

Most animals possess multiple sensory systems, which can be used during navigation. Different senses obtain environmental information on different spatial scales and thus provide a different basis for efficient navigation. Here we used the weakly electric fish *Gnathonemus petersii* to investigate how different sensory inputs influence the navigational strategy and whether landmark information can be transferred flexibly between two sensory systems. Fish were trained to swim through a maze using a particular route indicated by either visual landmarks, electrical landmarks or without any landmarks. In subsequent tests, egocentric (internal cues, such as motion patterns) and allocentric cues (external cues like landmarks) were put in conflict by relocating the local landmarks. We found that all fish, independent of the available sensory input, chose the egocentric over the allocentric route. However, visual landmarks significantly improved the training duration compared to the other groups, suggesting an involvement of allocentric visual cues during route acquisition. In a second experimental series, fish were trained to use either visual or electrical landmarks for navigation and were subsequently tested in sensory transfer tests. Fish trained with visual landmarks were able to learn this allocentric navigation task and were capable of cross-modal landmark recognition, although navigation based on electrical landmarks was less efficient. The fish trained with electrical landmarks did not learn the task at all, suggesting that the short perceptual range of the electric sense prevented learning of allocentric navigation. Together our results show that the type of sensory input influences the efficiency of allocentric navigation in *G. petersii* and that these fish are able to use egocentric and allocentric strategies flexibly to navigate successfully under varying environmental conditions.

Keywords: cross-modal landmark recognition, egocentric vs. allocentric cues, electrolocation, navigation, vision

The ability to navigate successfully is vital for most actively moving organisms and is therefore widely spread amongst animals. A range of different navigation strategies are known that allow animals to

return to food sources, mating sites or refuges across different spatial scales (Able, 1980; Benhamou, Sauvé, & Bovet, 1990; Bingman & Cheng, 2005; T. S. Collett & Rees, 1997; Etienne, Maurer, et al., 1998; Etienne, Maurer, & Séguinot, 1996; Rüdiger Wehner, 1998; Rüdiger Wehner, Michel, & Antonsen, 1996). While navigation is well studied in many species, little is known about how sensory input shapes the strategy that animals use, and how information can be used flexibly by different senses to navigate through their environment. Here we investigate these questions by using the weakly electric fish *Gnathonemus petersii*.

In order to navigate through space, animals must perceive information about their surroundings using sensory systems. Among other factors, the sensory equipment and the quantity and quality of sensory input determines whether an organism is only capable of performing simple phototaxis orientating towards or away from a light source (e.g. bacteria relying on simple photoreceptors (Häder, 1987; Jékely, 2009)) or whether it is capable of navigating successfully halfway around the world during migration (e.g. birds or mammals equipped with an array of complex sensory system (Alerstam, Gudmundsson, Green, & Hedenström, 2001; Gagliardo, 2013; Mouritsen, 2015; Wiltschko & Wiltschko, 2009). Besides influencing this basic navigational framework, the sensory input might also affect the navigational strategy within a single individual. Most animals possess multiple sensory systems, which can be used combined, redundantly or complementarily and provide different potentials which navigation strategy could be used efficiently (Able, 1991; Braithwaite & De Perera, 2006; Ernst & Bühlhoff, 2004; Hebets et al., 2014; Sutherland, Holbrook, & Burt De Perera, 2009; Wiltschko & Wiltschko, 2009).

A key factor affecting which navigational strategy is applied might be the perceptual range of the sensory system that is used to gather information about the environment (Able, 1991; Prevedello, Forero-Medina, & Vieira, 2010; Schooley & Branch, 2005; Sutherland et al., 2009). Depending on the sense that is employed and the limits of its perceptual range, an animal might obtain information only from its very near surroundings or at a greater distance (Smith, 2008). While navigation always involves an interaction with the surroundings and thus always requires sensory input, the degree to which individual navigation strategies depend on environmental information varies greatly. Egocentric navigation, for example, is based on internal cues such as learned motion sequences and is therefore less dependent of external information (Benhamou et al., 1990; Etienne, Berlie, Georgakopoulos, & Maurer, 1998; Etienne, Maurer, et al., 1998; Healy, 1998; Klatzky, 1998). A prominent example for

egocentric navigation is path integration (in mammals also called dead reckoning). For example, after extensive food searching walks, the desert ant *Cataglyphis fortis* is able to return to its nest on a straight direct path by integrating internal information on direction and distance that are based upon internal cues such as proprioception and odometry (Müller & Wehner, 1988; Wittlinger, Wehner, & Wolf, 2006). Similar mechanisms are also found in humans and other mammals (Etienne & Jeffery, 2004; Etienne, Maurer, et al., 1998; Loomis, Klatzky, Golledge, & Philbeck, 1999; M. -L. Mittelstaedt & Mittelstaedt, 1980; Marie-Luise Mittelstaedt & Mittelstaedt, 2001). An egocentric strategy provides the advantage that it is robust to changes in the environment. However, egocentric navigation is restricted to a defined known route and still needs some external cues, informing about the start point or for updating the current location (Benhamou et al., 1990). E.g. the desert ant uses visual, olfactory and tactical cues to optimise path integration (Buehlmann, Hansson, & Knaden, 2012; T.S. Collett, Collett, & Wehner, 2001; Seidl & Wehner, 2006; Rüdiger Wehner, 2003; Rüdiger Wehner et al., 1996). On the other hand, allocentric navigation relies on external information such as landmarks to return to a goal location. ~~For example, pigeons are famously known for relying on visual landmarks when navigating in a familiar environment (Biro, Guilford, & Dawkins, 2003; Burt, Holland, & Guilford, 1997), and olfactory cues in addition to a sun and magnetic compass during homing. Within this system~~ During such ~~allocentric navigation strategies~~, landmarks can be used in various ways, for example, they can directly indicate a goal (beacon), or many landmarks can be combined together in a map-like system (Braithwaite & De Perera, 2006; Healy, 1998; López, Broglio, Rodríguez, Thinus-Blanc, & Salas, 1999; Odling-Smee & Braithwaite, 2003; Rodriguez, Duran, Vargas, Torres, & Salas, 1994; Schluessel & Bleckmann, 2005). ~~For example, pigeons are famously known for relying on visual and olfactory cues in addition to a sun and magnetic compass during homing.~~ Allocentric navigation strategies require detailed information about the environment and thus might be most efficient when landmarks can be perceived from a longer distance (Pe'er & Kramer-Schadt, 2008). From this, it can be hypothesised that the available sensory input might determine which navigation strategy is employed. For example, the availability of a far range sense, such as vision, might promote allocentric navigation and the restriction to short range sensory input, might favour the use of an egocentric strategy.

