

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

Gerhard von der Emde and Stephan Schwarz

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# **THE ROTAL**<br> **Three-dimensional analysis of object properties**<br>
during active electrologation in mermurid **de-dimensional analysis of object properties**<br>during active electrolocation in mormyrid<br>sokly electric fiches (Gretheremus petereii) during active electrolocation in mormyrid<br>
weakly electric fishes (*Gnathonemus petersii*)

# **Gerhard von der Emde**\* **and Stephan Schwarz** *Gerhard von der Emde<sup>\*</sup> and Stephan Schwarz*<br>*Institut für Zoologie, Universität Bonn, Poppelsdorfer Schloss, 53115 Bonn, Germany*

Institut für Zoologie, Universität Bonn, Poppelsdorfer Schloss, 53115 Bonn, Germany<br>Weakly electric fishes are nocturnal and orientate in the absence of vision by using their electrical sense. Weakly electric fishes are nocturnal and orientate in the absence of vision by using their electrical sense.<br>This enables them not only to navigate but also to perceive and recognize objects in complete darkness.<br>They crea Weakly electric fishes are nocturnal and orientate in the absence of vision by using their electrical sense.<br>This enables them not only to navigate but also to perceive and recognize objects in complete darkness.<br>They crea This enables them not only to navigate but also to perceive and recognize objects in complete darkness.<br>They create an electric field around their bodies by producing electric signals with specialized electric<br>organs. Obje 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 a organs. Objects within this field alter the electric current at electroreceptor organs, which are distributed<br>over almost the entire body surface. During active electrolocation, fishes detect, localize and analyse<br>objects 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 p 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 *G. pete* 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. Th *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 betwee 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 ratio between two parameters (maximal slope and maximal amplitude) of the electrical image which<br>each object projects onto the fish's skin. During active electrolocation, electric fishes cannot only locate<br>objects in space each object projects onto the fish's skin. During active electrolocation, electric fishes cannot only locate<br>objects in space but in addition can determine the three-dimensional shape of an object. Up to certain<br>limits, ob objects in space but in addition can de<br>limits, objects are spontaneously categor<br>the materials of which they are made. limits, objects are spontaneously categorized according to their shapes, but not according to their sizes or<br>the materials of which they are made.<br>**Keywords:** electrical sense; depth perception; object shape; sensory analy

## **1. ACTIVE ELECTROLOCATION ACTIVE ELECTROLOCATION<br>AND ELECTRICAL IMAGES**

**AND ELECTRICAL IMAGES**<br>Certain freshwater fishes in Africa and South America **Certain freshwater fishes in Africa and South America**<br>regularly produce weak electric signals using specialized<br>electric organs. It was shown in behavioural training Certain freshwater fishes in Africa and South America<br>regularly produce weak electric signals using specialized<br>electric organs. It was shown in behavioural training<br>experiments that these weakly electric fishes use their regularly produce weak electric signals using specialized<br>electric organs. It was shown in behavioural training<br>experiments that these weakly electric fishes use their<br>electric organ discharges (EODs) for detecting objects electric organs. It was shown in behavioural training<br>experiments that these weakly electric fishes use their<br>electric organ discharges (EODs) for detecting objects<br>with electrical properties different from those of the experiments that these weakly electric fishes use their<br>electric organ discharges (EODs) for detecting objects<br>with electrical properties different from those of the<br>surrounding water (Bullock & Heiligenberg 1986; electric organ discharges (EODs) for detecting objects<br>with electrical properties different from those of the<br>surrounding water (Bullock & Heiligenberg 1986;<br>Lissmann & Machin 1958) Such objects cause distortions with electrical properties different from those of the surrounding water (Bullock & Heiligenberg 1986; Lissmann & Machin 1958). Such objects cause distortions surrounding water (Bullock & Heiligenberg 1986;<br>Lissmann & Machin 1958). Such objects cause distortions<br>in the three-dimensional (3D) electric field, which is<br>generated around the fish during each EOD. As a result Lissmann & Machin 1958). Such objects cause distortions<br>in the three-dimensional (3D) electric field, which is<br>generated around the fish during each EOD. As a result,<br>the current flow through epidermal electroneceptor orga in the three-dimensional  $(3D)$  electric field, which is<br>generated around the fish during each EOD. As a result,<br>the current flow through epidermal electroreceptor organs<br>is altered compared with the current flow in the a 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 the current flow through epidermal electroreceptor organs<br>is altered compared with the current flow in the absence<br>of an object. Each object projects an 'electrical image' onto<br>the skin surface, which consists of a skin ar is altered compared with the current flow in the absence<br>of an object. Each object projects an 'electrical image' onto<br>the skin surface, which consists of a skin area where the<br>EOD-evoked current density has changed (Assad of an object. Each object projects an 'electrical image' onto<br>the skin surface, which consists of a skin area where the<br>EOD-evoked current density has changed (Assad *et al.*<br>1999; Caputi *et al.* 1998; Rasnow 1996). The e 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 compare 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 dep image is defined as the difference in the spatial pattern of phase shifts and/or EOD waveform distortions convey<br>electric current flow evoked by an object compared with information about capacitive object properties, which 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 organ respond to the voltage drop across the skin and thus<br>collectively report the properties of the electrical image to<br>the brain via afferent fibres. This process, during which<br>the fish detects objects by the distortions collectively report the properties of the electrical image to<br>the brain via afferent fibres. This process, during which<br>the fish detects objects by the distortions that they cause in<br>its own EODs is called active electrolo the brain via afferent fibres. This process, during which<br>the fish detects objects by the distortions that they cause in<br>its own EODs, is called active electrolocation (Bastian<br>1989: Lissmann & Machin 1958: Von der Emde 19 the fish detects objects by the distortions that they cause in<br>its own EODs, is called active electrolocation (Bastian<br>1989; Lissmann & Machin 1958; Von der Emde 1998). own EODs, is called active electrolocation (Bastian 89; Lissmann & Machin 1958; Von der Emde 1998).<br>Electric fishes orientate in complete darkness by moni-<br>ring the electrical images of nearby objects. Different

