected in parallel. (15 kΩ) means that only a 15 kΩ resistor was put into the circuit, etc. To avoid the possibility of DC currents serving as an additional cue, a large capacitor of 5 μF was always placed in series in the circuit. This capacitance was far too large to cause any additional waveform or amplitude changes (Fig. 2) and thus is not mentioned in describing the electric properties of an object.

### Electric stimuli

During electrolocation, an electric fish attends to its own local EODs as these are changed by an electrolocation object. Electroreceptors in the skin monitor the amplitude and the waveform of the local EODs. These local EODs were affected in defined ways by a dipole object with certain resistive and capacitive properties. Each combination of resistors and capacitors produced a certain amplitude and a certain amount of waveform distortion of the local EOD. Local EOD waveform distortions can be measured in several ways. A good parameter describing waveform distortions quantitatively is the amplitude ratio of the positive (P) and negative (N) phase of an EOD (Fig 1). It was shown that it is correlated with all other measures of EOD waveform distortion such as (i) the amplitude of the second positive phase of the local EOD, (ii) the integral of the EOD, (iii) the slope of the main positive negative transient, (iv) the frequency with maximum power in the amplitude spectrum of a single EOD (von der Emde 1990; and personal observation). Because of these correlations we used the P/N amplitude ratio which proved to be a reliable indicator of EOD waveform changes (von der Emde 1990).

In order to assess the effects of objects on the local EOD quantitatively, experiments were conducted in which local EODs were recorded in the presence of different dipole objects. A *Gnathonemus petersii* was physically immobilized within a silk sock in the center of a circular tank (diameter: 1 m, water depth: 60 cm). The fish still emitted EODs at a regular rate. A pair of small carbon recording electrodes (diameter: 0.5 mm) isolated except for the tips, were placed close (<1 mm) to the pore of an electroreceptor organ near the skin of the fish. The tips of the electrodes were about 2 mm apart and their connecting axis was oriented perpendicular to the fish's skin. These electrodes were differentially amplified and thus recorded the local EOD close to the fish. The recorded signals resemble the signals that the fish perceives through its electroreceptors.

To mimic the effect of the dipole objects during electrolocation, a dipole object was placed close (about 2 mm) to the recording electrodes, with its longitudinal axis perpendicular to the fish's skin. For the importance of the distance between object and skin see Results. The local signal was then recorded in the presence of the object, whose electric properties were varied as in the behavioral experiments. By using this method it was possible to determine the amount of waveform and amplitude changes caused by each dipole object.

### Training

The fish were trained to discriminate between two dipole objects with different electric properties. Each trial started with the experimenter setting the electric properties of the dipole objects. The gates in the dividing wall of the experimental tank were opened, which exposed the dipole objects and made them accessible to the fish. The fish learned quickly to swim to the dividing wall and to examine each electrolocation object successively, after having

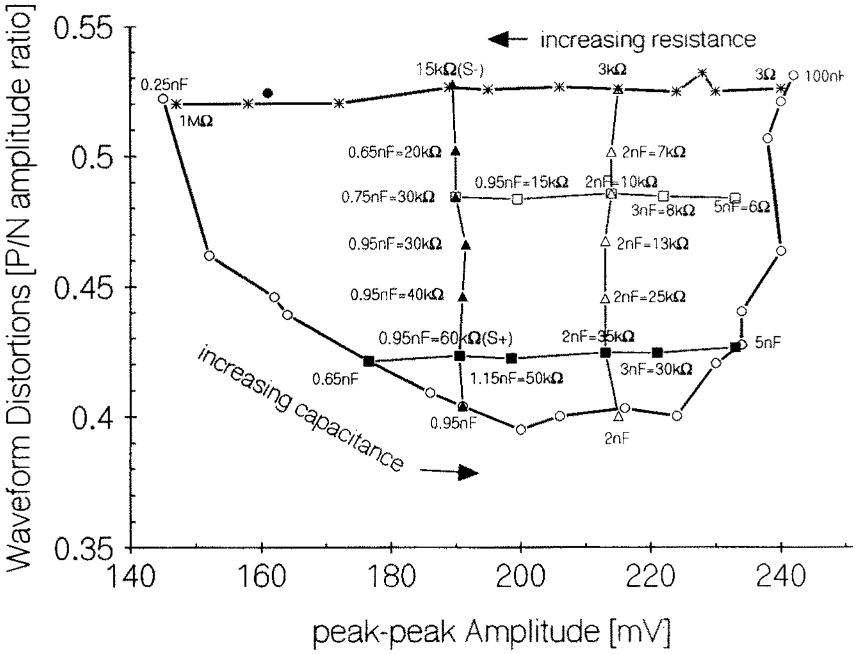


**Fig. 2** Physical stimulus space. The diagram shows the characteristics of local EODs, recorded in the presence of various dipole objects. The amount of waveform distortions of the EOD (measured as P/N amplitude ratio) is plotted versus its peak-to-peak amplitude. Each point represents the EOD parameters induced by a dipole object of different electric properties, some of which are written as *numbers* next to their corresponding points. The *closed circle* gives the values for an EOD without any object present. *Asterisks* (*) stand for resistive objects, *open circles* for purely capacitive objects. Filled triangles show objects of test series no. 1, that all cause approximately the same local amplitude but different waveform distortions. The objects used as the rewarded training stimulus (0.95 nF=60 kΩ; S+) and the unrewarded training stimulus (15 kΩ; S–) are both members of series no. 1. Objects of test series no. 2 (*filled squares*) cause the same waveform distortions but different amplitudes. The S+ is also a member of test series no. 2. Each member of test series no. 1 has a corresponding member in test series no. 3 (*open triangles*) that causes the same waveform distortions but at a different amplitude level. All members of test series no. 4 (*open squares*) cause the same waveform distortions but their signal amplitudes vary. Each member of test series no. 4 has a corresponding member of test series no. 2 causing the same amplitude, but at a different P/N ratio. *Symbols*: ○–○ capacitive objects; ✳–✳ resistive objects; ▲–▲ constant Amplitude (test series 1); ■–■ constant P/N-ratio (test series 2); △–△ constant Amplitude (test series 3); □–□ constant P/N-ratio (test series 4); ● no object present

heard the gates open. It finally chose one object by swimming through the corresponding gate into the smaller compartment. If the trial was a "training trial" and the fish's decision was correct, it received a food reward consisting of one chironomid larva. If the decision was wrong no food reward was given and the fish was chased back into the larger compartment. After having eaten the reward, the fish swam back through the gates into the larger compartment and the gates were closed behind it. After an intertrial interval of one to two minutes, a new trial started. Each fish made more than 100 choices in one session per day.