Here we used the African weakly electric fish *Gnathonemus petersii* as a model to investigate the influence of sensory input on navigation. With its active electric sense and a highly specialised visual system these fish possess two sensory systems that provide similar information about the environment on different spatial scales.

During active electrolocation, *G. petersii* is able to perceive its surroundings by detecting distortions in a self-generated electric field. These fish produce weak electrical pulses also called electric organ discharges (EOD) with an electric organ located in the caudal peduncle (Lissmann, 1958; Lissmann & Machin, 1958). With each EOD, a 3-dimensional electric field is built up around the fish, which is perceived with epidermal electroreceptor organs (Jorgensen, 2005). According to their electrical properties, objects within this electric field distort the spreading of the field lines, which leads to a local change of the perceived amplitude and waveform of the EOD (Lissmann & Machin, 1958; von der Emde, 1990; von der Emde et al., 2010). Using these object evoked distortions of the electrical field, *G. petersii* is able to detect and recognise objects within its environment (Graff, Kaminski, Gresty, & Ohlmann, 2004; Schumacher, Burt de Perera, & von der Emde, 2016; von der Emde & Fetz, 2007). However, the perceptual range of the active electric sense is restricted to approximately one or two fish length (ca. 10 - 20 cm) when detecting objects and to only a few centimetres during object recognition (Fechler & von der Emde, 2013; Moller, 1995; von der Emde, Schwarz, Gomez, Budelli, & Grant, 1998)

The visual system of *G. petersii* relies on a so-called grouped retina, which enhances light absorption under dim light conditions and reduces visual noise in turbid water (Kreysing et al., 2012; Landsberger et al., 2008). Thus it is perfectly adapted to the fishes' crepuscular (main activity during dusk and dawn) or nocturnal life style and their habitat in black water streams in Central and West Africa. Within this grouped retina, the photoreceptor cells are packed into bundles and are located at the bottom of a cup like structure formed by reflective retinal pigment epithelial cells (tapetum lucidum), which focuses incoming light on the outer segments of the cones (Francke et al., 2014; Kreysing et al., 2012; Landsberger et al., 2008). This organisation of the retina, however, results in a relatively low spatial resolution of the visual system of *G. petersii* (minimal visual angle of about 3°)(Kreysing et al., 2012; Schuster & Amtsfeld, 2002). Despite this poor spatial resolution these fish are able to use visual information for object recognition, applying template matching to do so (Schumacher, Burt de Perera, & von der Emde, 2017; Schuster & Amtsfeld, 2002).

Previous studies have shown that *G. petersii* is able to integrate information from vision and the active electric sense and that both senses can be used to recognise objects in the near field of the fish (Moller, 2002; Rojas & Moller, 2002; Schumacher, Burt de Perera, Thenert, & von der Emde, 2016; Schumacher et al., 2017). Furthermore, *G. petersii* is capable of cross-modal object recognition, i.e.

object information acquired and learned with one of the senses can be used by the other for object recognition (Schumacher, Burt de Perera, Thenert, et al., 2016). Both senses have a high temporal resolution which allows detailed perception of the environment even during fast swimming (Moller, 1980; Pusch et al., 2013; Schumacher, Burt de Perera, & von der Emde, 2016). Together, this means that both sensory systems are able to provide the information necessary for allocentric navigation. However due to the short perceptual range of the active electric sense, navigation based on the perception of landmarks might be inefficient.

So far little is known about how *Gnathonemus petersii* navigates in its environment and which senses they use primarily to do so. Studies have shown that during a vertical navigation task, *G. petersii* is able to use electrical and hydrostatic pressure cues for short range navigation (Cain, 1995; Cain, Gerin, & Moller, 1994; Cain & Malwal, 2002). In their natural environment *G. petersii* is known to possess home territories, which they leave to forage and where they regularly return to (Moller, Serrier, Belbenoit, & Push, 1979). In order to do this, they must be able to navigate successfully in their environment across a considerable range.

Here we investigate how the use of vision or the active electric sense affects the navigation strategy in *G. petersii* by training individual fish to swim through a maze using a particular route indicated by either visual landmarks, electrical landmarks or without landmarks. By putting egocentric and landmark-based allocentric cues into conflict, we tested whether the fish employed an egocentric or an allocentric strategy. In a second experimental series we explored whether the use of landmarks could be transferred between the senses, by testing visually trained fish with electrical landmarks and vice versa. Together our experiments inform us how the perceptual range of sensory systems influences navigation and how flexible navigation strategies can be employed within a species.

MATERIAL AND METHODS

Subjects and Setup

During this study we used 17 *G. petersii*, with a standard length of 8.5 - 13 cm as subjects. The fish were bought in a local store in Oxford (The Goldfish Bowl Oxford) and were imported, wild caught from Africa. The age and sex of the fish were unknown. The fish were housed individually in housing tanks

with the dimensions 60 cm x 35 cm x 40 cm. The experiments were conducted in a separate experimental tank (130 cm x 45 cm x 45 cm), which was divided into five compartments (Fig. 1). The outermost compartments acted as the start and goal area. They were divided from the other compartments with a partition containing one door and were, in contrast to the inner compartments, equipped with gravel on the floor. The other three compartments had the same size (30 cm) and were divided by partitions containing two gates, so that in order to get from the start area to the goal area the fish had to choose twice between two gates. A cage made of a plastic framework covered with fly screen net was attached to each gate. At each partition there was one open cage and one closed cage, therefore the passage into the next compartment was only possible if the fish chose the gate with the open cage behind. The cages were used in order to prevent the possibility of the fish detecting the difference between an open and a closed gate from afar. The cages could be taken off, and since the setup was symmetrical, the experiments could be conducted in both directions by relocating the cages to the other side of the partition. In other words, the goal area of the first trial was used as the start area of the second trial and vice versa.

The temperature, the pH-value and the conductivity of the water in the experimental as well as in the housing tanks were kept constant at $24\pm 1^{\circ}\text{C}$, 6-7 and $100\pm 10\ \mu\text{S/cm}$.

