

Three-dimensional spatial cognition: information in the vertical dimension overrides information from the horizontal

Robert I. Holbrook · Theresa Burt de Perera

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Abstract Fish live in three-dimensional environments, through which they swim with three translational and three rotational degrees of freedom. Navigating through such environments is recognised as a difficult problem, yet fish, and other animals that swim and fly, achieve this regularly. Despite this, the vast majority of research has considered how animals navigate horizontally from place to place and has ignored the vertical component. Here, we test the importance of the vertical axis of space for fish solving a three-dimensional spatial cognition task. We trained banded tetras (*Astyanax fasciatus*) to learn the route towards a goal in a rotating Y-maze in which the arms led either up and left or down and right in an environment that allowed access to visual landmarks providing horizontal and vertical information. Our results revealed that the landmarks increased navigational efficiency during training. However, these landmarks were ignored when the horizontal and vertical components were placed in conflict with each other by rotating the maze 90° during testing. From this surprising result, we conclude that the cues that are present in the vertical axis (presumably hydrostatic pressure) override landmark cues that have been shown to be salient in experiments that only consider the horizontal component of space.

Keywords Spatial cognition · Navigation · Three dimensions · Fish · Orientation · Volumes

Introduction

The difficulty of navigating through three-dimensional space is a recognised problem in animal behaviour (Holbrook and Burt de Perera 2009; Taylor et al. 2010). This arises because of the additional vertical dimension through which animals have to move, resulting in an increase in spatial complexity. The problem is exemplified in fish, which must navigate from place to place within their aquatic, volumetric habitats through which they can move with three translational degrees of freedom. Here, we aim to identify the importance of the, largely ignored, vertical component to a spatial cognition task by using the banded tetra fish (*Astyanax fasciatus*; Cuvier) as a model organism. This fish species is robust, easy to manipulate and highly motivated to obtain a food goal.

A limited number of studies have examined how animals navigate vertically, but these have considered each axis independently and have not aimed to ascertain how an animal navigates through a volume (e.g. Henderson et al. 2001, 2006; Wiegmann et al. 2000). Other work has considered how terrestrial animals navigate over undulating terrain, but these have been concerned with subjects that are constrained to surfaces (Grah et al. 2005, 2007; Grobety and Schenk 1992; Nardi and Bingman 2009; Nardi et al. 2010; Wohlgenuth et al. 2001). We therefore know very little about volumetric navigation in animals. In a previous experiment, we used a rotating Y-maze in which fish had to learn to swim along an arm to reach a goal. In probe trials, the maze was rotated 90 degrees, which placed the cues associated with the horizontal and vertical components of space in conflict. We showed that fish encode the vertical and horizontal axes of space separately, rather than as an integrated unit. Further, the fish revealed a strong preference for using the previously

R. I. Holbrook · T. Burt de Perera (✉)
Animal Behaviour Research Group, Department of Zoology,
University of Oxford, South Parks Road,
Oxford OX1 3PS, UK
e-mail: theresa.burt@zoo.ox.ac.uk

learned vertical direction over the horizontal (Holbrook and Burt de Perera 2009). Importantly, landmark cues were rendered uninformative throughout this study, and in a control, light cues were found not to have an effect; hence, the only cues that were available to learn and remember were either egocentric cues or hydrostatic pressure—an allocentric cue that only provides vertical information. This simulated an aquatic environment similar to the open ocean, which is landmark free. However, fish and other animals often inhabit landmark-rich environments such as coral reefs or densely weeded mangroves. These environments contain allocentric landmark cues that provide both vertical and horizontal information that fish may learn. These cues would then enable them to navigate from place to place. Such differences in the visual structure of the environment may affect the relative weighting given to the vertical axis.