Trials were divided into *training trials* and *test trials*. First, only training trials were conducted until a fish had learned its task. During all training trials, fish always had to decide between the same two dipole objects with the following properties: The positive, rewarded object (S+) was a (0.95 nF=60 kΩ) object, i.e. a 0.95 nF capacitor was placed in parallel with a 60 kΩ resistor into the circuit. The negative, unrewarded object (S–) was a purely resistive object: (15 kΩ). The position of each object (left or right gate) varied according to a pseudorandom schedule (Gellerman 1933).

Test trials began after a fish had reached a performance level of more than 90% correct choices in three subsequent training sessions. In that case, the following session was a mixed training and test session: it contained training trials but every fourth trial was a test trial. A test trial was only conducted, however, if at least two of the three previous training trials were solved correctly by the fish. During a test trial, there was no longer a S+ and a S–, but instead the preference for two new objects was tested. Test trials were always unrewarded in order to eliminate further learning. It was noted, which of the two objects was chosen by the fish. Since the learning level from the previous training trials was high, it was assumed that the fish's choices would reflect the similarity of the test objects with the previous S+, or the dissimilarity with the previous S–.

During a test trial a new combination of dipole objects was used. Each combination was presented at least 50 times to each fish. Test combinations were presented in a quasi-random order, and rarely were the same two objects presented in two successive test trials. The result of each test combination was expressed as a choice index (CI) with values between –1 and +1. The CI was calculated according to the formula:

$$\mathrm{CI}(X) = (x-y)/(x+y) \qquad (1)$$

with x being the number of choices for object X and y being the number of choices for object Y.

A value of +1 for a particular object X indicates that this object was chosen in 100% of the trials. A CI of –1 indicates that the other object (Y) was chosen in 100% of the trials, and an index of 0 indicates that 50% of the choices were directed towards each of the two objects.

## Test series

In several test series, the influence of the two signal parameters waveform and amplitude on the fish's choice behavior was evaluated. By varying the resistive and capacitive properties of the dipole objects, these two parameters could be set independently to almost every desired value. It was, for example, possible to change the amount of EOD waveform distortion without altering the local EOD amplitude, and vice versa (Fig. 2).

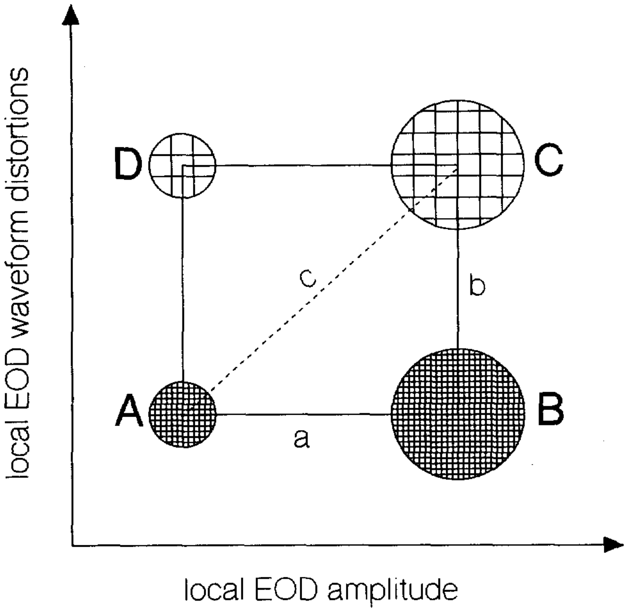


**Fig. 3** Scheme of the proposed two-dimensional perceptual space with four different objects (*A–D*). Objects *A* and *D* and objects *B* and *C* cause the same local EOD amplitude but different waveform distortions, while objects *A* and *B* and objects *C* and *D* cause the same waveform distortions. *Lines* represent perceptual distances for objects differing in amplitude (*a*), or waveform distortions (*b*), or for a stimulus pair differing in both parameters (*c*). Object pairs like the objects *B* and *D* were used for the trading experiments. Objects *A*, *B*, and *C* form a triplet like it was used for the metric experiments

All objects in Fig. 2 placed on the line connecting S+ with S– belong to test series no. 1 (filled triangles in Fig. 2). They all affected the EOD amplitude in the same way but caused different amounts of waveform distortion. The objects placed on the line running through S+ parallel to the abscissa belong to test series no. 2 (filled squares). They all caused the same waveform distortion as S+ but affected the local EOD amplitude differently. The line running vertically through the 2nF object belongs to a second series of test objects with constant EOD amplitude changes, i.e. test series no. 3 (open triangles). Each member of this series caused similar waveform distortions as a corresponding member of test series no. 1 but at a different amplitude level. Members of test series no. 4 (open squares), finally, resulted in similar amplitude effects as the members of test series no. 2 but at a different level of waveform distortions, which was held constant throughout this series. In order to find out how the fish rated differences in one dimension only, every combination of two objects within each series was presented in test trials.

In a kind of 'cross modality matching' (Stevens 1959) or 'trading' experiment, objects from amplitude series no. 1 were tested together with objects from waveform series no. 2. The goal of these tests was to find for each object from the amplitude series an object from the waveform series that was chosen equally often (CI=0). This choice index indicates that the perceptual distances between each object and the S+ are equal, although the two objects are located at different positions within the two-dimensional coordinate system of the perceptual space (such as objects B and D in Fig. 3).

### Determination of the "best" Minkowski metric

The perceptual differences between objects with different electric properties were evaluated with the two-dimensional scaling procedures mentioned above, using Minkowski metrics as a model for perceptual differences. The most appropriate Minkowski metric was determined from the pooled data of three fish, as well as from the data of each individual animal.

Minkowski metrics in the two-dimensional space can be written as:

$$c = (a^r + b^r)^{1/r} \tag{2}$$

with 'a' giving the subjective difference between EODs differing only in amplitude, 'b' standing for the differences only in waveform distortions, and 'c' indicating EODs that differ in both parameters (Fig. 3). Special cases of Minkowski metrics according to this formula are the City-block metric ($r$=1), the Euclidean metric ($r$=2), and the dominance metric ($r \rightarrow \infty$).

