Landmark use and development of navigation behaviour in the weakly electric fish *Gnathonemus petersii* (Mormyridae; Teleostei)

Peter Cain* and Sapna Malwal

Department of Psychology, St. Lawrence University, Canton, NY 13617, USA

*Author for correspondence (e-mail: pcain@stlawu.edu)

Summary

African mormyrids, such as *Gnathonemus petersii*, migrate: nocturnally, from daytime shelters to find food and return by morning, and seasonally, spawning in swamps flooded during the rainy season. The present study examined whether the fish use landmarks detected *via* electrolocation to locate an aperture, whether they detect changes in landmark size and respond appropriately, whether landmarks or hydrostatic pressure are the primary cues for navigation and whether fish of different developmental stages behave differently with respect to landmarks and navigation. The fish's task was to locate and swim through a circular aperture in a wall dividing an aquarium into two compartments. Two groups of fish were trained to find the aperture with a landmark present, while a control group had no such landmark. The water level remained constant throughout training. At the end of training, the fish's task was to locate the aperture after the landmark size had changed or the water level had increased. The results show that *G. petersii* use landmarks to orient and navigate. They can detect changes in landmark size and will modify their locomotor behaviour to integrate the change into an internal representation. If the water level changes, increasing hydrostatic pressure, the fish orient to a landmark, if present. If no landmark is present, the fish rely on an internal representation oriented to hydrostatic pressure. Larger, early-adult *G. petersii* located the aperture faster than smaller, sub-adult fish.

Key words: electric fish, *Gnathonemus petersii*, electrolocation, landmark, spatial navigation, development, cognitive map.

Introduction

Forming an internal representation or cognitive map (Tolman, 1932) of the environment based on sensory information is a part of spatial learning and has been demonstrated in many species, including birds, mammals and fish (Bennett, 1996; Healy, 1998; Poucet, 1993). Spatial learning allows animals to locate territories successfully and to return to abundant food sources (Cheng and Spetch, 1998). Moller et al. (1979) have described mormyrid fish leaving shelters inhabited during the day at sunset, swimming out into deeper waters to find food and returning by morning, while seasonal migrations by mormyrids have been observed during the rainy season (Corbet, 1960; Okedi, 1969).

According to Bennett (1996), successful navigation requires some memory of the position of landmarks. Local landmarks aid navigation by providing information about the environment, such as the distance and direction to a specific goal (Cheng and Spetch, 1998). Goldfish (*Carassius auratus*) learned to locate a food source more quickly if there was a visual landmark present (Warburton, 1990). Honeybees (*Apis mellifera*; Cartwright and Collett, 1983) and gerbils (*Meriones unguiculatus*; Collett et al., 1986) acquired information about the distance to a goal from the size of landmarks when the goal was reached. When the size of a previously learned landmark was modified, bees and gerbils adjusted their search for the goal relative to the size of the landmark.

As *G. petersii* learned the aperture location in the absence of local landmarks, they modified their approach and increased the height at which they made contact with the divider wall more closely to the aperture height (Cain, 1995; Cain et al., 1994). Both intact and 'electrically silent' fish increased the height at which they contacted the divider wall when the hydrostatic pressure was increased by increasing the water level (Cain, 1995) or when it was increased in a pressurized aquarium (P. Cain and J. Manchester, unpublished observations). Hydrostatic pressure acts as a global landmark or reference (Braithwaite, 1998). Similar to compass direction or distal visual information, it provides information about the location of a goal, especially to an organism that must orient and navigate in three dimensions.

G. petersii is a nocturnal bottom-dweller that lives in streams and lakes in Africa (Blake, 1977; Moller et al., 1979). These fish possess an electric organ in their tail that generates an electric organ discharge (EOD) used in communication and electrolocation (Heiligenberg, 1977; Lissmann and Machin, 1958; reviewed by Moller, 1995). *G. petersii* use electrolocation to navigate in novel environments. Once

familiar with the environment, they rely on an internal representation of their environment developed from electrosensory input and hydrostatic pressure (Cain, 1995; Cain et al., 1994). The present study investigated whether *G. petersii* uses landmarks in order to orient and acquire direction and distance information contributing to an internal representation of their environment.

Von der Emde et al. (1998) showed that *G. petersii* were able to determine the distance to different objects *via* electrolocation. The boundaries of more-distant objects were less sharply defined in the fish's electrosensory receptive field than closer objects. If fish learned to associate a landmark with an aperture and gauged the distance to the aperture based on the electrosensory image of the landmark, we hypothesized that modifying the size of the landmark would affect the locomotor trajectory that the fish took to the aperture. As with honeybees and gerbils, if the sphere increased in size, fish would maintain the electric image size by swimming upward towards the aperture sooner and, as a result, would contact the divider wall at a higher place; conversely, if the landmark size decreased, fish would contact the divider at a lower place. Because of the perceptual illusions for distance determination of spheres by weakly electric fish described by von der Emde et al. (1998), we believed that the fish would be more likely to modify their approach trajectory in order to match the learned electric image with the perceived image.

