PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 2000 **355**, 1143-1146
doi: 10.1098/rstb.2000.0655

THE ROYAL SOCIETY

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Three-dimensional analysis of object properties during active electrolocation in mormyrid weakly electric fishes (*Gnathonemus petersii*)

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Weakly electric fishes are nocturnal and orientate in the absence of vision by using their electrical sense. This enables them not only to navigate but also to perceive and recognize objects in complete darkness. They create an electric field around their bodies by producing electric signals with specialized electric organs. Objects within this field alter the electric current at electroreceptor organs, which are distributed over almost the entire body surface. During active electrolocation, fishes detect, localize and analyse objects by monitoring their self-produced electric signals. We investigated the ability of the mormyrid *Gnathonemus petersii* to perceive objects three-dimensionally in space. Within a range of about 12 cm, *G. petersii* can perceive the distance of objects. Depth perception is independent of object size, shape and material. The mechanism for distance determination through electrolocation involves calculating the ratio between two parameters (maximal slope and maximal amplitude) of the electrical image which each object projects onto the fish's skin. During active electrolocation, electric fishes cannot only locate objects in space but in addition can determine the three-dimensional shape of an object. Up to certain limits, objects are spontaneously categorized according to their shapes, but not according to their sizes or the materials of which they are made.

Keywords: electrical sense; depth perception; object shape; sensory analysis; orientation

1. ACTIVE ELECTROLOCATION AND ELECTRICAL IMAGES

Certain freshwater fishes in Africa and South America regularly produce weak electric signals using specialized electric organs. It was shown in behavioural training experiments that these weakly electric fishes use their electric organ discharges (EODs) for detecting objects with electrical properties different from those of the surrounding water (Bullock & Heiligenberg 1986; Lissmann & Machin 1958). Such objects cause distortions in the three-dimensional (3D) electric field, which is generated around the fish during each EOD. As a result, the current flow through epidermal electroreceptor organs is altered compared with the current flow in the absence of an object. Each object projects an 'electrical image' onto the skin surface, which consists of a skin area where the EOD-evoked current density has changed (Assad *et al.* 1999; Caputi *et al.* 1998; Rasnow 1996). The electrical image is defined as the difference in the spatial pattern of electric current flow evoked by an object compared with the situation without an object present, and depends on the object's electrical properties, its size, shape and distance. The electroreceptor cells in each electroreceptor organ respond to the voltage drop across the skin and thus collectively report the properties of the electrical image to the brain via afferent fibres. This process, during which the fish detects objects by the distortions that they cause in its own EODs, is called active electrolocation (Bastian 1989; Lissmann & Machin 1958; Von der Emde 1998).

Electric fishes orientate in complete darkness by monitoring the electrical images of nearby objects. Different image parameters provide different types of information about an object. The location of the image on the skin tells the fish where the object is located, relative to its own body coordinates. For example, when only receptors on the fish's left trunk are influenced by an object, the fish knows that the object must be located at its left side. The sign and amount of amplitude change reported by the electroreceptors to the brain inform the animal about the object's impedance, i.e. whether object impedance is low or high compared with the water resistance. EOD phase shifts and/or EOD waveform distortions convey information about capacitive object properties, which in turn inform the fish whether an object is composed of living or inanimate matter (Von der Emde 1990). Other object properties, such as object size or shape, the exact value of its impedance, and the object's distance must be computed through a process of calculations involving several image parameters. Here we report that these object properties can unequivocally be determined by electrolocating fishes by analysing certain electrical image parameters.

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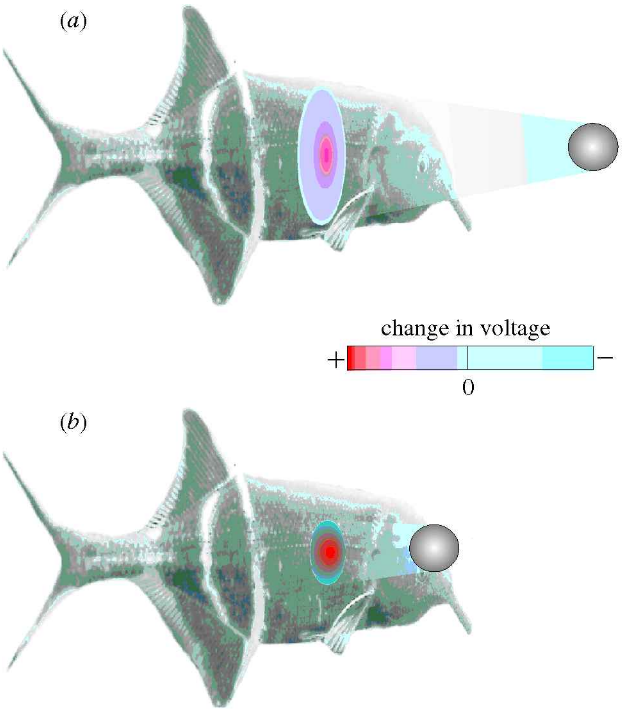