1989; Lissmann & Machin 1958; Von der Emde 1998).<br>Electric fishes orientate in complete darkness by monitoring the electrical images of nearby objects. Different<br>image parameters provide different types of information 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 toring the electrical images of nearby objects. Different<br>image parameters provide different types of information<br>about an object. The location of the image on the skin tells image parameters provide different types of information<br>about an object. The location of the image on the skin tells<br>the fish where the object is located, relative to its own<br>hody coordinates. For example, when only recept about an object. The location of the image on the skin tells<br>the fish where the object is located, relative to its own<br>body coordinates. For example, when only receptors on<br>the fish's left trunk are influenced by an object the fish where the object is located, relative to its own<br>body coordinates. For example, when only receptors on<br>the fish's left trunk are influenced by an object, the fish<br>knows that the object must be located at its left body coordinates. For example, when only receptors on the fish's left trunk are influenced by an object, the fish the fish's left trunk are influenced by an object, the fish<br>knows that the object must be located at its left side. The<br>sign and amount of amplitude change reported by the<br>electrorecentors to the brain inform the animal ab knows that the object must be located at its left side. The<br>sign and amount of amplitude change reported by the<br>electroreceptors to the brain inform the animal about<br>the object's impedance i.e. whether object impedance is 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 electroreceptors to the brain inform the animal about<br>the object's impedance, i.e. whether object impedance is<br>low or high compared with the water resistance. EOD<br>phase shifts and/or EOD waveform distortions convey the object's impedance, i.e. whether object impedance is<br>low or high compared with the water resistance. EOD<br>phase shifts and/or EOD waveform distortions convey<br>information about canacitive object properties which in low or high compared with the water resistance. EOD<br>phase shifts and/or EOD waveform distortions convey<br>information about capacitive object properties, which in<br>turn inform the fish whether an object is composed of living phase shifts and/or EOD waveform distortions convey information about capacitive object properties, which in<br>turn inform the fish whether an object is composed of living<br>or inanimate matter (Von der Emde 1990). Other object<br>properties, such as object size or shape, the exac turn inform the fish whether an object is composed of living<br>or inanimate matter (Von der Emde 1990). Other object<br>properties, such as object size or shape, the exact value of<br>its impedance, and the object's distance must or inanimate matter (Von der Emde 1990). Other object<br>properties, such as object size or shape, the exact value of<br>its impedance, and the object's distance must be computed<br>through a process of calculations involving sever properties, such as object size or shape, the exact value of<br>its impedance, and the object's distance must be computed<br>through a process of calculations involving several image its impedance, and the object's distance must be computed<br>through a process of calculations involving several image<br>parameters. Here we report that these object properties<br>can unequivocally be determined by electrolocation through a process of calculations involving several image<br>parameters. Here we report that these object properties<br>can unequivocally be determined by electrolocating fishes<br>by analysing certain electrical image parameters parameters. Here we report that these object pro<br>can unequivocally be determined by electrolocating<br>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  $G.\rho \text{ }e \text{ }t$ sii, Figure 1. Colour representation of the electrical images that<br>a sphere, placed at two different distances from a  $G. petersii$ ,<br>projects onto the fish's skin. The electrical image consists of<br>an area where the local EOD amplitu a sphere, placed at two different distances from a  $G. peters$ <br>projects onto the fish's skin. The electrical image consists<br>an area where the local EOD amplitude has changed<br>compared with the situation without an object presen projects onto the fish's skin. The electrical image consists<br>an area where the local EOD amplitude has changed<br>compared with the situation without an object present.<br>The amplitude change is colour coded: amplitude increas an area where the local EOD amplitude has changed<br>compared with the situation without an object present.<br>The amplitude change is colour coded: amplitude increases<br>are depicted in different shades of red -amplitude decrease compared with the situation without an object present.<br>The amplitude change is colour coded: amplitude increases<br>are depicted in different shades of red, amplitude decreases<br>in blue  $(a)$  A far-away sphere creates a larger The amplitude change is colour coded: amplitude increation<br>are depicted in different shades of red, amplitude decreation<br>in blue. (*a*) A far-away sphere creates a larger image<br>containing smaller amplitude changes compared are depicted in different shades of red, amplitude decreases<br>in blue. (*a*) A far-away sphere creates a larger image<br>containing smaller amplitude changes compared with (*b*) a<br>sphere at a close distance in blue.  $(a)$  A far-away sphe<br>containing smaller amplitud<br>sphere at a close distance.