General Procedure

Before the first trial was started, the door of the start area was closed and the door of the goal area opened. The goal area contained a plastic tube as a hiding place and a food reward in the form of a small amount of bloodworm (Chironomidae larvae). Both motivated the fish to swim into the goal area.

The fish was carefully netted, taken from its home tank and placed in the start area of the experimental tank. After a short habituation phase of two minutes, the door of the start area was opened. When the fish had left the start area, the door was closed in order to prevent a return of the fish. The fish was given 10 minutes to swim into the goal area. If it did not enter the area in this time the trial was aborted and the fish was placed back into the start area. If the fish did swim into the goal area the door was closed and the fish was given 3 minutes to feed and hide. In the meantime, the cages were replaced on the other side of the partitions and the new goal area was equipped with the

food reward and a plastic tube. Before the new trial was started the plastic tube was removed from the new start area.

Sensory Influence on Navigation

Training

Before the training started, pre-training sessions were conducted, during which the fish were trained to swim from the start area to the goal area without the two partitions in between. As described above the food reward and the hiding place were placed in the goal area to motivate the animals to perform. Once the fish had learned to swim directly from the start area to the goal area (after 2 - 3 days) the partitions with the cages were introduced.

To test the sensory influence on navigation during the first experimental series, the open cages were positioned in a pre-assigned order. For example, on the first partition (first decision) the open cage was attached to the right gate and on the second partition (second decision) it was placed behind the left gate, forcing the fish to swim a right - left route in order to reach the goal area. An object (landmark) was placed 3 cm in front of each correct gate with the open cage behind. For the first decision a sphere with a diameter of 5 cm was used as the landmark and a cross with the same volume was used for the second decision. The number of training trials conducted per day varied between two and eight trials per fish (only even numbers to avoid overrepresentation of one of the swimming directions in the two-directional design), all fish conducting the same number of trials each day..

The fish were divided into four training groups composed of five or four in each. In all training groups three or two fish were trained to the route, right - left and two to the route, left - right. The training groups were exposed to objects that were made from different materials, which influenced the senses that could be used to detect the objects:

1) The first training group (visual group, fish 1 - 5) could only use vision to detect the objects. This was achieved by making the objects from red coloured electrically transparent agarose. These objects had approximately the same conductivity as the tank water and were therefore electrically "invisible". To produce these objects, red food colour was added to deionised water until the conductivity of the mixture reached a value of ca. 40 $\mu\text{S}/\text{cm}$. Red colour was used because the cones of *G. petersii* are

most sensitive to red light (absorption maximum: 615 nm (Kreysing et al., 2012)). By adding agarose powder (Agarose BP 160-100, Fisher Scientific, Fair Lawn, New Jersey, USA) (2g per 100ml) the conductivity was increased to ca. 100 μ S/cm. This mixture was boiled and cast in moulds. After cooling down the agarose became stiff and the objects could be used. Since it wasn't possible to measure the conductivity of the stiffened agarose directly, the resistance of 250 ml stiff agarose within a beaker was compared with the resistance of 250 ml tank water using a multimeter (M-3650B, Voltcraft) to test whether their electrical properties were identical. For both measurements the measuring electrodes were positioned 5 cm apart. There was no measureable difference between the agarose and the tank water.

2) The second group (plastic group, fish 6 - 9) could use only their active electric sense to perceive the objects. In this case, visual detection of the landmark was prevented by covering plastic objects (detectable by the active electric sense) with hoods made of opaque, black cotton fabric. Identical hoods containing no landmark, were placed in front of the doors with the closed cages behind, therefore the fish had to use electrolocation to detect the navigational landmark.

3) Since the effect of plastic on the electrical field of the fish is relatively small, a third group (metal group, fish 10 - 13) was trained with metal objects covered by the cotton hoods instead of the plastic objects.

4) As a control a fourth group (control group, fish 14 - 17) was trained without any landmarks at all. The aim of this was to test whether the objects had an uncontrolled effect and whether these objects acted as positive or negative reinforcers on the training duration and the accuracy with which the fish navigated through the maze.

During training, the fish learned to swim from the start to the goal area on the pre-assigned route without directional errors. Directional errors were counted when the fish either swam into the dead-end of a closed cage or when the fish swam back through an open cage in the direction of the start area. The probability of completing this task without any errors at random was 16.67% (first decision: right or left gate (50:50), second decision: right, left or backwards (1/3:1/3:1/3)).

The number of errors as well as the trial duration, from leaving the start area to entering the goal area, were documented. Training was considered successful when the fish reached the pre-assigned learning criterion of 21 correct trials out of 24 (87.5 %).

To compare the training performance of the four different training groups, we plotted the number of trials taken to reach the learning criterion (e.g. a fish making errors only in three trials between trial 32 and 55 reached the criterion after 55 trials) in box plots, and we conducted a Kurskal Wallis test and a post hoc test. We calculated the mean trial duration, the mean number of errors and the percentage of correct trials of 8 trial intervals for each group and plotted them in learning curves. To compare the within-subjects effects of trial number and the interaction of trial number x training group as well as the between-subjects effect of training group, we conducted a mixed-design ANOVA with post-hoc-tests (Bonferroni correction) for trial duration, number of errors and percentage of correct trials. We arcsine-transformed the percentage of correct trials and back-transformed the mean and the standard error for plotting the learning curves.

Egocentric vs. allocentric navigation

After the fish had reached the preassigned learning criterion, probes were introduced every fifth trial, to test whether the fish learned the egocentric route or whether they learned to navigate by using the landmarks (allocentric route). To achieve this, the egocentric and the allocentric information were put into conflict by moving the landmarks. For these tests, all cages were opened and the objects were placed in front of the gates that were closed during training; e.g. in tests with fish that were trained to the route right - left, the objects were placed left - right. In the group trained without landmarks only, all cages were opened to control whether the closed cages had any effect on the performance. In order to prevent a training effect during the tests, no food reward or hiding place was placed in the goal area. Ten test trials were conducted with each fish.

