Integrative Zoology 2023; 0: 1–5 doi: 10.1111/1749-4877.12751

LETTER TO THE EDITOR

Individuals with spatial learning training experience increase group foraging efficiency in goldfish irrespective of landmark conditions

Wuxin LI,[1] Changxuan YU,[1] Shijian FU,[1] Shaun S. KILLEN[2] and Lingqing ZENG[1]

[1]Laboratory of Evolutionary Physiology and Behavior, School of Life Sciences, Chongqing Normal University, Key Laboratory of Animal Biology of Chongqing, Chongqing, Chinaand [2]Institute of Biodiversity, Animal Health & Comparative Medicine, College of Medical, Veterinary & Life Sciences, University of Glasgow, Glasgow, UK

INTRODUCTION

The ability to learn could enable animals to match their behavioral responses to a variable environment on the basis of experience. Animals move through habitats and monitor their locations in regard to a vast array of external environmental information. The spatial learning refers to the process by which animals encode information about their surroundings in order to enable movement across space and to remember the position of stimuli that are motivationally meaningful. Therefore, the spatial learning and memory capacity of animals play important roles in their daily life activities, including foraging, reproduction, competition, and predator avoidance (Wolbers & Hegarty 2010; Tierney & Andrews 2013). In laboratory experiments, fish are usually trained to complete specific spatial learning tasks (e.g. foraging) under single landmark condition, which, for instance, would have one landmark with only one color (Odling-smee & Braithwaite 2003a). However, in natural habitats such as rivers, ponds and streams, the visual landscapes around the habitat include various landmarks with different colors, such as green or red, creating a certain color background, all of which result in reliable indicators of local visual landmarks for fish orientation behavior. Additionally, color vision is a fundamental feature for fish that plays an important role in the way that organisms behave in their habitats (Luchiari & Pirhonen 2008). Fish have a color preference for local visual cues or light (Rodd *et al.* 2002; Luchiari & Pirhonen 2008; Ruchin 2018). However, to our knowledge, it is not clear whether individuals preferring either specific colors or numbers of landmarks for orientation and foraging vary within a fish species. The first goal of our study aimed to examine the effect of the amount of visual information on navigation in the goldfish.

Collective behavior in animal groups (i.e. fish shoals, bird flocks and insect swarms) is a widespread phenomenon in the animal kingdom. Animal groups often make decisions when faced with different environmental situations; however, their habitat conditions are not only very complicated but also change dynamically, which can influence their group decision-making (Yang *et al.* 2021). Although effective environmental information, such as habitat spatial information, is useful for individual survival and growth, the influence of this spatial information on decision-making in animal groups (e.g. motivation for foraging) remains largely unknown. Additionally, individual variations in phenotype, such as physiology (e.g. energy metabolism) and behavior (e.g. personality and spatial behavior) are thought to have important ecological and evolutionary consequences (Burton *et al.* 2011). This raised the question of how much the importance of

Correspondence: Lingqing Zeng, Room 127, Yifu Building, Laboratory of Evolutionary Physiology and Behavior, Colleges of Life Sciences, Chongqing Normal University, Chongqing 401331, China.
Email: lingqingzeng@cqnu.edu.cn

