Complex maze learning by fish

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Abstract

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 testing days. Learning occurred already in the first day of training, and guppies reached 80% correct responses in the fifth day. We found no difference between a condition in which colour cues marked differently each T-junction and a condition with no such cues. In contrast with the male advantage in spatial tasks previously observed in guppies and other fish, 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.

Keywords: fish cognition; maze learning; *Poecilia reticulata*; sex differences; spatial abilities.

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, mice 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 non-spatial information during discrimination learning (Olton, 1979). Furthermore, mazes are somewhat similar to the natural environment of these burrow-dwelling animals, giving rise to speculation that rodents might have been selected for enhanced learning performances in maze-like problems (Shettleworth, 1972). However, the scarcity of data from other taxa prevents us from testing this hypothesis.

Among the remaining vertebrates, only humans have been extensively tested in relation to such tasks, and they have shown abilities comparable to rodents in solving complex mazes (Gillner & Mallot, 1998; Husband, 1929; Moffat et al., 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 a 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. 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 Odling-Smee & Braithwaite, 2003a), but maze learning is usually assessed with very simple tasks, such as the T-maze. We tested male and female domestic guppies in a maze with six consecutive T-junctions. Half of the guppies were tested in a condition in which different colour cues marked each turn, and half were tested without such cues. Based on a previous study on this species (Lucon-Xiccato & Bisazza, in press), we expected to find a better spatial learning performance in the male fish. As we found an unpredicted female advantage in our task, we also performed a second experiment using the descendant of wild caught guppies to exclude the possible effect of domestication on sex differences in spatial cognition.

Materials and methods

Experimental subjects

Subjects were adult female and male guppies from an outbred aquarium stock, snakeskin cobra green (experiment 1) and descendants of wild-caught fish from the lower Tacarigua river, Trinidad (experiment 2). In experiment 1, we tested 32 females and 32 males, equally divided in the two experimental conditions (64 guppies overall). In the control experiment using wild-derived guppies (experiment 2), we tested a reduced number of subjects, 8 males and 8 females (16 guppies overall) and with only one condition (without colour cues) because these fish become easily stressed when employed in long training procedures.

The outbred aquarium stock was bred in our laboratory since 2012 starting from c.a. 200 individuals bought from local dealers. These guppies were maintained in 150-l tanks with gravel bottom, natural plants, water filter, aerator, and a 12:12 hour 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 two months in 400-l tanks with the same condition as the domestic guppies. In the laboratory, all fish were fed 3 times per day with commercial food flakes and live *Artemia salina* nauplii.

Apparatus

The apparatus was 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 a main sector and the maze. This main sector was enriched with plants and gravel to resemble maintenance tanks. Two subjects, one male and one female, inhabited the main sector permanently together with 25 immature guppies that served as social companions. The experimental maze was placed at one corner of the tank, 2 cm below the water surface (figure 1). The maze was built using green plastic. The walls of the maze were 5 cm high, and the corridors were 3 cm wide. We used narrow corridors because this is thought to motivate guppies to exit the maze (Kellogg & Gavin, 1960). The walls of the maze were perforated to favour water exchange with the main sector of the apparatus. The beginning of the maze consisted of a 9 × 6 cm start chamber. The end of the maze emerged into the main sector of the tank; this part was occluded with a plastic barrier outside the trials to prevent the fish from entering the maze spontaneously. The colour cues were panels made of coloured plastic (red, blue and orange) and were fixed to the walls or floor of the maze. The left wall of the first T-junction was blue, both the left and the right walls of the third T-junction were red, and the bottom of the sixth T-junction was orange (figure 1a).Two lamps placed in different positions and not directly above the maze, were used to light the apparatus. An HD camera placed on the ceiling recorded the experiments.

Procedures

The two subjects were introduced in the apparatus 48-hours before the beginning of the experiment for habituation to the tank. In the morning of the third day, subjects started the training. The training consisted of a series of 30 trials subdivided into 5 days. Each day trials started at 09:00 hour, and were separated by a 1-h interval, starting from. We tested the two subjects separately, counterbalancing the order between males and females in each trial. To start a trial, we gently moved one of the subjects into the start chamber of the maze using a fish net. The fish was free to find the way to the exit of the maze for 30 min. Trials taking longer than 30 min were considered null and not analysed. In addition to the social reward, we delivered a small quantity of food flakes when the fish exited the maze.