We calculated the percentage of trials during which the fish chose the previously trained to route (egocentric route) for all training trials after the fish had reached the learning criterion and for the test trials for each fish and conducted a Chi²-test to test whether the performance was significantly different from the 16.66% chance-level. To test whether there was a significant difference between the performances during training and tests and between the different training groups we arcsine-transformed the data and conducted a mixed design ANOVA. Subsequently we calculated the mean and the standard error and transformed the data back to percentage and plotted them in bar charts.

261 *Cross-modal Landmark Recognition During Navigation*

262 *Training*

263 After the first experimental series a second set of experiments was conducted with the group trained
264 with visual landmarks and the group trained with plastic landmarks, in which the fish were forced to
265 use the landmarks for navigation instead of following a pre-assigned route. To do this, the positions of
266 the correct gates with the open cages were changed pseudo-randomly every trial using the four
267 possible combinations (right - right, right - left, left - left, left - right). As in the first experimental series
268 the correct gates were indicated by the visual/plastic landmarks (red coloured electric transparent
269 agarose objects/ plastic objects covered with cotton hoods and empty cotton hoods).

270 Since none of the fish trained with plastic landmarks showed a training effect after 96 trials, the plastic
271 objects were replaced by metal objects. This was done because metal has a stronger effect on the
272 electrical field and therefore is easier to detect and can be perceived from a greater distance. The
273 learning criterion for this experimental series was set to 17 correct trials out of 25 (68%).

274 We plotted the number of trials to criterion for those fish that reached the learning criterion. For all fish
275 the percentage of correct trials of the last 25 training trials was calculated (either the fish reached the
276 learning criterion or the training was considered unsuccessful and stopped). We used a Chi²-test to
277 test whether the performance was significantly different from the 16.67% chance level. We plotted the
278 mean trial duration, the mean number of errors and the mean percentage of correct trials of 8 trial
279 intervals for each group and conducted a mixed-design ANOVA with post hoc-tests (Bonferroni
280 correction) to analyse the within-subjects effects of trial number and the interaction of trial number x
281 training group as well as the between-subjects effect of training group for trial duration, number of
282 errors and percentage of correct trials. To do this the percentage of correct trials was arcsine-
283 transformed and the mean and the standard error were back-transformed for plotting the learning
284 curves.

285

286 *Transfer tests*

287 After the fish had reached the learning criterion, we tested whether the ability to recognise the
288 landmarks and use them for navigation was transferable between the senses. To do this, the training
289 landmarks used by the visually trained fish were replaced by electrical landmarks (metal objects

covered with hoods) and vice versa. During these tests all cages behind the gates were open and no reward was used. A total of 20 probe trials were interspersed into training every fifth trial.

We calculated the percentage of correct trials for each fish for all training trials after the fish had reached the learning criterion and for the test trials. To test whether the performance was significantly different from chance level we used a Chi²-test and with exact Fisher-tests we compared the performance during training and tests for each fish. Furthermore, we compared the performance with electrical landmarks of the group trained with visual landmarks during the transfer tests and the group trained with electrical landmarks during training using a Mann-Whitney-U-test.

Analysis of decision behaviour

To record the decision behaviour of the fish during training and transfer test trials, a camera was placed above the tank. For each fish 22-35 training trials and 20 test trials were recorded and analysed. We observed the direction in which the fish swam after leaving the start area/ after passing the first barrier (right or left) and whether it changed the swimming direction. Training and test trials as well as correct and incorrect decisions were analysed separately. We plotted the mean relative frequency of decisions, during which the fish swam in the individual favoured direction (direction chosen with a relative frequency of more than 50%; the favourite direction was separately assigned for the first and the second decision for each fish) and of decision during which the fish changed direction (swimming towards one gate and at a distance of ca. 5 cm in front of the gate turning towards the other gate without entering the first) for the correct and the incorrect decisions during training and transfer tests. To analyse the main effects of training/transfer and correct/incorrect and the interaction of both factors (training/transfer x correct/incorrect) we arcsine-transformed the data and conducted a two-way repeated measures ANOVA with subsequent post hoc-tests (Bonferroni correction) for favourite direction and changed direction. For the plots the mean and the standard error were back-transformed into percentage data.

Ethical Note

Protocols used in this paper were approved by the Local Ethical Review Committee of Oxford University's Department of Zoology.

319

320 RESULTS

321 *Sensory Influence on Navigation*

322 To test whether the navigation strategy of *G. petersii* is influenced by the sensory system available for
323 landmark detection, we trained the fish to swim through a maze using a defined route, which was
324 indicated by landmarks that could be perceived only with vision (electrically transparent agarose
325 objects) or only with the active electric sense (plastic or metal objects) or no landmarks were present.

326

327 *Route acquisition*

328 All fish from the four training groups reached the pre-assigned learning criterion of 21 correct trials out
329 of 24 and therefore learned to swim from the start area to the goal area using the defined route.
330 However the number of trials the fish needed to learn the task differed between the groups (Fig. 2).
331 The fish, which were trained with the visual landmarks, learned the navigation task significantly faster
332 than all the other groups (Kruskal-Wallis-test: $H_3 = 11.504$, $P = 0.009$), reaching the learning criterion
333 with a median number of 55 training trials. The training duration of the other three groups did not differ
334 significantly. These results suggest that the visual landmarks had a positive influence on the training,
335 while the electrical landmarks (plastic and metal) had no significant influence compared to the control
336 group without landmarks.

337 In line with the significantly shorter training duration a comparison of the learning curves of the four
338 different training groups also indicates that the performance of the group trained with visual landmarks
339 improved faster than that of the other groups (Fig. 3). While there was no significant difference in trial
340 latency or number of errors between the four training groups (Fig. 3 a, b; mixed-design ANOVA:
341 between-subjects effects of training group: $F_{3,13} = 1.257$; $P = 0.33$ (trial latency); $F_{3,13} = 2.250$; $P =$
342 0.131 (No. of errors); within-subjects effects of interaction No. of trials x group: $F_{4,687,20.310} = 0.625$; $P =$
343 0.673 Greenhouse-Geisser correction $\varepsilon = 0.195$ (trial duration); $F_{5,982,25.924} = 0.807$; $P = 0.574$
344 Greenhouse-Geisser correction $\varepsilon = 0.195$ (No. of errors)), the percentage of correct trials differed
345 between the groups over the training period (Fig. 3 c; mixed-design ANOVA: within-subjects effects of
346 interaction trial No. x training group: $F_{24,104} = 2.09$; $P = 0.006$). On trials No.41-48, 49-56 and 57-64
347 the visually trained group reached a significantly higher performance than the other groups,

suggesting that during this training period the visual landmarks positively influenced the training performance (post-hoc-tests with Bonferroni correction $P \leq 0.006$).