Visual landmarks play an important role in the way many animals navigate horizontally between locations (Braithwaite and Burt de Perera 2006; Odling-Smee et al. 2006). Fish use landmarks to locate and navigate to foraging patches (Warburton 1990, 2003). They are also able to learn the spatial configuration of visual landmarks to indicate the position of foraging areas and can use this information to feed efficiently and accurately (Hughes and Blight 1999, 2000). Landmarks have been shown to override other cues such as egocentric information when fish navigate horizontally (Odling-Smee and Braithwaite 2003; Sutherland et al. 2009). There is some discussion over the way that landmarks and cues from the overall geometry of an experimental arena provide orientation information, with some evidence that in certain situations the geometry of an area is used to orient in preference to distant landmarks (Sovrano et al. 2005, 2007). However, experiments on rats suggest that global geometric features might not be learned or used (Pearce et al. 2004) and instead animals may use a view-based image matching mechanism (Cheng 2008; Cheung et al. 2008). The precise use of geometric information remains controversial (Cheng 2008; Shettleworth 2010), and the difference between geometric cues and landmarks has been recently called into question (Sutton 2009).

On the basis of the above studies, we hypothesise that fish will use allocentric visual landmarks when navigating through three dimensions. This will shift the previously observed preference for the vertical axis that exists in a landmark-free environment. We trained individual fish to swim either up and left or down and right through a Y-maze. As we had previously shown no difference in learning cues associated with arms position either left or right, fish were trained to these two arm positions only for simplicity (Holbrook and Burt de Perera 2009). In repeated probe trials, we rotated the Y-maze by 90° from its starting

position, so that the available directions were either up and right or down and left. This arrangement positioned previously learned horizontal and vertical cues in conflict. If fish use the landmark cues to navigate, the reliance on the vertically learned direction would be expected to decrease during probe trials, indicating that fish choose to use a mixture of both vertical and horizontal directions. Consistent with studies on other animals, this would imply that fish in landmark-rich and landmark-poor environments use different navigational mechanisms and that similar mechanisms are used during horizontal and volumetric short-range navigation.

Materials and methods

Subjects

Subjects were ten captive-bred banded tetras, *A. fasciatus* (eyed morph), from a population originally collected from Texas, U.S.A. These were raised with conspecifics in aquaria (0.3 × 0.6 m and 0.3 m high) that were environmentally enriched with Java moss, rocks with crevices and wooden structures. After completing the experiment, the fish were donated to a local tropical fish shop. The fish were between 6 months and 2 years old and between 4 and 5 cm total length. All fish were experimentally naïve. During the study, they were housed in aerated, filtered aquaria (0.6 × 0.3 m and 0.3 m high) that were divided into five compartments using perforated clear Perspex. The laboratory was maintained at 25°C on a 12:12 h diurnal light cycle and was illuminated with overhead fluorescent lighting and fluorescent lighting over each tank. Over the course of the study, the fish received food only during experimental sessions. This study was approved by the Local Ethics Review Committee in the Department of Zoology, Oxford, and did not require a Home Office License.

Apparatus

We used a clear Perspex rotating Y-maze (Fig. 1) that was placed into a transparent glass tank (0.58 × 0.58 m filled with water to 0.56 m), allowing the fish to view all the landmarks around it that were present in the laboratory. The surrounding landmarks included buckets of varying heights, colours and sizes, water pumps, an aluminium frame around the tank, the sink and a number of other basic aquatic laboratory features (see Fig. 2 for a photograph of the landmarks surrounding the apparatus). All of these landmarks were maintained in a constant location throughout the experiment and were placed between approximately zero and 3 m outside the glass tank.

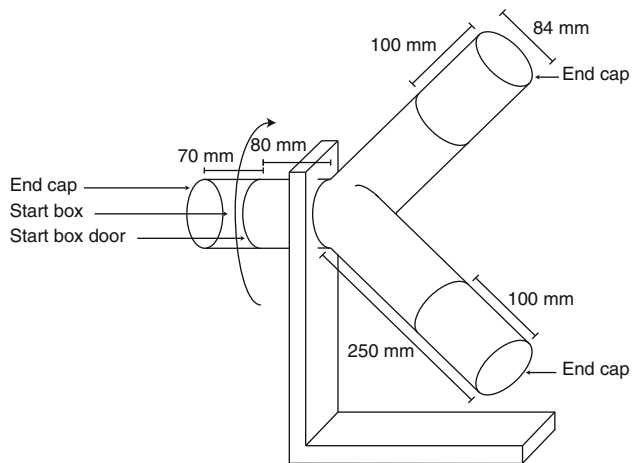


Fig. 1 The three-dimensional Y-maze. The maze is composed of 5-mm clear Perspex tubing and can be rotated around its axis allowing the arms to be positioned horizontally, vertically or at any point in between