#### **2. DEPTH PERCEPTION DURING ACTIVE ELECTROLOCATION**

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

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 During their nocturnal lives, they have to rely on active<br>electrolocation for finding food, locating obstacles and<br>determining their distances to other fishes. All of these<br>and many similar tasks appear to be impaired with electrolocation for finding food, locating obstacles and<br>determining their distances to other fishes. All of these<br>and many similar tasks appear to be impaired without<br>some means of distance determination. Therefore, we and many similar tasks appear to be impaired without some means of distance determination. Therefore, we conducted behavioural training experiments to resolve this issue. conducted behavioural training experiments to resolve

Individual *G.petersii* were trained to discriminate this issue.<br>
Individual *G. petersii* were trained to discriminate<br>
between two objects, each placed at a certain distance<br>
behind a gate in a dividing wall Experiments were Individual *G. petersii* were trained to discriminate<br>between two objects, each placed at a certain distance<br>behind a gate in a dividing wall. Experiments were<br>carried out under dim light conditions Control experibehind a gate in a dividing wall. Experiments were carried out under dim light conditions. Control experiments revealed that under these conditions fishes did not carried out under dim light conditions. Control experiments revealed that under these conditions fishes did not<br>use vision but instead completely relied on active electro-<br>location for object detection (Von der Emde et al ments revealed that under these conditions fishes did not<br>use vision but instead completely relied on active electro-<br>location for object detection (Von der Emde *et al.* 1998).<br>In order to obtain a food reward, the fishes use vision but instead completely relied on active electro-<br>location for object detection (Von der Emde *et al.* 1998).<br>In order to obtain a food reward, the fishes had to swim<br>through the gate behind which the correspondi location for object detection (Von der Emde *et al.* 1998).<br>In order to obtain a food reward, the fishes had to swim<br>through the gate behind which the corresponding object<br>was placed further away compared with the object In order to obtain a food reward, the fishes had to swim<br>through the gate behind which the corresponding object<br>was placed further away, compared with the object<br>behind the other gate. During the initial training phase through the gate behind which the corresponding object<br>was placed further away, compared with the object<br>behind the other gate. During the initial training phase,<br>we used two identical objects. Fishes learned within only was placed further away, compared with the object<br>behind the other gate. During the initial training phase,<br>we used two identical objects. Fishes learned within only<br>two weeks to pick the 'correct' object, no matter how la behind the other gate. During the initial training phase,<br>we used two identical objects. Fishes learned within only<br>two weeks to pick the 'correct' object, no matter how large<br>the absolute object distances were. However, t we used two identical objects. Fishes learned within only<br>two weeks to pick the 'correct' object, no matter how large<br>the absolute object distances were. However, this perform-<br>ance, did, not, demonstrate, that, fishes, co two weeks to pick the 'correct' object, no matter how large<br>the absolute object distances were. However, this perform-<br>ance did not demonstrate that fishes could measure<br>distance With two identical objects distance discrim the absolute object distances were. However, this performance did not demonstrate that fishes could measure distance. With two identical objects, distance discriminaance did not demonstrate that fishes could measure<br>distance. With two identical objects, distance discrimina-<br>tion could have been based on pure amplitude or image-<br>width measurements distance. With two ide-<br>tion could have been b<br>width measurements.<br>In a second step, w In could have been based on pure amplitude or image-<br>
In a second step, we presented two different types of<br>
iects to our fishes. Objects were, for example, of