Egocentric vs. allocentric navigation

After the fish reached the learning criterion, we tested whether they had learned the egocentric route or whether they had learned to rely on the landmarks by putting these navigational strategies in conflict.

During the conflict tests all fish chose the previously learned egocentric route over the landmark indicated allocentric route in at least 9 of 10 test trials (Chi²-test: $P < 0.001$). The comparison of the performance during tests and training shows that in all four groups the fish chose the egocentric route during tests with the same accuracy as during training (mixed design ANOVA, within-subjects effects: $F_{1, 13} = 0.93$, $P = 0.352$, interaction group x training/test: $F_{1, 13} = 0.993$, $P = 0.427$) (Fig. 4). Furthermore, there was no difference in the performances of the different training groups (mixed design ANOVA, between-subjects effects: $F_{3, 13} = 1.11$, $P = 0.381$), revealing that the fish chose the egocentric route no matter which sense was used for landmark detection.

Cross-modal Landmark Recognition During Navigation

To test whether *G. petersii* is able to navigate using landmarks that are transferred across two senses, we trained the fish from the visual and the plastic groups to use allocentric local landmark cues for navigation. To do this the landmark indicated correct route was altered pseudo-randomly every trial. After the fish had reached the pre-assigned learning criterion of 17 correct trials out of 25, we tested the fish with the previously untrained sense.

Training

In the group trained with visual landmarks four of the five fish reached the learning criterion. On average they needed 136 trials to do so (Fig. 5 a) and thus needed more than twice as many trials to learn the navigation task as during the first experimental series. After 168 trials, the fifth fish of this group showed a slight learning effect and reached a level of 40% correct trials within the last 25 trials,

which is significantly above the chance level of 16.67% but it did not reach the learning criterion (Chi²-test: $P=0.002$).

After 96 training trials none of the fish trained with plastic landmarks showed any training effect, therefore we replaced the plastic objects with metal objects. This was done because metal has a much stronger effect on the electric field than plastic and is therefore easier to detect for the fish. However even with the metal landmarks, none of the fish reached the pre-assigned learning criterion, so that the training was considered unsuccessful and was stopped after a minimum of 168 training trials. Within the last 25 training trials, none of the fish reached an accuracy of over 24% correct trials which is not significantly different from chance level (Chi²-test: $P > 0.05$) (Fig. 5 b).

The learning curves (Fig. 6) show that while there was no significant difference in the decrease of trial duration between the visual and the electrical group (mixed-design ANOVA: within-subjects effect of training group: $F_{1, 7} = 1.151$, $P = 0.319$, trial No. x training group: $F_{3.992, 27.942} = 1.307$, $P = 0.292$ Greenhouse-Geisser correction $\epsilon = 0.210$), the number of errors and the percentage of correct trials differed significantly between the groups from trial No. 121-128 until the end of training at trial No. 161-168 (mixed-design ANOVA: trial No. x training group: $F_{4.883, 34.179} = 2.908$, $P = 0.028$ Greenhouse-Geisser correction $\epsilon = 0.257$ (No. of errors) , $F_{4.537, 31.762} = 3.163$, $P = 0.023$ Greenhouse-Geisser correction $\epsilon = 0.239$ (correct trials) post-hoc-tests with Bonferroni correction $P < 0.05$). This reveals that the visually trained fish learned the task better than the electrically trained group.

The learning curves (Fig. 6 b and c) also show that there was no training effect over the entire training period in the electrical landmark group ~~(red lines)~~. There was no significant difference in the mean number of errors or in the mean percentage of correct trials between trials No. 1-8 and any other trial interval (mixed-designed ANOVA: trial No. x training group: $F_{4.883, 34.179} = 2.908$, $P = 0.028$ Greenhouse-Geisser correction $\epsilon = 0.257$ (No. of errors), $F_{4.537, 31.762} = 3.163$, $P = 0.023$ Greenhouse-Geisser correction $\epsilon = 0.239$ (correct trials) post-hoc-tests with Bonferroni correction $P > 0.05$). In contrast, the performance of the fish trained with visual landmarks significantly improved over time. After trial 64, the number of mistakes steadily decreased and the percentage of correct trials increased in line (mixed-designed ANOVA: trial No. x training group: $F_{4.883, 34.179} = 2.908$, $P = 0.028$ Greenhouse-Geisser correction $\epsilon = 0.257$ (No. of errors), $F_{4.537, 31.762} = 3.163$, $P = 0.023$ Greenhouse-Geisser correction $\epsilon = 0.239$ (correct trials) post-hoc-tests with Bonferroni correction $P < 0.05$). However, in

comparison to the first experimental series, where the fish were trained to use a defined route, the mean percentage of correct trials was much poorer and never exceeded 73%.

Transfer tests

Subsequent to training, the four fish of the group trained with visual landmarks were tested in transfer tests, during which the visual landmarks were replaced by electrical landmarks (metal objects covered with electrically transparent cotton hoods in front of one gate and empty hoods in front of the other gate).

During the transfer test, all four tested fish reached a performance significantly different from the 16.67% chance level (Chi²-test: $P \leq 0.05$; Fig. 7). However, in all fish the transfer performance with the electrical landmarks (38.75 % + 2.39 correct trials) was significantly worse than the training performance with the visual landmarks (70.87 % + 1.1 correct trials) (exact Fisher-test: $P < 0.001$). The comparison of the performance during the transfer tests with the training performance of the group trained with the electrical landmarks after at least 168 training trials shows that the visually trained group reached a significantly better performance during navigation with the electrical landmarks without any training with these landmarks (Mann-Whitney-U-test: $U = -2.337$, $N_1 = N_2 = 4$, $P = 0.029$; Fig. 8). This suggests that while the fish seemed to be able to transfer the use of the landmarks, the electrical input might not be sufficient for efficient allocentric navigation.

