Abstract

Flexible behavioural responses to the environment often require the suppressing of a strong internal predisposition or the overriding of external lures, tasks that are thought to be performed by a cognitive function called inhibitory control. The prevalent experimental paradigm for studying inhibitory control in non-human animals is the cylinder task: subjects are trained to find food inside an opaque cylinder; hence, the opaque cylinder is substituted with a transparent cylinder, and the subjects need to inhibit their tendency to directly reach the visible food and detour the cylinder. Inhibitory control is considered an effortful function, and a recent comparison of a large sample of vertebrate species found that performance in the cylinder task positively correlates with absolute brain size (MacLean et al., 2014). However, a tiny teleost fish, the guppy (*Poecilia reticulata*), scores higher than many mammals and birds in the cylinder task, thus challenging this view. Guppies could enjoy two advantages when performing the cylinder task: a greater familiarity with transparent surfaces due to maintenance in aquaria, and a better spread in the water of food odour from the lateral sides of the cylinder. We tested whether these two factors increase guppies' performance in the cylinder task by manipulating their experience with transparent surfaces and the diffusion of food odour cues from the cylinder. Guppies raised in transparent aquaria or with transparent panels placed inside the tank did not show advantages over guppies with no experience with transparent surfaces. Furthermore, we did not find a decrease in performance in guppies tested with a modified cylinder, pierced in the middle so that both visual and olfactory cues lured in the same direction. These results seem to exclude methodological explanations for the high inhibitory control score of guppies, and they indicate that efficient inhibitory control can evolve even in small-brained animals.

Keywords: fish cognition; inhibitory control; cylinder test.

1. Introduction

Inhibitory control is a cognitive function that allows an individual to inhibit a habitual or prepotent response, either innate or learned, to express a different behaviour that is appropriate for the specific circumstance. In humans, inhibitory control has received much attention because it is associated with quality-of-life outcomes. In infancy, self-control predicts academic achievements (e.g. Duckworth, Quinn, & Tsukayama, 2012; Duckworth, & Seligman, 2005): in adults, it positively correlates with general intelligence (Shamosh, DeYoung, Green, Reis, Johnson, Conway, Engle, Braver, & Gray, 2008), and it negatively correlates with the propensity to engage in criminal behaviour and in drug addiction (e.g. Feil, Sheppard, Fitzgerald, Yücel, Lubman, & Bradshaw, 2010; White, Moffitt, Caspi, Bastusch, Needles, & Stouthamer-Loeber 1994).

Non-human animals also have to deal with situations involving inhibition. For example, sit-and-wait predators need to inhibit predatory attacks and wait for the perfect timing to chase their prey (e.g. Curio 1976; Harper & Blake, 1991; Pritchard, 1965). Prey species such as chum salmons (*Oncorhynchus keta*) inhibit foraging activity when exposed to predation risk (Ryer & Olla, 1991). In several species of primates, subordinates that discover a food resource often inhibit consumption to tactically deceive other members about its presence (Whiten & Byrne, 1988).

The prevalent experimental paradigm for studying inhibitory control in animals and human infants is the detour task. An individual sees a reward (e.g. food) behind a transparent barrier, has to inhibit the tendency to reach the goal directly and must depart from it to detour the obstacle. A recent comprehensive study compared 36 different species belonging to several orders of birds and mammals using a variant of this task, the cylinder test (MacLean et al., 2014). Subjects were initially trained to find food inside an opaque cylinder; once they met the criterion, the opaque cylinder was substituted with a transparent one, and the researchers measured each species' ability to inhibit the tendency to go directly toward the visible food and instead retrieve it from the lateral, open sides. This comparative investigation found a large interspecific variation in task success, with the absolute brain size being the main predictor of performance.