To determine the Minkowski metric that best describes the perceptual space of *G. petersii* many behavioral tests were performed with triplets of stimuli of the form A, B, and C, as indicated in Fig. 3. For each triplet three stimuli were chosen from the grid of stimuli of Fig. 2 that could be arranged like the objects A, B, C in Fig. 3. Object A always was the S+ of the previous training experiments. A total of 15 different stimulus triplets were used in the metric experiments (not all of them are shown in Fig. 2 for the sake of clarity). The distances a, b, and c between the objects of each triplet were determined by offering two of the three objects as test stimuli. The choice index for each test combination was measured as an indicator for the perceptual distance between the two objects. To determine the "best" Minkowski metric, the observed distance c was compared with a prediction of c according to equation (2). For this purpose the function

$$SQ(r) = \Sigma\, [(a_i^r + b_i^r)^{1/r} - c_i]^2 \tag{3}$$

was defined for all $N$ data triplets. The minimum of this function was determined (Fig. 8) and the exponent $r$ at which the minimum occurred was taken as the "best" Minkowski exponent. For a detailed description of this procedure see Ronacher and Bautz (1985) and Ronacher (1992a).

## Results

### Recording of EODs and selection of stimuli

The signals emitted by an individual fish were extremely constant (see also von der Emde 1993a). Between fish, however, there were some variations in pulse characteristics. These were kept as small as possible by selecting fish of similar size that emitted similar EODs with respect to duration, frequency composition and amplitude. The pulses of the three *G. petersii* used for training were all biphasic with a duration between 390 and 410 µs. The peak power spectral frequencies of the EODs of the three fish were 5.02±0.18, 4.91±0.15, and 4.88±0.15 kHz (mean±SD; $n$>10). Because of this high similarity between the pulses of all fish used for training, the stimulus parameters in the presence of different objects were also very similar in all fish. Thus, the same objects could be used to cause the same amount of waveform distortions and amplitude changes of the local EOD in all fish. At the end of the whole series of experiments the EODs of all fish were measured again. These measurements showed that no considerable change of EOD parameters had occurred during the course of the experiment as has recently been described for mormyrids in captivity (Landsman 1993).

For a given fish, the local EODs recorded close to the skin without any object present were very similar in waveform and other pulse parameters to the EODs recorded instead with head-to-tail electrodes (see also von der Emde 1990). In the presence of a purely resistive or purely capacitive object, the local EODs of a discharging *G. petersii* changed in the same way as already reported (von der Emde 1990). Figure 2 summarizes these results by showing the EOD waveform distortion (measured as P/N amplitude ratio) as a function of EOD amplitude for some of the objects tested. Thus, Fig. 2 shows the two dimensional *physical stimulus space* with the orthogonal grid of the stimuli.

Purely resistive objects only affected the local EOD amplitude but left the EOD waveform unchanged. The P/N amplitude ratios were always about 0.52, which is also the case when no object is present. Highly resistive objects caused the local EOD amplitudes to decrease, while objects with a low resistance increased it (Fig. 2).

Capacitive objects, on the other hand, affected both the amplitude and the waveform of the local EOD (Fig. 2). The amplitude increased with increasing capacitive values up to about 100 nF. Larger capacitors did not increase the amplitude any further. P/N amplitude ratios were smallest at a capacitance of about 1 nF. Such a low P/N-amplitude ratio of only 0.39 corresponds to the strongest waveform distortions observed. Smaller as well as larger capacitances caused smaller waveform distortions, indicated by higher P/N values. Waveform distortions were not observed for capacitive values smaller than 0.25 nF or greater than 100 nF.

Objects with both a resistive and a capacitive component caused intermediate waveform distortions and amplitude effects (Fig. 2). By trying different combinations of resistive and capacitive values, 30 dipole-objects were chosen that caused desired changes of the EOD. Twenty of these objects belonged to 4 series of objects used in the experiments described below, the others were used only for the metric experiments and are not shown in Fig. 2. In each series, one stimulus parameter was held constant, while the other one varied. The series are represented by the four lines in Fig. 2 running parallel either to the abscissa or the ordinate.

It is important to note that the measured EOD changes depend on the distance between the object and the fish. Waveform distortions and amplitude changes decrease as the distance between fish and object increases. Thus, the values given in Fig. 2 for waveform distortions and amplitude only apply for the particular distance chosen in the corresponding experiments. The relative difference between any two objects, however, was found to be independent of distance. For example, if two objects affected only one stimulus dimension differently at one distance, the same held true at any other distance. Objects situated on a straight line in Fig. 2 remained on a straight line at other distances as well. This is an important prerequisite for the application of the quantitative dissimilarity scaling experiments reported here.

For the analysis of the experiments, it was assumed that fish positioned themselves at an "optimal" distance towards the objects to evaluate their electric properties, because in the training experiment they were rewarded only if they detected object differences. An optimal distance is a distance where differences between the two objects were most pronounced and thus best detected by the fish. Fish could position themselves freely relative to the objects during the choice experiments. In similar training experiments with *G. petersii* (von der Emde 1992), it was observed that during object inspection fish usually maintained a constant distance of 1–2 cm from an electrolocation object. In this situation, they performed so called "probing motor acts", i.e., stereotyped swimming movements near objects (Toerring and Belbenoit 1979). Fish usually displayed this behavior at both objects before deciding for one of them.

Two objects were chosen as training stimuli (Fig. 2): the positive, rewarded stimulus (S+) was an object with a capacitive component of 0.95 nF and a resistive component of 60 k$\Omega$ (0.95 nF=60 k$\Omega$). This object caused strong waveform distortion (P/N ration=0.423) and a medium amplitude (190.5 mV). The unrewarded object (S–) was a purely resistive object of 15 k$\Omega$ (15 k$\Omega$) that caused the same EOD amplitude change as the S+ but no waveform distortion (P/N ratio=0.524).

## The influence of the local EOD amplitude on the choice behavior

In a first series of tests, the influence of the EOD amplitude change on the choice behavior of the fish was tested by using stimulus objects that caused the same amount of waveform distortions but different EOD amplitude changes (test series no. 2 in Fig. 2).

Figure 4A summarizes the results of these experiments. For each curve, one "standard" object (the amplitude values of which is indicated to the left of each line) was tested against all other members of test series no. 2. The choice index indicates the choice frequency for the object given on the abscissa tested against the standard object. An object tested against itself usually yielded a choice index of zero. If the object with the amplitude value given at the abscissa was preferred over the standard object the choice index was positive. It was negative, however, if the standard object was preferred.