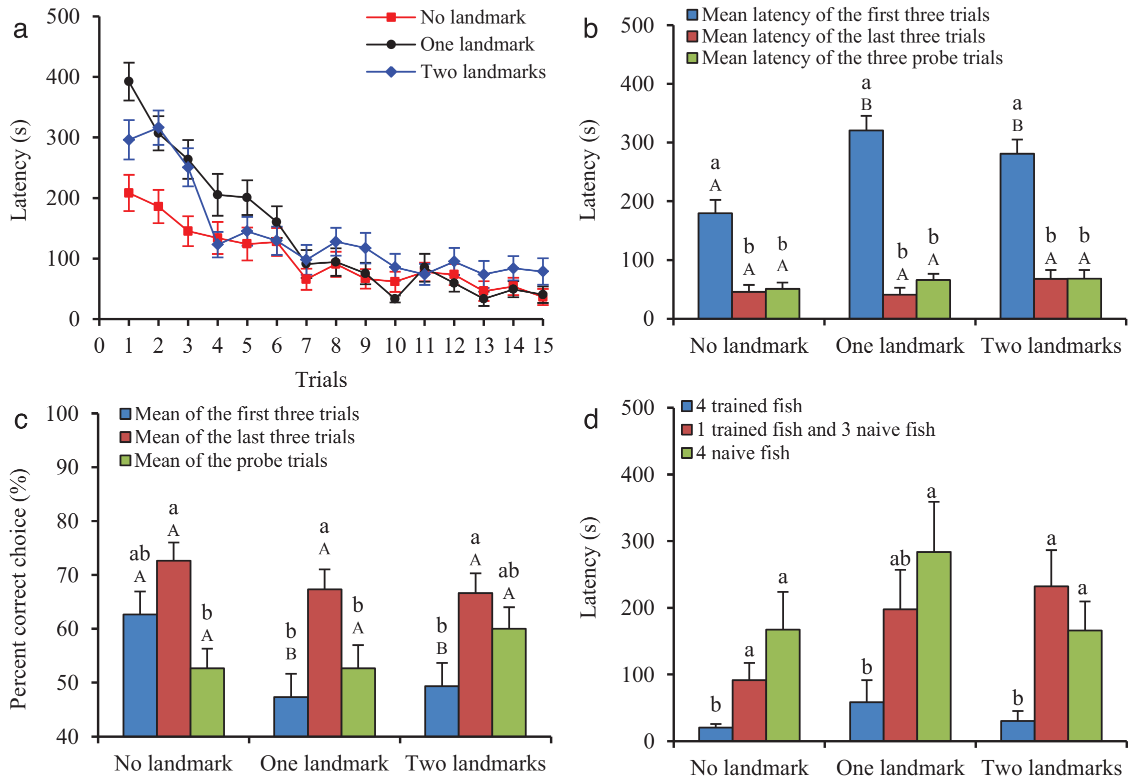

Figure 1 Latency to complete the foraging task and percent correct choice by the goldfish over the trials. Bars (mean ± s.e.) without sharing the same lowercase letter (a, or b) mean that difference in values existed among three stages within a given landmark condition. Bars (mean ± s.e.) without sharing the same capital letter (A, or B) mean that difference in values existed among three landmark conditions within the same stage.

environmental spatial information may be related to variation in the spatial learning ability of individuals within a group. Environmental spatial information is the premise and basis upon which animal groups evaluate movement-making decisions. Therefore, animal groups may use different decision-making strategies based on both external (i.e. spatial information) and internal stimuli (i.e. individual spatial learning ability). Here, we used goldfish (*Carassius auratus*) as the animal model and conducted two spatial learning experiments to investigate the individual spatial learning ability of goldfish under the three landmark conditions (e.g. no, one, and two landmarks) and the influence of this ability on the group foraging efficiency. All of the methods and materials are described in Supporting Information 1, and the Table S1, Table S2 and Figure S1 are presented in Supporting Information 2.

