FINDING FOOD: SENSES INVOLVED IN FORAGING FOR INSECT LARVAE IN THE ELECTRIC FISH *GNATHONEMUS PETERSII*

GERHARD VON DER EMDE* AND HORST BLECKMANN

Institut für Zoologie, Universität Bonn, Poppelsdorfer Schloss, 53115 Bonn, Germany

*e-mail: unb308@ibm.rhrz.uni-bonn.de

Summary

The weakly electric fish *Gnathonemus petersii* searches at night for insect larvae in tropical African streams. The aim of this study was to determine the contributions of different sensory modalities to foraging. The time that fish needed to find two randomly placed chironomid larvae was measured. The influence of various senses on search time was investigated by blocking the use of one or more senses. Active electrolocation was used by most fish for prey detection in the dark. In addition, passive electrolocation played a role in some individuals. If light was available, vision could become the dominant sense in some individuals, replacing active electrolocation. The presence of chemical cues decreased prey detection time in most fish. Prey movements also shortened search times when active electrolocation and vision were not possible, indicating that the mechanosensory lateral line also plays a role in the detection of moving prey. The results show that *G. petersii* uses several senses simultaneously during foraging. Each individual favours a specific combination of the available sensory inputs. If one sensory modality is eliminated, fish can switch to other modalities, indicating that the food detection system is flexible and plastic.

Key words: electrolocation, vision, sensory plasticity, food search, multimodal integration, electric fish, *Gnathonemus petersii.*

Introduction

Animals have to find food in their natural habitat. To achieve this, they must orient towards potential food sources, detect and localise possible prey items, and finally analyse the nature of these items to classify them as edible. Different animals devote different senses to these problems. Some species use only one or a few senses, such as some echolocating bats which only use hearing (echolocation) (Kalko, 1995; Obrist, 1995; Schnitzler, 1987) (but see Höller and Schmidt, 1996), or diurnal birds of prey, which concentrate on vision (Martin, 1991; Waldvogel, 1990). Other animals have to recruit several senses simultaneously in order to find their natural prey successfully (Dusenbery, 1992).

Many fishes use vision for foraging (Blaxter, 1988; Warburton, 1990), but most weakly electric fish are nocturnal (Moller *et al.* 1979; Westby, 1988) and therefore do not normally use vision. Instead, they have developed an active electrolocation system that allows them to hunt successfully in complete darkness (Bastian, 1994; Lissmann, 1958; Lissmann and Machin, 1958). Electric fish of the family Mormyridae possess an electric organ in their tail, which generates a pulse-type electric signal in the water. Electroreceptors in the skin are distributed over most of the body surfaces of the fish. They respond to the transdermal potential difference created by the electric organ discharge (EOD) and thus measure the local electric field strength. Nearby objects with electrical properties different from those of the surrounding water distort the self-produced electric field and lead to amplitude and/or waveform changes in the signals stimulating the electroreceptors. Fish can detect, localise and analyse objects in their vicinity by perceiving these local electric field distortions (Bastian, 1986, 1994; Heiligenberg, 1984; von der Emde, 1998).

During active electrolocation, mormyrids are able not only to detect and localise objects but also to analyse their electrical properties. Object impedance determines the amplitude of the locally perceived signal, which fish can measure quantitatively and thus discriminate between non-conductors (such as most stones) and conductors (such as water plants or insect larvae) (von der Emde and Ronacher, 1994). Living objects such as water plants, other fishes and insect larvae have a complex impedance with both an ohmic and a capacitative component (Heiligenberg, 1973; Schwan, 1963; von der Emde, 1990). The capacitative properties distort the waveform of the electric signals stimulating the electroreceptors. Mormyrids can detect these waveform distortions and use them to identify capacitative objects and to measure their capacitative component quantitatively (capacitance detection, von der Emde, 1990; von der Emde and Ringer, 1992; von der Emde and Ronacher, 1994). This ability allows mormyrids to discriminate between animate and inanimate objects and probably provides an additional cue for prey identification.

Not much is known about the ecology of most mormyrids. They live a nocturnal life in freshwater rivers, small streams

and lakes of tropical Africa (Hopkins, 1981; Kramer, 1996; Moller, 1975; Moller *et al.* 1979; Okedi, 1965). Most mormyrids feed on aquatic insect larvae, and many species have specialised on chironomids (Blake, 1977; Corbet, 1961; Hyslop, 1986; Okedi, 1971). It is usually assumed that weakly electric fish use active electrolocation for food detection, but there are only a few studies that support this hypothesis (Cain, 1995; Cain *et al.* 1994; Lannoo and Lannoo, 1993; Marrero and Winemiller, 1993; von der Emde, 1994, 1995). Previous experiments with the mormyrid fish *Gnathonemus petersii* showed that active electrolocation helps these animals to find natural food (von der Emde, 1994). These experiments also showed that electrically silenced fish that are unable to electrolocate actively can still find food and orient in the experimental tanks even in complete darkness.

In the present paper, we investigated the foraging success of *Gnathonemus petersii* under various sensory conditions. Our goal was to determine the contributions of active electrolocation and other sensory modalities to food searching. We find that active electrolocation is only one of several senses that are used simultaneously during foraging for insect larvae. Individual fish have different sensory preferences and are flexible with respect to exploiting the available sensory information. They can compensate for a loss of a particular sensory modality quickly, enabling them to find their food successfully even under changing environmental conditions.

Materials and methods

Animals

Twelve *Gnathonemus petersii* L. obtained from a commercial fish dealer were used in this study. Their lengths (mouth to fork of tail) were between 10 and 14 cm. For an experimental period, which lasted for several weeks, fish were housed one at a time in a 100 l experimental tank. Fish were maintained in an artificial 12 h:12 h light:dark cycle. Water temperature was kept constant at 27±1 °C, water conductivity at 100±5 μS cm^{-1} (10 kΩ cm).

Experimental apparatus

Individuals of *G. petersii* were trained to search for food in the larger compartment (36 cm×40 cm×32 cm) of a 100 l aquarium divided by an opaque plastic wall containing a gate (6 cm×6 cm; 5 cm above the floor). Fish lived in the smaller compartment (25 cm×40 cm×32 cm) of the tank and could swim through the gate for feeding only during experimental hours. The glass floor of the larger compartment was divided in 3 cm×3 cm squares with black lines visible from above (Fig. 1A). The tank floor was loosely covered with quartz gravel (pebble size between 2 and 10 mm diameter). An infrared video camera and an infrared light were mounted above the experimental tank in order to view the food search of the fish in the absence of visible light.

For a single trial, two chironomid larvae were placed at random in two different squares of the grid on the tank floor between the pebbles. Dead (commercially available frozen larvae) or living chironomid larvae or artificial larvae made out of gelatine (see below) were used. Five additional objects were also placed at random in the arena: two flat bricks (sizes 15 cm×2.5 cm×11 cm and 12 cm×2.5 cm×9 cm), two plastic columns (circular diameter 3 cm, height 12 cm) and one artificial plastic water plant (height approximately 12 cm, 15 thin 'leaves' with a diameter of approximately 1 cm). A given object arrangement was called an 'environment', and object placement within it was determined at random. After five trials, the objects in the search compartment were rearranged in order to present a new, unfamiliar 'environment' to the fish. A set of 15 environments with five trials conducted in each was used to test a fish for each experiment. Fish were given one experimental session per day, each consisting of at least 15 trials, i.e. three environments. Fish were fed only during the experimental sessions. This ensured a high motivation to search for food.

Training and foraging experiments

Before each trial, two prey items were placed on the floor of the test arena. A trial started when the door in the dividing wall between the two compartments was opened. The fish quickly learned to swim into the larger compartment and to search for the two insect larvae. The search was observed from above with aid of the video camera on each trial. The times from passing the gate until taking the first and second larvae were measured. Fish usually searched without interruption until the larvae were found and eaten. Very rarely, a fish stopped searching and moved upwards in the tank. When this happened, the clock was stopped; it was restarted when the fish started its food search again. After having eaten the two larvae, the fish had to swim back into the smaller compartment. The door was then closed and two new larvae were positioned for the next trial. To obtain median search times, the results of 75 trials (in 15 'environments' with five trials each) were averaged.