Figure 4A shows that for each standard object there was a gradual change of preference if the amplitude of the alternative object was increased. Those test objects that caused an amplitude closer to the amplitude caused by the rewarded training stimulus (S+) were always preferred. The larger the amplitude difference between two objects the larger was this preference. This trend continued when the local EOD amplitude became smaller than that caused by the S+, which was the case when the standard objects were tested against the 175 mV object. Because this object differed from the S+, it was less often chosen than the S+. The animals obviously determined the absolute difference between each test object and the S+, independently of the "sign" of the difference. Thus,

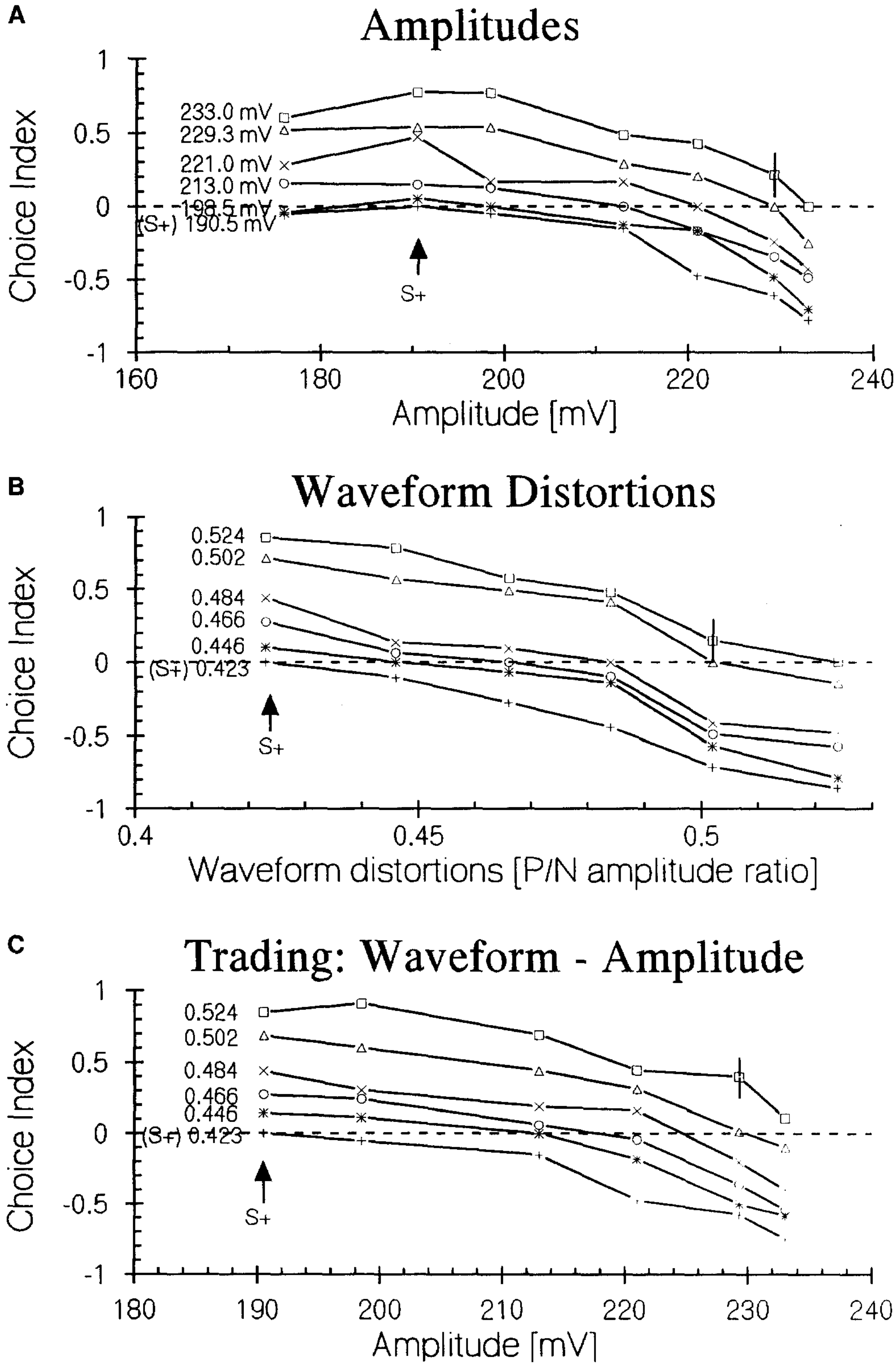


**Fig. 4A–C** Test results of the dissimilarity scaling experiments. Each point gives the global mean of three fishes, which is the mean of the means of three individual fishes. For each point, each fish made at least 50 decisions. The *vertical bars* in each diagram indicate the 95% confidence range of an arbitrary chosen point. The confidence ranges of the other points were of the same size. *Ordinate*: Choice index for the object given on the abscissa. Written to the left of each curve is the value of the amplitude (or the P/N amplitude ratio) of the "standard object" that was tested against the objects with the value given on the abscissa. A choice index of +1 is a 100% choice for the object on the abscissa, −1 means 100% choice of the standard object, and CI=0 means that both objects were chosen equally often. The straight crosses (+) always give the results using the rewarded training stimulus (S+) as standard object. **A** Responses of the fish to objects causing different EOD amplitudes but constant P/N ratios (test series no. 2 in Fig. 2), which were the same as those caused by the S+. **B** Responses to objects generating the same EOD amplitude changes but different waveform distortions (test series no. 1). This series also contains the S− (P/N ratio= 0.524). **C** Results of the trading experiments. Standard objects were members of test series 1, which were tested against members of test series 2, whose amplitude value is given on the abscissa. A choice index of 0 represents the equivalence point (see Fig. 6)

the curves of Fig. 4A reach a maximum at S+ and decline towards both sides.