width measurements.<br>In a second step, we presented two different types of<br>objects to our fishes. Objects were, for example, of<br>different sizes or shapes or were made out of different In a second step, we presented two different types of<br>objects to our fishes. Objects were, for example, of<br>different sizes or shapes or were made out of different<br>materials. Now fishes could no longer solve the discrimiobjects to our fishes. Objects were, for example, of<br>different sizes or shapes or were made out of different<br>materials. Now, fishes could no longer solve the discrimi-<br>nation task by measuring just one image parameter such 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 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 ta nation task by measuring just one image parameter, such<br>as image amplitude. Surprisingly, however, none of our<br>fishes needed any extra training to solve these new tasks<br>correctly. They immediately continued to chose the ob as image amplitude. Surprisingly, however, none of our fishes needed any extra training to solve these new tasks<br>correctly. They immediately continued to chose the object<br>located further away as long as a certain threshold fishes needed any extra training to solve these new tasks<br>correctly. They immediately continued to chose the object<br>located further away, as long as a certain threshold value<br>of inter-object distances was exceeded (Schwarz correctly. They immediately continued to chose the object<br>located further away, as long as a certain threshold value<br>of inter-object distances was exceeded (Schwarz & Von<br>der Emde 2000) This demonstrated that *G hetersii* located further away, as long as a certain threshold value<br>of inter-object distances was exceeded (Schwarz & Von<br>der Emde 2000). This demonstrated that *G. petersii* indeed<br>can determine object distance and that distance d of inter-object distances was exceeded (Schwarz & Von der Emde 2000). This demonstrated that  $G. petersii$  indeed can determine object distance and that distance discrimider Emde 2000). This demonstrated that *G. petersii* indeed<br>can determine object distance and that distance discrimi-<br>nation is independent of object size, shape or impedance<br>(Von der Emde *et al* 1998) can determine object distance<br>nation is independent of obj<br>(Von der Emde *et al.* 1998).<br>In order to discover the r tion is independent of object size, shape or impedance<br>
In order to discover the mechanism that fishes use for<br>  $\Omega$  denth percention, we measured the electrical images

(Von der Emde *et al.* 1998).<br>In order to discover the mechanism that fishes use for  $3D$  depth perception, we measured the electrical images In order to discover the mechanism that fishes use for<br>3D depth perception, we measured the electrical images<br>which the training objects projected onto the fish's skin.<br>Our goal was to find those image parameters that corr 3D depth perception, we measured the electrical images<br>which the training objects projected onto the fish's skin.<br>Our goal was to find those image parameters that corre-<br>lated only with object distance and did not depend o which the training objects projected onto the fish's skin.<br>Our goal was to find those image parameters that correlated only with object distance and did not depend on<br>other object properties. Finally, we found one paramete 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 lated only with object distance and did not depend on<br>other object properties. Finally, we found one parameter<br>combination that fulfilled these conditions: the ratio of<br>the maximal amplitude in the image centre and the other object properties. Finally, we found one parameter<br>combination that fulfilled these conditions: the ratio of<br>the maximal amplitude in the image centre and the<br>maximal slope at the image's edges. The slope indicates combination that fulfilled these conditions: the ratio of<br>the maximal amplitude in the image centre and the<br>maximal slope at the image's edges. The slope indicates<br>how fast the amplitude changes from the rim areas of the 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 how fast the amplitude changes from the rim areas of the 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 o image to its centre. It is a measure of the 'fuzziness' of the<br>image, or of how much the image is in 'focus'. Both image<br>slope and image amplitude decrease when an object<br>moves away. However, both parameters decrease at image, or of how much the image is in 'focus'. Both image<br>slope and image amplitude decrease when an object<br>moves away. However, both parameters decrease at<br>different rates. Thus, the slope-to-amplitude ratio slope and image amplitude decrease when an object<br>moves away. However, both parameters decrease at<br>different rates. Thus, the slope-to-amplitude ratio<br>decreases when object distance increases and it usually 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 denend on the type of object involved 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. creases when object distance increases, and it usually<br>es not depend on the type of object involved.<br>Our electrical image measurements also revealed that<br>ere was one exception to this rule. Precisely spherical

