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From fish out of water to new insights on navigation mechanisms in animals

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ABSTRACT

Navigation is a critical ability for animal survival and is important for food foraging, finding shelter, seeking mates and a variety of other behaviors. Given their fundamental role and universal function in the animal kingdom, it makes sense to explore whether space representation and navigation mechanisms are dependent on the species, ecological system, brain structures, or whether they share general and universal properties. One way to explore this issue behaviorally is by *domain transfer methodology*, where one species is embedded in another species' environment and must cope with an otherwise familiar (in our case, navigation) task. Here we push this idea to the limit by studying the navigation ability of a fish in a terrestrial environment. For this purpose, we trained goldfish to use a Fish Operated Vehicle (FOV), a wheeled terrestrial platform that reacts to the fish's movement characteristics, location and orientation in its water tank to change the vehicle's; i.e., the water tank's, position in the arena. The fish were tasked to "drive" the FOV towards a visual target in the terrestrial environment, which was observable through the walls of the tank, and indeed were able to operate the vehicle, explore the new environment, and reach the target regardless of the starting point, all while avoiding dead-ends and correcting location inaccuracies. These results demonstrate how a fish was able to transfer its space representation and navigation skills to a wholly different terrestrial environment, thus supporting the hypothesis that the former possess a universal quality that is species-independent.

Navigation is a fundamental behavioral capability which facilitates survival in many species. It involves the continuous estimation of the animal's position and direction in the environment which leads to the planning and execution of movements and trajectories towards spatial target locations. In this study we explored the fundamental questions of space representation and navigation in animals, though for practical reasons we focus on a particular animal model, in our case, a fish.

Fish navigation capabilities have been studied extensively in labs and natural environments. Specifically, it was shown that goldfish are capable of orienting themselves using both allocentric and egocentric maps in a plus-shaped maze [1–4]. The neural basis of goldfish navigation exhibits similarities with the neural basis found in the hippocampal formation of mammals and birds [5–7], as revealed by recordings from freely swimming fish [8–13]. Picasso triggerfish for example are able to estimate their swimming distance [14] and Redtail splitfin can differentiate geometric attributes in their environment [15]. In the natural environment, salmon were shown to be able to navigate on the macro and micro scales [16,17]. Studies have indicated that rabbitfish maintain a stable home range and can return to it after being displaced outside this range [18,19].

Although these findings demonstrate the capacity of fish to carry out navigational tasks of different complexities while in aquatic environments, they do not address issues concerning their universality. Mammals and birds can also accomplish these tasks in their own natural environments [20,21]. These functional similarities raise the question of whether all these species do so in a same manner. In particular, is space representation similar or different in all these species? Does the environment affect the representation and how it is used? Are navigation

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strategies universal or confined to specific species? Here, we propose one way to address these questions which we term *domain transfer methodology*. Basically, this methodology takes one species from its own environment and challenges it to perform behavioral tasks in a completely different environment. If the species performs successfully despite this change, the more likely the supposition that its spatial cognition, internal representations and behavioral strategies are independent of the environment and thus may be universal. Here we explored this idea in the context of space representation and navigational skills by taking a fish out of its aquatic environment and challenging it to cope with navigational tasks in a terrestrial environment.

It goes without saying that fish, in general, are not naturally equipped to explore terrestrial environments. Here, this was made possible by using a Fish Operated Vehicle (FOV, Fig. 1A). The FOV is a self-propelled platform whose motion is controlled by the fish placed in an onboard water tank. Control is mediated by an onboard camera and a computer vision system that detects the fish's position in real time and activates the vehicle motors accordingly. Whenever the fish is near one of the water tank walls and facing outwards, the FOV is automatically propelled in this direction. When this mapping is learned by the fish, it can drive the vehicle to any location in the terrestrial environment.

Fish face several critical challenges when navigating the environment using the FOV. First, the fish needs to learn new motor skills to drive the vehicle since these are very different from the muscle power applied to fins to enable swimming. Second, the fish needs to learn how to navigate the vehicle in an alien environment despite the significant distortion in vision due to refraction through the air-to-water interface that results in a distorted projection of the visual world to the eye.