Decision behaviour

The analysis of the recorded trials shows that each fish tended to swim in an individually preferred direction during most decisions (Fig. 9). This preferred direction did not depend on the direction the fish was trained to in the first experimental series. The fish chose this individually preferred direction on average in 62.4 % (training) and 68.6 % (transfer tests) of the correct decisions and in 78.7 % (training) and 81.7 % (transfer tests) of the incorrect decisions, indicating a non-significant trend towards choosing the favourite direction more often during incorrect trials (two-way repeated measures ANOVA: main effect correct/incorrect: $F_{1, 3} = 5.947$, $P = 0.093$ Greenhouse-Geisser correction $\epsilon = 1.000$).

Furthermore during the correct decisions, the fish changed directions (swimming in one direction and changing direction shortly before (ca. 5cm) entering the gate) on average in 43.25% of the training decisions and in 53.74% of the transfer decisions. In comparison, during the incorrect decisions the fish changed directions with an average 6.39% of the training decisions and 7.24% of the transfer decisions significantly less often (two-way repeated measures ANOVA: main effect correct/incorrect: $F_{1,3} = 2021.877$; $P < 0.001$ Greenhouse-Geisser correction $\epsilon = 1.000$). This suggests that during correct trials the fish changed the direction towards the correct gate when noticing the absence of the landmark on an initially incorrect route and tended to swim less often in the individually preferred direction maybe in favour of swimming towards the landmark.

During both decision behaviours (favourite direction and changed direction), there was no significant difference between training and test (two-way repeated measures ANOVA: main effect training/transfer: $F_{1,3} = 0.671$, $P = 0.473$ (favourite direction); $F_{1,3} = 3.646$, $P = 0.152$ (changed direction)) and no significant interaction between training/transfer and correct/incorrect (two-way repeated measures ANOVA: training/transfer x correct/incorrect: $F_{1,3} = 0.530$, $P = 0.833$ (favourite direction); $F_{1,3} = 0.250$, $P = 0.651$ (changed direction) Greenhouse-Geisser correction $\epsilon = 1.000$).

DISCUSSION

Sensory Influence on Navigation

Route acquisition

Our results show that *G. petersii* is able to learn a determined route highly accurately. All fish, no matter whether trained with visual landmarks, electrical landmarks or without landmarks, were able to navigate through the maze with an accuracy of nearly 100% correct trials after training (Fig. 4). However, the performance during training shows that task acquisition was influenced by the available sensory input (Fig. 2 and 3). The fish trained with visual landmarks learned the task significantly faster than all other groups. These fish were probably able to see the visual landmarks in front of the correct doors from their start position or after swimming through the first partition, therefore the visual landmarks might have affected the decision in which direction to swim, improving route acquisition.

The electrical landmarks (plastic and metal objects) had no significant influence on the training duration compared to the group trained without landmarks. Because of the short perceptual range of the electric sense and the distance of ca. 27 cm between the door and the objects, the fish could not perceive the electrical landmarks from their start position. In this case, the landmarks were unlikely to guide the directional decision, and thus had no influence on task acquisition. This does not correspond with the results of studies of Cain et al. showing that in a vertical navigation task *G. petersii* did use electrical cues during task acquisition (Cain, 1995; Cain et al., 1994; Cain & Malwal, 2002). These differences might be explained by differences in the navigational task and differences in the experimental setup. During the experiments of Cain et al the fish had to find a hole in a partition located at a certain height, vertically navigating in the range of ca. 20 cm, while during our experiments the fish had to swim a specific more complex route, navigating over a total range of 90 cm (from start area to goal area). During a very short range navigation task such as that used in the studies by Cain et al., the electric sense seems to be much more efficient than in our experiments.

However, our results might also be influenced by a systematic difference in landmark presentation of the visual and the electrical cues. During the experiments with the visual landmarks there was only one object present for each decision. In contrast, during the experiments with the electrical landmarks, the hoods were placed in front of both gates. The presence of visually detectable hoods in front of both doors while only one of them contained an electrically detectable object, introduced an additional conflict between the visual and electrical information, which might have made the electrical landmarks less reliable.

Egocentric vs. allocentric navigation

The results of the test in which egocentric and allocentric cues were put in conflict reveal that all fish no matter which landmarks were available preferred the previously learned egocentric route over the use of landmarks (Fig. 4). This suggests that there is an inherent dominance of the egocentric navigation strategy in *G. petersii* when navigating on a familiar route, which is not influenced by the availability of certain senses. This corresponds with findings in fruit bats (*Rousettus aegyptiacus*) showing a very similar dominance of an egocentric representation of space over displaced local landmarks during a familiar navigation task independent of whether the bats used vision or echolocation for landmark detection (Holland, Winter, & Waters, 2005). Together with studies e.g. in

pigeons and hummingbirds this indicates the importance of egocentric representation of space (Hurly & Healy, 1996; Strasser & Bingman, 1996). Egocentric navigation is more robust against changes in the environment and is therefore the more reliable strategy in a variable environment. The natural habitats of *G. petersii* are rivers in West and Central Africa, which provide a highly variable environment (Moller, 1995). Because of the water current of rivers, local landmarks are likely to be relocated and seasonal changes of the water level (rainy and dry seasons) will additionally affect the structure of the fish's habitat. Within such unstable environments, allocentric navigation based on local landmarks is probably less reliable than egocentric navigation, especially if the route is very well known and used repeatedly. Therefore river fish might be more likely to use an egocentric strategy than fish that live in more stable habitats like lakes or ponds, as for example shown in sticklebacks (Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003). Our results, however, do not correspond with maze studies in the closely related African weakly electric fish *Mormyrus rume*, which used landmark based navigation when electrical landmarks were available and only chose egocentric navigation in the presence of visual landmarks (Walton & Moller, 2010). The experimental setup and landmark presentation were very different in this study so that the results are not directly comparable.

An additional factor, which might have influenced our results, is that we might have created a conflict between local and global landmark as we not only put egocentric and allocentric cues in conflict but we also changed the position of the local landmarks within the tank. While we minimised global cues by shielding the tank from the outside and by using the setup in two directions, the availability of uncontrolled cues cannot be completely excluded. Such global landmarks might have supported the egocentric navigation strategy and reduced the reliability of the local landmarks.