Each fish was 'trained' to perform in the experiments before testing. Fish had to learn to swim through the gate in the partition when it opened and to search for food on the other side. All fish learned this within a few days. Fish also had to become accustomed to being chased back after having eaten two insect larvae. Training consisted of going through the usual test procedure with real, dead insect larvae in complete darkness. Median search times decreased over time during training and finally reached a constant level with no further improvement. When median performance was constant for at least 5 days, the actual tests began.

Testing

A test usually consisted of 75 trials in 15 environments under constant conditions. The standard test for each fish was conducted in complete darkness using dead chironomid larvae. All other tests (see below) were conducted in the same 15 environments (except for the test with electrical noise, see below) and with the larvae placed at the same positions within the test arena. This allowed paired statistical comparisons of search times. Median search times and inter-quartile values were calculated separately for the first- and second-found larva in each trial. To compare the performance of a given fish in different tests, a non-parametric paired Wilcoxon rank-sign test was

usually used (Statgraphics 5.5 Software). In some tests, prey items to be compared were not positioned in identical places. This was the case when electrical noise was used, with artificial insect larvae, and when comparing moving and motionless larvae (see below). For statistical analysis, an unpaired Wilcoxon test (Statgraphics 5.5) was used in these cases.

Silenced fish

After going through the complete training and testing procedure, the electric organ of some fish was surgically silenced by cutting the efferent innervation under MS-222 anaesthesia. This was achieved by inserting a small surgical needle into the spinal cord just rostral to the electric organ. This destroyed the spinal fibres innervating the motor neurones, which in turn innervate the electric organ. Because the electric organ is the most caudal innervated structure in *G. petersii* (the tail fin is moved by tendons running parallel to the spinal cord), this procedure did not cause any motor deficits but only lesioned the electromotor efferents. The procedure prevented a fish from discharging its electric organ and thus from using active electrolocation. Fish

recovered from the surgery within 1 day, after which they were tested again. With their electric organs silenced, fish showed no overt behavioural changes and swimming was unaffected while searching for food compared with the situation before the surgery. Median search times obtained with a particular fish before silencing were compared with the results for that same fish after silencing while solving the same search tasks. Two sham-operated fish, which were anaesthetised and treated in the same way as silenced fish except that the surgical needle was inserted into the spinal cord caudal to the electric organ, leaving the electromotor efferents intact, served as controls.

Visible light

To assess the contribution vision makes to food searching, experiments were conducted under different light conditions. Most experiments were conducted in complete darkness, i.e. only infrared light was present, which is invisible to *G. petersii* (Ciali *et al.* 1997). Fish were observed with an infrared video camera. In other experiments, a dim light was turned on above the experimental tank, with a maximum of approximately
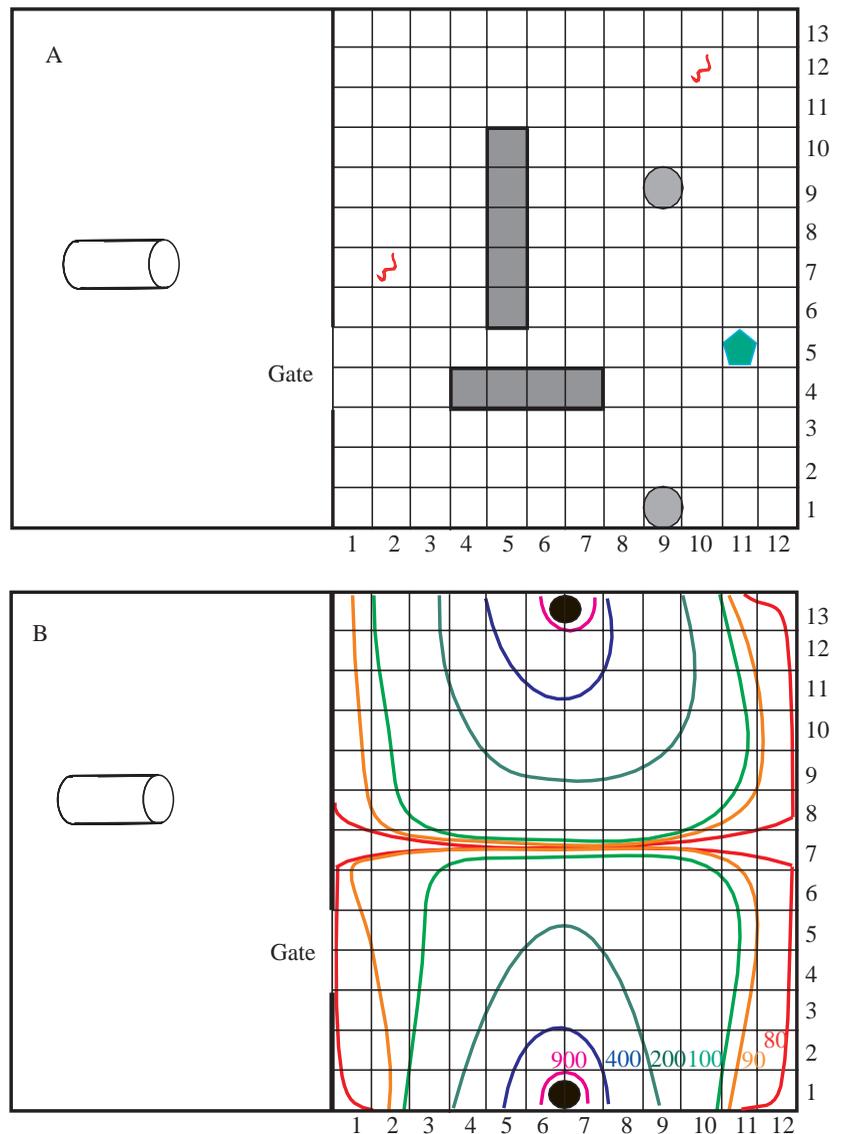

Fig. 1. (A) Experimental arrangement. View of the experimental tank with the search arena (environment 1) on the right seen from above. The cylinder on the left depicts the hiding place (ceramic tube) of the fish. Objects in the search arena are marked by bordered areas: two flat bricks (rectangles), two plastic columns (grey circles) and one artificial water plant (green pentagon). Two chironomid larvae (red worms) were placed at coordinates (2,7) and (10,12), respectively. (B) Distribution of noise amplitudes in the test arena during the presentation of high-frequency electric noise through two carbon electrodes marked as black dots. Each line connects the points where a certain noise amplitude was measured. Values are noise amplitudes in mV cm^{-1} (RMS).

0.75 lx in the centre of the search arena. In some experiments, a bright light was used. It had a maximum amplitude of 75 lx above the floor of the test arena. Even with visible light present, fish were observed with the video camera to ensure identical measurement conditions.

Electrical noise

During some experiments, bandpass-filtered electrical white noise was introduced into the search arena to mask either the EODs of the fish (high-frequency noise) or the low-frequency electric signals emitted by the prey (low-frequency noise). Two carbon electrodes (diameter 0.6 cm; length 5 cm) were placed opposite each other close to the glass walls of the experimental compartment (Fig. 1B). Their connecting axis was oriented parallel to the dividing wall in the middle of the experimental compartment. Bandpass-filtered white noise was produced by an arbitrary waveform generator (Wavetek, model 395), attenuated by a defined value (custom-built attenuator) and delivered through an isolation unit (custom-built with a flat frequency response between 1 Hz and 70 kHz) to the carbon electrodes.

The electrical field strengths of the noise were measured using two chloridised silver wire electrodes, insulated except for the tips, separated by 1 cm. The electrode arrangement was placed 1 cm above the floor in each of the squares painted on the floor of the search arena. It was turned at each spot, until a maximum amplitude was measured. Signals were amplified using a custom-built amplifier with a flat frequency response between 1 Hz and 50 kHz.

The measured electric fields (Fig. 1B) were strongest close to the electrodes and declined towards the centre and the four corners of the experimental chamber. Lowest field strengths were measured in a small area at the centre of the tank and in the corners. The amplitude of the noise was adjusted so that a certain amplitude was still exceeded even at the corners. During the experiments with electric noise, no objects were present in the search arena to prevent them from altering the electric field.