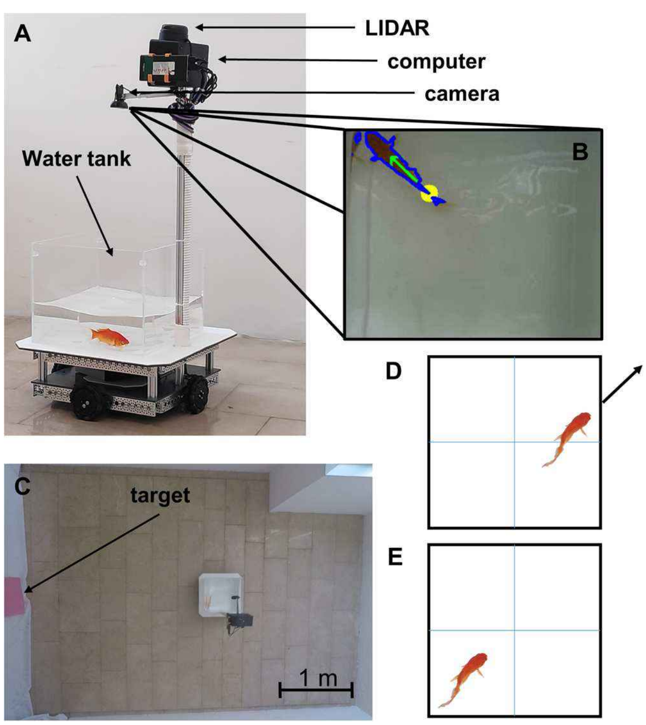

Fig. 1. The fish operated vehicle. A. The fish operated vehicle is composed of a chassis with 4 electric motors equipped with omni wheels, and a camera together with a LIDAR to collect data on fish position and vehicle position in space, respectively. B. View of a fish from the camera: fish contour (blue), tail (yellow), direction vector (green) are automatically extracted from the image and fed to the control system of the wheels. C. The fish operated robot and arena, bird's eye view. The enclosure was created by the room walls and a curtain where the target was placed. D. Instance of fish quadrant location and direction correlating; as a result, the vehicle moves in the direction of the arrow. E. Fish location is far from the water tank wall; the vehicle motors do not generate movement.

Finally, there are inherent differences in the natural structure of the terrestrial and aquatic environments. This raises the question of whether fish can use the unrecognizable elements in the new environment for navigation. The findings here show that the fish were able to control the FOV and solve navigation tasks in this terrestrial environment. These behavioral results thus suggest a level of universality in space representation and navigation strategies.

1. Animals

All the experiments on the goldfish were approved by the Ben-Gurion University of the Negev Institutional Animal Care and Use Committee and were in accordance with the government regulations of the State of Israel. Goldfish (*Carassius auratus*), 15–18 cm in body length, and 80–120 g body weight were used in this study. A total of six fish were used for the study, one female, three males and two undetermined. Specifically: fish 2 was female, fish 3, 4, 5 were males and fish 1, 6 could not be determined. The fish were kept in a water tank at room temperature. The room was illuminated with artificial light on a 12/12 h day-night cycle. The fish were kept in their home water tank and were relocated to the experimental FOV water tank for behavioral experiments. Prior to the beginning of the experiments the fish were fed and habituated to the same food that will be used as a reward for at least two weeks.

2. Fish operated vehicle

The FOV was composed of a chassis measuring 40×40×19 cm that housed the platform on which the water tank was placed. Underneath the platform four engines (Brushed DC motors) connected to four omni wheels (4″ OMNI, 595671, Actobotics) were mounted on 4 sides of the metal skeleton (Fig. 1A). A Perspex water tank was placed (35×35×28 cm) on the platform so that the water level reached 15 cm. A relatively shallow water level of 15 cm was selected to reduce surface waves while the FOV was moving. The main computer (Raspberry Pi 3B+), a LIDAR (RPLIDAR A2M8, Slamtec) and a battery (power bank, 10Ah Type-C 18 W PD) were mounted with a side pole at 40 cm above the platform. The computer was enclosed in a box measuring 17×11×8 cm, the removable power bank was attached on the side and the LIDAR was placed on top (Fig. 1A). Extending another 20 cm inward toward the middle of the vehicle, the TGB camera (C270 HD WEBCAM, Logitech) was mounted facing down to record the fish's position in the water tank below. The operating system of the vehicle can be accessed through MobaXterm [22].

The algorithm operating the vehicle was written in Python with a robot operating system (ROS) module. An extensive list of parts, assembly directions and the code are available for use at the github repository FishOperatedVehicle [23].

3. Vehicle motor control system

The fish's control of the vehicle was enabled by streaming the video signal from the camera to the computer which performed segmentation and detection to find the fish's location and orientation in the water tank (Fig. 1B). If the fish was located near a boundary (i.e., wall) of the water tank while facing outward (Fig. 1D), the vehicle moved in that direction. If, however, it was facing inward (Fig. 1E), no motion occurred. If at any point, based on measurements from the LIDAR, the vehicle came closer than 20 cm to any of the walls or any other obstacle in the terrestrial environment, the computer overrode the fish control algorithm and disallowed any further motion in that direction to avoid a collision. Throughout the experimental session the computer recorded the fish's positions within the water tank and the FOV position in the room and kept a log for further analysis.