This led us to examine whether or not a change in the size of such landmarks would affect the fish's navigation once an internal representation was established. When sticklebacks were presented with conflicting information from local and global cues after becoming familiar with a feeding situation, about two-thirds oriented using global cues, while the remainder relied on local cues (Huntingford and Wright, 1989). We were therefore interested to see whether global cues, such as hydrostatic pressure, or local landmarks were the primary sensory input to guide the fish's locating behaviour.

Mormyrids of different sizes responded differently in an earlier investigation of navigation behaviour (P. Cain and W. Nolin, unpublished observations). During the breeding season, mormyrids migrate to newly flooded swamps to spawn (Corbet, 1960; Okedi, 1969). It is possible to distinguish juvenile, sub-adult and reproductively mature adult developmental stages in *G. petersii* based on anal-fin ray-bone expansion (Pezzanite and Moller, 1998). Ontogenetic shifts in habitat preference by saltwater fishes provide evidence of changes in behaviour as fish mature (Danilowicz, 1997; Macpherson, 1998). In addition, significant age-related differences in exploratory and investigatory behaviour have been documented in rats (*Rattus norvegicus*; Renner et al., 1992; Renner and Pierre, 1998; Renner and Rosenzweig, 1986). These findings led us to investigate the effect of development stage on landmark use by fish in navigation.

The current investigation examines the following hypotheses: (1) *G. petersii* learn to find a goal faster with a landmark present than without one; (2) once fish learn the location of the goal in the presence of a constant-size landmark,

they will modify their locomotor behaviour to maintain the original, learned distance/size relationship between the goal and the landmark if the landmark size is changed; (3) when the fish have a choice between hydrostatic-pressure cues and landmarks, they will choose hydrostatic-pressure cues because of their universal (and therefore primary) presence; and (4) navigation behaviour changes during development from juvenile to adult.

Materials and methods

Animals

Twenty-seven *Gnathonemus petersii* L., ranging in standard length (SL) from 110 mm to 181 mm, were obtained from a commercial fish dealer (Quality Tropicals, Mahwah, NJ, USA). Fish were housed individually and maintained on a phase-shifted 12 h:12 h L:D cycle (lights on at 24.00 h) and fed live blackworms. Water temperature was maintained at $21\pm2°C$ and conductivity was $175\pm5\,\mu S\,cm^{-1}$.

Experimental apparatus

Experiments were conducted in a dark room with an apparatus similar to that described and illustrated in Cain et al. (1994). An aquarium (92 cm×46.5 cm×45.5 cm) was divided into two equally sized compartments with a clear plastic wall. The divider was split in the middle and slotted to receive four clear plastic squares measuring 10 cm×10 cm. A circular aperture (diameter 6.85 cm) in one of the squares provided the only access from one compartment to the other. The aperture was positioned with its centre 25.5 cm from the floor (Fig. 1). Based on computations by Heiligenberg (1977) and our previous work (Cain, 1995; Cain et al., 1994), there was no evidence that fish at or beyond 15 cm from the divider wall, the electrolocation boundary, could detect the aperture using electrolocation or any other sense. Water depth was marked in 5 cm increments at the divider wall and the electrolocation boundaries on the front of the aquarium. Each compartment was illuminated independently by two red 5 W lamps (C7½, Osram Sylvania, Yonkers, NY, USA) placed behind translucent white paper covering the back wall of the aquarium. *G. petersii* can detect long-wavelength light (575–725 nm), although the fish are most sensitive to 525 nm light (Ciali et al., 1997). Under these conditions, we were able to observe and videotape the behaviour of the fish while providing them with a nearly dark environment.

We constructed three sets of landmarks, one of each diameter (3.9 cm, 6.8 cm or 8.3 cm), by attaching one end of a plastic tube to two plastic spheres of equal diameter. The opposite end of each tube was attached to a Plexiglas square. Each plastic tube was cut such that the maximum distance each plastic sphere extended was 12.5 cm from the divider wall (Fig. 1). Each square could be placed in the slotted opening so that the center of the landmarks was 20 cm directly below the aperture and 6 cm off the floor.

Training

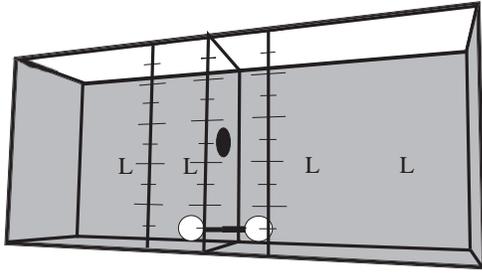The fish were divided into two groups: small fish (N=8)

Fig. 1. The experimental tank with landmark and aperture shown (not to scale). The wooden cover, lined with aluminum screen and grounded to reduce electrical interference, was removed to show the placement of the four lamps (L). The aperture, in black, was centred 25.5 cm from the floor, and the landmarks (white circles) were centred 6 cm from the floor and extended 12.5 cm on both sides of the divider wall. The electrolocation boundaries are marked on both sides of the divider wall and the depth is marked in 5 cm increments.

ranging from 113 mm to 135 mm SL (124±6.6 mm, mean ± S.D.) and large fish (*N*=9) ranging from 145 mm to 178 mm SL (159±14.4 mm). These assignments reflect two developmental stages: sub-adults and early adults, respectively (Pezzanite and Moller, 1998). Each group was trained with the medium landmark (diameter 6.8 cm). A control group of large fish (*N*=4) ranging from 145 mm to 181 mm SL (157±16.5 mm) and a control group of small fish (*N*=6) ranging from 110 mm to 132 mm SL (121±6.9 mm) were trained without landmarks.