Data were collected from the video recordings played back on a computer monitor. For each T-junction, we scored whether the subject entered the correct or incorrect arm of the maze at first. To perform this measurement, we superimposed two lines at the beginning of the lateral arms of the T-junction; we considered the fish to have entered one arm when its snout crossed the line (figure 1b). We also measured the time in which the subject solved the task, calculated from when the subject left the start chamber to when it exited the maze.

Statistical analysis

We analysed the number of errors in each trial with generalized linear-mixed-effects models (binomial error distribution and logic link function), fitting sex and presence/absence of coloured cues as fixed effects and individual ID as a random effect. Since preliminary plotting suggested a linear decrease of the number of errors across trials, we fitted the serial number of the trial (1-30) as the covariate. Interactions involving the covariate were removed from the model when they were not significant (Engqvist, 2005). We analysed the time to exit the maze (log transformed) with a linear mixed-effects model built with the same independent variables described above. Wild guppies in experiment 2 were compared with the domestic guppies of the corresponding condition in experiment 1 (without colour cues). The models of experiment 2 were fitted as above, but we added strain as a fixed effect.

Ethical note

Experiments were conducted in accordance with the law of the country in which they were performed (Italy, D.L. 4 Marzo 2014, n. 26). The Ethical Committee of Università di Padova reviewed and approved all the experimental procedures (protocol n. 22/2016). No physical invasive manipulations were performed on the fish during the experiments. At the end of the experiments, all subjects were released into stock tanks.

Results

Experiment 1: domestic guppies

The number of errors significantly decreased across the trials ($\chi^2_1 = 216.204$, $P < 0.0001$; figure 2a, 2b). Females made less errors than males ($\chi^2_1 = 8.787$, $P = 0.003$; figure 2a, 2b), but there was no significant sex × trial interaction, indicating the absence of sex differences in the learning rate. The presence of coloured cues did not affect learning ($\chi^2_1 = 0.147$, $P = 0.702$), and there was no significant sex × cues interaction ($\chi^2_1 = 0.499$, $P = 0.480$). In the first day of training, the number of errors was already significantly smaller than expected by chance (mean ± SD: 11.234 ± 2.93; chance: 18; one-sample *t* test: $t_{63} = 18.496$, $P < 0.0001$). Exploring the performance of the fish in each turn of the maze, we found that guppies made more errors when the correct arm was left compared to when it was right (left: 32.22 ± 9.65; right: 8.08 ± 4.51; paired-sample *t* test: $t_{63} = 17.253$, $P < 0.0001$).

As regards time to solve the task, we found a significant decrease across the trials ($F_{1,1848} = 175.905$, $P < 0.0001$; figure 3a, 3b). Sex and presence of coloured cues did not affect the time to solve the task ($F_{1,60} = 1.928$, $P = 0.170$ and $F_{1,60} = 0.777$, $P = 0.382$, respectively). The only significant interaction was trial × sex × cues ($F_{1,1848} = 6.047$, P = 0.014; figure 3a, 3b).

Experiment 2: wild-derived guppies

When we compared the number of errors of the domestic and wild-derived guppies, we found a significant decrease in the number of errors across trials ($\chi^2_1 = 126.058$, $P <$ 0.0001), and a better performance of the females ($\chi^2_1 = 8.016$, $P = 0.005$). There was no difference between the wild and domestic strain ($\chi^2_1 = 0.256$, $P = 0.613$). The sex × strain interaction was not significant ($\chi^2_1 = 0.005$, $P = 0.943$). None of the interactions involving the covariate were significant, although the trial × sex interaction was close to the threshold (χ^2_1 = 3.827, $P = 0.050$).

As regards time to solve the task, we found a significant effect of trial ($F_{1,1386}$ = 90.021, $P < 0.0001$; figure 3c). Wild-derived guppies were faster in solving the task ($F_{1,44}$ = 7.838, $P = 0.008$; figure 3c). Sex had no significant effect in the model ($F_{1,44} = 0.078$, P = 0.781), and sex × strain interaction was not significant ($F_{1,44} = 2.902$, $P = 0.096$).