However, cross-species comparison is often problematic in cognition research due to the presence of unaccounted confounding factors (Bitterman, 1960, 1965). Two factors in particular could have affected the study of MacLean and co-workers (2014). The first has to do with between-species variation in experience with obstacles and transparent materials. Some species have been tested in laboratories and zoos and thus might have extensive previous experience with transparent surfaces, whereas other species have been maintained in wire mesh cages or in large enclosures and could have less familiarity with transparent materials. In the study by MacLean and colleagues, subjects underwent only 10 trials with a transparent cylinder, so species with experience with transparent materials could have enjoyed an advantage compared with animals with less or no experience. The second issue has to do with the prevalent sensory modality used to solve the given task. Whereas primates or birds, which are mostly microsmatic species, may be strongly attracted to the sight of food and try to reach it via the shortest way possible, macrosmatic species, such as dogs or rats, might ignore visual information and instead be attracted by the smell of food that flows from the lateral openings of the cylinder. This factor could potentially bias the results in favour of the species that rely less on vision to locate food sources.

Recently, a small teleost species, the guppy *(Poecilia reticulata*) was examined in the cylinder task (Lucon-Xiccato, Gatto, & Bisazza, 2017). The performance of guppies was considerably lower than that of primates, parrots and corvids, but it was higher than that of several other mammals and birds (MacLean et al., 2014; Kabadayi, Taylor, von Bayern, & Osvath, 2016). As a guppy's brain is much smaller than that of the smallest warm-blooded vertebrate, the performance of this fish is clearly challenging the hypothesis that brain size is the main determinant of how an animal scores in inhibitory control tasks. However, the aforementioned methodological challenges in the comparison made by MacLean et al. (2014) might also provide alternative explanations for guppies' performance. First, guppies studied in laboratories spend their entire lives in glass aquaria. This possibly provides them with an advantage over the other species due to their unique experience with transparent surfaces. Second, guppies are the only aquatic species so far studied, and odour diffusion has quite different properties in water compared with air, potentially facilitating guppies in retrieving food from the open sides of the cylinder.

In the present study, we tested the importance of previous experience with transparent materials and of olfactory cues in the cylinder test within the same species, *Poecilia reticulata*. To study the effect of experience, we compared guppies grown without any experience with transparent surfaces, guppies maintained in a standard glass aquarium (with experience with glass but no experience with detouring a transparent surface) and guppies maintained in a tank with inner transparent panels so that they could also experience the detouring of transparent obstacles. To study the importance of olfaction, we compared guppies tested in the standard cylinder task with guppies tested with a modified transparent cylinder, perforated in the middle, so that olfactory cues could not provide directional cues regarding the cylinder entrance.

2. Materials and methods

a. Subjects and experimental treatments

Fifty-eight adult female guppies (see below) were tested in this study. The subjects belonged to an ornamental strain ("snakeskin cobra green") bred in our laboratory since 2012. The strain was maintained in large opaque plastic tanks (400 L) that had gravel bottoms, abundant vegetation (*Hygrophila corymbosa* and *Taxiphyllum barbieri*), water filters, and two 30-w fluorescent lamps (12 h:12 h light/dark photoperiod). Water temperature was maintained at 26 ± 1 °C. At the onset of sexual maturity, fish were collected and randomly assigned to one of the four treatment tanks (see below). Guppies were fed with commercial food flakes (Aqua tropical, Padovan®) and *Artemia salina* nauplii two times per day.

Experimental guppies were then maintained for three weeks in treatment tanks filled with 80 L of water provided with gravel, filter, and illumination as described for the previous large tanks. Guppies in these tanks underwent four different treatments. For one group (“No experience”), the walls of the tank were covered with a grey plastic sheet so that they were made opaque. In a second group (“Glass experience”), the tank had normal glass walls. In the third group (“Detour experience”), the aquarium was a normal glass tank but provided with four vertical transparent panes (10 x 20 cm) that the fish had to detour while swimming in the tank. For the fourth group (“Odour control”), the conditions were the same as those of the “Glass experience” group.

b. Apparatus for the cylinder test

The apparatus consisted of a 60 x 40 x 38 cm tank filled with natural gravel and 30 cm of water at 26 ± 1 °C (Lucon-Xiccato et al., 2017; Figure 1). We covered the long walls of the tank with green plastic, and we divided the tank into three compartments: a back compartment, a frontal test compartment, and a central start box. In the back compartment, we provided natural plants and four immature companions, which did not take part in the experiment, to enrich the environment. The cylinder test took place in the frontal compartment. The start box was connected to the test compartment by means of a semi-transparent guillotine door, but it was separated from the back compartment by means of a green net wall. Two fluorescent lamps and a video camera were placed above the tank to illuminate the apparatus from 07:30 to 19:30 h. Experiments were conducted in a dark room.