Cross-modal Landmark Recognition During Navigation

Training

The training results of the second experimental series show that while the fish preferred the egocentric route in the first series, *G. petersii* is able to use visual landmarks for allocentric navigation (Fig.5). However, with an accuracy of ca. 70% correct trials and a more than twice as long training duration, this allocentric navigation was much less efficient than the egocentric strategy. This might result from the possible conflict between the local landmarks and global cues. Under natural conditions using

objects for navigation, which vary their position relative to unchanging global cues, probably would not be efficient. Therefore it was proposed that a conflict between local and global cues is solved based on the perceived stability (a priori reliability) of the cues (Biegler & Morris, 1996). Since in our experiments only the local landmarks changed their position and the rest of the setup stayed constant throughout the experiments, the local landmarks were probably perceived as less reliable. Hence to learn the task, the fish might first had to learn to rely on the local cues.

Caution should be taken, however, as the training performances during the first and the second experimental series are not independent. The previous experience of the first experimental series, during which the fish were trained using one defined route, might have influenced the training of the second experimental series. The fish were already familiar with the setup and knew that they had to swim from the start area to the goal area, which might have positively influenced the training performance. This positive effect is shown in the trial duration (Fig. 3 and 6). While at the start of the second experimental series the trial duration slightly increased compared to the end of the first series, the fish were much faster than at the start of the first series. Alternatively, the previous experience might also have had a negative influence on training. The new task contradicted with the previously learned information, hence to learn the new task the previously learned task had to be overwritten. It is therefore possible that naive fish would have learned the allocentric navigation task faster.

The difference in the training performance of the fish trained with visual landmarks and the fish trained with electrical landmarks is probably based on the difference in perceptual range of both senses (Fig. 5 and 6). As described above the fish could not perceive the electrical landmarks from their start position or directly after they had passed the first barrier. Therefore, the fish could have made the decision in which direction to swim before they could detect the electrical landmarks and thus did not associate the decision and its consequences with the landmark.

The visual landmarks, on the other hand, could be perceived from a greater distance, so the fish might have been more likely to associate the landmark with the directional decision and thus to learn the task. However, the analysis of the swimming behaviour of the fish trained with visual landmarks shows that these fish also tended to swim in a preferred direction independently of whether this direction was indicated by a landmark or not (Fig. 9). This was especially the case when they made an incorrect decision, suggesting that in these cases the fish swam in their preferred direction without attending to the landmarks. During trials in which correct decisions were made, the fish seem to have used the

landmarks in two different ways. In 56.75% of the correct training decisions the fish directly swam in the direction of the correct landmark indicated direction, suggesting that the fish might have used the landmarks for guiding the decision. In the other 43.25% of the correct decision, the fish first swam in the direction of the incorrect gate and then changed the direction, suggesting that the fish noticed the absence of the landmark when swimming in the direction of the incorrect gate and reacted with a change of direction.

Transfer tests

The results of the transfer tests with electrical landmarks show that all four visually trained fish tested reached a performance significantly different from chance level (Fig. 7). However, with only 35% - 45% correct trials the performance was significantly worse than during training with visual landmarks and navigation was not very efficient. The comparison of this test performance with the training performance of the group trained with electrical landmarks shows that under the same conditions the visually trained fish without any training with the electrical landmarks reached a significantly higher performance than the electrically trained group after more than 160 training trials (Fig. 8). This suggests that the visually trained fish were able to transfer the use of landmarks from vision to the electric sense, however, the short working range of the electric sense made the landmark recognition ineffective. During the transfer tests with the electrical landmarks, the hoods and thus some visual cues were present in front of both gates. From this, the fish received ambiguous visual information, which made the task more difficult to solve. The fact that despite this ambiguous visual input the fish reached a performance significantly different from chance level, might suggest that the fish had not just learned to swim to any visible object but recognised the landmarks more specifically and were able to transfer this information from vision to the electric sense. This corresponds with the findings of an earlier study that *G. petersii* is capable of cross-modal object recognition (Schumacher, Burt de Perera, Thenert, et al., 2016).

The comparison of the recorded decision behaviour during training and transfer tests supports the hypothesis that the fish were able to transfer the use of the landmarks but that navigation was impaired, because of the small perceptual range of the electric sense. The decision behaviour during training and test was very similar but during the transfer test the fish chose slightly more often the favoured direction and changed the direction slightly more often (Fig. 9). During the transfer trials the

fish could not perceive the landmarks from their start position but could only detect their presence or absence when close to the gate and therefore might have changed the direction more often than during the trials with visual landmarks.

CONCLUSION

Our results show that *G. petersii* is able to navigate highly efficiently in a familiar environment using egocentric cues. After learning the navigational task, an egocentric strategy, perhaps supported by global landmarks, dominated over an allocentric strategy, independently of the available sensory system. Nevertheless, our results suggest that navigation is influenced by the employed sensory system in subtle ways. In contrast to electrical landmarks, visual landmarks significantly improved task acquisition and allowed allocentric navigation. This suggests that there might be a task division of allocentric and egocentric navigation. *G. petersii* might tend to use allocentric cues during route acquisition in less familiar environments whereas the egocentric strategy might be employed when following familiar routes. This hypothesis is supported by the results of Cain et al. showing that *G. petersii* used electrical cues during acquisition of a short range vertical navigation task and relied on an egocentric representation when the fish were familiarised with the task (Cain, 1995; Cain et al., 1994). Furthermore, our results in conjunction with the above cited results from Cain et al. and previous studies showing a dominance of the electric sense at close range (Schumacher, Burt de Perera, Thenert, et al., 2016; Schumacher et al., 2017), suggest that there is also a task division between vision and the active electric sense. Vision might be used for detecting larger landmarks from some distance, which aids longer range navigation, whereas active electrolocation is probably used to perceive fine-scale information about its close surroundings, orientating at very close range.

The results of the allocentric training and the transfer tests show that, although egocentric navigation seems to be inherently dominant during navigation in a familiar environment, *G. petersii* is able to adjust its navigation strategy if necessary, and is able to use cross-modal landmark recognition to further increase the flexibility of the navigational system. These results, together with previous research in other taxa, underpin the importance of navigation mechanisms being flexible in order to cope with environmental challenges (T. S. Collett & Graham, 2004). A flexible multisensory system

allows an animal to navigate successfully within the environment under varying conditions in diverse environments, providing a clear adaptive advantage.

ACKNOWLEDGEMENTS

This study was supported by the German Research Foundation (DFG Em43/17-1) and the German Academic Exchange Service.