In order to determine whether the amplitude effect of an object is perceived independently of the waveform distortions it generates, test series no. 4 was used. All stimuli of test series no. 4 caused the same waveform distortions (P/N amplitude ratio of 0.48), which differed from the constant waveform distortions of test series no. 2 (P/N ratio of 0.42) (Fig. 2). For each member of test series no. 4 a member of test series no. 2 existed that generated the same amplitude change of the local EOD. All members of test series no. 4 were tested with the (0.75 nF=30 kΩ) object. This object generates the same amplitude effect as the S+ but at a different level of

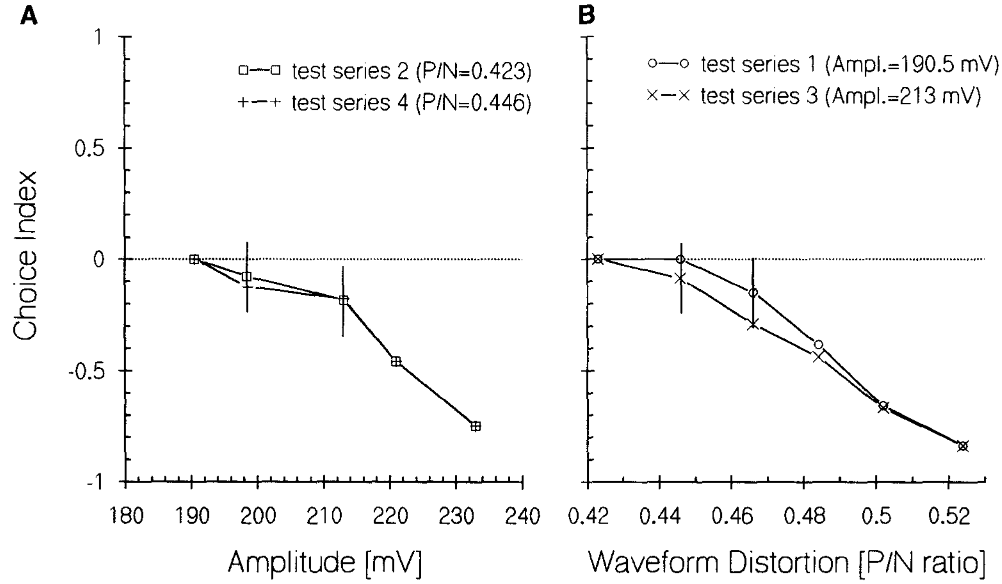


**Fig. 5A,B** Results showing the independence of the two stimulus dimensions local EOD amplitude and waveform distortion. The data represent the mean of two fishes and at least 100 decisions per data point. In each diagram, one example of the 95% confidence range of a point is indicated by the vertical bar. **A** Test for independence of the amplitude dimension. *Squares* give results with the S+ being the standard object, which was tested against all other members of test series no. 2. *Crosses* show results of test series no. 4 with the (0.75 nF=30 kΩ) object being the standard object, which was tested against all other members of test series no. 3. **B** Test of independence of the waveform dimension. *Circles* depict results of tests with the S+ being the standard object tested against all members of test series no. 1, like in Fig. 4B. *Crosses* give results for the corresponding test series no. 3 with the (2 nF=35 kΩ) object being the standard object

waveform distortions. The results of these experiments are shown in Fig. 5A together with the "S+ curve" of Fig. 4A. The results are virtually identical. This indicates that relative distance in the perceptual space continued to correspond to relative distance in physical space in spite of a shift in waveform distortions, which in turn suggests that differences in stimulus amplitude were perceived independently of the amount of waveform distortions.

## The influence of EOD waveform distortions on the choice behavior

The influence of the EOD waveform distortions on the choice behavior of the fish was tested in a second series of tests. In these tests, the objects of series no. 1 (Fig. 2), which all caused the same local EOD amplitude change but different EOD waveform distortions, were used as test stimuli. The EOD amplitude effect was maintained constant and was the same as that caused by the rewarded stimulus (S+), which allowed us to test the influence of waveform distortions of the local EOD on the choice behavior of the fish.

In Fig. 4B, each curve represents the results of tests of a standard object (the P/N amplitude ratio of which is written to the left of the line) against all other members of test series no. 1. As was the case with varying EOD amplitudes (see Fig. 4A), the choice behavior of the fish changed gradually with varying waveform distortions. The CI increased with increasing difference in P/N amplitude ratio.

As with amplitude, it was again tested whether waveform distortion differences are perceived independently of the other stimulus dimension, i.e. the amplitude effect. For this purpose, stimulus series no. 3 was used (open triangles in Fig. 2). Each member of this series had a corresponding member in test series no. 1 that caused the same amount of waveform distortions. As in test series no. 1, the amplitude effect was maintained constant throughout this series, however at a different level of waveform distortion. Stimuli of test series no. 3 were tested with the (2 nF=35 kΩ) object, which generated the same P/N-ratio as the S+ but a higher amplitude change. Figure 5B shows the results and compares them with the values for the "S+ curve" from Fig. 4B. Again, both curves are similar, thus indicating that the two stimulus dimensions were rated independently.

## Trading of waveform distortions with EOD amplitude

By using trading experiments it is possible to compare perceptual distances across perceptual parameters (cf. Stevens 1959). In our trading experiments, the fish had to choose between objects causing constant local EOD amplitudes (test series no. 1) and objects generating constant P/N amplitude ratios (test series no. 2). The standard objects were objects of test series no. 1 (constant amplitude effect), whose P/N-values are written to the left of each curve in Fig. 4C.