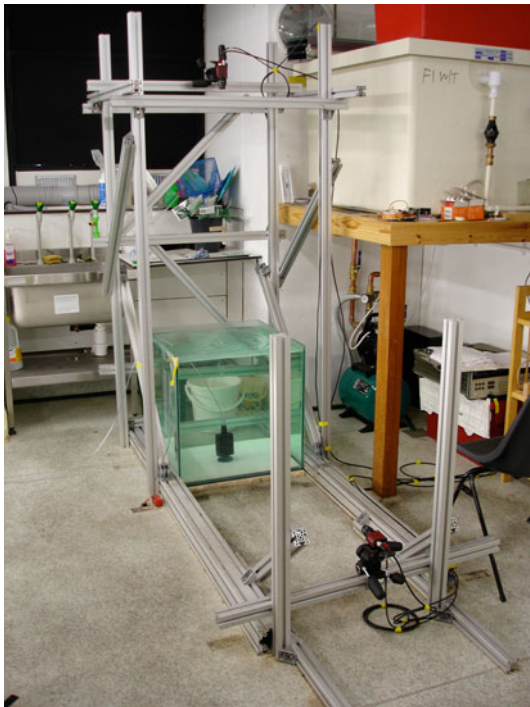


Fig. 2 A photograph showing the position of the landmarks around the apparatus. The maze shown in Fig. 1 was placed in the glass tank in the centre of this photograph

Training and testing

Fish were trained to swim from the start box, through the maze to one of the arms. These arms were rewarded with food and a stimulus shoal. Vaseline was used to attach a food reward of a 5-mm square of red TetraMin fish flake to the end cap of the rewarded arm. These fish are highly motivated to associate with other conspecifics. This

propensity allowed us to use a stimulus shoal as an additional reward. We did this by placing a conspecific in a small glass tank outside the maze at the end of the rewarded arm as an additional complementary reward. The subject fish could not see either the food or the conspecific fish from the starting point; they could only see the reward once they had made a decision to swim in a particular direction.

Each fish completed four training trials on alternate days. To begin each trial, fish were placed individually into the start box of the Y-maze. After 60 s, the fish were released into the maze by removing the door to the start box indicated in Fig. 1. The door was a clear piece of acrylic shaped to fit the maze precisely. We defined a correct choice as crossing a line drawn at 0.1 m from the end of the rewarded arm of the maze. The time taken from exiting the door to crossing this line was recorded as latency to the goal. During training, if the subject selected the correct arm first, the trial ended. If the fish initially selected the incorrect arm, the trial continued until the fish swam out of that arm and down the correct arm (terminating the trial) or until 600 s had elapsed. Once the trial had ended, the fish was given 120 s to consume the reward and interact with the conspecific. After this time, we removed the end cap to the start box and the fish was given 180 s to swim out of the Y-maze. If the fish was still in the Y-maze after 180 s, the maze was manually rotated in the water to a position to allow the fish to swim out easily. This last procedure only occurred during the initial training phase. Both the food and conspecific rewards were removed from the maze during probe trials. As the start box door was on one side of the maze, the direction of the door was randomised in the first training trial. The maze was rotated through 180° (as indicated in Fig. 1) each subsequent training day, alternating the position of the maze door. This rotation maintained the position and directions of the arms while controlling for the potential door cue.

To test the effect of multiple stable three-dimensional landmarks on the fishes' preference for using the vertical direction, we placed the maze inside the glass tank described above, enabling the fish to see and potentially use all the landmarks surrounding it. The position of the maze was maintained throughout all training trials. We positioned the maze at a 45° angle from the vertical, with one arm allowing the fish to swim up and left and the other allowing the fish to swim down and right. Five fish were trained in each direction. All fish were trained until they reached the preset criterion of nine out of ten correct trials. Once this criterion had been reached, the stimulus shoal was removed from further training trials and the fish received additional training with only the food reward. Fish again had to reach a criterion of nine out of ten correct

trials under these conditions. We added this second criterion to ensure that the fish was not using the stimulus shoal or the associated Perspex tank as a beacon to aid navigation. When a fish had reached this criterion, it completed four test trials. Fish also experienced training trials between each test trial to prevent extinction of the learned task. As the fish had already learned the task, the criterion for these inter-test training sessions was completing four out of five correct trials (four were completed per day).