Each fish was released into an illuminated compartment at the wall opposite the divider. The task was for the fish to locate and swim through the aperture to the non-illuminated compartment during a 300 s interval. As fish became familiar with the compartment and learned the aperture location, they would spend less time near the floor of the compartment, reduce the amount of time in the illuminated compartment and swim more directly to the aperture. These changes in locomotor behaviour resulted in faster times to and through the aperture, increased height of contact with the divider wall as the fish's trajectory more closely approached the height of the aperture, and increased number of crossings. The side of the aquarium in which the fish were released was alternated by trial-day. The fish's movements were monitored with a low-light video camera and recorded on videotape for later analysis.

If the fish swam through the aperture within 300 s, lights were turned off, and, after 15 s of darkness, the lights in the compartment where the fish was located were turned on and the fish was again allowed 300 s to swim to the non-illuminated compartment. In this way, it was possible for the fish to make numerous crosses from an illuminated to a non-illuminated compartment. However, if the fish failed to locate the aperture after 300 s, it was returned to its home tank after 60 s in darkness and given a time score of 301 s. This procedure was followed for a maximum of 10 min per day (one trial) for 10 days. The water level remained constant at 35 cm, the aperture was 25.5 cm from the floor, and the landmark was always 6.8 cm in diameter and 15 cm directly below the

aperture. Testing followed immediately upon completion of 10 training trial-days. Fish were netted and either the water level was raised or a larger or smaller landmark replaced the medium-sized landmark. Presentation of novel stimuli was counterbalanced across fish over subsequent trial-days after 5 min refresher trials under training conditions.

Landmark tests

Each fish was netted and confined at the water surface while the medium landmark was replaced with the large (8.3 cm diameter) or small landmark (3.9 cm diameter). The test began when the fish was released from the net into the illuminated compartment. Because we were not interested in how long it took the fish to learn the new conditions, we scored dependent variables for each fish for 180 s. If the fish swam through the aperture, the lights were turned off for 15 s, then turned on in the compartment where the fish was located. If the fish did not swim through the aperture, the lights were turned off, the fish was given a time score of 181 s and was returned to its home tank after 60 s.

Water-level test

A fish was netted and held in the net at the water surface while the water level was raised by 10 cm (from 35 cm to 45 cm) within 5 min with all other conditions remaining the same. The test began when the fish was released into the illuminated compartment. Each fish was allowed 180 s to locate and swim through the aperture. When the fish swam through the aperture, lights were turned off for 15 s and turned on in the compartment where the fish was now located. If the fish did not swim through the aperture, the lights were turned off and the fish was returned to its home tank after 60 s. We scored dependent variables for 180 s.

Analysis

We recorded three dependent variables: (1) the time (s) that the fish needed to locate the aperture after it crossed a 15 cm boundary corresponding to the electrolocation distance (see Moller, 1995), (2) the height (cm) at which the fish first made physical contact with the divider wall and (3) the number of times that the fish crossed through the aperture from an illuminated compartment to a non-illuminated compartment. Data are expressed as means ± S.E.M. Learning the location of the aperture was defined by a decrease in the time to locate the aperture, an increase in the height at which the fish contacted the divider and an increase in the number of aperture crossings. In earlier investigations, fish learned the aperture location within four trial-days (Cain, 1995; Cain et al., 1994). We compared the mean time to locate the aperture for the first three trial-days with the mean time over trial-days 4–10. We also determined the responses of fish to changes in landmark size and water depth. We compared these dependent measures for the first 3 min of trial-day 10 with those of the first 3 min of each of the test situations.

Data were analyzed using mixed factors or univariate analysis of variance (ANOVA; SPSS V.10; SPSS Inc.,

Chicago, IL, USA). For the within-subject analyses, violations of the sphericity assumption, as shown by Mauchly's test, were corrected using the Huynh–Feldt epsilon correction for degrees of freedom. Pair-wise comparisons were conducted with independent and paired-sample *t*-tests (SPSS V.10). A confidence level of 95% (*P*<0.05) determined significance.

Results
Time

Both large and small control and experimental fish learned to find the aperture over the 10 trial-days as determined by a decrease in the amount of time needed to find the aperture ($F_{6.7,153.2}$=22.25, *P*<0.001) (Fig. 2). There was also a significant interaction between trial-days and group ($F_{19.98,153.2}$=1.73, *P*=0.033) in the amount of time needed. Over the 10-day training period, there were significant differences in the amount of time that fish in each group needed to locate the aperture ($F_{3,23}$=4.39, *P*=0.014). However, there was no significant difference in the amount of time needed to locate and swim through the aperture by the large and small control groups over the 10 trial-days; therefore, the interaction effect was not due to the size difference between the control groups. We therefore combined the data from the large and small control fish into one control group.