Two types of noise were used. (1) Low-frequency noise (LF noise) was filtered between 0.1 Hz and 150 Hz. It was used to mask the weak low-frequency electric signals emitted by living and dead chironomid larvae (Kalmijn, 1987; Peters and Bretschneider, 1972; R. C. Peters, personal communication), which might be detected through the ampullary electroreceptors of *G. petersii*. The noise had a minimum amplitude of 0.7 mV cm^{-1} (RMS) in the corners of the search arena. Close (2 mm) to the electrodes, the amplitude was as high as approximately 9 mV cm^{-1} (RMS). These amplitude values were chosen because they are well above threshold values reported for ampullary receptors of teleosts ($<100 \mu$V cm^{-1}; Bennett and Clusin, 1979). The ampullary receptors of *G. petersii* have a similar threshold (G. von der Emde, personal observation). (2) High-frequency noise (HF noise) was filtered between 3 and 5 kHz and had a minimum RMS amplitude of 70 mV cm^{-1} and a maximum amplitude of 900 mV cm^{-1} close to the electrodes (Fig. 1B) in order to mask the high-frequency EODs the fish emits during food searching and uses for active electrolocation (von der Emde, 1990). The amplitude of the HF noise at every point in the search arena was as strong or stronger than the EODs of the fish (G. von der Emde, unpublished measurements).

The noise was turned on before a trial started. Each fish was given 1 week of training with electrical noise to become accustomed to its presence. Usually, it took a fish approximately 2 days, after which it readily swam through the gate into the search arena containing the noise and searched for food.

During a session with electrical noise, every second trial was conducted without turning on the noise. These trials served as controls for the noise experiments. Median search times with and without noise were subsequently calculated and compared.

Living insect larvae

Experiments were also conducted using living chironomid larvae. The experimental procedures were otherwise identical. For each larva, it was noted whether it moved while in the arena or whether it remained motionless. When a larva started to move at any time during a trial, it was counted as moving. Larval movement was a continuous wriggling motion that usually remained constant throughout a search trial. The number of moving larvae was approximately twice as high as the number of motionless larvae. Care was taken to ensure that each larva used was still alive when placed in the search arena and that there was no size difference between moving and motionless larvae. Median search times to find moving and motionless larvae were calculated separately and compared.

Artificial insect larvae

In order to examine the contribution of chemical cues during foraging, we used artificial 'insect larvae' during some experiments. These dummies were made from red-coloured gelatine and glycerol. They were briefly fixed in 0.5 % formalin, to prevent them from swelling in aquarium water, and washed several times with distilled water. They had a similar size and a shape to those of a typical real chironomid larva. Artificial larvae 'with flavour' were prepared by using the fluid from squeezed-out frozen insect larvae. Artificial larvae 'without flavour' were prepared with water. To ensure that the latter had the same electrical conductivity as larvae with flavour, NaCl was added to the water used for making larvae without flavour until it had the same conductivity as the larval extract.

As with the electrical noise experiments, only every second trial was conducted with two artificial insect larvae placed in the arena. The other trials served as controls. They were performed in the usual way using real, dead larvae. In three fish (10, 11, 12), another procedure was used: instead of placing two artificial larvae in the arena, one real and one artificial larva were used simultaneously. After completion of all the trials, median search times for artificial and real larvae were calculated separately and compared.

Results

After a fish had become accustomed to the task, median search times to find two insect larvae did not change

significantly when fish were tested repeatedly under the same conditions. Even though search times varied considerably in individual trials, median values calculated from 75 trials conducted in 15 different environments differed only slightly and always insignificantly (compare, for example, open columns for fish 6–12 in Figs 3 and 4) under identical experimental conditions. This allowed us to compare median search times measured under different sensory conditions.

Silenced fish

Silenced fish did not show any overt behavioural differences compared with intact fish. Their motivation to start searching for food and their foraging behaviour were normal, and it was impossible to recognise a silenced fish only through behavioural observations. After recovery from surgery, silenced fish were motivated to perform in the food-search task equally well as before surgery, even in complete darkness.

Fig. 2 shows the performance of the five silenced fish and one sham-operated control fish before and after surgery. While the control fish did not show any difference in performance, four out of the five silenced fish performed significantly better before the surgery then after, i.e. when they could still actively electrolocate. There was no change in the performance of fish 4.

Electrical noise

High-frequency noise

Even though fish became accustomed to the presence of HF electrical noise in the search arena, their searching behaviour differed somewhat from the behaviour without the noise present. They more frequently interrupted searching and swam upwards into the open water. When they did so, the clock was stopped; it was restarted when the fish resumed its search. The control experiments with silenced fish showed, however, that the median search times of these fish were not affected by the presence of HF noise in the search arena (Fig. 3), indicating that an increase in search time in intact fish was not caused by a general disturbing effect of HF noise on the fish.

Seven fish were tested with HF noise present during foraging (Fig. 3). Two of these were retested under identical conditions after their electrical organ had been silenced. Six out of the seven fish took longer to search for prey in the presence of HF noise than they did in the absence of noise. This trend was absent in electrical silenced fish (fish 6 and 7) (Fig. 3).

Low-frequency noise

In contrast to the effects of HF noise, the search behaviour of the fish was not altered when LF electrical noise was present during foraging. Nevertheless, LF noise could interfere with foraging success. Eight fish were tested in the presence of LF noise. Three silenced fish, two of which had been tested before under the same conditions, served as controls. In three out of the seven intact fish, the presence of LF noise prolonged food search times significantly; in another three fish, search times did not increase significantly. In one fish, median search times were the same in the presence and absence of LF noise. The three
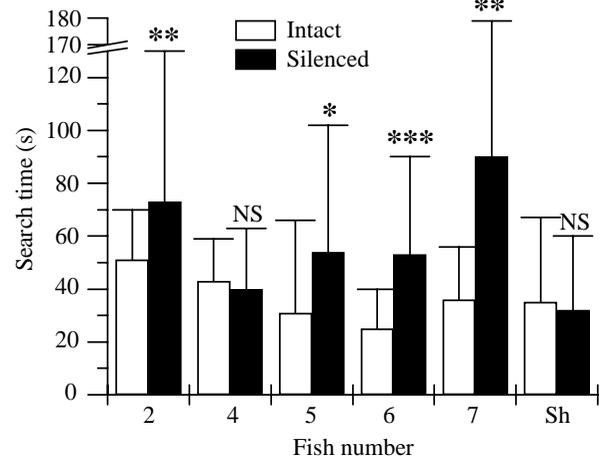

Fig. 2. Median search times of six fish for finding two randomly placed dead chironomid larvae in the search arena in darkness. Each column is the median of 75 trials conducted in 15 different 'environments'. Error bars represent the upper quartiles. Each fish was tested before (open columns) and after (filled columns) surgically silencing its electric organ. One fish (Sh) was sham-operated without silencing. Note that silenced fish could no longer use active electrolocation. In this and subsequent figures: NS, no significant difference; $*P<0.05$; $**P<0.01$; $***P<0.001$. Asterisks denote significance levels between the right- and left-hand columns of each group. Except in Figs 9 and 10, column heights represent the median time needed by a fish to find *two* food items.

silenced fish were also affected by LF noise: search times were significantly prolonged when LF noise was present (Fig. 4).

Light

Six fish, two of which were electrically silenced, were tested to determine whether they could find their food more quickly when visible light was present, i.e. when they could use vision for food searching. The two silenced fish found food faster when the lights were on than in complete darkness. The results with intact fish varied: one of the intact fish found food faster when light was present (9); two fish performed the same whether visible light was present or not (11, 12); and one fish found food significantly faster in darkness than in the light (10) (Fig. 5).

Light and noise

Four fish were tested under different light conditions in combination with LF or HF electrical noise to determine whether fish still use active or passive electrolocation when they can use visual cues (Fig. 6). The performance of all except one fish was significantly impaired by HF noise in the dark (see also Fig. 3). When the light was on, this changed: only one out of four fish still searched longer in the presence of HF noise, while the other three fish were not affected (Fig. 6B).