4. Vehicle motor response characteristics

To characterize the FOV response dynamics and precision, we measured the vehicle's performance by recording the vehicle location over time after receiving a step command to move forward. Fig. 2A shows the distance traversed as a function of the time from the onset of the motion command. The results are pooled from 28 trials, with seven trials for each main axis of the vehicle. Fig. 2B presents the speed of the vehicle after a command to move forward. In addition, we evaluated the accuracy of the *directional* progression of the vehicle in relation to the orientation of the fish itself. For this purpose, an artificial fish model was set at different angles and locations on the platform, in a total of eight directions at 45° intervals. For each direction, over seven trials, the motion of the vehicle was recorded. The results of these measurements are shown in Fig. 2C, where the orange oval represents the fish head's direction, the arrows represent the mean vehicle motion direction and the standard deviation of the direction. The standard error never exceeded 3°. Given the low standard error and the one second response time, the motor response and its accuracy were thus sufficient.

5. Behavioral arena

The behavioral arena was a three by four-meter enclosure with an indent on the top right corner. Three sides consisted of the room walls painted white, one with a window, and the fourth side had an adjustable white curtain. Depending on the task, one or more colored corrugated polypropylene boards (60 cm × 40 cm) were placed on the walls to constitute the target or distractors. A bird's eye view of the arena can be seen in Fig. 1C.

6. Behavioral experiments

Each session started by placing the fish in the water tank of the FOV as seen in Fig. 1A. The vehicle started out in the middle of the arena or otherwise as stated (Fig. 1C). We tested whether the fish could drive the vehicle towards a target in return for a food pellet reward which was identical to the fish regular food. Every time the fish reached the target, which was defined as the moment the vehicle touched the pink corrugated board, a single 0.002 g food pellet was dropped by the experimentalist into the water tank, the water tank was then covered to prevent any visual feedback to the fish and the FOV was driven manually back to the starting position for the next trial.

Each session lasted 30 min in total, during which the number of times the fish reached the target, how long it took it each time, and the distance it traveled each time were recorded. To avoid over-feeding, the sessions were terminated after a maximum of 20 trials. The fish were kept in separate water tanks throughout the duration of the study. Sessions were conducted three times a week every two days and unless more than a day passed between sessions the fish were not fed between sessions. If there was a break for more than a day between sessions, then