The amount of time to locate and swim through the aperture decreased significantly for each group: controls ($F_{5.5,49.8}$=5.97, *P*<0.001); large fish ($F_{9,72}$=11.9, *P*<0.001); small fish ($F_{9,63}$=12.4, *P*<0.001). Over the 10-day period, large fish in the presence of the medium landmark did not differ from controls (with no landmark present) in the amount of time taken to find the aperture. Small fish took significantly longer to locate and use the aperture than controls ($F_{1,16}$=8.4, *P*=0.01). Large fish found the aperture faster than small fish with the same landmark present (Fig. 2; $F_{1,15}$=9.15, *P*=0.009).

We divided the trial-days into two blocks and compared trial-days 1–3 with trial-days 4–10 (Cain, 1995; Cain et al., 1994). There was a significant difference in the amount of time to the aperture between the blocks ($F_{1,23}$=28.31, *P*<0.001) across groups. There was also a significant difference between groups ($F_{1,23}$=4.59, *P*<0.012). The amount of time (228.5± 21.5 s) that small fish in the presence of the medium landmark took to find the aperture over the first three trial-days was significantly greater ($F_{1,16}$=8.14, *P*=0.012) than that observed in controls (112.9±25 s) and significantly greater ($F_{1,15}$=12.68, *P*=0.003) than the time taken by large fish (116±21.1 s). There was no difference in time taken between large and control fish over the first three trial-days.

Height

All groups increased the height at which they contacted the divider wall ($F_{7.4,177.7}$=22.52, *P*<0.001) over the 10 trial-days (Fig. 3). There was no significant difference in the height at which large and small control groups contacted the divider over 10 trial-days. Each group – controls ($F_{9,81}$=9.95, *P*<0.001), large fish ($F_{9,72}$=9.03, *P*<0.001) and small fish ($F_{9,63}$=6.21, *P*<0.001)
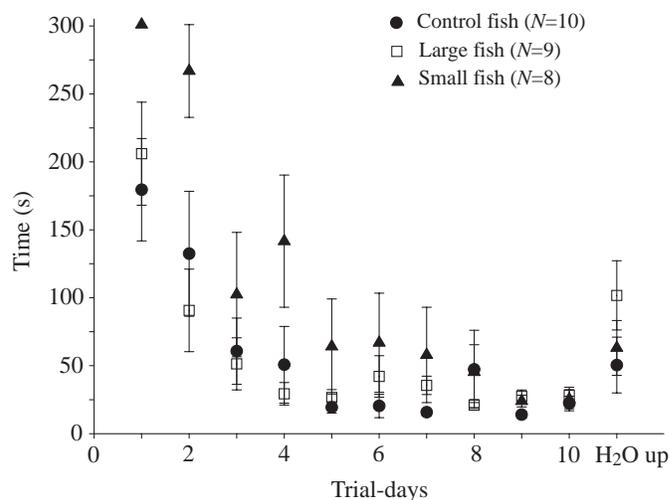

Fig. 2. Amount of time *Gnathonemus petersii* needed to find the aperture. Data represent mean times ± S.E.M. per trial-day. At some points, the error bars are smaller than the symbols. Trial-days 1–10: water depth was held constant at 35 cm. H₂O up: water level increased by 10 cm and time was recorded for the first 3 min; aperture height was maintained at 25.5 cm from aquarium floor; medium landmark size was maintained for large and small fish. All fish significantly decreased the time to find the aperture over the first 10 trial-days. After the water level was raised, large fish with a landmark significantly increased the time to find the aperture over the time taken on trial-day 10. Values for the first 3 min of each group in trial-day 10 were nearly identical to the 10 min values and were not plotted because they would obscure the other data.

– significantly increased the height at which they contacted the divider wall. While the mean height at which controls (16.7±1.43 cm) and large fish (14.8±6.8 cm) contacted the divider did not differ over 10 trial-days, the mean height that small fish (12.2±7.58 cm) contacted the divider was significantly lower than that for controls ($F_{1,16}$=4.64, *P*=0.047).

When we compared the heights of contact between trial-day blocks 1–3 and blocks 4–10, we found no significant difference across groups or between groups. Also, there was no significant difference in the height at which controls, large and small fish contacted the divider over the first three trial-days. Control fish continued to increase the height of contact, approaching the bottom edge of the aperture (22.1 cm from the floor), until trial-day 7, while the large and small fish levelled out. On trial-day 7, there was a significant difference ($t_{22.8}$=2.82, *P*=0.014) between controls (21.3±1.38 cm) and large and small fish (15.9±1.4 cm). In the first 3 min of trial 10, small fish contacted the divider at a significantly lower height than did the larger fish (t_{15}=2.18, *P*=0.045) (Figs 3, 5B medium landmark).