Discussion

Guppies were able to solve the complex maze, as evinced by the decrease in both the number of errors and the time to solve the task across trials. Learning was found to occur early: guppies showed a number of errors significantly below the chance level since the first day of training, and by the fifth session of the test, they reached 80% correct responses, a performance fully comparable with that observed in mammals.

Thus, the ability to learn complex mazes thus does not appear to be a prerogative of burrowing rodents and humans. Rather, our results suggest that this ability might be similar between mammals and fish, independently of the specialization for fossorial habitats and nervous system complexity. Other works on spatial cognition have drawn similar conclusions. For example, fish can encode ordinal information and use it to solve spatial problems, an ability previously thought to be typical of mammals and a few avian species (de Perera, 2004; Miletto Petrazzini et al., 2015). The similarities between fish and mammals are fascinating given the ecological diversity and phylogenetical distance between the two clades and might be indicative of shared cognitive abilities across all vertebrates or of convergent evolution due to similar selective pressures.

The hypothesis of shared cognitive mechanisms due to shared ancestry in vertebrates has been proposed for visual perception and for numerical abilities (e.g., Beran, 2008; Gori et al., 2014), and this might be an interesting possibility to evaluate in relation to maze learning abilities. Even if the idea of shared ancestry is supported in the future by further studies, the fact that maze-learning ability and other sophisticated spatial abilities are present in phylogenetically distant vertebrate species does not imply that these traits do not undergo selection or that the accuracy of the different species is similar. It is possible that, even if all vertebrates possess the basic ability to learn complex mazes, some species might have been selected for better performance. An analogous scenario has been observed, for example, concerning spatial memory for food caches in storing versus non-storing bird species (Shettleworth & Hampton, 1998). Testing the existence of between-species differences in maze learning abilities would require the development of novel maze paradigms suitable for a wide number of species (Gatto et al., 2016; Prétôt et al., 2016).

Our results can also be explained by convergent evolution due to similar selective pressures. While maze-learning abilities are certainly useful for an animal with fossorial habits, they might be also favoured for animals living in environments characterized by a complex spatial structure, like riverine habitats typical of guppies. In some parts of their distribution range and in some seasons, guppies inhabit areas of considerable physical complexity, such as streams that fragment into pools and riffles with an abundant presence of stones, roots and vegetation. Because of this complex environment, guppies might have evolved sophisticated navigation skills in parallel to what hypothesised for fossorial rodents. The hypothesis of enhanced maze learning abilities selected by complex spatial environment potentially applies to a large number of species. The few data available are compatible with this hypothesis. Complex maze learning abilities have also been found also in insects such as the German cockroach, *Blattella germanica*, and honeybees (Hullo, 1948; Zhang et al., 1996). Cockroaches show fossorial habits that are similar to those of rodents; honeybees, on the other hand, base their survival on the capacity to learn and memorise the location of a large number of food sites dispersed across a wide area, frequently with a complex tri-dimensional structure. To confirm this hypothesis, it is necessary to test whether the same abilities are shown by species that live in spatial environments with a low level of complexity, such as deserts or pelagic habitats. To date, it is difficult to disentangle between these two possible explanations for the similarities between fish and rodents, especially because of the limited number of species investigated.

In some species, maze learning is improved in the presences of visual cues (Zhang et al., 1996). In our experiment, there is no evidence that the presence of colour cues improved performance, suggesting that guppies did not rely on these cues to learn the maze. Odling-Smee and Braithwaite (2003b) have reported that three-spined sticklebacks, *Gasterosteus aculeatus*, collected from rivers generally do not rely on visual cues for spatial learning, perhaps because in such environments visual cues are not stable and are continually disrupted by water flow. In line with this finding in sticklebacks, guppies, which typically live in streams with flowing water, might prefer to ignore local visual cues when learning spatial tasks as these cues may be ephemeral.