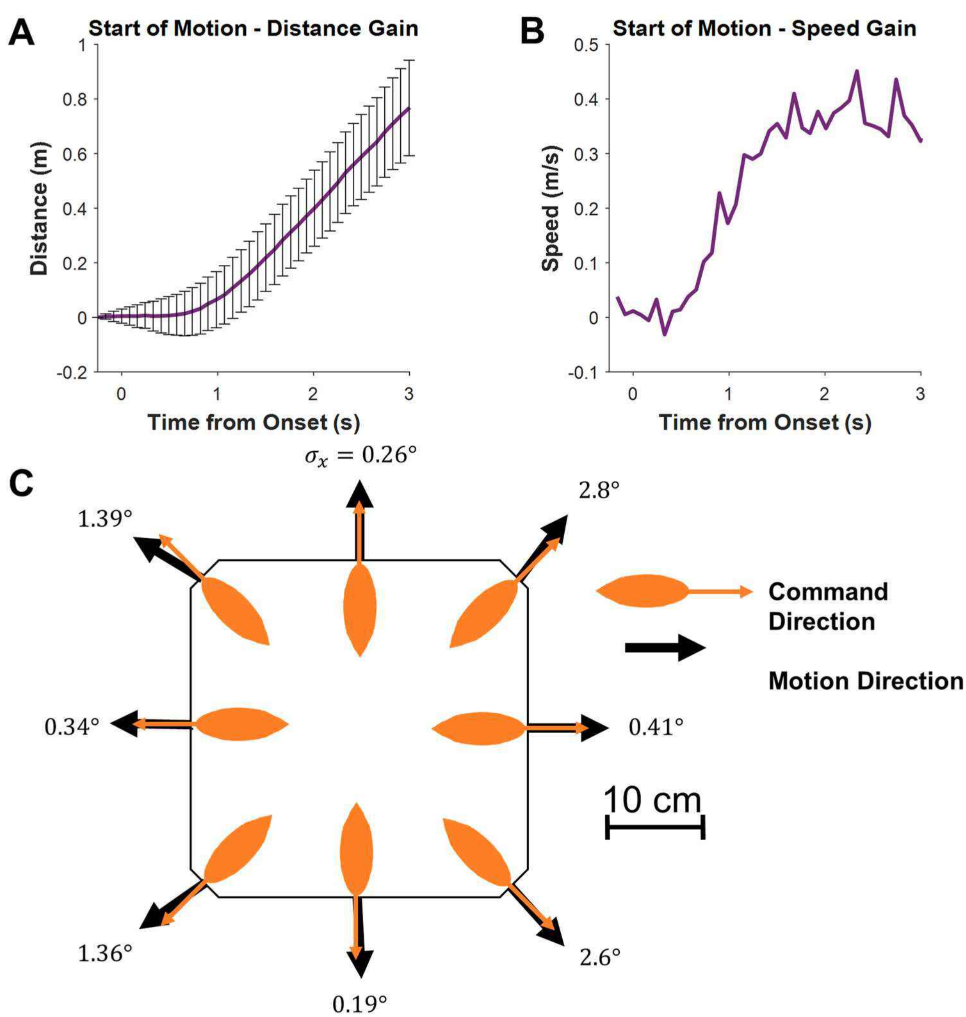

Fig. 2. Vehicle motor response characteristics. A. Dynamic profile in response to step motor command to move forward. B. Velocity profile following a step motor command. C. Reliability of motor command in different directions: eight examples of fish motion along with the mean direction of vehicle movement from seven trials together with the standard deviation.

the fish were given food in the home water tank. The experiments started by first letting the fish habituate to the vehicle environment and experience control of the vehicle for 15 min before the first session began. Overall, six fish took part in the experiments.

7. Statistical analysis

For all fish we have performed t-text between success rate between the first and last sessions. For fish 1 and 2 which participated in different start location control trials, two one-tailed *t*-tests were conducted between different session results to determine whether they were equivalent. The comparisons were between each fish's success rates throughout the manipulations versus its last days of training.

The goal of this study was to test the ability of goldfish to control the FOV and navigate in a terrestrial environment. For this purpose, we tested whether fish could drive the vehicle towards a target in return for a food pellet reward (see Methods). The vehicle was designed to detect the fish's position in the water tank and react by activating the wheels such that the vehicle moved in the specific direction according to the fish's position. In this way, the vehicle's reaction to the fish's position allowed the fish to drive the vehicle in the environment.

As a first test of the fish's ability to navigate the environment, we let the fish navigate from the center of the arena to a target on the arena wall marked by a pink board. The vehicle with the fish inside the tank was placed in the center. The opaque cylinder that prevented the fish from seeing the room prior to the experiment was removed and the computerized control of the vehicle's motion as result of the fish's position was activated. This navigation task could be accomplished using a simple beacon navigation strategy; namely, steering the vehicle towards the target.

Fig. 3A and C show the trajectories on the first session of training of two of the six fish. At that point in time the fish were naïve to the operation of the FOV, the environment, and the task. Both fish appeared to explore the arena randomly. After the first session, the fish were continuously tested every two days (see Methods) and performance was recorded.

The fish became progressively more proficient on the task and by the last session exhibited control of the FOV and a high level of success. Fig. 3B and D show the fish trajectories during the best session, near the end of the training sessions (due to variability, not necessarily the final session). The fish improved in terms of the total number of food pellet rewards during the session (paired *t*-test, $p < 0.005$) and the direct routes to the target.

To quantify the learning curve of the fish, Fig. 4A shows the number of successful trials in each training session and trends over the course of training. Fig. 4B and C present the mean time and mean distance traveled for all trials per session respectively, again clearly indicating that control improved over time. Finally, Fig. 4D compares the number of successful navigations in early and late sessions, averaged across all fish. The statistically significant result of the learning process is evident (t_5 ($tstat = 5.44$), $p = 0.002$, power = 99%).

8. Fish can overcome environmental manipulation

To further explore fish navigational skills, we challenged the fish with several control sessions in which we manipulated the environmental settings to explore different skills or strategies.