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Figure 1: Top view of the experimental tank with a symmetrical two-directional design. Start and goal area switched after each trial as the fish either had to swim from left to right or from right to left. The correct landmark indicated route allowed passage via open cages, whereas incorrect doors denied passage via closed cages (dead end). To maintain motivation the goal area was equipped with a refuge (plastic tube) and a food reward (bloodworms). To minimise uncontrolled external cues a black curtain was placed around the setup.

Figure 2: Box plots of the number of training trials the different training groups needed to reach the pre-assigned learning criterion of 21 correct trials out of 24. The fish were trained to swim from the start area to the goal area using a pre-assigned landmark indicated combination of gates (either right - left or left - right). The number of fish within each group is indicated in the figure. The lines of the box plot indicate the lower quartile (25 %), the median (50%) and the upper quartile (75 %) and the whiskers indicate the minimum and maximum values. A Kurskal Wallis-test and a post hoc test was conducted to ascertain whether the training duration of the groups differed significantly (KW: $H_3 = 11.504$, $P=0.009$). The letters above the box plots indicate which training durations are significantly different. Groups with the same letter do not differ significantly ($P > 0.05$). Groups with different letters are significantly different ($P \leq 0.05$).

Figure 3: Learning curves of the four different groups trained with visual landmarks (~~diamonds~~~~blue~~), plastic landmarks (~~squares~~~~red~~), metal landmarks (~~triangles~~~~dark-red~~) and without landmarks (~~circles~~~~grey~~). Mean trial duration (a), mean number of errors (b) and mean percentage of correct trials (c) of 8 trials of each group. The trial duration was measured from the moment the fish left the start area to the moment it entered the goal area. It was counted as an error when the fish swam into a dead end of the incorrect gate or swam back in the direction of the start through an open gate. During a correct trial the fish swam from the start to the goal area without any errors. The error bars indicate the standard error within each group. The dashed line in c indicates the chance level of 16.67% which results from a 50% chance for the first decision (correct or incorrect gate) and a 33.33% chance for the second decision (correct, incorrect or backwards).

Figure 4: Mean choice of the training route of the four different groups trained with visual landmarks (~~light grey~~~~blue~~), plastic landmarks (~~grey~~~~red~~), metal landmarks (dark ~~grey~~~~red~~) and without landmarks (~~white~~~~grey~~) during training (~~lighter bars~~) and during tests where egocentric and landmark cues were put in conflict (~~shaded~~~~darker bars~~). The error bars indicate the standard error and the number of tested fish is given within the bars. The chance level of 16.67% is marked by the dashed line.

822

823 **Figure 5:** Training performance of the fish trained with visual landmarks (a) and the fish trained with electrical
824 landmarks (b) during the experiments where the fish were trained to use an allocentric navigation strategy. The
825 black bars on the primary y-axis (left) show the number of training trials the fish needed to reach the learning
826 criterion of 17 correct trials out of 25 (68%). If the fish did not reach the criterion no bar is shown. The
827 ~~greyblue/red~~ columns on the secondary y-axis (right) show the percentage of correct trials the fish reached within
828 the last 25 trials of training before the fish reached the learning criterion or before training was stopped. To test
829 whether the performance of the fish was significantly different from the 16.67% chance level, Chi²-tests were
830 conducted (NS: $P > 0.05$, *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$). The dashed line indicates chance level and the
831 dotted line indicates the learning criterion.

832

833 **Figure 6:** Learning curves of the groups trained with visual landmarks (~~diamondsblue~~) and with electrical
834 landmarks (~~squaresred~~). Mean trial duration (a), mean number of errors (b) and mean percentage of correct trials
835 (c) of 8 trials of each group. Within the first 24 trials the route the fish were previously trained to (right - left or left -
836 right) was not used during training (black framed data points). Subsequently all four possible routes were shuffled
837 pseudo-randomly and were used with the same frequency. After 96 trials there was still no consistent trainings
838 effect in all fish trained with plastic landmarks, therefore the plastic objects were replaced by metal objects from
839 trial 97 on (~~dark~~~~er~~ ~~grey~~ ~~red~~). For further description see Fig. 3.

840

841 **Figure 7:** Percentage of correct trials of the four fish trained with visual landmarks that reached the learning
842 criterion during training (~~light~~ ~~grey~~ ~~blue~~) and during transfer tests with electrical landmarks (~~grey~~ ~~purple~~). The
843 training performance was calculated for each fish using all training trials after the fish had reached the learning
844 criterion. Chi²-tests were conducted to test whether the performances were significantly different from the 16.67%
845 chance level. The results are indicated by the asterisks within the bars (*: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$).
846 To test whether there was a significant difference between the performance during training and during the transfer
847 tests exact Fisher-tests were conducted (***: $P \leq 0.001$).

848

849 **Figure 8:** Box plots of the percentage of correct trials of the group trained with visual landmarks during transfer
850 tests with electrical landmarks and of the group trained with electrical landmarks during training. For each fish of
851 the group trained with visual landmarks the percentage of correct trials was calculated from the 20 transfer test
852 trials. For the fish trained with electrical landmarks, the last 25 trials before the training was stopped were

analysed. A Mann-Whitney-U-test was conducted to test whether there was a significant difference between the performances ($U = -2.337$, $N_1 = N_2 = 4$, $P = 0.029$). For further description see Fig. 4.

Figure 9: Mean relative frequency of decisions (two decisions per trial), during which the fish swam in its favoured direction and changed directions during training (light greyblue) and during the transfer tests (grey) of the four fish trained with visual landmarks that reached the learning criterion. Correct (+; shaded bars) and incorrect (-; lighter bars) decisions were analysed separately. The favourite direction is defined as the direction the fish chose with a frequency of more than 50% and it was assigned for each fish for both decisions separately. The fish changed direction when swimming in the direction of one of the gates but then swam in the direction of the other gate before entering the first gate. For each fish, 22-35 training trials after reaching the criterion (44-70 decisions, 34-55 correct decisions, 10-25 incorrect decisions) and 20 transfer test trials (40 decisions, 20-24 correct decisions, 16-20 incorrect decisions) were analysed. The percentage data was arcsine transformed and a two-way repeated measures ANOVA was conducted independently for the favourite direction and for changed direction. The mean and the standard error (error bars) were back transformed into percentage data.