does not depend on the type of object involved.<br>Our electrical image measurements also revealed that<br>there was one exception to this rule. Precisely spherical<br>metal spheres vielded slope to amplitude ratios that were Our electrical image measurements also revealed that<br>there was one exception to this rule. Precisely spherical<br>metal spheres yielded slope to amplitude ratios that were<br>smaller than those of other objects placed at an iden there was one exception to this rule. Precisely spherical<br>metal spheres yielded slope to amplitude ratios that were<br>smaller than those of other objects placed at an identical metal spheres yielded slope to amplitude ratios that were<br>smaller than those of other objects placed at an identical<br>distance. We hypothesized that if our fish indeed had used<br>the slope-to-amplitude ratios to determine obj smaller than those of other objects placed at an identical<br>distance. We hypothesized that if our fish indeed had used<br>the slope-to-amplitude ratios to determine object distance,<br>then they would have made mistakes when elec distance. We hypothesized that if our fish indeed had used<br>the slope-to-amplitude ratios to determine object distance,<br>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<br>objects, a metal pyramid and a metal cube. The time spent close to each of the objects within objects, a metal pyramid and a metal cube. The time spent close to each of the objects within 10 min intervals was measured and<br>is depicted on the ordinate. Closed triangles, time spent close to the pyramid; open squares, objects, a metal pyramid and a metal cube. The time spent close to each of the objects within 10 min intervals was measured and<br>is depicted on the ordinate. Closed triangles, time spent close to the pyramid; open squares, is depicted on the ordinate. Closed triangles, time spent close to the pyramid; open squares, time spent close to the cube. During<br>the second 70 min period, the fish's presence close to the cube was rewarded by playback of the second 70 min period, the fish's presence close to the cube was reward<br>period, the locations of the objects were changed and the metal cube was<br>gives the average time spent by the fish close to a non-rewarded object.

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> spheres: they would have judged spheres to be located<br>further away than other types of objects, even if their spheres: they would have judged spheres to be located<br>further away than other types of objects, even if their<br>actual distances, were the same. In particular, we spheres: they would have judged spheres to be located<br>further away than other types of objects, even if their<br>actual distances were the same. In particular, we<br>predicted that a sphere placed at 3 cm from a fish should further away than other types of objects, even if their<br>actual distances were the same. In particular, we<br>predicted that a sphere placed at 3 cm from a fish should<br>annear to be at the same distance as a cube at a distance actual distances were the same. In particular, we<br>predicted that a sphere placed at 3 cm from a fish should<br>appear to be at the same distance as a cube at a distance<br>of 4.5 cm. Behavioural experiments exactly confirmed our predicted that a sphere placed at 3 cm from a fish should<br>appear to be at the same distance as a cube at a distance<br>of 4.5 cm. Behavioural experiments exactly confirmed our prediction. The fishes indeed made mistakes when discriof 4.5 cm. Behavioural experiments exactly confirmed our<br>prediction. The fishes indeed made mistakes when discri-<br>minating between a sphere and a cube. They fell victim<br>to an 'electrical illusion', which led them to misjud prediction. The fishes indeed made mistakes when discriminating between a sphere and a cube. They fell victim<br>to an 'electrical illusion', which led them to misjudge the<br>distance of the sphere by about 1.5 cm (Von der Emde minating between a sphere and a cube. They fell victim<br>to an 'electrical illusion', which led them to misjudge the<br>distance of the sphere by about 1.5 cm (Von der Emde *et*<br> $d$  1998) 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). stance of the sphere by about 1.5 cm (Von der Emde  $et$  1998).<br>The use of the slope-to-amplitude ratio constitutes a<br>w-found natural mechanism of denth perception by