8.1. Controlling for the initial position

Whereas the main experiment initiated all trials from the same central position, to control for the effect of this position we ran the experiment again but this time the trials were initiated at different random locations in the arena. The objective of this control was to eliminate the possibility that the fish merely learned a set of movements to receive a reward. If that were the case, we would expect the fish to fail once the starting position was altered. If, on the other hand, the fish was successful despite the change, this would help confirm that its ability to

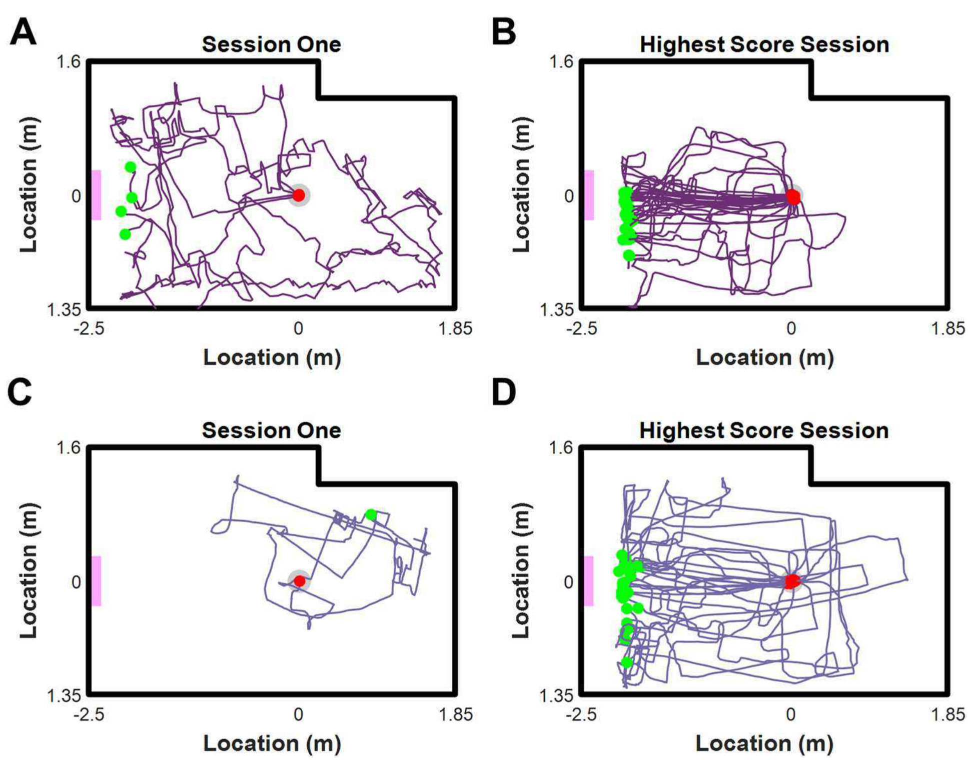

Fig. 3. View of trajectories from two sessions of two fish. A. Trajectories of fish 1 on the first session, starting point (red dot), finish point (green dot), target (pink rectangle). B. Trajectories of fish 1 on the session with the highest score. C. Trajectories of fish 2 on its first session. D. Trajectories of fish 2 on the session with the highest score.