LF noise had a less clear effect. In the dark, only one individual (fish 10) was slower in the presence of LF noise than without noise (see also Fig. 4). With the light on, one fish (fish 9) was impaired by the noise; however, this was a different individual from that affected by noise in darkness (Fig. 6A).
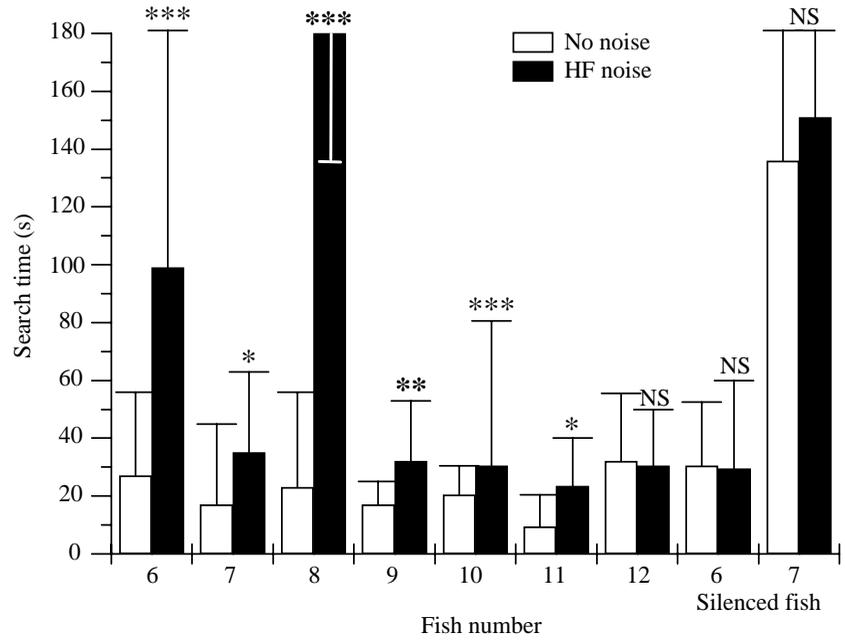
Fig. 3. The effect of high-frequency (HF) electrical noise on search times in the dark. Fish were tested in an empty search arena without (open columns) and in the presence of (filled columns) HF noise. HF noise prevents active electrolocation by interfering with the perception of the self-produced electric organ discharges of the fish. Two fish (6 and 7) were tested twice: before and after silencing their electrical organs. While silenced they served as controls. Symbols as in Fig. 2.

Living insect larvae

Seven fish were tested with living insect larvae, and their performance was compared with that when dead larvae were used (Fig. 7). One fish was retested after surgery had rendered it electrically silent. Four out of the seven intact fish took significantly longer to find living *versus* dead insect larvae. One fish was significantly faster when living larvae were used, and two showed no significant difference in performance. Fish 6 found dead larvae significantly faster when it was still able to use active electrolocation, whereas after surgical silencing of its electric organ, living larvae were found faster (Fig. 7).

Living larvae and electrical noise

In order to test whether living larvae were detected by active or passive electrolocation, masking experiments with different types of electrical noise were conducted with fish 9 (Fig. 8). Low-frequency noise, which prevents passive electrolocation, interfered with food searching only when living larvae were used. High-frequency noise, in contrast, significantly increased the times to find both dead and living larvae (Fig. 8).

Moving versus motionless larvae

In order to determine whether movement of larvae increased their detectability by weakly electric fish, prey movements
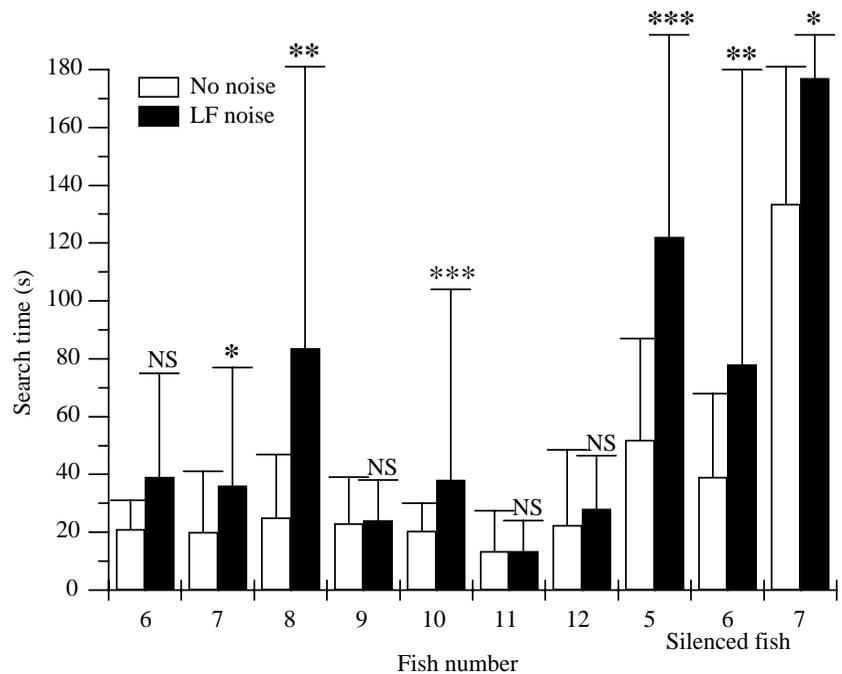
Fig. 4. The effect of low-frequency (LF) noise on search times in the dark. LF noise jammed the fishes' passive electrolocation system (filled columns). All except one of the intact fish took longer to find their prey when LF noise was present, the difference was significant, however, in only three cases. All three silenced fish were also affected by the noise because silencing does not affect passive electrolocation. Symbols as in Fig. 2.
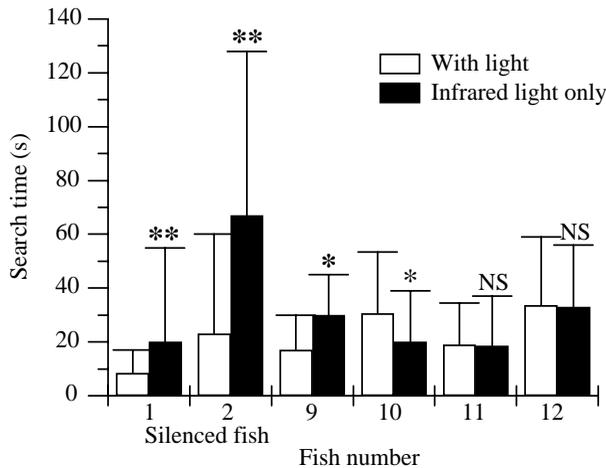
Fig. 5. The effect of visible light on search times. Six fish, two of which were electrically silenced, were tested to determine whether they found their prey faster when visible light was present (open columns) or absent (filled columns). Symbols as in Fig. 2.

0.05 mmol l^{-1} Co^{2+}, as used successfully in *Aplocheilus lineata* (Vogel and Bleckmann, 1997) and in the goldfish (D. Vogel, personal communication), led to severe behavioural disorders in *G. petersii*. Even at a concentration of 0.01 mmol l^{-1} Co^{2+}, our fish were no longer motivated to feed, moved around very slowly and appeared unwell. Therefore, experiments involving lateral line blocking with Co^{2+} were abandoned.

Prey movement and noise

One fish (12) was tested with wriggling and motionless live larvae in presence of HF and LF electrical noise and in the presence and absence of light. This individual always found wriggling larvae faster, no matter whether masking noise interfered with active (HF noise) or passive (LF noise) electrolocation (Fig. 10). The presence of visible light did not change this finding: again, moving larvae tended to be found faster than motionless ones, but only one of the tests resulted in a statistically significant difference between moving and non-moving larvae (Fig. 10).

Artificial insect larvae

In order to test whether chemical cues play a role during food searching, artificial insect larvae with or without 'chironomid flavour' were used as prey items. Six fish were tested, one of which was electrically silent (Fig. 11). Even when artificial larvae with flavour were used, a fish would eat only one artificial insect larva. Thereafter, it only made a characteristic head movement towards the dummy larva after localising it, without taking it into its mouth. Because of this behaviour, it was still possible to measure the time the fish needed to find the artificial larvae.

It took all fish longer to find artificial insect larvae than real larvae. All except one fish found artificial larvae with flavour

were noted for four *G. petersii*. Three out of four fish tended to find wriggling larvae faster than motionless ones. However, this difference was not statistically significant in any case. Similar results were obtained whether fish were tested in the dark or with visible light present (Fig. 9).

