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Original Research Paper

Object discrimination through active electrolocation: Shape recognition and the influence of electrical noise

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A B S T R A C T

The weakly electric fish *Gnathonemus petersii* can recognise objects using active electrolocation. Here, we tested two aspects of object recognition; first whether shape recognition might be influenced by movement of the fish, and second whether object discrimination is affected by the presence of electrical noise from conspecifics. (i) Unlike other object features, such as size or volume, no parameter within a single electrical image has been found that encodes object shape. We investigated whether shape recognition might be facilitated by movement-induced modulations (MIM) of the set of electrical images that are created as a fish swims past an object. Fish were trained to discriminate between pairs of objects that either created similar or dissimilar levels of MIM of the electrical images. As predicted, the fish were able to discriminate between objects up to a longer distance if there was a large difference in MIM between the objects than if there was a small difference. This supports an involvement of MIMs in shape recognition but the use of other cues cannot be excluded. (ii) Electrical noise might impair object recognition if the noise signals overlap with the EODs of an electrolocating fish. To avoid jamming, we predicted that fish might employ pulsing strategies to prevent overlaps. To investigate the influence of electrical noise on discrimination performance, two fish were tested either in the presence of a conspecific or of playback signals and the electric signals were recorded during the experiments. The fish were surprisingly immune to jamming by conspecifics: While the discrimination performance of one fish dropped to chance level when more than 22% of its EODs overlapped with the noise signals, the performance of the other fish was not impaired even when all its EODs overlapped. Neither of the fish changed their pulsing behaviour, suggesting that they did not use any kind of jamming avoidance strategy.

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1. Introduction

Weakly electric fish, *Gnathonemus petersii*, possess multiple senses, which can provide information about objects within the environment. Besides vision and the lateral line systems these fish can use active electrolocation to obtain object information. During active electrolocation the fish use object-evoked changes in a self-generated electric field (Lissmann and Machin, 1958) to detect and recognise objects (von der Emde et al., 2010). To achieve this, *G. petersii* emit brief weak electric pulses called electric organ discharges (EODs) at a highly variable rate (Carlson, 2002; Moller, 1980; von der Emde, 1992). Each EOD builds up an electric field around the fish, which is perceived locally by mormyromast electroreceptor organs. Nearby objects with different electrical properties than the surrounding water distort the electrical field leading to changes of the locally perceived EOD, forming an "electrical image" of the object on the fish's skin (Caputi et al., 1998; Rasnow, 1996).

Although the detection and recognition of objects through active electrolocation in *G. petersii* has been studied extensively, many open questions remain concerning the parameters that enable the recognition of objects. In this study we investigated two aspects of object recognition in *G. petersii*: (1.1.) whether the recognition of object shape is dependent upon the modulations of a series of self-induced electric images that are created as a fish swims past an object, and (1.2.) whether object recognition is influenced by electrical noise.

1.1. Recognition of object shape

While object properties such as object resistance, capacitance, size, volume, distance and location can be linked to certain combinations of parameters within the electric image (von der Emde,

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2006), so far no combination has been found that would allow object shape to be encoded. One possibility is that the fish might recognise shape by engaging in movements relative to the object. Inspecting an object from different angles will modulate the successive electrical images (Hofmann et al., 2013a,b) and the magnitude of these modulations will depend on the shape of the object. Electric images of objects depend on several parameters, in particular on the distance of the fish from the object and on the part of the fish (flank, head, etc.) that faces the object. Nevertheless a few general statements regarding the differences of electric images of spheres and cubes on the one hand and elongated objects (ellipsoid) can be made. For example, when perceived from a constant distance, the electric images of a sphere are constant for each angle of perspective, while the electric images of an elongated object, e.g. an ellipsoid, differ depending on whether it is perceived facing its longer or its shorter side. Therefore, the modulations in a series of electrical images that are induced by a fish swimming past an object might provide useful information that could be used to recognise object shape. We define the changes in the electrical images that occur as a fish swims past an object, as movement-induced modulations (MIM). Here we tested whether movement-induced modulation is used to encode object shape by comparing the performance of the fish when they had to discriminate between two objects (a cube and a sphere), which both evoked similar levels of MIMs, or between objects (an ellipsoid (presented with its longer side facing the observation gate) and a sphere), which produce very different MIMs. If the fish indeed use the difference in MIM for object shape discrimination, we would predict that it should be easier for them to discriminate between the sphere and the ellipsoid than to discriminate between the sphere and the cube. Accordingly, discrimination between the sphere and the ellipsoid should be possible up to a greater distance compared to discrimination between the sphere and the cube.