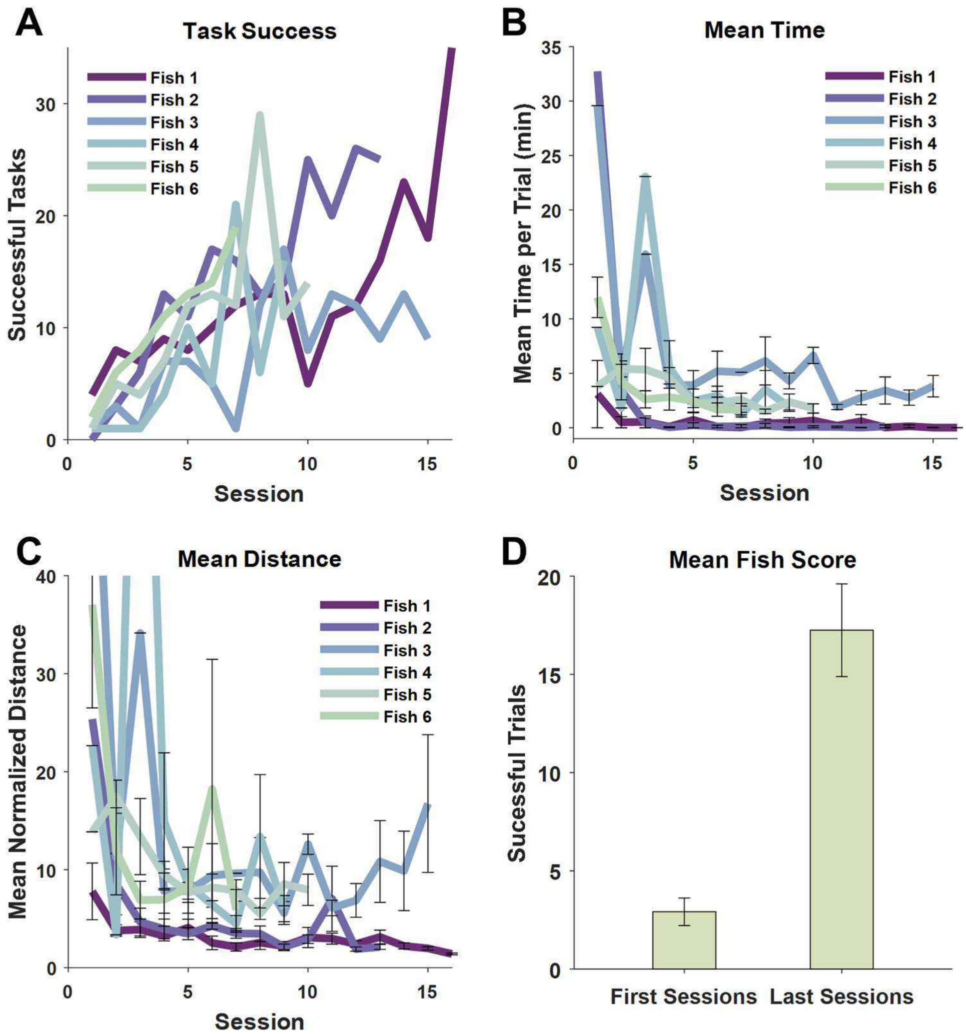

Fig. 4. Learning curves of six fish show improved performance over sessions. A. Number of successful trials per session. B. Mean trial time per session. C. Mean distance travelled by fish within a session. D. Mean successful trials across all fish for first sessions and last sessions throughout the entire experiment along with standard deviation.

reach the target stemmed not from muscle memory but from real-time spatial analysis and navigation, as indeed emerged in the results. Examples of trajectories with different starting points can be seen in Fig. 5A.

To determine whether the initial position affected the navigation behavior of the fish, we tested for equivalence of path lengths between the original and control conditions. If the fish recognized the target, we expect it to head directly to it. Since path lengths are affected by the starting position, we compared the efficiency coefficient of each path. The efficiency coefficient is the path length divided by the Euclidean distance between the initial and target positions (also representing the shortest and most efficient trajectory in each trial). We then compared the distribution of these efficiency coefficients in the original and control sessions. Persistence on a navigational strategy (as opposed to dead reckoning or movement recall) should result in equivalence between these two distributions, as indeed is shown in Fig. 5B.

8.2. Decoy target control

We tested whether the fish identified the target by its mere existence, shape, or other attributes. As a second control, we therefore challenged the fish with decoy targets that were placed along all four walls of the arena and had the same rectangular shape but different colors. We repeated the experiment for 15 trials, all from the central position in the arena as in the original experiment. The fish did not attempt to reach any of the decoy targets and still headed toward the correct target (Fig. 5C), showing conclusively that color was an attribute associated with the target or that the fish used color in combination with other cues as we show in the next experiment.

8.3. Target location control

In the previous experiments, the target remained in the same location throughout the training sessions and the first several controls. We tested whether the fish could accommodate target position manipulation, thereby exhibiting navigation skills that require some sort of path planning. For this purpose, the target was repositioned on the opposite wall of the arena. There were three possible outcomes to this control test. The first was that the fish would head toward the original location of the target and persevere. The second was that the fish would head to the original position, learn that it would not receive a reward and head toward the new target position. The third was that the fish would head straight toward the board target in its new location. Each of these outcomes provides different insights into space representation and navigational planning. In terms of the first outcome, the board does not play any role in the fish's navigation strategy and another attribute of the reward location is key for the fish. In the second outcome, the board is a secondary attribute, and the secondary attribute is only given more