Crossing

The number of crossings, across all three groups, increased significantly ($F_{6.7,160.3}$=13.77, *P*<0.001), with the control group crossing more times than both the large and small fish. Controls ($F_{6.6,59.2}$=6.12, *P*<0.001), large ($F_{9,72}$=3.87, *P*<0.001), and small fish ($F_{9,63}$=4.92, *P*<0.001) significantly
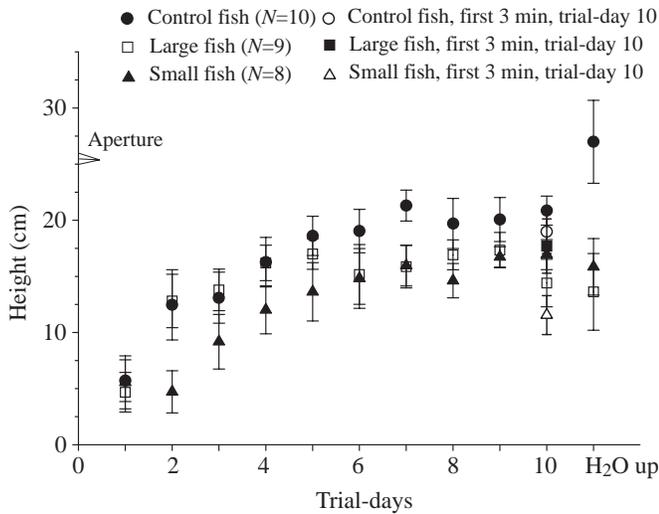
Fig. 3. Height of contact with the divider wall for each group. The centre of the aperture (arrow) was maintained 25.5 cm from the aquarium floor. Data represent the mean heights ± S.E.M. per trial-day. At some points, the error bars are smaller than the symbols. Trial-days 1–10: water depth was held constant at 35 cm. H_2O up: water level increased by 10 cm, height of contact was recorded for the first 3 min; medium landmark size was maintained for large and small fish. The controls increased the height at which they contacted the divider wall, while the fish with a landmark did not.

Fig. 4. Number of times per trial-day that fish crossed from one compartment to the other. Data represent the mean number of crossings ± S.E.M. per trial-day. Trial-days 1–10: medium landmark for large and small fish; water depth was held constant at 35 cm. H_2O up: water level increased by 10 cm and the number of crossings was recorded for the first 3 min; aperture height was maintained at 25.5 cm from the aquarium floor; medium landmark size was maintained for large and small fish. The controls increased the number of crossings after trial-day 4; the large and small fish did not.

increased the frequency with which they crossed from one compartment to the other over the 10 trial-days (Fig. 4). The controls crossed more frequently than did small fish over 10 trial-days ($F_{1,16}$=4.19, P=0.057), although this was not significant. However, there was no difference in the number of crossings between the large and small control groups over the 10 trial-days. There were significant differences in the number of crossings between trial-day blocks 1–3 and 4–10 ($F_{1,24}$=147.48, P<0.001) across groups. There were no significant differences between groups in the number of crossings over trial-days 1–3, trial-days 4–10 or over the total 10 trial-days. Over trial-days 1–3, the difference in the number of crossings between controls (22.3±5.3) and small fish (7.9±4.1) is significant (t_{16}=2.07, P<0.025).

Tests

Water level

At 35 cm water depth, the distance from the aperture centre to the water surface was 9.5 cm; at a depth of 45 cm, this distance increased to 19.5 cm. The floor-to-aperture distance was 25.5 cm, with the landmark surface 15 cm below the aperture and 12.5 cm from the divider wall. These did not change with the increase in water depth.