In order to test whether the mechanosensory lateral line system was involved in detecting moving prey, we tried to block the mechanosensitivity of the lateral line by adding cobalt ions to the water (Hassan *et al.* 1992; Karlsen and Sand, 1987). A concentration of 0.1 mmol l^{-1} Co^{2+} (at a Ca^{2+} concentration of less than 0.1 mmol l^{-1}), as recommended for the roach (Karlsen and Sand, 1987), or a concentration of
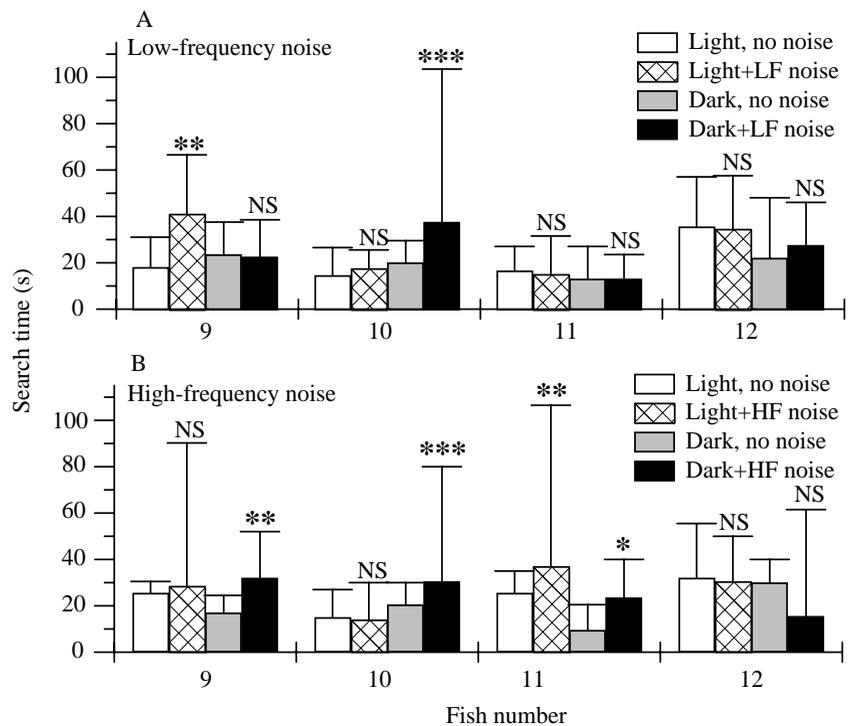

Fig. 6. The cumulative effects of light and electrical noise on search times. (A) Four intact fish were tested in the light and in the dark with and without low-frequency (LF) noise. (B) The same individuals as in A were tested with combinations of light and HF noise. Symbols as in Fig. 2.
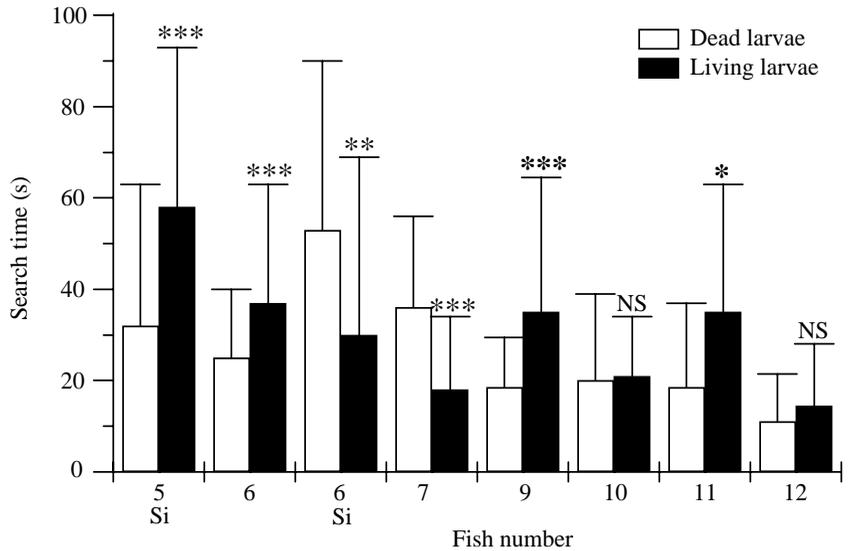
Fig. 7. Comparison of search times for two dead (open columns) or two living (filled columns) chironomid larvae. Some fish took longer to find living larvae, in others the opposite happened. Fish 6 was tested before and after silencing (Si). Fish were tested in the dark. Symbols as in Fig. 2.

faster than flavourless larvae. Statistical tests revealed, however, that only some of these results were significant (Fig. 11).

Discussion

Our results revealed that the weakly electric fish *Gnathonemus petersii* uses many senses during foraging for insect larvae, some of which have been examined in the present study. Another sensory modality, which we did not include in our tests, might be touch. Foraging fish use their flexible chin appendix as a probe and search with it amongst the gravel on the floor. Besides being densely packed with electroreceptors, this organ may also contain chemical and touch receptors (Harder, 1968). Thus, touching an insect larva might have contributed to its detection and identification as a possible prey item.

Active electrolocation

Because weakly electric fish have developed a special active electrolocation system, it seems likely that active electrolocation is crucial during food searching, particularly since the brain and many peripheral structures of *G. petersii* have changed dramatically during the evolution of the electric sense and active electrolocation (Bell and Szabo, 1986; Bullock *et al.* 1982; Finger *et al.* 1986). The enormous increase in size of several brain structures assumed to be used exclusively for active electrolocation implies an evolutionary advantage in being able to electrolocate actively. One of these advantages is the ability of mormyrids to feed at night, which involves orientation without vision and prey detection in the dark. Active electrolocation might allow mormyrids to access extra food resources available at night and to avoid visually guided predators.

Therefore, it was a surprise to find that electrically silenced fish moved around effortlessly in complete darkness and found their prey successfully, even though they were unable to electrolocate actively. Silenced fish and fish prevented from using active electrolocation by electrical noise needed a little
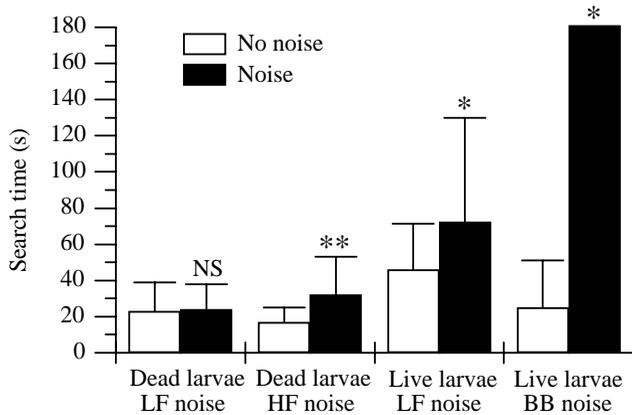

Fig. 8. Results of experiments conducted with fish 9, involving dead and living larvae and electrical noise. Open columns depict median search times in the absence of noise; filled columns give results in the presence of noise. Low-frequency (LF) noise, high-frequency (HF) noise or both (broadband noise, BB) were used. Symbols as in Fig. 2.
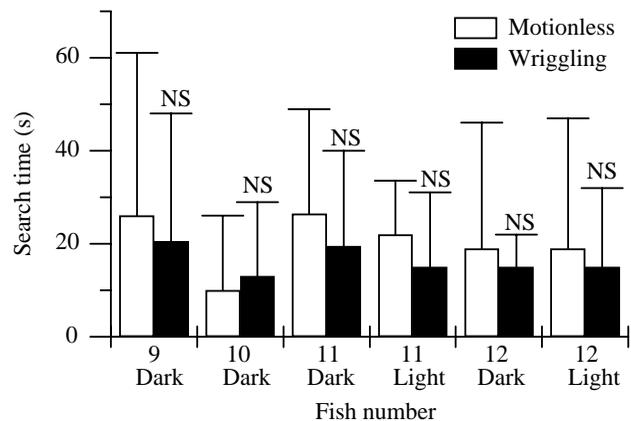

