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Figure–ground separation during active electrolocation in the weakly electric fish, *Gnathonemus petersii*

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ABSTRACT

The weakly electric fish *Gnathonemus petersii* uses active electrolocation to detect and discriminate between objects in its environment. Objects are recognised by analysing the electric images, which they project onto the fish's skin. In this study, we determined whether different types of large backgrounds interfere with the fishes' ability to discriminate between objects. Fish were trained in a food-rewarded two-alternative forced-choice procedure to discriminate between two objects. In subsequent tests, structured and non-structured as well as stationary and moving backgrounds were positioned behind the objects and discrimination performance between objects was measured at different object distances. To define the electrosensory stimuli during the tests, the electric images of the objects and backgrounds used were measured. Without a background *G. petersii* was able to discriminate between objects up to distances of about 3–4 cm. Even though the electric images of background and object superimposed in a complex way, the addition of stationary structured or plain backgrounds had only minor effects on the range of object discrimination. However, two types of moving backgrounds improved electrolocation by extending the range of object discrimination up to a distance of almost 5 cm. This suggests that movements in the environment plays an important role for object identification and improves figure–ground separation during active electrolocation.

1. Introduction

Sensory perception plays an important role for all animals to gather information about their surroundings, for example to find food, to identify conspecifics and predators, and to discriminate between objects used as landmarks during orientation. Nocturnally active weakly electric fish from Africa and South America employ a strategy called active electrolocation for these tasks (Lissmann and Machin, 1958; Bastian, 1986; von der Emde et al., 2008; Pereira and Caputi, 2010). The African weakly electric fish *Gnathonemus petersii* has an electric organ in its tail with which it emits brief electric current pulses called electric organ discharges (EODs) (Lissmann, 1951). During each EOD, a three-dimensional electric field builds up around the fish which the sender fish perceives through an array of epidermal electroreceptor organs distributed over almost its entire skin surface. Nearby objects are detected and analysed because they distort the electric field and thus alter the electric current flow at those electroreceptor organs located at skin regions opposite the object. The changed pattern of electrical input at a certain skin area is called the 'electric image' of the object (Rasnow, 1996; Caputi et al., 1998; Budelli and Caputi, 2000; Rother et al., 2003; Babineau, 2006; Pusch et al., 2008).

By analysing the electric images, weakly electric fish not only can detect nearby objects but they also can analyse their electrical and spatial properties (Lissmann and Machin, 1958). The mormyrid *G. petersii* has been intensely used to investigate object discrimination during active electrolocation. These fish can discriminate between objects of different materials and can perceive the complex electrical impedance of an object quantitatively (von der Emde, 1990, 1993, 1998). They can also discriminate between objects based on their shapes or sizes (von der Emde et al., 2010), and they can measure the distance of an object from the fish (von der Emde et al., 1998; Schwarz and von der Emde, 2001; Lewis and Maler, 2002). Shape recognition persists even when the objects are rotated in space, indicating a viewpoint-independent recognition of objects (von der Emde et al., 2008). *G. petersii* also demonstrates size constancy during object recognition, i.e. they can recognise an object of a certain shape or size even if its electric image appears larger or smaller because of variations in the object's distance (von der Emde et al., 2010).

Active electrolocation allows weakly electric fish to perceive a detailed electrical picture of their surroundings even in complete darkness. However, in the natural habitat of *G. petersii*, freshwater rivers and streams in tropical Africa, the environment is much

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more complex than what has been used in behavioural laboratory experiments in the past. On the ground of the river, objects are scattered in a complex way with small objects often being next to or in front of large objects or surrounded by moving or stationary water plants. The detection and identification of a small object in front of a large, more or less cluttered background is much more difficult than the recognition of a single, free standing object (Babineau et al., 2007; Aguilera et al., in press). The problem of recognising the shape of a figure and to separate it from the background is difficult to solve for most sensory systems. In vision, for example, various strategies are used involving edge assignment, colour and contrast differences, relative object motion, distance differences and several more (e.g. in Fahle, 1993; Tang and von der Malsburg, 2008; Browning et al., 2009; Fang and Grossberg, 2009; Grossberg et al., 2011).

During active electrolocation figure–ground separation is even more difficult than during vision, because the electric images of two nearby objects will fuse in a nonlinear manner leading to a single, complex image (Caputi and Budelli, 2006; Engelmann et al., 2008; Caputi et al., 2011). If two objects are located in the electric field of an electrolocating fish, they will polarise each other and thus mutually change their electric images on the fish's skin even if they do not touch each other (Aguilera et al., in press; Caputi et al., 2011). It can be expected that a large background behind a small object has an especial strong effect on the electric image of the small object, probably making it more difficult for the fish to recognise the small object's shape especially at larger distances. In spite of this, *G. petersii* has been shown to be able to discriminate between objects even when they were positioned right in front of a large background (Folde, 2006; von der Emde et al., 2010). However, until now it was not tested whether fish can still do so at longer distances. Furthermore, cluttered or moving backgrounds might provide even more challenges for object recognition (Babineau et al., 2007).