Large fish took longer (t_8=–2.96, P=0.018) to find the aperture, from 26.8±4.8 s in the first 3 min of trial-day 10 to 115.0±33.0 s in the first 3 min after the water level was raised (Fig. 2). By contrast, the amount of time to locate and swim through the aperture by controls and small fish did not change significantly after the water level was increased.
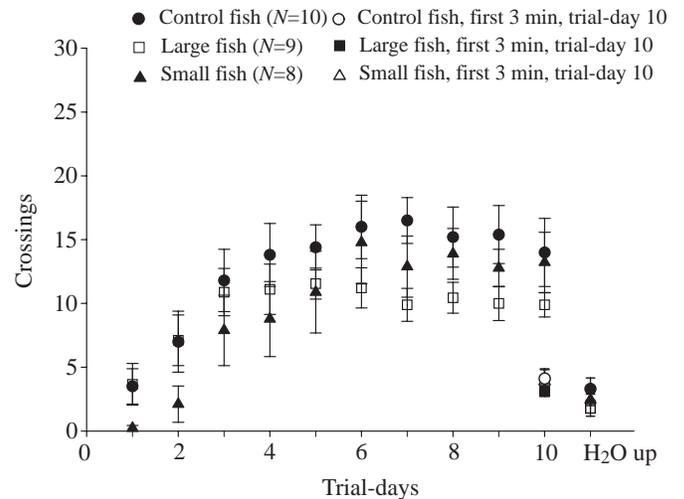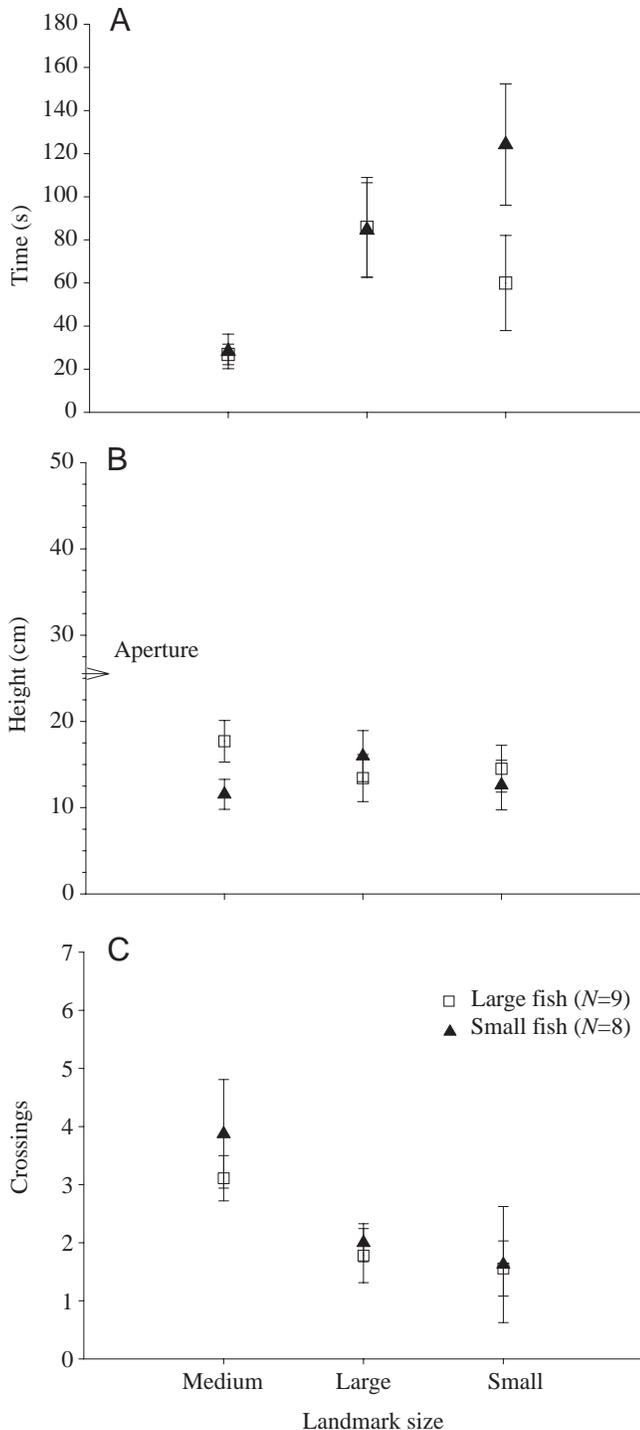
The height at which the controls (no landmark) contacted the divider wall increased significantly from 18.2±1.95 cm in the first 3 min of trial-day 10 to 27.7±3.9 cm (t_9=–2.47, P=0.036) (Fig. 3). Fish in the presence of a landmark contacted the divider at a lower height than did the controls after the water depth was increased: large fish at 13.6±3.4 cm (t_{17}=2.7, P=0.015), small fish at 15.8±2.8 cm (t_{16}=2.39, P=0.03). There was no difference between large and small fish on this measure.

When we compared the number of crossings by all three groups in the first 3 min of trial-day 10 with the number of crossings in the first 3 min after the water level had been increased (Fig. 4), we found a significant difference ($F_{1,24}$=6.24, P=0.02). A paired-samples *t*-test revealed no difference in the frequency of crossing in the first 3 min before and after the water-level increase by controls and small fish. However, large fish decreased their number of crossings from 3.11±0.39 in the first 3 min of trial-day 10 to 1.78±0.62 after the water level had been raised (t_8=2.31, P=0.05).

Large landmark (8.3 cm diameter)

Both large and small fish took significantly longer to swim through the aperture after the landmark increased in size (Fig. 5A). The large fish took significantly longer (85.8±23.1 s; t_8=–2.48, P=0.038) to swim through the aperture when the landmark size was increased than on trial-day 10 (26.8±4.8 s). The small fish also increased the time taken to swim through the aperture (84.6±22 s; t_7=–3.63, P=0.008) after the size increased as compared with trial-day 10 (28.3±8.0 s).

In the first 3 min of trial-day 10, small fish contacted the

Fig. 5. (A) Amount of time for large and small fish to find the aperture with different landmark sizes. The control fish had no landmarks so they were not included. Data represent the mean time ± S.E.M. of each group for the first 3 min of trial-day 10 (medium landmark size; 6.8 cm) and the first 3 min after the landmark either increased (to 8.3 cm) or decreased (to 3.9 cm) in size. Both the large and small fish increased the amount of time to find the aperture after the landmark size increased. When the landmark size decreased, the large fish did not change the amount of time to find the aperture, the small fish took longer. (B) Height at which large and small fish made contact with the divider wall in the presence of different sized landmarks. Data represent the mean height ± S.E.M. that each group made contact with the divider wall in the first 3 min of trial-day 10 (medium landmark size) and the first 3 min after the landmark increased or decreased in size. The height of the aperture (25.5 cm above the aquarium floor) is marked. (C) Mean number of times per trial-day that fish crossed from one compartment to the other for the first 3 min of trial-day 10 (medium landmark size) and the first 3 min after the landmark increased or decreased in size. Both the large and small fish decreased the number of times that they crossed through the aperture after the landmark changed size.

while the small fish (t_7=2.86, P=0.024) reduced their crossings from 3.8±0.93 for the first 3 min of trial-day 10 to 1.75±0.41.