Intriguingly, guppies made significantly fewer errors in relation to the three T-junctions in which they were required to turn right. One explanation for this unexpected result is the existence of functional brain asymmetries that cause a turning bias. Cerebral lateralization has been shown to influence many behaviours and cognitive functions in fish, including mating, aggression, shoaling abilities, prey capture and some spatial functions (reviewed in Bisazza & Brown, 2011). In another poeciliid fish, *Brachyraphis episcopi*, Brown and Braithwaite (2005) found a significant difference between high and low predation populations in a task that required to locate of a foraging patch in one of four compartments using spatial cues. As their apparatus was asymmetric, the authors suggested that these inter-population differences may be mediated by different degrees of cerebral lateralization in the different populations, which hampered spatial learning via turning bias.

An important finding of our experiment is that females showed a small (around 15%) but significant advantage with regard to the number of errors they made in the maze. 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; Lucon-Xiccato & Bisazza, 2016; Lucon-Xiccato & Dadda, 2016; Lucon-Xiccato et al., 2015; Miletto Petrazzini et al., 2015). Females achieved better scores in tasks involving cognitive flexibility, were faster in recognizing the larger of two shoals and showed enhanced social learning (Lucon-Xiccato & Bisazza, 2014; Lucon-Xiccato et al., 2016; Lucon-Xiccato & Bisazza, in press; Reader & Laland, 2000). Spatial abilities are by far the most widely studied topics with regard to cognitive sex differences. In humans, non-human primates, rodents and carnivorans, males generally possess enhanced spatial abilities compared to females, with the notable exception of monogamous species, which usually do not show appreciable sex differences (reviewed in Jones et al., 2003). A similar sex difference was recently found in guppies in relation to a task that consisted of learning the correct door in two consecutive choices in order to find refuge in proximity to a shoal of conspecifics (Lucon-Xiccato & Bisazza, in press). The latter study was performed on the descendant of wild-caught guppies and the possibility exists that the difference between our present study and the previous one is due to the effects of domestication on either the endocrine system (Shishkina et al., 1993) or the cognition (Lewejohann et al., 2010) of the domestic strain we used. The results of the control experiment, in which we tested wild-descendent male and female guppies, almost completely overlapped with the results obtained using the domestic strain, indicating that domestication is unlikely to explain the difference between the present and the previous study.

In the present work, guppies were tested in an environment somewhat familiar to them. They had experienced the environment for five consecutive days during the training, and it was permeated by the water, and thus the odours, of their home tank. In the previous work, the fish were tested in only five trials in a completely unknown environment (Lucon-Xiccato & Bisazza, in press). As previously found in rats (Beiko et al., 2004), it is possible that the spatial-learning performance of females improved as a result of familiarization with the testing apparatus. It should be said that in the present study we did not detect a difference in the learning rate as would be the case in a significant sex × trial interaction; rather, the average accuracy of females was higher. This might be suggestive of a difference in motivation to flee the maze, perhaps because female guppies tend normally to inhabit deeper water compared to males (Darden & Croft, 2008).

Our study did not reveal cognitive differences in spatial learning abilities between wild-descendent and domestic guppies as previously reported for zebrafish, *Danio rerio* (Spence et al., 2012). The learning curve of domestic and wild-derived guppies is roughly the same concerning both the decrease in the number of errors and the decrease in the time to solve the maze. One difference between strains, however, emerged when considering the average time to solve the task, which was reduced in the wild-descendent guppies. This can reflect differences in sociability and thus in the motivation to reach the social reward (Seghers & Magurran, 1995) or differences in swimming speed (Walker et al., 2005).

In conclusion, guppies showed maze-learning abilities comparable to those observed in primates and rodents. These results align with growing evidence that, despite their relatively small brains, bony fish possess cognitive abilities that were previously thought to be present only in mammals and birds. For example, fish can recognize individual conspecifics, learn novel behaviours from experienced individuals, finely discriminate numerosities, use tools and transmit cultural traditions (reviewed in Bisazza, 2011; Bshary et al., 2002; Brown & Laland, 2003). These abilities could have contributed to the remarkable success and extreme niche diversification of this group and might be associated with the whole-genome duplication event occurred after their separation from lobe-finned fishes (the lineage leading to terrestrial vertebrates), as suggested by the unexpectedly high rate of duplicate genes implicated in cognition that are retained in this fish group (Meyer & Schartl, 1999; Schartl et al., 2013).