Figure 1. Colour representation of the electrical images that a sphere, placed at two different distances from a *G. petersii*, projects onto the fish's skin. The electrical image consists of an area where the local EOD amplitude has changed compared with the situation without an object present. The amplitude change is colour coded: amplitude increases are depicted in different shades of red, amplitude decreases in blue. (*a*) A far-away sphere creates a larger image containing smaller amplitude changes compared with (*b*) a sphere at a close distance.

2. DEPTH PERCEPTION DURING ACTIVE ELECTROLOCATION

Can *Gnathonemus petersii* determine its distance to an object during electrolocation? Distance measurements to novel objects was hardly thought to be possible, because several parameters of the electrical image change simultaneously when an object moves away from an electrolocating fish (figure 1). Even worse, all of these image parameters depend upon other object features such as size and impedance. In general, it can be said that the closer an object the stronger is its effect on the pattern of electric current through the electroreceptors. Figure 1 shows that the electrical image of a spherical metal object consists of a centre zone with an increased amplitude and a smaller rim zone with an amplitude decrease. If the same object is placed at a larger distance from the fish, the diameter of the electrical image widens. This is in contrast to visual images on the retina, where an object at a large distance produces a smaller image compared with one located close by. During electrolocation, an increase in object distance not only causes an increase in electrical image size but also reduces the maximum amplitude in both the centre and rim zones. Thus, the overall image amplitude decreases, reducing the overall contrast of images of far-away objects.

We considered it very unlikely that electric fishes would not possess a means of determining object distance. During their nocturnal lives, they have to rely on active electrolocation for finding food, locating obstacles and determining their distances to other fishes. All of these and many similar tasks appear to be impaired without some means of distance determination. Therefore, we conducted behavioural training experiments to resolve this issue.

Individual *G. petersii* were trained to discriminate between two objects, each placed at a certain distance behind a gate in a dividing wall. Experiments were carried out under dim light conditions. Control experiments revealed that under these conditions fishes did not use vision but instead completely relied on active electrolocation for object detection (Von der Emde *et al.* 1998). In order to obtain a food reward, the fishes had to swim through the gate behind which the corresponding object was placed further away, compared with the object behind the other gate. During the initial training phase, we used two identical objects. Fishes learned within only two weeks to pick the 'correct' object, no matter how large the absolute object distances were. However, this performance did not demonstrate that fishes could measure distance. With two identical objects, distance discrimination could have been based on pure amplitude or image-width measurements.

In a second step, we presented two different types of objects to our fishes. Objects were, for example, of different sizes or shapes or were made out of different materials. Now, fishes could no longer solve the discrimination task by measuring just one image parameter, such as image amplitude. Surprisingly, however, none of our fishes needed any extra training to solve these new tasks correctly. They immediately continued to chose the object located further away, as long as a certain threshold value of inter-object distances was exceeded (Schwarz & Von der Emde 2000). This demonstrated that *G. petersii* indeed can determine object distance and that distance discrimination is independent of object size, shape or impedance (Von der Emde *et al.* 1998).

In order to discover the mechanism that fishes use for 3D depth perception, we measured the electrical images which the training objects projected onto the fish's skin. Our goal was to find those image parameters that correlated only with object distance and did not depend on other object properties. Finally, we found one parameter combination that fulfilled these conditions: the ratio of the maximal amplitude in the image centre and the maximal slope at the image's edges. The slope indicates how fast the amplitude changes from the rim areas of the image to its centre. It is a measure of the 'fuzziness' of the image, or of how much the image is in 'focus'. Both image slope and image amplitude decrease when an object moves away. However, both parameters decrease at different rates. Thus, the slope-to-amplitude ratio decreases when object distance increases, and it usually does not depend on the type of object involved.