Fig. 9. Comparison of search times of four fish that had to find living insect larvae that were actively moving (filled columns) or were motionless (open columns). Columns depict the median time to find only one insect larva. Fish 11 and 12 were tested both in the presence of visible light and in the dark. Symbols as in Fig. 2.
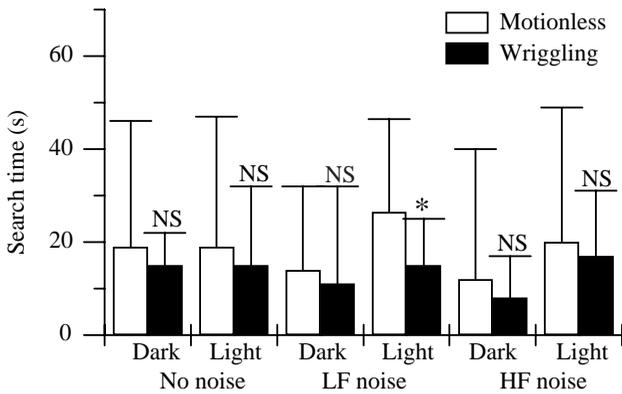
Fig. 10. Tests with fish 12 involving visible light and two types of electrical noise. Column heights represent the median times to find only one larva. This fish always found moving larvae faster then motionless ones, no matter whether vision, passive electrolocation (prevented by low-frequency noise) or active electrolocation (prevented by high-frequency noise) was possible, although the difference was only significant in one case. Symbols as in Fig. 2.

longer to find two insect larvae (Figs 3, 6B), but they were not seriously impaired. Their movements in the dark were fast and seemed to be unchanged compared with those of intact fish. Previous studies showed that *G. petersii* relies on active electrolocation much more when the environment is complex and unfamiliar (Cain, 1995; Cain *et al.* 1994; von der Emde, 1994). In an empty search arena, for example, without any objects and without floor covering, fish find and identify prey items even without electrolocation so quickly that jamming or silencing the fish has no significant effect on its search time. The more natural the environment, the greater the advantage conferred by electrolocation. Therefore, in our experiments, we ensured that the fish had to search for food in unfamiliar

and structured surroundings by constantly using different 'environments' with randomly arranged objects. The advantages of active electrolocation might be even more apparent in the complex natural habitat of the fish, where many more demands for prey location and identification exist.

Passive electrolocation

Weakly electric mormyrids possess a special set of very sensitive ampullary electroreceptor organs that respond to low-frequency electric signals (Bennett, 1971; Kalmijn, 1974; Zakon, 1987). Although ampullary organs do respond to the fish's EOD, this response is not greatly modulated by nearby objects (Bell and Russell, 1978), and ampullary receptors are not believed to be involved in active electrolocation (C. C. Bell, personal communication). Ampullary organs do respond to changes in low-frequency electric fields, some of which come from prey items. The detection of such external fields is called passive electrolocation (Peters and Bretschneider, 1972). The most important biotic electric fields are caused by biochemical processes. Peters and Bretschneider (1972) were able to measure stationary electric fields of the dipole type in fresh water that were generated by fishes, aquatic insect larvae, tadpoles and snails. Kalmijn (1987) reports low-frequency electric fields around more than 60 marine vertebrate and invertebrate species representing nine phyla. In particular, strong electric signals were found to radiate from wounded crustaceans. Because of these results, it is likely that dead chironomid larvae may also be a source of low-frequency electric fields (R. Peters, personal communication), which might be detectable through ampullary electroreceptors.

Our results support the hypothesis that passive electrolocation can play a role during food searching in *G. petersii* (Figs 4, 6). All fish needed longer to find food when the electrical currents originating from the prey were jammed
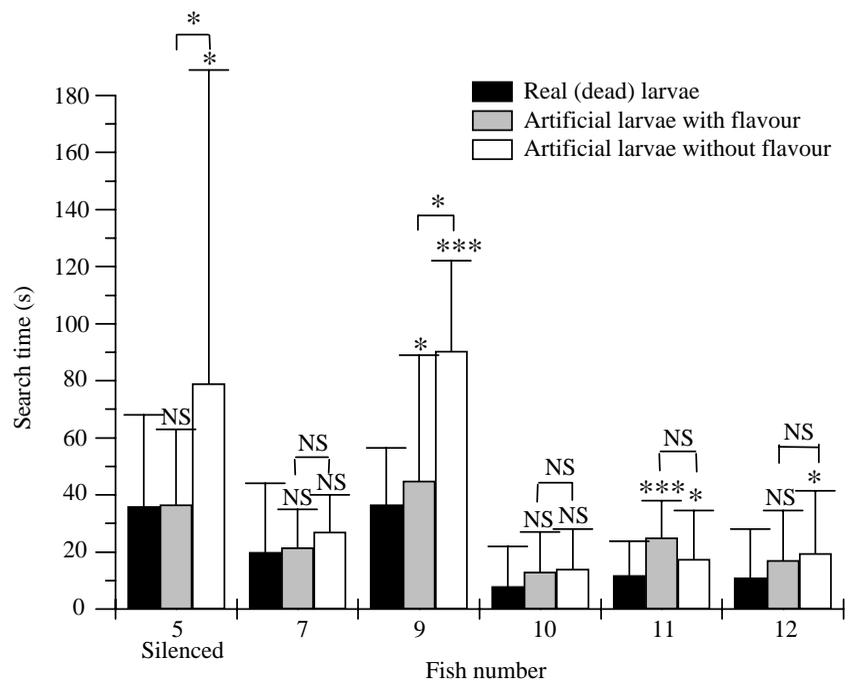

Fig. 11. Comparison of search times for real (dead) insect larvae (black columns), artificial 'larvae' made with larval extract (with flavour, grey columns) and artificial 'larvae' made only with water (without flavour, white columns) in the dark. Results for fish 5, 7 and 9 indicate search times for two larvae, for fish 10, 11 and 12 median times to find only one larva are given. Symbols as in Fig. 2.

by low-frequency electrical noise. Silenced fish, which are deprived of active electrolocation, appeared to rely even more on passive electrolocation as a substitute (Fig. 4).

Passive electrolocation plays a dominant role in many marine elasmobranchs, which possess the most sensitive ampullary receptor organs reported so far and use them to find their prey electrically (Kalmijn, 1987). Siluriforms are electroreceptive teleosts, which also use passive electrolocation for prey detection and orientation (Peters and Bretschneider, 1972). Kalmijn (1974) reports that catfish (*Ictalurus nebulosus*) were able to locate passively the position of a goldfish hidden behind a layer of electrically transparent agar. The hunting behaviour of several *Clarias* species in South African rivers provides another example of the probable use of passive electrolocation by catfish. These catfish selectively hunt two species of mormyrids by a method termed 'pack-hunting' (Merron, 1993), which is probably based on passive electrolocation (Hanika and Kramer, 1997).

Vision

Like most mormyrids (Hopkins, 1981; Moller *et al.* 1979), *G. petersii* are nocturnal. Nevertheless, they have large eyes specialised for vision in blackwater habitats with adaptations to the spectral distribution of ambient light (Ciali *et al.* 1997; Moller *et al.* 1982). Our results provide some indication that vision is used for prey detection. When searching for food in the light, the search times of some fish are shorter than those measured in complete darkness (Fig. 5). Vision can even play such an important role that active electrolocation no longer contributes greatly to foraging success when light is present. This is indicated in Fig. 6, where some fish were not influenced by jamming HF electrical noise when the lights were on but were influenced only during darkness. Activity periods in the wild start at dusk, shortly before sunset (Moller *et al.* 1979). At these times, and also when moonlight is present during the night, vision may be used in foraging and may contribute to food searching. In contrast, one fish (10) in Fig. 5 searched longer for food when the lights were on than in darkness. This might be explained by the observation that some fish are disturbed by light and tend to move more slowly and cautiously than in darkness. Newly caught fish introduced into a tank are even more pronounced in their reluctance to be active during daytime and avoid open illuminated spaces. After some time in captivity and after becoming accustomed to feeding during the day, this fear of light usually disappears.

Living insect larvae

When comparing the performance of fish finding living *versus* dead insect larvae, an ambiguous picture emerges. While some fish were faster at finding dead larvae, others found living larvae more quickly (Fig. 7). This result shows again that different individuals employ different strategies for foraging. Different sensory cues might have been involved in finding dead *versus* living larvae: dead larvae probably emitted more chemical cues then living ones, because most of the former were not completely intact, leaking their internal fluid into the water (see below). Many of the living larvae, however,

performed wriggling movements when placed in the search arena, which provided additional mechanical and other cues (see below). It is not known whether there were also differences between living and dead larvae in their electrical properties (active electrolocation) or in the amount of electrical current they produced (passive electrolocation).