*al.* 1998).<br>The use of the slope-to-amplitude ratio constitutes a<br>new-found natural mechanism of depth perception by<br>animals. It enables *G betersii* to measure object distance The use of the slope-to-amplitude ratio constitutes a<br>new-found natural mechanism of depth perception by<br>animals. It enables *G.petersii* to measure object distance<br>with a single receptor surface that does not have to be 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 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 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  $(e, \alpha)$  the two retinas of our eves during stereonsis) moved. This is unique because all other mechanisms<br>discovered so far employ either multiple receptor surfaces<br>(e.g. the two retinas of our eyes during stereopsis) or<br>movement of a single receptor surface (e.g. the retina discovered so far employ either multiple receptor surfaces<br>(e.g. the two retinas of our eyes during stereopsis) or<br>movement of a single receptor surface (e.g. the retina of a<br>single eye). The mechanism is also unknown in h (e.g. the two retinas of our eyes during stereopsis) or<br>movement of a single receptor surface (e.g. the retina of a<br>single eye). The mechanism is also unknown in human<br>technology and could provide new solutions for distanc 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. single eye). The mechanism is also unknown in human

#### **3. PERCEPTION OF OBJECT SHAPE**

Recent results obtained in our laboratory suggest that **S. PERCEPTION OF OBJECT SHAPE**<br>Recent results obtained in our laboratory suggest that<br>fishes might be able to compensate for distance measure-<br>ment errors which occur when natural objects resembling Recent results obtained in our laboratory suggest that<br>fishes might be able to compensate for distance measure-<br>ment errors, which occur when natural objects resembling *Phil. Trans. R. Soc. Lond.* B (2000) *Phil. Trans. R. Soc. Lond.* B (2000)

spheres are electrolocated. When a fish was trained for a<br>considerable time-period with variable types of objects spheres are electrolocated. When a fish was trained for a considerable time-period with variable types of objects, the electrical illusions described above  $(8.2)$  disappeared spheres are electrolocated. When a fish was trained for a considerable time-period with variable types of objects, the electrical illusions described above ( $\S 2$ ) disappeared completely (Von der Emde & Schwarz 2000) This considerable time-period with variable types of objects,<br>the electrical illusions described above  $(\S 2)$  disappeared<br>completely (Von der Emde & Schwarz 2000). This indi-<br>cates that the fish might be able to recognize the the electrical illusions described above  $(\S 2)$  disappeared<br>completely (Von der Emde & Schwarz 2000). This indi-<br>cates that the fish might be able to recognize the shape of<br>an object and take the 'errors' which occur dur 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 cates that the fish might be able to recognize the shape of<br>an object and take the 'errors', which occur during<br>distance determination of spherical objects, into account.<br>The fish might 'subtract' this error from the dista an object and take the 'errors', which occur during<br>distance determination of spherical objects, into account.<br>The fish might 'subtract' this error from the distance<br>value obtained while calculating the slope-to-amplitude distance determination of spherical objects, into account.<br>The fish might 'subtract' this error from the distance<br>value obtained while calculating the slope-to-amplitude<br>ratio and thus arrive at an accurate distance estima 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. value obtained while calculating the slope-to-amplitude