Our electrical image measurements also revealed that there was one exception to this rule. Precisely spherical metal spheres yielded slope to amplitude ratios that were smaller than those of other objects placed at an identical distance. We hypothesized that if our fish indeed had used the slope-to-amplitude ratios to determine object distance, then they would have made mistakes when electrolocating

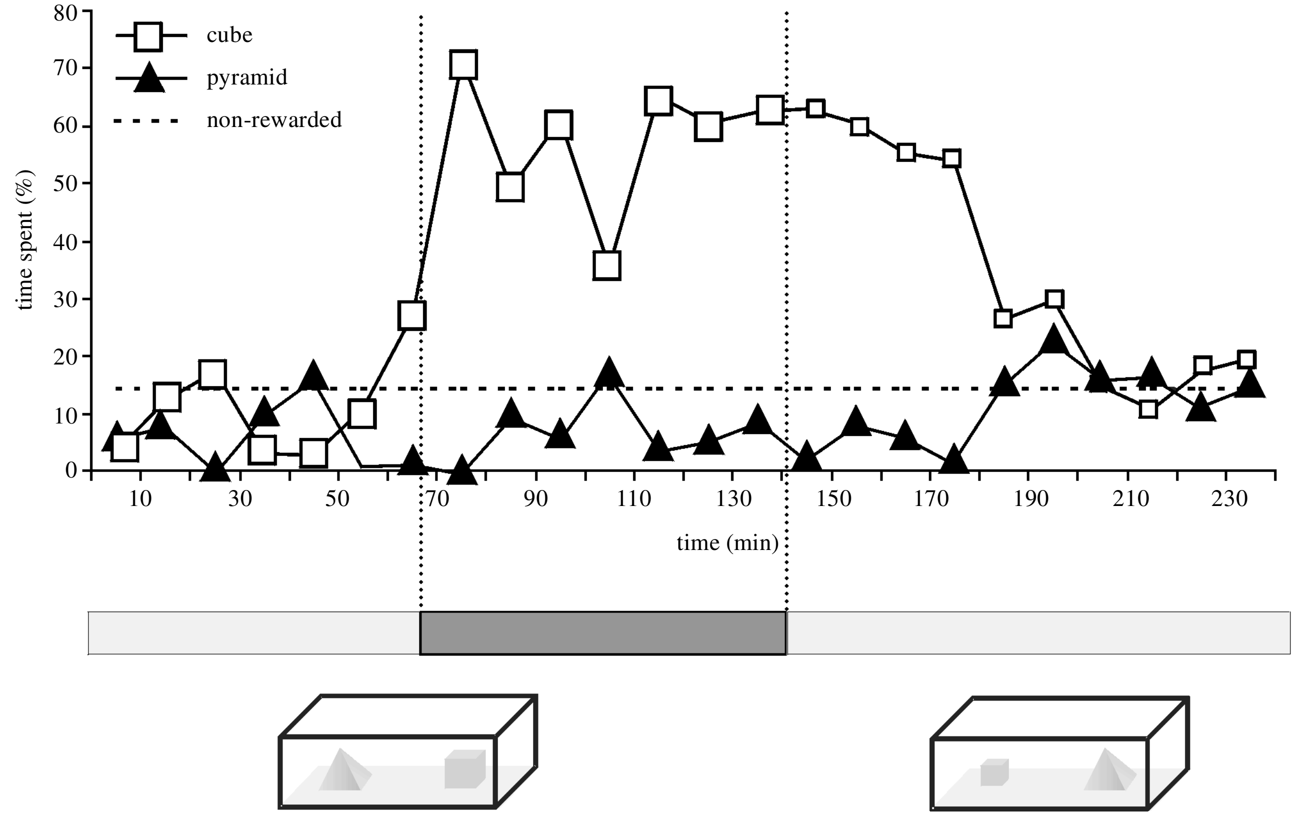

Figure 2. Time-course of a 4 h experiment during which a *G. petersii* could freely move in an experimental arena containing two objects, a metal pyramid and a metal cube. The time spent close to each of the objects within 10 min intervals was measured and is depicted on the ordinate. Closed triangles, time spent close to the pyramid; open squares, time spent close to the cube. During the second 70 min period, the fish's presence close to the cube was rewarded by playback of EOD signals. During the last 100 min period, the locations of the objects were changed and the metal cube was replaced by a smaller-sized metal cube. The dashed line gives the average time spent by the fish close to a non-rewarded object.

spheres: they would have judged spheres to be located further away than other types of objects, even if their actual distances were the same. In particular, we predicted that a sphere placed at 3 cm from a fish should appear to be at the same distance as a cube at a distance of 4.5 cm. Behavioural experiments exactly confirmed our prediction. The fishes indeed made mistakes when discriminating between a sphere and a cube. They fell victim to an 'electrical illusion', which led them to misjudge the distance of the sphere by about 1.5 cm (Von der Emde *et al*. 1998).