The first test trial was conducted with the maze positioned exactly as it had been during training, but with the food reward removed. This was to ensure that the fish had learned the task and would perform it in the absence of a reward. If the fish completed this successfully, they went on to complete the other three test trials. If they failed, they resumed training from the point where the shoal was removed. During the three repeated test trials, we rotated the maze through 90° about the axis shown in Fig. 1, placing the previously learned vertical and horizontal directions in conflict with each other, while maintaining the arrangement of the landmarks.

The latency to choose an arm for each trial was recorded using a digital stopwatch. Latencies are defined as the period from when the end of the fish's tail went past the door slot for the start box until it crossed the line 0.1 m from the end of one of the arms (indicated in Fig. 1). If fish failed to meet the criterion after 50 training trials, they were removed from the experiment (one individual).

Results

The fish preferred the arm that was consistent with the vertical direction they had previously learned (Wilcoxon signed-ranks test: $T = 45$, $N = 9$, $P = 0.005$; Fig. 3). There was no evidence of a difference in the rate of learning between the up-and-left and down-and-right treatments (Mann–Whitney U test: $U = 26.5$, $N_1 = 4$, $N_2 = 5$, $P = 0.1248$).

To test whether three-dimensional visual landmarks affected the learning of the route, we compared two measures of learning between experiment 3 (in which no landmarks were present) in Holbrook and Burt de Perera (2009) and the current study. These measures were the number of trials to reach criterion and learning speed. The latencies in the final training trial before the probe trials began measured navigational efficiency. For consistency, only trials where fish were trained up and left or down and right were used from the experiment in Holbrook and Burt de Perera (2009) as these match the training conditions of the current study. We found no difference in the number of trials to criterion between the two experiments (Mann–Whitney U test: $U = 71.5$, $N_1 = 8$, $N_2 = 9$, $P = 1$;

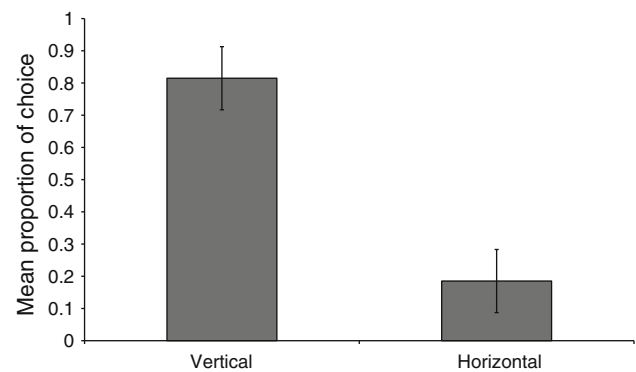


Fig. 3 Arm selection when horizontal and vertical components were placed in conflict with the position experienced during training. This shows the mean proportion of choice over three probe trials when nine fish trained with the Y-maze at a 45° angle from the horizontal, four trained to *up* and *left* and five to *down* and *right*, were presented with the maze in the opposite orientation where the choices were either *up* and *right* or *down* and *left*. Error bars indicate \pm SE

Fig. 4). However, comparing the latencies to the reward during the final probe trial showed that the fish that were able to use landmarks were faster at getting to the reward than those that learned the task in the featureless environment (Mann–Whitney U test: $U = 102$, $N_1 = 8$, $N_2 = 9$, $P = 0.0045$; Fig. 5).

Discussion

Our results show that, despite the presence of allocentric horizontal cues, fish prefer to use the previously learned vertical component of their three-dimensional environment when the learned vertical and horizontal components are