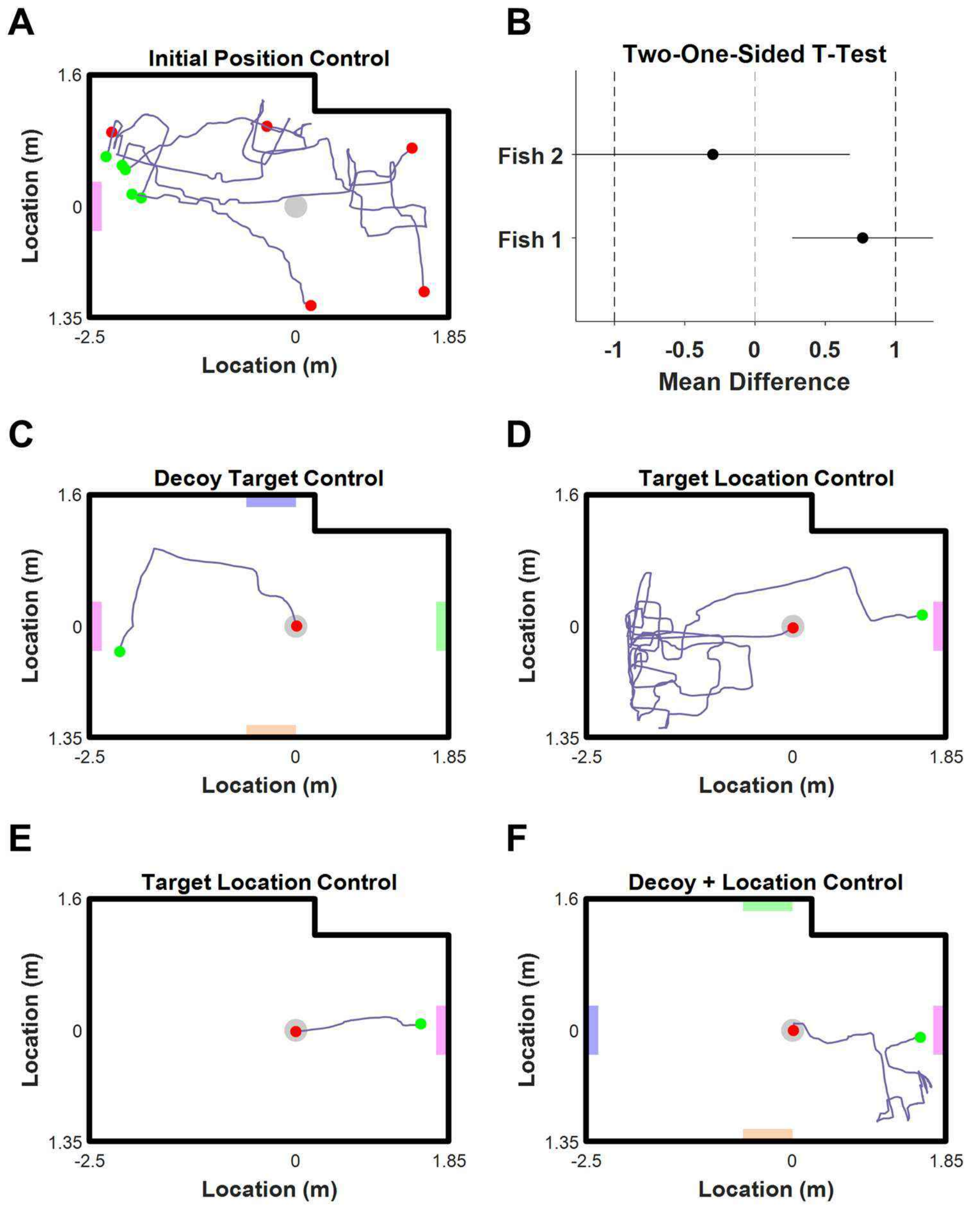

Fig. 5. Results of behavioral arena controls. A. Shifting the initial starting position to different locations in the arena. Original starting point is depicted by a grey dot, new starting points red dots, green dots correspond to end points. B. Two one-tailed *t*-test result for two fish comparing last training sessions and manipulation results. Horizontal lines are the 90% confidence intervals, equivalence borders are at $\Delta L = \pm 1$. C. Despite adding decoy targets (green, blue, and orange), the fish can find the target. D. Moving the target to other side of the arena, first trial. E. Third trial after relocating the target. **F.** Combination of decoy targets and different target locations.

weight when the main attribute results in failure. In the third, the board is the main attribute. Whereas in the first and third scenarios the fish presumably focuses on a single attribute of the environment, the second scenario suggests that the fish has a wider representation of the space which allows it flexibility in navigational planning and re-planning.

In Fig. 5D we show the trajectory of the first encounter for this manipulation. At first the fish headed to the original location of the target. The fish came back to that location repeatedly from different angles. After several failed attempts, it headed straight to the pink target at the other end of the enclosure. This result, corresponding to the second outcome hypothesized above, suggests that the fish took in more of the environment than just the board as a cue for the location of the reward, but the board remained part of it, even though it was not the main attribute. Fig. 5E shows the trajectory of the third trial, when this time the fish headed straight toward the new location of the target, implying a reconsolidation of its internal representation of the environment.

8.4. Conjunction control

Fig. 5F shows a fish that reached the target when the target location was changed, and decoy targets were present. Here, we tested whether the fish could indeed internalize the target as we hypothesized. The supposition was that if the fish reached the target it is likely that it had recognized the pink board as the attribute corresponding to the location of the reward.