The latency to complete the foraging task by goldfish under three landmark conditions all showed a first decreasing and then a leveling-off trend as training times increased (Fig. 1a; Fig. S1, Supporting Information 2). Compared to the first trial, the latencies to complete the foraging task profoundly decreased at the 7th, 3nd, and 4th trials for the no, one, and two landmark treatments, respectively (Fig. S1, Supporting Information 2). For each of the three landmark treatments, the latency to complete the foraging task of the three probe trials did not decrease compared to the latency of the last three learning trials (Fig. 1b, landmark: $F = 2.730$, $P = 0.066$; stage: $F = 142.127$, $P < 0.001$; interaction: $F = 5.520$, $P < 0.001$. Covariable effects, body mass: $F = 2.420$, $P = 0.121$; body length: $F = 0.018$, $P = 0.892$). Additionally, no difference in this latency was found among three landmark treatments at either the last three trials or three probe trials (Fig. 1b). In addition to the no-landmark condition, the percent correct choice increased greatly in both the one- and two-landmark conditions between the first and last three trials (Fig. 1c, landmark: $F = 0.406$, $P = 0.666$; stage: $F = 13.871$, $P < 0.001$; interaction: $F = 1.952$, $P = 0.101$. Covariable effects, body mass: $F = 1.581$, $P = 0.209$; body length: $F = 0.043$, $P = 0.836$). Only the percent correct choice did not change between the first and last three learning trials in the no-landmark condition. However, both the one- and two-landmark condition had a higher percent correct choice in the last three learning trials than in the first three learning trials (Fig. 1c). When probe trials were performed, the percent correct choice in both the no- and one-landmark condition decreased but did not change in the two-landmark condition (Fig. 1c). No differences in percent correct choice were found among three landmark treatments at either the last three trials or three probe trials (Fig. 1c). Shoals composed of four trained fish had a shorter latency to complete the group foraging task than those composed of four untrained fish in all three landmark conditions with shoals composed of one trained fish and three naïve fish to be intermediated (Fig. 1d, landmark: $F = 2.370$, $P = 0.100$; stage: $F = 9.893$, $P < 0.001$; interaction: $F = 0.965$, $P = 0.431$). No differences in latency to complete the group foraging task within the same group composition were found among the three landmark conditions (Fig. 1d).

Our study found that both latency to complete the foraging task and first-choice accuracy for fish in the one-landmark and two-landmark condition improved greatly with spatial learning experience, which was consistent with previous studies on fish (Warburton 1990; Rodriguez *et al.* 1994; Swaney *et al.* 2001; Roy & Bhat 2017). As expected, goldfish in the no-landmark condition did not improve in their first-choice accuracy but exhibited greatly shortened latency to complete the foraging task under the no-landmark condition, suggesting that goldfish may increase their swimming speed after numerous spatial trainings but make more mistakes. Two previous studies on goldfish also showed that first choice accuracy in an unmarked condition was close to chance and did not improve with experience, but latency to complete the foraging task decreased greatly during training (Warburton 1990; Rodriguez *et al.* 1994). In nature, many resources, such as food or habitat, are often widely separated in space or time such that animals, including fish, cannot rely purely on chance encounters (Odling-Smee & Braithwaite 2003b). Hence, the fitness of an animal may increase if it can guide its daily life activities by using local spatial information on the basis of its spatial learning and memory. For example, visual landmarks facilitate the spatial navigation of rodents and lizards (Youngstrom & Strowbridge 2012; Noble *et al.* 2012). In our study, the four arms of the maze were symmetrical and equiaxial; hence, no difference in spatial features between the left and right arms could be found by goldfish when performing spatial learning training. Additionally, olfactory and gustatory cues such as food pheromones in the T-maze were well controlled between the left and right arms. Compared to the no-landmark condition, local visual cues such as plastic plants were presented in the T-maze in the one- or two-landmark condition, which provided reliable indicators of local visual landmarks for food location and resulted in goldfish having higher performance of locating food accurately. Our results suggested that goldfish can keep track of their location with respect to an external point of reference by using their spatial learning and memory capacity.