Small landmark (3.9 cm diameter)

The small fish took longer (124.97±28.4 s) to find the aperture after the landmark size decreased from 6.8 cm to 3.9 cm diameter (t_7=−3.78, P=0.007), while the large fish showed no difference (Fig. 5A). As with the large landmark, there were no differences in the heights at which the large and small fish made contact with the divider wall after the small landmark replaced the medium landmark (Fig. 5B). However, the large fish decreased (t_8=2.58, P=0.03) the number of crossings (1.56±0.47) from that recorded at trial-day 10 (3.11±0.39). The decrease by small fish from 3.8±0.93 crossings in the first 3 min of trial-day 10 to 1.62±0.99 was not significant (Fig. 5C).

Discussion

Exploratory and investigatory behaviours have been demonstrated in a wide range of species, including fish (Glickman and Sroges, 1966; Kleerekoper et al., 1974). Exploratory behaviour provides information that enables an organism to avoid predation (Ambrose, 1972; Metzgar, 1967). In earlier studies with *G. petersii* ranging in length from 140 mm to 220 mm, intact fish without a landmark present learned to locate and use an aperture within four trial-days. Fish deprived of vision but with an intact electric organ were able to locate the aperture, while sighted fish without active electrolocation were not. Fish deprived of both sight and active electrolocation but with an intact lateral line and olfactory and gustatory systems were unable to locate the aperture (Cain, 1995; Cain et al., 1994). Fish relied on electrolocation even when vision is possible (von der Emde et al., 1998; but see Cain, 1995; also see von der Emde and Bleckmann, 1998).

divider at a significantly lower height than did the larger fish (t_{15}=2.18, P=0.045) (Fig. 5B, medium landmark). However, contrary to what we expected, the heights at which both groups of fish made contact with the divider wall did not change after the landmark size increased from 6.8 cm to 8.3 cm diameter.

Both large and small fish made fewer crossings after the landmark increased in size (Fig. 5C). In the first 3 min after the increase in landmark size, the large fish reduced (t_8=2.6, P=0.032) the number of crossings from 3.1±0.39 to 1.7±0.5,

After becoming familiar with their environment, *G. petersii* may continue to swim from one compartment to another as an operant response to changes in their environment such as (1) the mormyromast electroreceptor response pattern across the fish's body as it swims through the aperture, (2) changes in the external electric field as a result of the lights turning on and off and (3) a change in light intensity when swimming from an illuminated compartment to a non-illuminated one (Cain et al., 1994). Our data show that *G. petersii* of different developmental stages (1) responded differently to similar navigation and orientation tasks, (2) incorporated landmarks into their navigation and orientation behaviour, (3) were able to detect and respond to changes in landmark size and (4) relied on landmarks as the primary source of information in the presence of conflicting information between hydrostatic-pressure cues and landmarks.

Size/development differences in performance

G. petersii display a sexually dimorphic ventral body wall indentation resulting from anal-fin ray bone expansion (Pezzanite and Moller, 1998). Pezzanite and Moller (1998) defined developmental stages in *G. petersii* based upon this characteristic and correlated them with standard body length. According to their categories, our large fish are large sub-adults and adults (145–181 mm) and our small fish are large juveniles and sub-adults (110–132 mm). In the current study, we expected that intact *G. petersii* would locate and swim through an aperture in a clear plastic wall more rapidly in the presence of a landmark. Our expectations were accurate for large fish (large sub-adults and adults) but not small fish (large juveniles and sub-adults). *G. petersii* consistently demonstrated size-related orientation and navigation behavioural differences. Small fish initially took longer to swim through the aperture after crossing the electrolocation boundary, made contact with the divider wall at a lower height and made fewer crossings in the first three days.

Armstrong et al. (1997) examined the effects of trials or experience, starting region, and size on the propensity of wild Atlantic salmon *(Salmo salar)* parr (69–114 mm fork length) in a group situation to explore novel surroundings. They found no effect of trial or starting region, but larger parr were more likely to explore than smaller fish. No size breakdown of larger and smaller fish was provided. Similar differences in behaviour have been reported for juvenile and adult rats. Renner et al. (1992) reported that 30-day-old rats (*R. norvegicus*) took significantly longer to cross through an aperture and enter an open field arena than 60- and 90-day-old rats. They also spent significantly less time in the arena than 60- and 90-day-old rats. The authors suggested that, as rats mature, they develop behaviours capable of investigating novel environments.

Previous studies showed that fish rely on landmarks to orient and navigate (Braithwaite, 1998; Braithwaite et al., 1996; Girvan and Braithwaite, 1997; Reese, 1989; Warburton, 1990). We examined the effects of adding a landmark and found that it affected the behaviour of both large and small fish differently. Once large fish learned the aperture location in the

presence of the landmark, they did not increase their contact height to match the aperture but instead oriented to the landmark and then swam up to and through the aperture (Fig. 2).