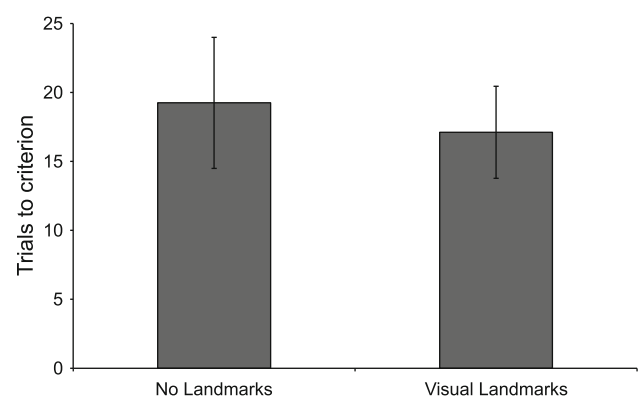


Fig. 4 Rate of learning: trials to criterion. Mean trials to reach criterion for eight fish that were trained to swim either *up* and *left* or *down* and *right* in an environment devoid of landmarks, and nine fish that were trained in the same two directions, but had three-dimensional visual landmarks around their environment. Data from the “No Landmarks” experiment are from Holbrook and Burt de Perera (2009) and the “Visual Landmarks” data are from this study. Error bars indicate \pm SE

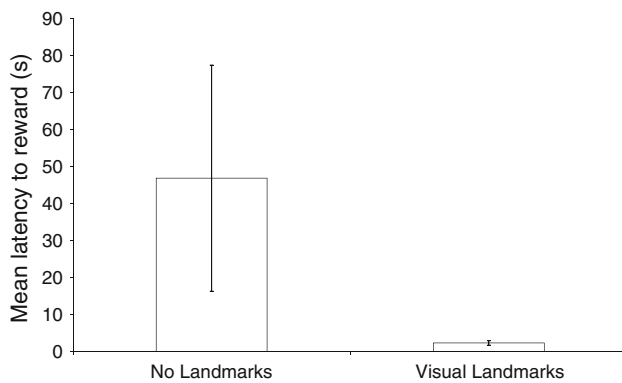


Fig. 5 Time to complete the task. The mean latency for the last training trial for eight fish that were trained to swim either *up* and *left* or *down* and *right* in an environment devoid of landmarks, and nine fish that were trained in the same two directions, but had three-dimensional visual landmarks around their environment. Data from the “No Landmarks” experiment are from Holbrook and Burt de Perera (2009) and the “Visual Landmarks” data are from this study. Error bars indicate \pm SE

placed in conflict with each other. This highlights the crucial role of the vertical component in three-dimensional navigation.

Our results are surprising and run contrary to previous findings of how fish and other animals use visual landmarks while learning to navigate horizontally. Using landmarks to navigate provides accurate location information and can constitute an efficient navigation tool. Animals from a wide range of taxa and environments have been shown to use visual landmarks to navigate in the horizontal dimension (e.g. honey bees (*Apis mellifera*; Linnaeus), Cheng et al. 1987; pigeons (*Columba livia*; Gmelin), Cheng 1994; dogs (*Canis familiaris*; Linnaeus), Fiset 2009; Clark’s nutcracker (*Nucifraga columbiana*; Wilson), Kelly et al. 2010; corksling wrasse (*Symphodus melops*; Linnaeus) and fifteen-spined sticklebacks (*Spinachia spinachia*; Linnaeus), Hughes and Blight 1999; and butterfly fish (family: Chaetodontidae), Reese 1989). In addition, landmarks have been shown to override other cues, such as egocentric information when spatial information from these cues conflict (Odling-Smee and Braithwaite 2003; Sutherland et al. 2009). However, in this experiment in which the fish were navigating through three-dimensions, visual landmarks did not override other cues. Even if the propensity for animals to use landmarks to navigate was translated into the vertical dimension in the same way they are used in the horizontal, we would have expected fish to show this by choosing to use the previously learned horizontal and vertical directions equally.

The preference for using vertical cues in this experiment could be the result of the fish using hydrostatic pressure as a navigational tool. Hydrostatic pressure is a global, stable cue that is present in all bodies of water. Fish have been

shown to be highly sensitive to pressure changes (Blaxter 1980; Blaxter and Tytler 1972; Burt de Perera et al. 2005; McCutcheon 1966) and the sign of the change (Qutob 1962), so could therefore use the hydrostatic pressure gradient to determine the vertical direction of their movement. In our previous study, hydrostatic pressure was the only allocentric cue available to the fish and we argued that the fish showed greater reliance on vertical cues because they did not have access to allocentric horizontal information during training; thus, they used hydrostatic pressure to aid their navigation. We hypothesised that this preference would be disrupted when allocentric horizontal cues were added to the system, as they were in this experiment, but the preference for the vertically learned direction has remained.