Our study found that shoals composed of individuals with spatial training experience had a shorter latency to complete the foraging task than those composed of individuals without any experience irrespective of the local visual landmark environment. Trained experience influenced group foraging efficiency in guppies (*Poecilia reticulata*), which demonstrated that well-trained individuals had better performance in completing the foraging task than poorly trained individuals over the trials (Swaney *et al.* 2001). In our study, all fish were from the same population and were familiar with each other before or during laboratory acclimation. In guppies, however, well-trained individuals facilitated learning in observers via demonstration only in the short term, perhaps by directing attention to the hole in the partition through a local enhancement process (Swaney *et al.* 2001). Such situation may have also existed in our study, especially in goldfish shoals composed of one well-trained fish (demonstrator) and three untrained fish (observer) though their group foraging did not perform well compared to those shoals composed of four naïve fish. It was indicated that social learning (e.g. naïve fish imitates trained fish) might not happen during only two group foraging events. However, goldfish shoals composed of fish with spatial learning training experience performed better in the foraging task compared to other types of shoals. It is possible that the trained goldfish with experience were more familiar with the spatial structure of the T-maze and, hence, were more relaxed and less vigilant when performing the foraging task compared to untrained shoals. In contrast, although untrained goldfish had two chances to familiarize themselves with the spatial features in the T-maze, they still spent more time exploring the T-maze, which was an unfamiliar or novel environment for them. Therefore, these shoals may have solved the foraging task more slowly and carefully in such an environment.

Our study found that the color of external cues (i.e. plastic plants) did not influence the training effectiveness of spatial learning of individual goldfish under the two-landmark condition. In nature, color signals have been found to be important for a large range of animal behaviors (Bradbury & Vehrencamp 1998). Numerous studies have suggested that fish have color vision to enable them to discriminate local visual cues around their habitats (Warburton 1990; Neumeyer 1992; Rodd *et al.* 2002; Wyzisk & Neumeyer 2007; Luchiari & Pirhonen 2008; Sovrano *et al.* 2020). The Atlantic salmon (*Salmo salar*) were able to distinguish between two similar visual landmarks and may use multiple forms of cues (e.g. different visual landmarks in the same arena) to facilitate their spatial learning tasks (Braithwaite *et al.* 1996). In our study, one green aquatic plant and one red aquatic plant, both of which had very similar shapes and geometries, were placed at the opening of each arm in the T-maze, in which goldfish were trained to complete the foraging task in the presence of two landmarks of different colors. Additionally, trainings for combinations of specific color and food reward (e.g. green and food) were randomly carried out at either of the two arms in the T-maze. Our statistical analysis showed that both latency controlling for green plants and latency controlling for red plants had similar decreased rates over the 15 trials, indicating that goldfish did not have a color preference for using external cues to guide their spatial behavior to locate food resources but have the ability to form spatial representations of food resources to solve foraging tasks under the conditions of multiple cues.

In conclusion, our study documented that goldfish subjected to three types of landmark conditions could all solve a spatial task of locating a food source, as indicated by a shortened latency to complete the foraging task and an increased percentage of correct first choices after 15 trials of spatial learning training, suggesting that goldfish have spatial abilities in navigating by using the local spatial information. During the probe trials, goldfish made more mistakes in the spatial task compared to the number of mistakes made at the end of spatial learning training, but the number of mistakes was dependent on the landmark condition. Additionally, intraspecific variation in spatial learning ability existed among the goldfish. As expected, shoals composed of fish that underwent spatial learning tasks located food resources faster than shoals without fish that had completed spatial training, suggesting that the spatial learning ability of individual fish might partly contribute to their group foraging efficiency.

ACKNOWLEDGMENTS

We thank Huihuang Ma and Shuang Liu for their help with the experiments. This work was supported by grants from the National Natural Science Foundation of China (31300341), the Project of the Natural Science Foundation of Chongqing (cstc2021jcyj-msxm0498), the Science and Technology Research Program of Chongqing Municipal Education Commission (KJQN201900540 and KJQN202000539), and the Venture and Innovation Support Program for Chongqing Overseas Returnees (cx2019153) granted to L.Q.Z.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Latency to complete the foraging task by the goldfish over the trials.

Figure S2 Diagram of the T-shape maze.

Cite this article as:

Li W, Yu C, Fu S, Killen SS, Zeng L (2023). Individuals with spatial learning training experience increase group foraging efficiency in goldfish irrespective of landmark conditions. *Integrative Zoology* **00,** 1–5. https://doi.org/10.1111/1749-4877.12751