Can *G. petersii* determine the shape of an object by the particular object.<br>
Can *G. petersii* determine the shape of an object by<br>
using only its electrical sense? To answer this question, we<br>
conducted behavioural experiments during which a fish 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 obs using only its electrical sense? To answer this question, we<br>conducted behavioural experiments during which a fish<br>was offered two differently shaped objects in an observa-<br>tion arena illuminated only by infrared light, wh conducted behavioural experiments during which a fish<br>was offered two differently shaped objects in an observa-<br>tion arena illuminated only by infrared light, which is<br>invisible to the fish. The animal was observed by an was offered two differently shaped objects in an observation arena illuminated only by infrared light, which is<br>invisible to the fish. The animal was observed by an<br>infrared camera mounted above the arena. The output of tion arena illuminated only by infrared light, which is<br>invisible to the fish. The animal was observed by an<br>infrared camera mounted above the arena. The output of<br>the camera was fed into a computer which calculated invisible to the fish. The animal was observed by an<br>infrared camera mounted above the arena. The output of<br>the camera was fed into a computer, which calculated<br>online the movements and whereabouts of the fish within infrared camera mounted above the arena. The output of<br>the camera was fed into a computer, which calculated<br>online the movements and whereabouts of the fish within<br>the arena (Viewer: BiObserve Bonn Germany) During the camera was fed into a computer, which calculated<br>online the movements and whereabouts of the fish within<br>the arena (Viewer; BiObserve, Bonn, Germany). During online the movements and whereabouts of the fish within<br>the arena (Viewer; BiObserve, Bonn, Germany). During<br>an initial period of 2 h, the time spent by the fish next to<br>each of the two objects was monitored and added up f the arena (Viewer; BiObserve, Bonn, Germany). During<br>an initial period of 2 h, the time spent by the fish next to<br>each of the two objects was monitored and added up for<br>every 10 min. In a following 'training period' of abo 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  $70 \text{ min}$ , pre-stored electric signals (EODs of a each of the two objects was monitored and added up for<br>every 10 min. In a following 'training period' of about<br>70 min, pre-stored electric signals (EODs of another *G.p etersy* 10 min. In a following 'training period' of about 70 min, pre-stored electric signals (EODs of another *G.p etersii*) were played back to the fish through electrodes mounted near one of the two objects wheneve 70 min, pre-stored electric signals (EODs of another  $G.\rho \text{ }etersii)$  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 defin 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

<sup>'</sup>positive' by the experimenter. *G.petersii* is attracted by the EODs of its own species and therefore preferred to "positive" by the experimenter.  $G.\rho \varepsilon$  is attracted by the EODs of its own species and therefore preferred to stay near that object in whose vicinity the "rewarding" '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 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 stay near that object in whose vicinity the 'rewarding'<br>signals were given. As soon as a fish had learned that<br>social signals were only presented when it stayed close to<br>the positive and not near the alternative object it signals were given. As soon as a fish had learned that<br>social signals were only presented when it stayed close to<br>the positive and not near the alternative object, it spent<br>most of its time in the vicinity of the positive social signals were only presented when it stayed close to<br>the positive and not near the alternative object, it spent<br>most of its time in the vicinity of the positive object<br>(figure 2) the positive and not near the alternative object, it spent most of its time in the vicinity of the positive object (figure 2).

(figure 2).<br>
After the 'training period', the object arrangement in the arena was changed by moving both objects to new<br>
nositions. During the following 'testing period' of 2 h no After the 'training period', the object arrangement in<br>the arena was changed by moving both objects to new<br>positions. During the following 'testing period' of 2 h, no<br>playback signals were presented when the fish stayed ne the arena was changed by moving both objects to new<br>positions. During the following 'testing period' of 2 h, no<br>playback signals were presented when the fish stayed next<br>to any of the objects. In order to find out which of positions. During the following 'testing period' of 2 h, no<br>playback signals were presented when the fish stayed next<br>to any of the objects. In order to find out which of the two<br>objects was more attractive to the fish aft playback signals were presented when the fish stayed next<br>to any of the objects. In order to find out which of the two<br>objects was more attractive to the fish after training, the<br>time it spent near both of the objects was to any of the objects. In order to find out which of the two<br>objects was more attractive to the fish after training, the<br>time it spent near both of the objects was determined by<br>the computer program. It turned out that des objects was more attractive to the fish after training, the<br>time it spent near both of the objects was determined by<br>the computer program. It turned out that despite the fact<br>that no more social signals were given the fish time it spent near both of the objects was determined by<br>the computer program. It turned out that despite the fact<br>that no more social signals were given, the fish still<br>preferred to stay close to the previously rewarding the computer program. It turned out that despite the fact<br>that no more social signals were given, the fish still<br>preferred to stay close to the previously rewarding object<br>for a time-period of about 45 min (figure 2) Contr that no more social signals were given, the fish still<br>preferred to stay close to the previously rewarding object<br>for a time-period of about 45 min (figure 2). Control<br>experiments revealed that the type of the 'negative' o preferred to stay close to the previously rewarding object<br>for a time-period of about 45 min (figure 2). Control<br>experiments revealed that the type of the 'negative' object<br>did not matter for the fish's choice behaviour du for a time-period of about 45 min (figure 2). Control<br>experiments revealed that the type of the 'negative' object<br>did not matter for the fish's choice behaviour during the<br>testing period i.e. that fishes were not condition experiments revealed that the type of the 'negative' object<br>did not matter for the fish's choice behaviour during the<br>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 avoid the negative object.<br>In order to learn which cues the fishes used to recognize<br>the 'rewarding' object, we presented new objects during<br>the testing period, which deviated in certain parameters In order to learn which cues the fishes used to recognize<br>the 'rewarding' object, we presented new objects during<br>the testing period, which deviated in certain parameters<br>from the previously used objects. When we changed f the 'rewarding' object, we presented new objects during<br>the testing period, which deviated in certain parameters<br>from the previously used objects. When we changed, for<br>example only the size of the positive object by replac the testing period, which deviated in certain parameters<br>from the previously used objects. When we changed, for<br>example, only the size of the positive object by replacing<br>it with an object of the same shape but half as big from the previously used objects. When we changed, for<br>example, only the size of the positive object by replacing<br>it with an object of the same shape but half as big, the<br>fishes still preferred it over the alternative obje 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 plasti 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 thoug same result was obtained when the material of an object was changed but its shape was maintained: a plastic cube<br>was still preferred over a metal sphere even though<br>rewarding signals were previously presented next to a<br>metal cube in the training phase. The results of many was still preferred over a metal sphere even though<br>rewarding signals were previously presented next to a<br>metal cube in the training phase. The results of many<br>choice experiments clearly showed that fishes categorized rewarding signals were previously presented next to a<br>metal cube in the training phase. The results of many<br>choice experiments clearly showed that fishes categorized<br>objects according to their shapes and not according to metal cube in the training phase. The results of many<br>choice experiments clearly showed that fishes categorized<br>objects according to their shapes and not according to their sizes or the material they were made of. An electroobjects according to their shapes and not according to<br>their sizes or the material they were made of. An electro-<br>locating *G. petersii* is thus able to recognize an object's<br>shape and uses this information to memorize an their sizes or the material they were made of. An electro-<br>locating *G. petersii* is thus able to recognize an object's<br>shape and uses this information to memorize an object. In<br>addition fishes might use three-dimensional locating  $G$ , *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 shape and uses this information to memorize an object. In addition, fishes might use three-dimensional object shape<br>to 'calibrate' their distance measurements in order to<br>avoid electrical illusions addition, fishes might use<br>to 'calibrate' their distan<br>avoid electrical illusions.