The aim of this study was to test up to what distance *G. petersii* can still discriminate between objects when they are placed in front of large backgrounds of different materials. We used structured and non-structured backgrounds, which were either stationary or moving. We aimed at testing the following hypotheses: (1) Addition of a background will decrease the distance up to which *G. petersii* can discriminate between objects. (2) Metallic backgrounds will deteriorate the discrimination between metallic objects, while they should be more easily discriminated in front of plastic backgrounds because of increased contrast. (3) Structured backgrounds degrade object recognition compared to homogeneous backgrounds. (4) Moving backgrounds will impair figure–ground separation especially at larger distances because of increased background noise, which might aggravate the recognition of weak object-caused electric signals.

2. Materials and methods

2.1. Animals

All experiments were done with six individuals of the weakly electric fish *G. petersii* (standard length: 12–15 cm). Two animals were used in the training experiments and four for the measurement of electric images. All animals were kept in individual tanks (75 × 42 × 40 cm). The water temperature was 26 ± 1 °C, water conductivity was 100 ± 5 μS/cm, and the light–dark cycle was set to 12:12 h. Fishes were fed with frozen mosquito larvae (*Chironomidae*). Animals were housed in registered facilities conforming to German, European and international regulations concerning animal care (European Directive 86/609/EEC and the Treaty of Amsterdam Protocol on Animal Welfare 1997).

2.2. Experimental setup for training experiments

The setup was nearly the same as described in von der Emde et al. (2010). Fish were kept singly in tanks (75 × 42 × 40 cm), which were also used for the training and testing. A plastic mesh partition, which contained two gates (9 × 10 cm) that could be opened and closed by the experimenter, divided each tank into a living area (35 × 40 cm) and an experimental area (40 × 40 cm). During training, behind each of the two gates an object was placed on a platform in such a way that the fish had to pass it to access the experimental area. On the ground of the experimental area, a cm-scale was placed to position the objects at a defined distance from the gates. When the object distance was increased in the test trails, the fish had to inspect the objects from the gate. In order to restrict the minimal distance between the fish and the object, a widely perforated plastic mesh grid (10 × 13 cm) was placed in front of the object 0.5 cm behind the respective gate in the experimental area. Object distance was taken as the distance of the object from the grid. The grids prevented the fish from approaching the objects before making a decision. In addition, the grids had the function to prevent the fish from touching the objects at close distances.

2.3. Training procedure

First, the animals learned to swim through the open gates by passing the grids and to get food in the experimental area of the tank. When the fish were accustomed to the general set-up, a food rewarded two-alternative forced-choice (2AFC) training started. Before each trial, the experimenter placed both objects on the platforms behind the gates. Fish learned to pass through that gate, behind which a rewarded object (S+) was positioned, and to avoid the alternative gate with a non-reinforced negative object (S−). The position of the objects behind the left or the right gate was chosen randomly (Gellermann, 1933). The choice for the correct gate with the positive stimulus (S+) was rewarded by a few mosquito larvae (*Chironomidae*). A decision for the wrong object (S−) was punished by chasing the fish back to the living area immediately. After eating the food reward, the fish had to swim back through one of the gates into the living area, the gates closed and a new trial started with repositioning the objects. Even if the positions of the objects were identical in the next trial, objects were always replaced to avoid giving hints about the new position of the S+. On average, 30 trials per day, 5 days a week, were conducted for each fish. The learning criterion was reached when the fish performed with 70% correct choices during three consecutive days.

2.3.1. Object discrimination

Fish 1 was trained to discriminate between a small (2 × 2 × 2 cm) and a large (3 × 3 × 3 cm) metal cube. During training, the small cube (S+) and the large cube (S−) were presented 1 cm behind the gates.

Fish 2 had to learn to discriminate between two metal objects of different shapes and sizes. The positive stimulus (S+) was a pyramid (base area: 3 × 3 cm, height: 3 cm), while the S− was a cube (3 × 3 × 3 cm). Both objects were presented at a distance of 1 cm. In all cases objects were oriented with their sides placed parallel to the respective gate, i.e., the fish were facing the side of the cube or the pyramid. The tip of the pyramid was pointing upwards.

2.4. Testing procedures

When the fish had learned to discriminate between the S+ and the S− in more than 70% of the trials in at least three consecutive sessions, test trials were started. During testing, the discrimination performance of the fish was tested in new situations, either with the objects placed at different distances or in the presence of