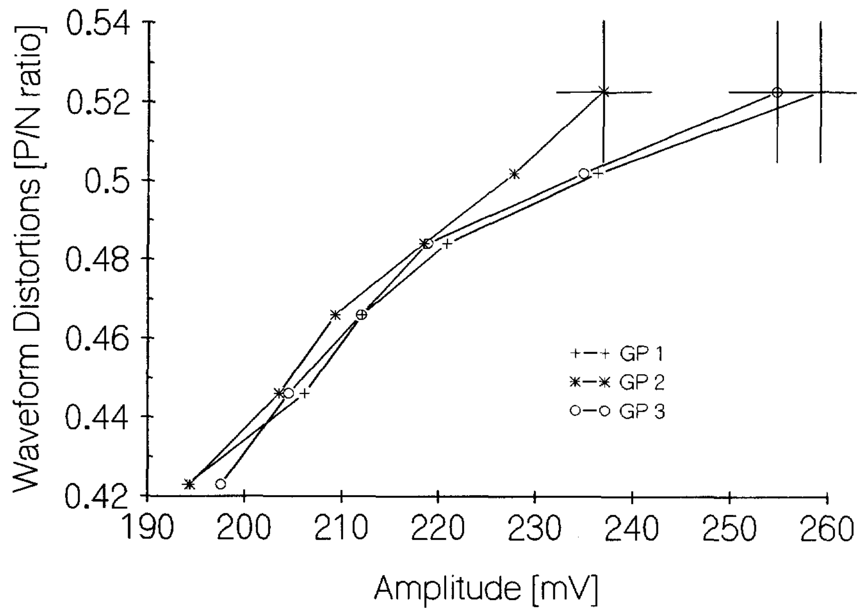


**Fig. 6** Equivalence curves of three fish for the two dimensions local EOD amplitude and waveform distortion (P/N amplitude ratio). *Points* are zero crossings of trading curves of individual fish similar to those shown in Fig. 4C. The *abscissa* gives the corresponding amplitude value of the object of test series no. 2, while on the *ordinate* the waveform value of the object of test series no. 1 is given. Each point indicates that the two objects of the trading experiments were chosen equally often (CI=0) and gives therefore the P/N-ratio and amplitude values of equal perceptual distance to the S+. The *vertical* and *horizontal* bars indicate the 95% confidence range for a typical point of each fish

As in the previous experiments, the animals gradually judged the similarities between the test objects (Fig. 4C). Note, however, that in these tests neither of the two objects had the same properties as S+. Nonetheless, it was possible to find for each object of test series no. 1 (e.g. the 0.65 nF=20 kΩ object that differed only in waveform from the S+ and caused a P/N ratio of 0.502) another object of test series no. 2 (in this example, the 3 nF=30 kΩ object that differed only in its higher amplitude effect of 229.3 mV from S+), so that in pairwise comparison these two objects were chosen equally often (CI=0). The amplitude values and the P/N-values that were chosen equally often are plotted in Fig. 6 for three fish. Because the earlier experiments had proven that the animals can clearly discriminate these objects (Fig. 4A,B) this 50:50 choice must be interpreted as indicating two perceptually equivalent objects. In other words, the two objects, differing in two different parameters, were perceived to be equally dissimilar from S+ and were therefore chosen equally often.

## Determination of the best Minkowski metric

Minkowski metrics are only applicable if some prerequisites are met. Beals et al. (1968) and Tversky and Krantz (1970) established two main criteria which have to be met if Minkowski metrics are to be applied. The first is "intradimensional subtractivity", i.e. the requirement that distances along a perceptual parameter can be combined additively. This was verified in these experiments by the results shown in Fig. 4A,B and by direct testing of many triplets of three stimuli that varied only in one dimension (located on a straight line in the physical stimulus space of Fig. 2). It turned out that the dissimilarity between the two stimuli being furthest apart was the sum of the two dissimilarities between the stimuli in the middle and the other two stimuli. Thus, the requirement of intradimensional subtractivity was fulfilled.

The second important condition for the applicability of Minkowski metrics is the independence of perceptual dimensions ("interdimensional additivity"). This was tested for the two dimensions waveform and amplitude of the electrolocation stimuli. In both cases the perception of differences in one dimension proved to be independent of the value of the other dimension (Fig. 5A,B). Apparently, the data fulfill the second criterion and the application of Minkowski metrics is possible.

Figure 7A and B shows two evaluations of possible metrics, the Euclidean metric and the City-Block metric, for the same data set. In each case, the measured value of c (Fig. 3) was plotted against the expected value of c calculated according to Eq. 2 (see Methods), with an $r$-value of 2 for the Euclidean metric and $r$=1 for the City-Block metric.

Figure 7A,B shows that the solid regression line for all fishes matches the dotted bisectrix quite well in the case of the City-Block metric while in the Euclidean metric the measured c values are almost always too large compared with the expected values. When comparing the data for individual fish, there again is a better match for the City-Block metric. It follows that the data fit the City-Block metric much better than the Euclidean metric.

This result is confirmed by the determination of the 'best' exponent $r$ using Eq. 3 (see Fig. 8). The minimum SQ-value is found at $r$=0.98 (arrow in Fig. 8), which corresponds closely to the exponent $r$=1 of the City-Block metric.

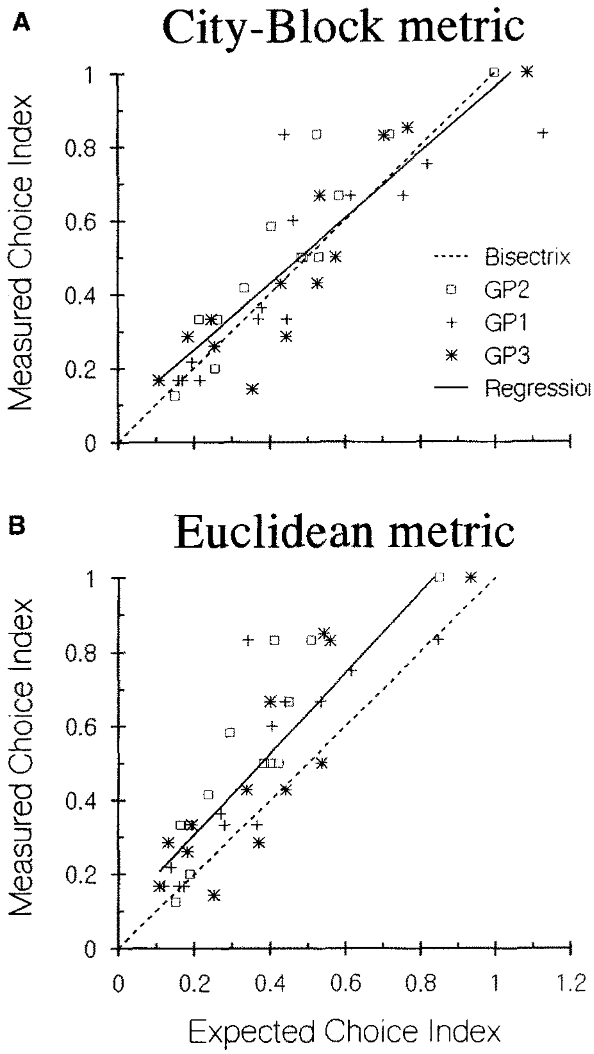


**Fig. 7** Evaluation of two-dimensional differences according to the City-Block metric (**A**) and the Euclidean metric (**B**). Data of three fish (each fish shown with a different symbol), based on at least 50 decisions per point. *Abscissa*: expected values for complex distances determined according to formula (2) with $r$=1, for the City Block metric, and $r$=2 for the Euclidean metric from the choice index data. Ordinate: measured complex perceptual difference c. *Dashed lines*: bisectrix; *solid lines*: regression lines (regression coefficients in **A** 0.88, in **B** 0.86). The regression line in **A** corresponds much better to the bisectrix than that in **B**, i.e. the fit of measured and expected data is better for the City-Block metric

