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Complex maze learning by fish

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Rats, mice and other rodents are well-known for their ability to solve complex spatial tasks, such as learning to negotiate complicated mazes. This ability might be an adaptation for the fossorial habit that characterizes most rodents, but the scarcity of data from other taxa prevents us from confirming this hypothesis. We tested guppies, *Poecilia reticulata*, for their ability to navigate a maze consisting of six consecutive T-junctions. Guppies learned to solve the complex maze, and both the number of errors and the time to exit significantly decreased during the training period, which consisted of 30 trials over 5 test days. Guppies reached 68% correct responses on the first day of training and they exceeded 80% correct responses by the last day of training. We found no difference between a condition in which colour cues made each T-junction distinct from the others and a condition with no such cues. In contrast with the male advantage in spatial tasks previously observed in guppies, we found a small but significant female advantage in complex maze learning. Our work suggests that the ability to learn complex mazes is not a prerogative of those species that inhabit burrow systems such as mice and rats, but it might be common in vertebrates.

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At the dawn of comparative psychology, the experiments of Edward Tolman on complex maze learning in rats led to the development of important concepts such as latent learning and cognitive maps and marked the birth of spatial cognition studies on animals (Tolman, 1948). Rats, *Rattus norvegicus*, mice, *Mus musculus*, and other rodents can promptly learn to solve complex spatial problems such as mazes formed by a series of sequential right-left turns (reviewed in Thinus-Blanc, 1996). Their notable spatial learning performance might be associated with a natural predisposition to process spatial information (Fagan & Olton, 1987). For instance, rats prefer to exploit spatial rather than nonspatial information during discrimination learning (Olton, 1979). Furthermore, complex mazes are somewhat similar to the natural environment of these burrow-dwelling animals, giving rise to the idea that rodents might have been selected for enhanced learning performances in maze-like problems (Shettleworth, 1972). However, the scarcity of data on complex maze learning from other taxa prevents us from testing this hypothesis.

Among the remaining vertebrates, only humans have been extensively tested in relation to complex mazes formed by multiple T-junctions, and they have shown learning abilities comparable to rodents (Gillner & Mallot, 1998; Husband, 1929; Moffat, Hampson, & Hatzipantelis, 1998). However, it is difficult to associate the maze-learning ability of humans to a specific ecological specialization in their evolutionary past. It could equally be that their spatial abilities are associated with the extraordinary complexity of their nervous system or the fact that nowadays most humans experience rather complex environments such as buildings and cities.

Here, we asked whether vertebrates phylogenetically distant from rodents and humans, and that live in a very different habitat, can learn to solve complex mazes similar to those classically adopted to study rodents' spatial cognition. We used the guppy, *Poecilia reticulata*, a fish that typically inhabits freshwater streams, to address our question. Spatial abilities have been found in a large number of fish species including guppies (reviewed in Broglio, Rodríguez, & Salas, 2003; Odling-Smee & Braithwaite, 2003a). Fish can solve rather difficult spatial problems (de Perera, 2004), are capable of latent learning (Gómez-Laplaza & Gerlai, 2010) and can form an internal representation of the environment (Broglio et al., 2003; Cain & Malwal, 2002). However, in fish, maze learning is usually studied with very simple tasks, such as T-mazes, radial mazes or two-chamber apparatuses (Cain, 1995; Cain & Malwal, 2002; Odling-Smee & Braithwaite, 2003b; Sison & Gerlai, 2010; Spence, Magurran, & Smith, 2011). In experiment 1 of this study, we tested whether male and female domestic guppies can learn to solve a complex maze formed by six consecutive T-junctions.

We also considered two additional factors. The first regards the information made available to guppies. Ideally, our complex maze

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can be decomposed into a series of T-maze problems whose solutions, right or left turn, are different. If each T-junction is visually distinct from the others, guppies can independently learn each T-maze problem. However, if the T-junctions are visually identical, guppies additionally need to learn how to recognize each specific T-junction, for example by using distant landmarks to encode a spatial map (de Perera, 2004) or by learning the order in which the T-junctions are encountered from the starting point (Miletto Petrazzini, Lucon-Xiccato, Agrillo, & Bisazza, 2015). To investigate the contribution of these factors, we tested half of the guppies in a condition in which each T-junction was made recognizable by the presence of colour cues, and half of the guppies without such cues. We expected that the presence of colour cues should help guppies in identifying their position in the maze and, thus, boost their learning performance.