The use of the slope-to-amplitude ratio constitutes a new-found natural mechanism of depth perception by animals. It enables *G. petersii* to measure object distance with a single receptor surface that does not have to be moved. This is unique because all other mechanisms discovered so far employ either multiple receptor surfaces (e.g. the two retinas of our eyes during stereopsis) or movement of a single receptor surface (e.g. the retina of a single eye). The mechanism is also unknown in human technology and could provide new solutions for distance determination in human-made sensors.

3. PERCEPTION OF OBJECT SHAPE

Recent results obtained in our laboratory suggest that fishes might be able to compensate for distance measurement errors, which occur when natural objects resembling spheres are electrolocated. When a fish was trained for a considerable time-period with variable types of objects, the electrical illusions described above (§ 2) disappeared completely (Von der Emde & Schwarz 2000). This indicates that the fish might be able to recognize the shape of an object and take the 'errors', which occur during distance determination of spherical objects, into account. The fish might 'subtract' this error from the distance value obtained while calculating the slope-to-amplitude ratio and thus arrive at an accurate distance estimate for the particular object.

Can *G. petersii* determine the shape of an object by using only its electrical sense? To answer this question, we conducted behavioural experiments during which a fish was offered two differently shaped objects in an observation arena illuminated only by infrared light, which is invisible to the fish. The animal was observed by an infrared camera mounted above the arena. The output of the camera was fed into a computer, which calculated online the movements and whereabouts of the fish within the arena (Viewer; BiObserve, Bonn, Germany). During an initial period of 2 h, the time spent by the fish next to each of the two objects was monitored and added up for every 10 min. In a following 'training period' of about 70 min, pre-stored electric signals (EODs of another *G. petersii*) were played back to the fish through electrodes mounted near one of the two objects whenever the fish stayed close to it. This object was previously defined as 'positive' by the experimenter. *G. petersii* is attracted by the EODs of its own species and therefore preferred to stay near that object in whose vicinity the 'rewarding' signals were given. As soon as a fish had learned that social signals were only presented when it stayed close to the positive and not near the alternative object, it spent most of its time in the vicinity of the positive object (figure 2).

After the 'training period', the object arrangement in the arena was changed by moving both objects to new positions. During the following 'testing period' of 2 h, no playback signals were presented when the fish stayed next to any of the objects. In order to find out which of the two objects was more attractive to the fish after training, the time it spent near both of the objects was determined by the computer program. It turned out that despite the fact that no more social signals were given, the fish still preferred to stay close to the previously rewarding object for a time-period of about 45 min (figure 2). Control experiments revealed that the type of the 'negative' object did not matter for the fish's choice behaviour during the testing period, i.e. that fishes were not conditioned to avoid the negative object.

In order to learn which cues the fishes used to recognize the 'rewarding' object, we presented new objects during the testing period, which deviated in certain parameters from the previously used objects. When we changed, for example, only the size of the positive object by replacing it with an object of the same shape but half as big, the fishes still preferred it over the alternative object. The same result was obtained when the material of an object was changed but its shape was maintained: a plastic cube was still preferred over a metal sphere even though rewarding signals were previously presented next to a metal cube in the training phase. The results of many choice experiments clearly showed that fishes categorized objects according to their shapes and not according to their sizes or the material they were made of. An electrolocating *G. petersii* is thus able to recognize an object's shape and uses this information to memorize an object. In addition, fishes might use three-dimensional object shape to 'calibrate' their distance measurements in order to avoid electrical illusions.

4. CONCLUSIONS

Electric fishes have a remarkable ability to locate and analyse objects three-dimensionally in space during active electrolocation. They use the electrical images that objects project onto their skin to accurately measure object distances and 3D shapes. Electrolocation thus provides the fishes with a 3D picture of their surroundings that helps them to orientate in complete darkness and thus to lead a nocturnal life in their freshwater habitats free of competition from other visually dominated fishes.

We thank Horst Bleckmann for providing laboratory space and constant support. This research was supported by the Deutsche Forschungsgemeinschaft (Em 43/5-1,3; Em 43/8-1).

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