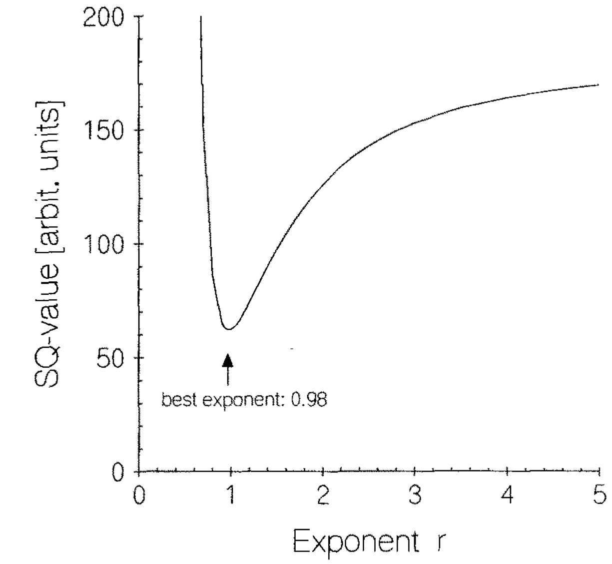


**Fig. 8** Determination of the best Minkowski metric by means of the SQ-function (Eq. 3). The SQ values are arbitrary units to avoid artifacts during the calculation process. The lowest SQ-values are found at a $r$=0.98, which corresponds very closely to the $r$-value of 1 used in the City-Block metric

## Discussion

The results of this study demonstrate that the weakly electric fish *G. petersii* attends to, and also assesses quantitatively the two physical stimulus dimensions local EOD amplitude and waveform distortion during electrolocation. Other object dimensions, such as size or shape, could not be used in our experiments, because they remained constant throughout the experiment. When stimuli varying only in one dimension were used, the fish judged differences between them in a quantitative way. Objects that were physically more similar yielded smaller choice indices compared to physically more distant objects. This means that they were also perceived to be more similar, because choice frequencies were used in our experiment as indicators for dissimilarities.

Interestingly, both the amplitude and waveform dimensions were rated in the above mentioned fashion. Apparently, both dimension were important to the fish and thus were both evaluated during the electrolocation experiments. This inference is confirmed by our trading experiments. If differences in waveform distortions of a certain amount were offered alternatively to amplitude differences, the fish decided according to the subjectively smaller difference to the previously rewarded training stimulus (S+). Differences in one dimension could "trade off" differences in the other dimension. This was exactly the case at the points shown in the equivalence curves of Fig. 6, where the fish rated the two stimuli as being equally different from S+, although they differed in another dimension. Again, differences were measured quantitatively, i.e., a greater amplitude difference required a greater waveform difference to result in equal choice frequencies.

The impression given from the trading experiments is that both stimulus dimensions were weighted about equally (Fig. 6). As Fig. 2 shows, the stimuli used cover a large percentage of the possible values in both dimensions. About 75% of the maximum waveform distortion that can be induced by dipole objects and approximately 50% of all possible amplitude values were generated. The equivalence curves show that neither amplitude nor waveform changes dominated clearly over the other, which would be the case if relatively small changes in one dimension were perceived as being equal to large changes in the other dimension.

An important prerequisite for the construction of a certain perceptual space has been introduced by Dunn

(1983), namely the requirement of "correspondence". Correspondence is given, if a set of stimuli that vary in two physical dimensions is also perceived to vary in a corresponding pair of psychological dimensions. In our experiments, correspondence is confirmed by the trading experiments and also by the fulfillment of interdimensional additivity (see Results).

In the experiments reported here, fish were trained to discriminate stimuli varying only in waveform distortions and not in amplitude. Nevertheless, in the test experiments they also judged differences in stimulus amplitude, even in the absence of any waveform differences. During training the fish obviously had learned all parameters of the object including those that were not different in S+ and S–. It would be interesting to investigate whether similar influence of training as found in other systems, e.g. bees (Ronacher 1979a, 1992b), can also be found with electrolocating weakly electric fish.

The evaluation of waveform distortions is important for the discrimination between capacitive objects, which are mainly animate objects, and resistive, i.e. nonliving objects. The latter only affect the amplitude of the perceived electrolocation signals, whereas the former also distort their waveforms (Fig. 2). The detection and quantitative evaluation of capacitive objects is thus possible by paying attention to the waveform distortions. In analogy to vision, waveform distortions add some "color" to the otherwise black and white electrolocation picture. Different shades of "electric color" are perceived by detecting differences in the amount of waveform distortions. Thus, signal waveform obviously carries some important information about the environment of the fish. This importance is reflected by the elaborate analyzing mechanisms *G. petersii* has developed to determine even small differences in the shape of the waveform and the amplitude of their signal (Bell 1990; von der Emde and Bell 1994; von der Emde and Bleckmann 1992). The experiments reported here show that electric fish indeed employ of these mechanisms to form a quantitative, psychological representation of different stimulus features.

The electric sense shows similarities to other senses such as vision or audition, because a quantitative representation of different stimulus parameters is formed by the fish during electrolocation. Therefore it is conceivable that also during electrolocation similar rules may apply concerning the quantitative judgement of dissimilarities between stimuli, i.e. the "laws" of generalization (Shepard 1987) may also govern electric fish.

The determination of the best Minkowski metric revealed that distances in the perceptual space of electrolocation stimuli were best described by a City-Block metric (Figs. 7, 8). Garner (1974) proposed that a City-Block metric applies for so called analyzable stimuli (see also Burns et al. 1978; Dunn 1983; Treisman 1986). These are stimuli that are easily separated into their perceptual dimensions. They are not perceived holistically like stimuli of integral dimensions for which an Euclidean metric produces a better fit.