Here, fish learned the route to the reward in an environment that contained both horizontal and vertical visual landmarks. Fish were able to use any of these to aid the learning of the goal position. The potential conflict between information given from landmarks in the horizontal and vertical components during probe trials compared with that which was present during training (due to maze rotation) may mean that under these circumstances, the fish chose to attend to the more reliable hydrostatic pressure cue, which provides global stable information. This cue was constantly present and was stable throughout the experiment, providing reliable information about the vertical dimension. It is possible that the fish learn a route to the reward or the position of the goal using multiple mechanisms, but when some of these become unreliable during testing, they ignore previous information given by the landmarks and they rely on a cue that maintains stability.

Together with G. Taylor, we have recently proposed a possible mechanism for fish to determine their absolute vertical location in a column of water (Taylor et al. 2010; Holbrook and Burt de Perera 2011). This mechanism theorises that fish can use the rate of change of pressure while moving vertically through the water column to determine their absolute depth. Fish are acutely sensitive to changes in hydrostatic pressure, with some fish being sensitive to changes of 0.02% (Blaxter 1980; Blaxter and Tytler 1972, 1978; Burt de Perera et al. 2005; McCutcheon 1966); theoretically meaning only small vertical movements are required to sense their change in depth. Not only are fish highly sensitive to pressure changes, they can also determine the sign of this change, with an increase in firing rate from the neurons coming from the swim-bladder if it is expanding (meaning the fish is moving up), and a depression in the firing rate if it is contracting (meaning the fish is swimming down) (Qutob 1962). This simple mechanism could inform the fish that it is travelling up or down and could be used to navigate in this experiment.

During training, fish could use egocentric cues, directional cues based on the orientation of their body, to aid in finding the goal. Fish are able to obtain body-centred kinesthetic and proprioceptive cues that register rotations, i.e. yaw and pitch and roll. However, in order to navigate from point to point, translational movements (move left, right, up or down) are important in addition to rotations. To use egocentric signals for navigational translations, they must first calibrate these against an external cue. For fish, this means fixing their body orientation in the volume before making a rotational and translational movement. Fish have a vestibular system similar to mammals in their inner ear and can fix their body orientation using the direction of gravity (Watanabe et al. 1991; Rahmann and Anken 2000). It is possible that they use only a vertical egocentric cue during the probe trials in this experiment, but this cue is still calibrated by gravity, which also causes hydrostatic pressure.

The results show that the fish were using the visual landmarks to aid their navigation during training. Analysis of the latencies to swim to the reward in the final training trial showed that fish with access to visual landmarks located the reward significantly faster than those trained in a landmark-free environment. The standard error of these latencies was also lower in the condition with landmarks. Both of these measures demonstrate that landmarks increase within trial navigational efficiency during training.

However, when we compared the number of trials to reach the first criterion between the two groups, we found no significant difference. This result could reflect a similarity in the speed at which the task is learned with and without landmarks. However, it is more likely that this is an artefact of our arbitrarily set criterion, which imposed an artificial lower limit of nine trials. If any of the fish had learned the task in fewer than nine trials, we would not have detected this in this experiment.

It is possible that vertical visual cues in general, or just those in this particular experiment, are more salient to the fish than the horizontal visual cues, but we have no reason to suspect this is the case. Such a method of navigation would be a very inefficient, and sometimes ineffective, way of navigating in a landmark-rich environment, as it would only allow the fish to use landmarks to navigate in the vertical dimension, ignoring any information provided from horizontal landmarks. There is also strong evidence for fish using landmarks to navigate horizontally in a number of other studies (Burt de Perera 2004a, b; Burt de Perera and Macias Garcia 2003; Odling-Smee and Braithwaite 2003; Sutherland et al. 2009; Warburton 1990). Fish are able to learn and later extract and use the horizontal component of a route through a volume devoid of visual landmarks that comprised all three dimensions (Holbrook and Burt de Perera 2009). It is therefore unlikely that the fish were unable to learn the horizontal component

in the current study. Our results strongly corroborate the hypothesis that the vertical dimension of space is vitally important for navigating through volumes.

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