The results obtained when testing fish 6 (Fig. 7) indicate that active electrolocation was used to find dead larvae but to a lesser extent to find living larvae. Living larvae were obviously found not by active electrolocation but by other means, perhaps by monitoring prey movements using the mechanosensory lateral line system.

Fig. 8 shows that prey searching by fish 9 could only be jammed by HF noise when it had to find dead larvae. In contrast, both high- and low-frequency noise interfered with the search for living insect larvae. This means that, in this fish, passive and active electrolocation contributed to the detection of living larvae, while only active electrolocation was involved in finding dead larvae. In the latter case, chemical cues may have played an important role, pushing the other senses into the background and speeding up detection. This hypothesis is supported by the results of experiments conducted with artificial insect larvae depicted in Fig. 11.

Mechanosensory lateral line

The mechanosensory lateral line system of fishes is used for the detection of relative water movements. Some fish species employ this sense for the detection of moving prey (Bleckmann, 1993; Montgomery *et al.* 1988). In the present study, we tested whether *G. petersii* also finds wriggling prey, which produce hydrodynamic stimuli, faster than motionless prey. Our results show that this assumption may be correct, because all except one fish consistently found moving prey faster than motionless prey (Fig. 9). Neither the addition of light nor jamming of the electric sense by LF or HF noise could abolish this ability. This indicates that it is indeed the mechanosensory lateral line that decreases search times and not the detection of visual or electrical motion.

Chemical sense

As mentioned above, dead insect larvae emit a chemical 'flavour', which may be detected by the fish. Many fish species, e.g. catfish or goldfish, can use chemical cues for prey detection (Lamb and Finger, 1995; Valentincic and Caprio, 1994). *G. petersii* possesses a well-developed olfactory system, which may be involved in food searching (Rooney *et al.* 1989). Our experiments showed that some fish indeed failed to find larval dummies without flavour as fast as those with flavour or real insect larvae. When flavour was added to the larval dummies, they were found as fast as real larvae (Fig. 11). It may be that there is a profound electrical difference between real larvae and the dummies used. Artificial larvae (even those with flavour) were never taken into the mouth after a fish had tried them once. Obviously, the prey identification system, possibly involving capacitance detection (von der Emde and Ronacher, 1994), recognised them as inedible before they were swallowed. An alternative explanation would be that, despite

the careful rinsing of the dummy larva, there was some residual formalin left which was sensed by the fishes. However, the fact that larvae with flavour were detected as fast as real larvae by some fish indicates that the formalin was not an important factor. Instead, chemical food cues probably play an important role in prey localisation.

Multimodal integration

Our results revealed that *G. petersii* is not completely dependent on just one sense for finding food. This contrasts strongly with another active orientation system used by insectivorous bats: active echolocation. If a bat is unable to produce sound or is jammed so strongly by continuous acoustic noise that it is prevented from receiving the echoes of its echolocation calls, it is completely helpless and will no longer fly or catch insects on the wing (Neuweiler, 1990; Schnitzler, 1984; G. von der Emde, personal observation). Similarly, a blind hawk or a deaf owl is no longer able to find food in the wild. Weakly electric mormyrids, in contrast, are able to compensate immediately for the loss of active electrolocation and to use their other senses instead. They are flexible in their ability to exploit environmental cues indicating the location of their food and substitute an available sense for one that is not available (see also Cain, 1995; Cain *et al.* 1994). For example, some fish might use vision and not active electrolocation when enough light is available. Under these circumstances, they are not impaired by jamming high-frequency electrical noise. The same individuals actively electrolocate, however, when the lights are turned off and are then jammed by the addition of HF electrical noise (Fig. 6B).

The results of our study also show that each individual fish uses its own strategy when searching for food. In almost every test, there was no uniform result over all individuals tested. Some fish were not impaired by silencing their electric organs, but others were (Fig. 2). Some fish relied greatly on chemical cues and thus were more impaired then others when they had to find an artificial insect larva without flavour (Fig. 11). Individual sensory strategies for foraging were also adopted when searching for living *versus* dead insect larvae. Some fish found living larvae faster than dead ones, while others were significantly faster when dead larvae were used (Fig. 7). In some cases, the fish may have relied more on larval movements for prey detection, which were detected by the mechanosensory lateral line system, and less on chemical cues. In other cases, chemical cues could have been more dominant.

References

BASTIAN, J. (1986). Electrolocation: behavior, anatomy and physiology. In *Electroreception* (ed. T. H. Bullock and W. Heiligenberg), pp. 577–612. New York: John Wiley & Sons.

BASTIAN, J. (1994). Electrosensory organisms. *Physics Today* **47**, 30–37.

BELL, C. C. AND RUSSELL, C. J. (1978). Effect of electric organ discharge on ampullary receptors in a mormyrid. *Brain Res.* **145**, 85–96.

BELL, C. C. AND SZABO, T. (1986). Electroreception in mormyrid fish. Central anatomy. In *Electroreception* (ed. T. H. Bullock and W. Heiligenberg), pp. 375–421. New York: John Wiley & Sons.

BENNETT, M. V. L. (1971). Electroreception. In *Fish Physiology* (ed. W. S. Hoar and D. J. Randall), pp. 493–574. New York: Academic Press.

BENNETT, M. V. L. AND CLUSIN, W. T. (1979). Transduction at electroreceptors: origin of sensitivity. In *Membrane Transduction Mechanisms* (ed. R. A. Cone and J. E. Dowling), pp. 91–116. New York: Raven Press.

BLAKE, B. F. (1977). Food and feeding of the Mormyrid fishes of Lake Kainji, Nigeria, with special reference to seasonal variation and interspecific differences. *J. Fish Biol.* **11**, 315–328.

BLAXTER, J. H. S. (1988). Sensory performance, behavior and ecology of fish. In *Sensory Biology of Aquatic Animals*, chapter 8 (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 203–232. New York, Berlin, Heidelberg: Springer Verlag.

BLECKMANN, H. (1993). Role of the lateral line in fish behaviour. In *Behaviour of Teleost Fishes*, chapter 7 (ed. T. J. Pitcher), pp. 201–246. London: Chapman & Hall.

BULLOCK, T. H., NORTHCUTT, R. G. AND BODZNICK, D. A. (1982). Evolution of electroreception. *Trends Neurosci.* **5**, 50–53.

CAIN, P. (1995). Navigation in familiar environments by the weakly electric elephantnose fish, *Gnathonemus petersii* L. (Mormyriformes, Teleostei). *Ethology* **99**, 332–349.

CAIN, P., GERIN, W. AND MOLLER, P. (1994). Short-range navigation of the weakly electric fish, *Gnathonemus petersii* L. (Mormyridae, Teleostei), in novel and familiar environments. *Ethology* **96**, 33–45.

CIALI, S., GORDON, J. AND MOLLER, P. (1997). Spectral sensitivity of the weakly discharging electric fish *Gnathonemus petersii* using its electric organ discharges as the response measure. *J. Fish Biol.* **50**, 1074–1087.

CORBET, P. S. (1961). The food of non-cichlid fishes in the Lake Victoria basin, with remarks on their evolution and adaptation to lacustrine conditions. *Proc. zool. Soc., Lond.* **136**, 1–101.

DUSENBERY, D. B. (1992). *Sensory Ecology, How Organisms Acquire and Respond to Information*. New York: W. H. Freeman and Company. 558pp.

FINGER, T. E., BELL, C. C. AND CARR, C. E. (1986). Comparison among electroreceptive teleosts: Why are electrosensory systems so similar? In *Electroreception* (ed. T. H. Bullock and W. Heiligenberg), pp. 465–481. New York: John Wiley & Sons.

HANIKA, S. AND KRAMER, B. (1997). Predation on weakly electric fish by the African Sharptooth Catfish, *Clarias gariepinus*: electrosensory detection distance. *Verh. dt. zool. Ges.* **90. 1**, 351.

HARDER, W. (1968). Die Beziehungen zwischen Elektrorezeptoren, elektrischen Organen, Seitenlinienorganen und Nervensystem bei den Mormyridae (Teleostei, Pisces). *Z. vergl. Physiol.* **59**, 272–318.