City-Block metrics were found in several experiments involving both animals and humans. In humans and bees, for example, size and brightness in vision are separable dimensions for which a City-Block metric applies (Garner 1977; Ronacher 1979b; however see Ronacher and Bautz 1985). In bees, also color vision can best be described by this metric (Backhaus et al. 1987). This was surprising, since in humans, multidimensional scaling procedures with different colors always yield a Euclidean metric (Garner 1974; Handel and Imai 1972). In other experiments as well, the perceptual system of bees could be described according to a City-Block metric and this has led Ronacher (1992a) to speculate that the City-Block metric could be generally valid for the bees‘ perceptual system.

Here we report another example for the applicability of the City-Block metric. Electrolocation stimuli proved to be *analyzable* for weakly electric fish and the overall dissimilarity is derived *additively* from the component differences.

The applicability of the City-Block metric is not too surprising, if one suspects that the two dimensions of electrolocation signals, waveform and amplitude, correspond to two uniquely defined independent variables in the world. According to Shepard's (1987) reasoning about generalization contours, this metric can be expected for such stimuli, whereas the Euclidean metric is assumed to be valid for stimuli with dimensions that are not uniquely defined in the world. Thus, our metric experiments again point to the importance and uniqueness of the waveform and the amplitude dimensions during electrolocation. Waveform stands for animate versus inanimate, a dimension which is certainly useful for a fish to attend to.

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## References

Backhaus W, Menzel R, Kreißl S (1987) Multidimensional scaling of color similarities in bees. Biol Cybern 56: 293–304

Beals R, Krantz DH, Tversky A (1968) Foundations od multidimensional scaling. Psychol Rev 75: 127–142

Bell CC (1990) Mormyromast electroreceptor organs and their afferent fibers in Mormyrid fish. III. Physiological differences between two morphological types of fibers. J Neurophysiol 63: 319–33

Bergland DG, Doland MT (1979) Fast Fourier Transform Algorithms. In: Digital Signal Processing Committee IEEE Acoustics, Speech and Signal Processing Society (ed) Programs for digital signal processing. IEEE Press, New York, pp 1.2-1–1.2-18

Burns B, Shepp BE, McDonough D, Wiener-Ehrlich WK (1978) The relation between stimulus analyzability and perceived dimensional structure. In: Bower G (ed) The psychology of learning and motivation, vol 12. Academic Press, New York, pp 77–115

Dunn JC (1983) Spatial metrics of integral and separable dimensions. J Exp Psychol (Hum Perc) 9: 242–257

Garner WR (1974) The processing of information and structure. Wiley, London

Garner WR (1977) The effect of absolute size on the separability of the dimensions of size and brightness. Bull Psychol Soc 9: 380–382

Gellerman LW (1933) Chance orders of alternating stimuli in visual discrimination experiments. J Genet Psychol 42: 206–208

Handel S, Imai S (1972) The free classification of analyzable and unanalyzable stimuli. Percept Psychophys 12: 108–116

Heiligenberg W (1977) Principles of electrolocation and jamming avoidance in electric fish. In: Braitenberg V (ed) Studies of brain function, vol 1. Springer, Berlin Heidelberg New York, pp 1–85

Hering E (1875) Zur Lehre vom Lichtsinne. 6. Mittheilung: Grundzüge der Theorie des Farbensinnes. Sitzungsber Kaiserl Akad Wissenschaften in Wien. Mathem-Naturw Classe, Abth III, Bd 70: 169–204

Landsman RE (1993) The effect of captivity on the electric organ discharge and plasma hormone levels in *Gnathonemus petersii* (Mormyriformes). J Comp Physiol A 172: 619–631

Lissmann HW, Machin KE (1958) The mechanism of object location in *Gymnarchus niloticus* and similar fish. J Exp Biol 35: 451–486

Ronacher B (1979a) Äquivalenz zwischen Größen und Helligkeits-Unterschieden im Rahmen der visuellen Wahrnehmung der Honigbiene. Biol Cybern 32:63–75

Ronacher B (1979b) Beitrag einzelner Parameter zum wahrnehmungsgemäßen Unterschied von zusammengesetzten Reizen bei der Honigbiene. Biol Cybern 32: 63–75

Ronacher B (1992a) Pattern recognition in honeybees: multidimensional scaling reveals a City-Block metric. Vision Res 32: 1847–1843

Ronacher B (1992b) Influence of unrewarded stimuli on the classification of visual patterns by honey bees. Ethology 92: 205–216

Ronacher B, Bautz W (1985) Human pattern recognition: Individually different strategies in analyzing complex stimuli. Biol Cybern 46: 173–182

Shepard RN (1964) Attention and the metric structure of the stimulus space. J Math Psychol 1: 54–87

Shepard RN (1980) Multidimensional scaling, tree fitting, and clustering. Science 210: 390–398

Shepard RN (1987) Towards a universal law of generalization for psychological science. Science 237: 1317–1323

Stevens SS (1957) On the psychophysical law. Psychol Rev 64: 153–181

Stevens SS (1959) Cross-modality validation of subjective scales for loudness, vibration, and electric shock. J Exp Psychol 57:201–209

Toerring MJ, Belbenoit P (1979) Motor programs and electroreception in mormyrid fish. Behav Ecol Sociobiol 4: 369–379

Torgerson WS (1958) Theory and methods of scaling. Wiley, New York

Treisman A (1986) Properties, parts and objects. In: Boff K, Kaufmann L, Thomas J (eds) Handbook of perception and human performance. Wiley, London, pp 1–71

Tversky A, Krantz DH (1970) The dimensional representation and the metric structure of similarity data. J Math Psychol 7: 572–596

von der Emde G (1990) Discrimination of objects through electrolocation in the weakly electric fish, *Gnathonemus petersii.* J Comp Physiol A 167: 413–421

von der Emde G (1992) Electrolocation of capacitive objects in four species of pulse-type weakly electric fish. II. Electric signalling behaviour. Ethology 92: 177–192

von der Emde G (1993a) The sensing of electrical capacitances by weakly electric mormyrid fish: Effect of water conductivity. J Exp Biol 181: 157–173

von der Emde G (1993b) Capacitance discrimination in electrolocating, weakly electric pulse fish. Naturwissenschaften 80: 231–233

von der Emde G, Bell CC (1994) Responses of cells in the mormyrid electrosensory lobe to EODs with distorted waveforms: implications for capacitance detection. J Comp Physiol A 175: 83–93

von der Emde G, Bleckmann H (1992) Differential responses of two types of afferents to signal distortions may permit capacitance measurement in weakly electric fish, *Gnathonemus petersii.* J Comp Physiol A 171: 683–694