1.2. Influence of electrical noise on object recognition

In their natural environment, *G. petersii* are confronted with electrical noise during active electrolocation, e.g. arising from other nearby electric fish also emitting EODs. In contrast to gymnotiform pulse-type electric fish, mormyrid weakly electric fish can clearly separate their own EODs from those of other nearby fish as long as they do not overlap, by using their corollary discharge (Bell, 1989). However, when temporally overlapping with a foreign signal, the waveform and amplitude of the fish's own EOD can be changed. These noise related changes in the electric field could potentially mask or jam the object evoked changes and thus interfere with object recognition (Heiligenberg, 1974, 1976). While there are many investigations into the jamming avoidance response of South American wave-type electric fish (for example (Watanabe and Takeda, 1963), however, relatively little is known about how the African pulse-type Mormyridae cope with electrical noise (Heiligenberg, 1974, 1976; Moller and Bauer, 1973; Westby, 1981).

A possible mechanism for avoiding jamming in mormyrids could be the so-called echo response, during which one fish emits its EODs with a preferred short (usually 10–14 ms) latency after the EODs of another fish (Heiligenberg, 1976; Russell et al., 1974; Schuster, 2001). Pulsing with a latency of ca. 10–14 ms decreases the probability of overlaps, because the non-focal fish is unlikely to emit another EOD in this timeframe. The echo response is described in many different species of pulse-type electric fish, but in addition to being a possible jamming avoidance response, it is also described as an electrical communication behaviour (Arnegard and Carlson, 2005; Gebhardt et al., 2012; Heiligenberg, 1976; Lücker and Kramer, 1981; Russell et al., 1974). Here, we tested whether electrical noise, either from conspecifics or artificial electrical signals, influences the object discrimination performance of *G. petersii*. Furthermore, we recorded the electrical signals emitted during object discrimination to investigate whether the fish used any type of jamming avoidance response.

2. Material and methods

2.1. Animals and set up

During our experiments we used four experimental fish of the species *Gnathonemus petersii* (two for shape recognition (fish 1 and 2) and two for the influence of electrical noise (fish 3 and 4)). Two additional fish of the same species were used to serve as "jamming fish" (fish 5 and 6). The experimental fish were kept individually in tanks (75 cm × 40 cm × 40 cm), which also served as an experimental arena. The jamming fish were kept in separate housing tanks (75 cm × 40 cm × 40 cm) and were only put into the experimental tanks during the experiments. The water conditions in all tanks were kept constant with a temperature of 26 ± 1 °C, a pH-value of 7 ± 0.5 and a conductivity of 100 ± 10 μS/cm. The artificial dark:light-cycle was set to 12:12 h. All experiments except for the dark controls were conducted under ambient light level of ca. 65 lux (measured just above the water surface). Under these bright light conditions the ability of *G. petersii* to discriminate between objects visually deteriorates (Schuster and Amtsfeld, 2002).

The experimental tanks were divided into two compartments (40 cm × 40 cm, 35 cm × 40 cm) with a partition containing two gates (Fig. 1). The smaller compartment was used as the living area of the fish and contained hiding places, while the bigger compartment served as experimental area, which was again divided into two sections with a divider. During training, an object was placed 1 cm behind each gate. In order to ensure that the fish kept this minimal distance to the object, distance grids, made of a plastic frame stringed with thin cotton threads (mesh size 15 mm diagonal), were placed directly behind the gates (between gate and object). These grids allowed unimpaired electrolocation but in order to pass them, the fish had to push them aside.

The fish were trained individually in a two-alternative forced-choice procedure (2AFC) to swim through the gate with the positive object behind (associated with a food reward) and to avoid the gate with the negative object behind (associated with a mild punishment of being chased back into the living area). The position of the positive object was changed pseudo-randomly after Gellermann (1933). Each fish conducted 20–40 trials per training day.

2.2. Training groups

The fish were divided into two different training groups. Although all fish underwent the same principal training procedure described above, the different groups were trained with different objects and under different conditions.

2.2.1. Recognition of object shape

Two naive fish were trained to discriminate between two aluminium objects, which only differed in shape. In the first training phase, fish 1 was trained to discriminate between a sphere (Ø 3 cm, S+) and a cube (side length 2.42 cm, S−, presented with its side directly facing the door) and fish 2 was trained to discriminate between the sphere and an ellipsoid (length: 4.78 cm, Ø: 2.39 cm, S−, presented with its longer side facing the door) (Fig. 1). After the fish reached a pre-assigned learning criterion of 75% correct choices on three consecutive training days, test trials were introduced every third trial, during which the distance of the object to

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