We challenged goldfish to navigate in a terrestrial environment. For this purpose, we developed a fish-operated vehicle that enabled the fish to move in a non-aquatic environment. This required the fish to learn and acquire the vehicle motor control to allow navigation. Given the mechanical response of the vehicle, the fish had to overcome the delay in the vehicle's response (Fig. 2A and B) and inaccuracies due to the coarse mapping between the fish's location in the water tank and the movement of the vehicle (Fig. 2C).

Importantly, the view of the room through the water tank walls was distorted as a function of Snell's law of light ray refraction at the interface between the three optical media of air, plexiglass and water. The effect of the refraction is non-linear, because light rays striking directly perpendicular to the water tank walls were not affected but the effect was increased as the angle from the perpendicular is increased. The distortion was exaggerated further when looking at the corners of the water tank. Despite the non-linearity from the fish's perspective the fish still managed to direct the FOV to the target similar to other fish that can overcome this type of distortion while performing complex tasks [24–29].

While comparable to other studies in mammals focusing on the ability to learn how to control vehicles [30,31], here, we added the complexity of controlling the FOV, and the difficulty of overcoming the domain transfer methodology by having the fish navigate through an alien environment. This study is not the first to describe a fish-machine interaction [32–35]. While most studies have discussed a machine designed to emulate a conspecific interaction, in the current study the fish's interaction with the FOV was purely a heterospecific one.

The ability to control the vehicle allowed the fish to orient the vehicle towards the target in a terrestrial environment. Since this study constitutes the first attempt to test domain transfer methodology, we used simple scenery that enabled beacon navigation [20,36]. Further studies are needed to extend these findings to more complex scenery such as an open terrestrial environment. The findings nevertheless suggest that the way space is represented in the fish brain and the strategies it uses may be as successful in a terrestrial environment as they are in an aquatic one. This hints at universality in the way space is represented across environments. Future studies should test this methodology on a terrestrial animal in an aquatic environment to reach more decisive conclusions.

The navigational strategies of the fish also pointed to its ability to adapt to changing target positions. In the current study, the fish had to drive the vehicle toward the target when the target could be seen from every vantage point in the experimental arena. However, as shown when the pink target was moved to the opposite side of the arena, the fish did not use simple beaconing toward the target except for the first attempt after the switch (Fig. 5C), when the fish drove to the previous location of the target. In most cases, after the third attempt, the fish drove directly to the new location of the target (Fig. 5D). This behavior may imply that the fish registered more attributes of its surroundings than simply the beacon constituting its destination. The fish may have ascribed more weight to the location in the room where the food was located than to the proximity to any specific landmark. That said, the fish were able to adjust their strategy to correct for unsuccessful initial attempts.

It is important to note that the concept of an animal that controls a vehicle draws on previous work. Previous studies on rodents have explored their ability to reach a target using an automated vehicle [31]. A related attempt to teach dogs to drive was conducted to develop insights for Artificial Intelligence solutions [30]. While fish were shown to be able to "drive" in a wheeled water task [37], this was an observational report, rather than a scientific study, and did not include a methodological examination of navigational capacities. Overall, this study suggests that fish can learn to control a vehicle and use simple navigation strategies to successfully perform a task. Further studies are needed to elucidate the capabilities and limitations of fish navigation in a terrestrial environment and can lead to a better understanding of fish navigation in general. In addition, the fish operated vehicle can be used to study motor adaptation in fish in general since the computerized control system can be modified to include a constant distortion in the mapping between fish behavior and vehicle response.

Finally, we argue that the *domain transfer methodology* was used in the past without defining the term as we do here. Notable examples are studies involving mammals in zero gravity conditions. Performance of different procedures, emergencies and experimental tasks were tested in humans at zero gravity [38] and can be classified as using this methodology. In addition, astronauts working in zero gravity often experience visual disorientation illusions [39] which is consistent with recording in the rat head direction cells system. These cells, which are active when the animal directs its head in a particular direction in space are believed to be the compass used by the brain's navigation system. Measurements in rats in reveal that this system shows disorientation when the animals are in microgravity conditions [40]. Another example is the effect of microgravity on the development of the rat fetus's vestibular system and function due to the mother's behavior during space flight. It was found that significant differences exist in the post-natal animals [41]. In addition, experiments with rats exposed to partial gravity, that is gravity between zero and one G, revealed several behaviors that were more frequent than in regular gravity [42]. Thus, our newly definition of domain transfer methodology is relevant for past and future studies with a growing pool of subjects and environments.

CRediT authorship contribution statement

Shachar Givon: Formal analysis, Investigation, Methodology. **Matan Samina:** Investigation, Methodology, Software. **Ohad Ben-Shahar:** Investigation. **Ronen Segev:** Conceptualization, Investigation.

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