#### **4. CONCLUSIONS**

ost of its time in the vicinity of the positive object<br>gure 2).<br>After the 'training period', the object arrangement in<br>e fishes with a 3D picture of their surroundings that helps<br>e arena was changed by moving both objects Electric fishes have a remarkable ability to locate and 4. CONCLOSIONS<br>Electric fishes have a remarkable ability to locate and<br>analyse objects three-dimensionally in space during active<br>electrolocation. They use the electrical images that objects Electric fishes have a remarkable ability to locate and<br>analyse objects three-dimensionally in space during active<br>electrolocation. They use the electrical images that objects<br>project onto their skin to accurately measure analyse objects three-dimensionally in space during active<br>electrolocation. They use the electrical images that objects<br>project onto their skin to accurately measure object<br>distances and 3D shanes. Electrolocation thus pro electrolocation. They use the electrical images that objects<br>project onto their skin to accurately measure object<br>distances and 3D shapes. Electrolocation thus provides the<br>fishes with a 3D picture of their surroundings th project onto their skin to accurately measure object<br>distances and 3D shapes. Electrolocation thus provides the<br>fishes with a 3D picture of their surroundings that helps<br>them to orientate in complete darkness and thus to l distances and 3D shapes. Electrolocation thus provides the<br>fishes with a 3D picture of their surroundings that helps<br>them to orientate in complete darkness and thus to lead a<br>nocturnal life in their freshwater habitats fre fishes with a 3D picture of their surroundings that helps<br>them to orientate in complete darkness and thus to lead a<br>nocturnal life in their freshwater habitats free of competi-<br>tion from other visually dominated fishes them to orientate in complete darkness an<br>nocturnal life in their freshwater habitats f<br>tion from other visually dominated fishes.

tion from other visually dominated fishes.<br>We thank Horst Bleckmann for providing laboratory space and We thank Horst Bleckmann for providing laboratory space and<br>constant support. This research was supported by the Deutsche<br>Forschungsgemeinschaft (Em 43/5-13: Em 43/8-1) We thank Horst Bleckmann for providing laborator<br>constant support. This research was supported by t<br>Forschungsgemeinschaft (Em 43/5-1,3; Em 43/8-1).

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