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Figure captions

Figure 1

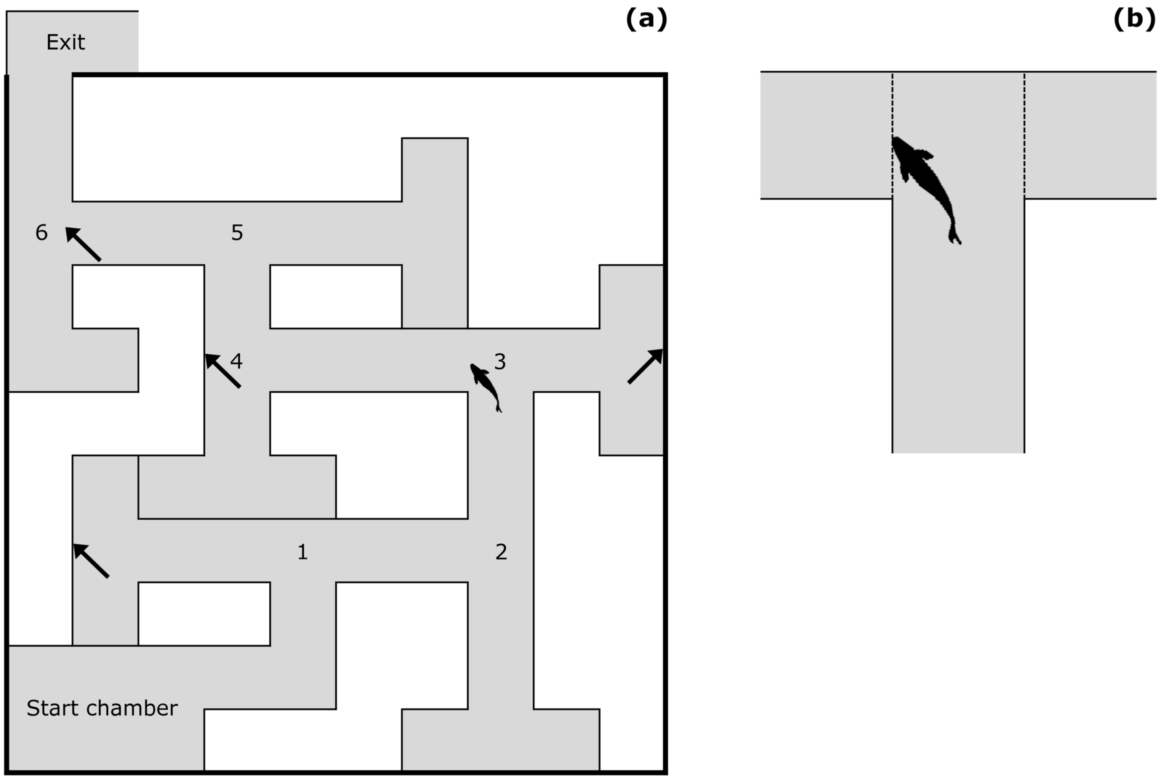
(a) Aerial view of the maze used in the experiments and (b) detail of a T-junction. Arrows indicate the position of the coloured cues used for half of the subjects in experiment 1. Dashed lines indicate the line used to score the left-right choice of the fish.