HASSAN, E.-S., ABDEL-LATIF, H. AND BIEBRICHER, R. (1992). Studies on the effects of Ca^{++} and Co^{++} on the swimming behavior of the blind Mexican cave fish. *J. comp. Physiol.* A **171**, 413–419.

HEILIGENBERG, W. (1973). Electrolocation of objects in the electric fish *Eigenmannia* (Rhamphichthyidae, Gymnotoidei). *J. comp. Physiol.* **87**, 137–164.

HEILIGENBERG, W. (1984). Neural mechanisms of electrolocation and jamming avoidance behavior in electric fish. In *Comparative Physiology of Sensory Systems* (ed. L. Bolis, R. P. Keynes and S.

H. P. Maddrell), pp. 475–495. Cambridge, London: Cambridge University Press.

Höller, P. and Schmidt, U. (1996). The orientation behaviour of the lesser spearnosed bat, *Phyllostomus discolor* (Chiroptera) in a model roost. Concurrence of visual, echoacoustical and endogenous spatial information. *J. comp. Physiol.* A **179**, 245–254.

Hopkins, C. D. (1981). On the diversity of electric signals in a community of Mormyrid electric fish in West Africa. *Am. Zool.* **21**, 211–222.

Hyslop, E. J. (1986). The food habits of four small-sized species of Mormyridae from the floodplain pools of the Sokoto-Rima river basin, Nigeria. *J. Fish Biol.* **28**, 147–151.

Kalko, E. K. V. (1995). Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). *Anim. Behav.* **50**, 861–880.

Kalmijn, A. J. (1974). The detection of electric fields from inanimate and animate sources other than electric organs. In *Handbook of Sensory Physiology*, vol. III/3 (ed. A. Tessard), pp. 148–200. Berlin: Springer Verlag.

Kalmijn, A. J. (1987). Detection of weak electric fields. In *Social Communication in Aquatic Environments* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 151–186. Berlin, Heidelberg, New York: Springer Verlag.

Karlsen, H. E. and Sand, O. (1987). Selective and reversible blocking of the lateral line in freshwater fish. *J. exp. Biol.* **133**, 249–262.

Kramer, B. (1996). Electroreception and communication in fishes. In *Progress in Zoology*, vol. 42, pp. 1–119. Stuttgart: Gustav Fischer Verlag.

Lamb, C. F. and Finger, T. E. (1995). Gustatory control of feeding behavior in goldfish. *Physiol. Behav.* **57**, 483–488.

Lannoo, M. J. and Lannoo, S. J. (1993). Why do electric fish swim backwards? An hypothesis based on gymnotiform foraging behavior interpreted through sensory constraints. *Env. Biol. Fish.* **36**, 157–165.

Lissmann, H. W. (1958). On the function and evolution of electric organs in fish. *J. exp. Biol.* **35**, 156–191.

Lissmann, H. W. and Machin, K. E. (1958). The mechanism of object location in *Gymnarchus niloticus* and similar fish. *J. exp. Biol.* **35**, 451–486.

Marrero, C. and Winemiller, K. O. (1993). Tube-snouted gymnotiform and mormyriform fishes: convergence of a specialized foraging mode in teleosts. *Env. Biol. Fish.* **38**, 299–209.

Martin, G. R. (1991). The question of polarization. *Nature* **350**, 194.

Merron, G. S. (1993). Pack-hunting in two species of catfish *Clarias gariepinus* and *C. ngamensis* in the Okavango Delta, Botswana. *J. Fish Biol.* **43**, 575–584.

Moller, P. (1981). Ecology and ethology of electric fish in West Africa. *Nat. geogr. Soc. Res. Rep.* **1981**, 519–526.

Moller, P., Serrier, J., Belbenoit, P. and Push, S. (1979). Notes on the ethology and ecology of the Swashi river mormyrids (Lake Kainji, Nigeria). *Behav. Ecol. Sociobiol.* **4**, 357–368.

Moller, P., Serrier, J., Squire, A. and Boudinot, M. (1982). Social spacing in the mormyrid fish *Gnathonemus petersii* (Mormyriformes): A multisensory approach. *Anim. Behav.* **30**, 641–650.

Montgomery, J. C., Macdonald, J. A. and Housley, G. D. (1988). Lateral line function in an Antarctic fish related to the signal produced by planktonic prey. *J. comp. Physiol.* A **163**, 827–833.

Neuweiler, G. (1990). Auditory adaptations for prey capture in echolocating bats. *Physiol. Rev.* **70**, 615–641.

Obrist, M. K. (1995). Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* **36**, 207–219.

Okedi, J. (1965). The biology and habits of the Mormyrid fishes: *Gnathonemus longibarbis*, *G. victoriae*, *Marcusenius grahami*, *M. nigricans*, *Petrocephalus catostoma*. *J. appl. Ecol.* **2**, 408–409.

Okedi, J. (1971). The food and feeding habits of the small mormyrid fishes of Lake Victoria, East Africa. *Afr. J. trop. Hydrobiol. Fish* **1**, 1–12.

Peters, R. C. and Bretschneider, F. (1972). Electric phenomena in the habitat of the catfish *Ictalurus nebulosus* LeS. *J. comp. Physiol.* **81**, 405–410.

Rooney, D. J., New, J. G., Szabo, T. and Ravaille-Veron, M. (1989). Central connections of the olfactory bulb in the weakly electric fish, *Gnathonemus petersii*. *Cell Tissue Res.* **257**, 423–436.

Schnitzler, H.-U. (1984). The performance of bat sonar systems. In *Localization and Orientation in Biology and Engineering* (ed. D. Varju and H.-U. Schnitzler), pp. 211–224. Berlin, Heidelberg: Springer Verlag.

Schnitzler, H.-U. (1987). Echoes of fluttering insects – Information for echolocating bats. In *Recent Advances in the Study of Bats* (ed. M. B. Fenton, P. Racey and J. M. V. Rayner), pp. 235–274. Cambridge, London, New York: Cambridge University Press.

Schwan, H. P. (1963). Determination of biological impedances. In *Physical Techniques in Biological Research*, vol. VI (ed. W. L. Nastuk), pp. 323–407. New York: Academic Press.

Valentincic, T. B. and Caprio, J. (1994). Chemical and visual control of feeding and escape behaviours in the channel catfish *Ictalurus punctatus*. *Physiol. Behav.* **55**, 845–855.

Vogel, D. and Bleckmann, H. (1997). Water wave discrimination in the surface-feeding fish *Aplocheilus lineatus*. *J. comp. Physiol.* A **180**, 671–681.

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

von der Emde, G. (1994). Active electrolocation helps *Gnathonemus petersii* to find its prey. *Naturwissenschaften* **81**, 367–369.

von der Emde, G. (1995). Sensory information used during food search in the weakly electric fish, *Gnathonemus petersii*. In *Nervous Systems and Behavior. Proceedings of the 4th International Congress on Neuroethology* (ed. M. Burrows, T. Matheson, P. L. Newland and H. Schuppe), p. 410. Stuttgart, New York: Georg Thieme Verlag.

von der Emde, G. (1998). Electroreception. In *The Physiology of Fishes* (ed. D. H. Evans), pp. 313–343. Boca Raton, FL: CRC Press.

von der Emde, G. and Ringer, T. (1992). Electrolocation of capacitive objects in four species of pulse-type weakly electric fish. I. Discrimination performance. *Ethology* **91**, 326–338.

von der Emde, G. and Ronacher, B. (1994). Perception of electric properties of objects in electrolocating weakly electric fish: two-dimensional similarity scaling reveals a City-Block metric. *J. comp. Physiol.* A **175**, 801–812.

Waldvogel, J. A. (1990). The bird's eye view. *Am. Sci.* **78**, 342–353.

Warburton, K. (1990). The use of local landmarks by foraging goldfish. *Anim. Behav.* **40**, 500–505.

Westby, G. W. M. (1988). The ecology, discharge diversity and predatory behaviour of gymnotiform electric fish in the coastal streams of French Guiana. *Behav. Ecol. Sociobiol.* **22**, 341–354.

Zakon, H. H. (1987). The electroreceptors: diversity in structure and function. In *Sensory Biology of Aquatic Animals* (ed. A. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 813–850. Berlin, Heidelberg, New York: Springer-Verlag.