Both controls and large fish located the aperture faster than small fish over the first four trial-days and 10 trial-days. There was no difference between the large and small controls. Why were small fish with a landmark slower than small fish without a landmark? The landmark was directly below the aperture and within the electrolocation boundary, and moving from one compartment to another was a two-stage event for small fish. Small fish crossed the electrolocation boundary and remained stationary under the landmark before crossing through the aperture. By contrast, controls of both sizes and large fish swam through the aperture after crossing the electrolocation boundary.

Cue conflicts

Von der Emde and Bleckmann (1998) found that *G. petersii* foraging for food rely on multiple sources of sensory input and that each individual may rely on a specific combination of sensory input. Cain (1995) found that *G. petersii* use electrolocation in conjunction with hydrostatic-pressure cues to form a spatial representation of their environment. Hydrostatic-pressure cues provided the fish with information of relative 'height' in the water column. These hydrostatic-pressure cues became the primary sensory cue after the aperture location was familiar. Without a local landmark, the internal representation and hydrostatic pressure controlled orientation and navigation to the aperture (Cain, 1995; Cain et al., 1994).

In these experiments, the relationship between hydrostatic pressure (a global cue), the landmark (a local cue) and the aperture remained stable during training for both large and small fish. The changes in the dependent variables indicate that large and small fish with the landmark present apparently learned the relationship between water depth, landmark and aperture.

When we increased the water level after training, this presented conflicting cues and we expected that all fish would orient according to the hydrostatic pressure, the distal cue. For control fish, the conflicting cues were hydrostatic pressure and internal representation *versus* the actual aperture location. After we raised the water level, controls increased the height at which they contacted the divider wall and did not significantly change the amount of time to the aperture. In the presence of conflicting information between hydrostatic pressure, landmark position and aperture location, large and small fish oriented to the landmark, as evidenced by the decreased height of contact, and increased the amount of time before crossing through the aperture. All fish reduced the number of crossings through the aperture in response to the increased water level. These changes suggest that fish detected novel sensory information, oriented to the landmark and took time to adjust to the new information. The data show that the landmark was a critical and preferred reference point for

orientation. Biegler and Morris (1996) found similar results when they changed the location of the landmark and held the distal cues constant.

We were interested in determining if *G. petersii* would modify their locomotor trajectory if the size of the landmark changed. Biegler and Morris (1993, 1996) showed that a single, reliable landmark, a proximal or local cue, exerts greater control over search location in a stable environment than does a variable environment in which local cues vary with respect to global cues. Their evidence supports a hierarchical organization of spatial representations. We changed the size of the landmark, not its location, and obtained similar results.

We predicted that because fish could determine the distance to an object *via* electrosensory means and that, because of the potential for error in determining the distance to a sphere (von der Emde et al., 1998), fish would rely on their internal representation and modify their approach path to the aperture in a predictable manner. We expected that the internal representation would provide an expectation of the electrosensory image size of the landmark as the fish approached the real landmark. The fish would attempt to match this image with the perceived image and modify its trajectory. However, fish of both sizes did not significantly change their trajectory. Instead, they appeared to perceive the changes in landmark size, approached it and investigated the novel stimulus.

Fish respond to detected changes in their environment with an increase in exploratory behaviour (Kleerekoper et al., 1974; Russell, 1967; Welker and Welker, 1958). After the landmark size increased, both large and small fish increased the amount of time to cross and decreased the number of crossings through the aperture. When the landmark size decreased, the small fish took longer to use the aperture but did not significantly decrease the number of crossings. Large fish did not increase the amount of time to the aperture but decreased the number of crossings through the aperture. Neither large nor small fish significantly modified the height at which they contacted the wall in response to changes in landmark size. Fish oriented to the stable cue. When the landmark changed size, the location of the landmark did not change, but the relationship between it and the substrate and aperture shifted. These discrepancies triggered responses similar to those displayed during the first three days of training when the fish were unfamiliar with the environment.

Biegler and Morris (1996) proposed that an organism will resolve a conflict between global and local cues in a previously stable environment based on 'a priori reliability' and the 'extent of the discrepancy' between current and previous information. This could explain the reliance of the fish on the local landmark when the hydrostatic pressure changed. When the hydrostatic pressure increased at both the landmark and the aperture, the relationship between the landmark, the substrate and the aperture did not change.

Significant, rapid increases in the water depth of rivers and streams during the rainy season are normal phenomena in subtropical Africa and act as a cue for reproduction in mormyrids (reviewed by Moller, 1995). The relationship between proximal and distal cues, which is relatively stable during the dry season, would change significantly. Spatial learning of proximal landmarks and their relation to hydrostatic pressure could help fish solve navigational problems encountered during migrations to and from nocturnal feeding grounds in their natural environment. In addition, the ability to detect and respond to changes in these relationships adaptively would facilitate predator avoidance and feeding in young fish with limited experience and would facilitate reproduction in mature fish as they moved from familiar areas into newly flooded swamps to breed.

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