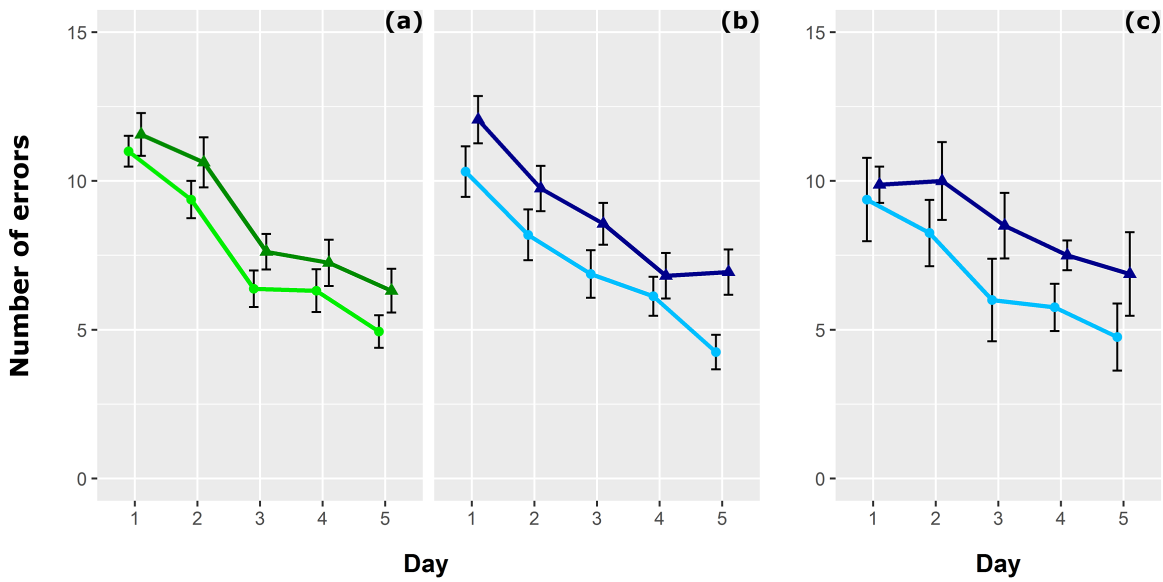
Figure 2

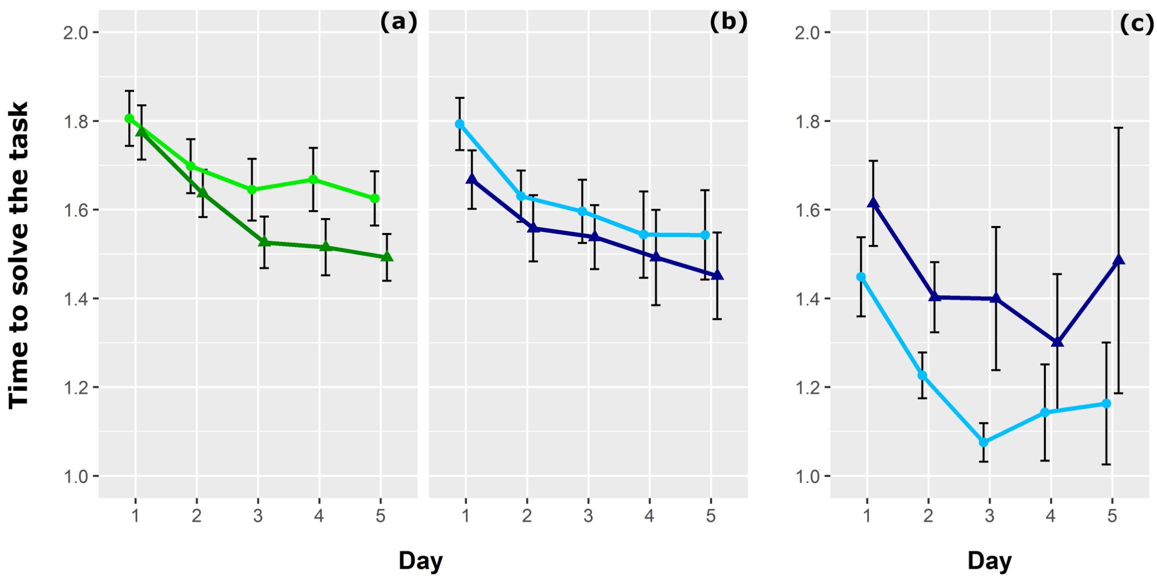
Number of errors (mean ± SE) across the 5 days of training. (a) Domestic guppies with colour cues; (b) domestic guppies without colour cues; (c) wild-descendent guppies without colour cues. Light colours: females; dark colours: males.

Figure 3

Time to solve the task (mean ± SE s; logarithmic transformation) across the 5 days of training. (a) Domestic guppies with colour cues; (b) domestic guppies without colour cues; (c) wild-descendent guppies without colour cues. Light colours: females; dark colours: males.


(a)
(b)
Exit
6
5
4
3
1
2
Start chamber


(a)
(b)
(c)
Number of errors
15
10
5
0
1
2
3
4
5
Day
Day


(a)
(b)
(c)
Time to solve the task
2.0
1.8
1.6
1.4
1.2
1.0
1
2
3
4
5
Day
Day