Second, we compared the performance of the two sexes. Previous studies on guppies have found no sex differences for shape discrimination, object recognition, concept learning, use of ordinal information and discrimination of food quantities (Lucon-Xiccato & Bisazza, 2014, 2016; Lucon-Xiccato & Dadda, 2016; Lucon-Xiccato, Miletto Petrazzini, Agrillo, & Bisazza, 2015; Miletto Petrazzini et al., 2015). However, females achieved better scores in tasks involving cognitive flexibility and social learning, and were faster in recognizing the larger of two shoals (Lucon-Xiccato & Bisazza, 2014, 2017; Lucon-Xiccato, Dadda, & Bisazza, 2016; Reader & Laland, 2000). Regarding spatial abilities, in a recent study performed on the descendants of wild-caught guppies, we found better male learning performance (Lucon-Xiccato & Bisazza, 2017). Based on this latter study, we expected to find a similar sex difference in complex maze learning. As we found an unpredicted female advantage, we performed a second experiment using the wild-derived guppies to exclude the possible effect of domestication on sex differences in spatial cognition. While it was not the primary aim of experiment 2, this offered the chance to verify whether many generations of breeding in captivity have affected guppies' spatial abilities.

METHODS

Experimental Subjects

In experiment 1, we tested 32 females and 32 males (64 guppies overall) from an outbred aquarium stock (snakeskin cobra green), equally divided into the two experimental conditions (with or without colour cues). In the control experiment (experiment 2), we used descendants of wild-caught guppies from the lower Tacarigua river, Trinidad; here, we tested fewer subjects, eight males and eight females (16 guppies overall) and with only one condition (without colour cues). This was done because in previous studies we observed that, in long training procedures, wild-derived guppies sometimes showed signs of distress such as freezing for long periods or completely ceasing to participate in the trials (e.g. Lucon-Xiccato & Bisazza, 2014).

The domestic guppies have been bred in our laboratory since 2012 starting from about 200 individuals bought from local dealers. These guppies were maintained in 150-litre tanks with a gravel bottom, natural plants, water filter, aerator and a 12:12 h light:dark cycle. Wild-derived guppies were collected from a large outdoor pond with warm water in Padova, Italy, into which they had been introduced in 2012. Before the experiment, wild-derived guppies were maintained in the laboratory for at least 2 months in 400-litre tanks with the same conditions as the domestic guppies. In the laboratory, all fish were fed three times per day with commercial food flakes and live *Artemia salina* nauplii.

Apparatus

The apparatus was built in a 68 × 68 cm glass tank filled with 25 cm of water, placed in a dark room, and surrounded by black plastic to prevent the subjects from seeing the room. The apparatus consisted of the maze and a home sector (the remaining part of the tank). The maze (32 × 32 cm) was built using green plastic and it was placed at one corner of the tank, 2 cm below the water surface (Fig. 1). The beginning of the maze consisted of a 9 × 6 cm

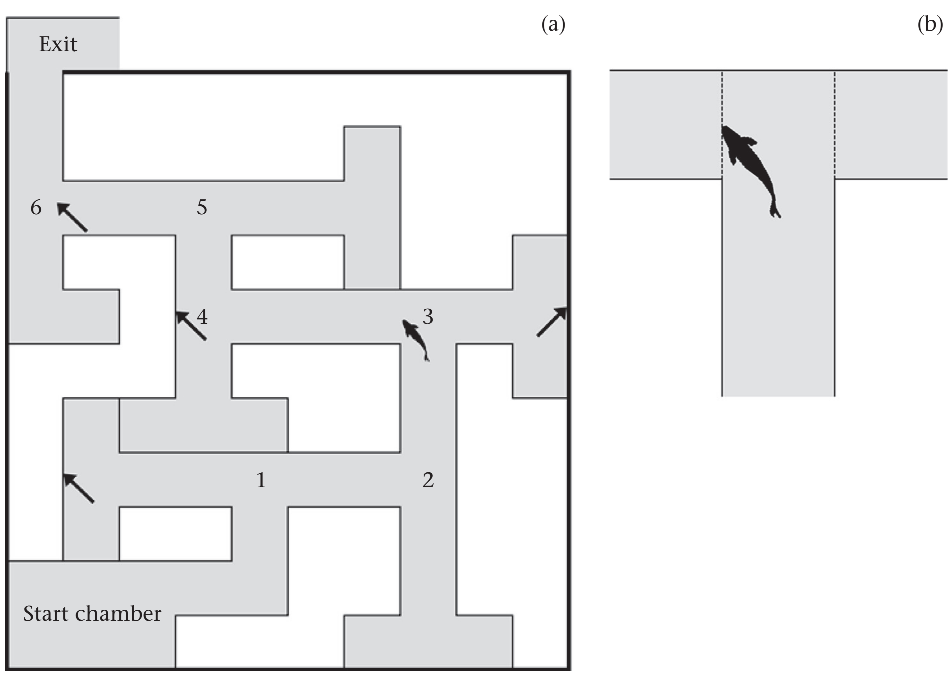

Figure 1. (a) Aerial view of the maze used in the experiments and (b) detail of a T-junction. Arrows indicate the position of the colour cues used for half of the subjects in experiment 1. Dashed lines indicate the lines used to score the left-right choice of the fish.

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