We used two types of cylinders in different phases of the procedure: both were 3 cm in length and 2.5 cm in diameter, but the training cylinder was opaque (green plastic), whereas the test cylinder was transparent (acetate). Both cylinders were glued on a green plastic base (4 x 4 cm). The transparent cylinder used for the Odour control group was pierced both in the front and in the back (six holes of 0.2 cm in diameter on both sides in correspondence to food).

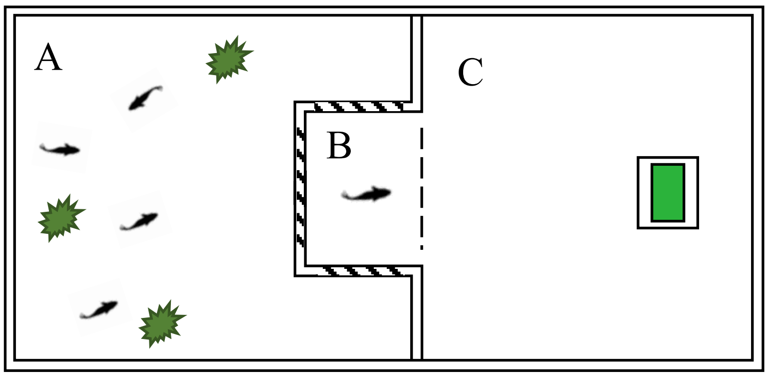

Figure 1. Above representation of the experimental apparatus: back compartment with plants and social stimuli (A), central start box (B) and frontal test compartment (C).

c. Procedures

Habituation phase

The procedure consisted of three phases as in the previous study on this species (Lucon-Xiccato et al., 2017). The habituation phase lasted three days. On the first day, the subjects were moved from the treatment tanks and inserted individually into the experimental apparatuses. On the second day, the subjects were fed five times with a Pasteur pipette with crumbled flakes mixed with water to train them to approach the pipette and to get the food from it as soon as it was released into the water. On the last day of this phase, before the subjects were fed, they were gently pushed into the start box with a transparent panel, and the guillotine door was closed. After a few minutes, the guillotine door was opened, and the Pasteur pipette was inserted into the tank to feed the subjects. After this phase, the guppies that did learn to get food from the pipette (10 out of 58) were substituted with new subjects.

Training phase

During this phase, the guppies had to learn to obtain food inside the opaque cylinder. The subjects performed five trials per day with a 1-h interval between each trial. Before each trial, the subjects were enclosed in the start box; the experimenter inserted the opaque cylinder into the middle of the test compartment and with a Pasteur pipette inserted the food inside of it while the subject was looking in the direction of the pipette. After two minutes, the guillotine door was opened so that the subject could enter the test compartment. The guppies had 15 minutes to exit the start box; otherwise, the trial was considered to be null and was repeated successively. If the subject exited within 15 minutes, it had 30 minutes to find the food inside the opaque cylinder; otherwise the trial was considered to be null and was repeated. Instead, if the subject entered the cylinder, we waited five minutes before removing the cylinder to allow the fish to consume the food. From the second day of the training phase, the subjects could pass to the test phase if they achieved four out of five correct trials in a day. A trial was considered to be correct if the subject entered the cylinder directly from the lateral openings without touching the transparency. All subjects met the learning criterion within five days.

Test phase

The test phase was similar to the training phase with the exception that the opaque cylinder was replaced with a transparent cylinder. Subjects of the "Odour control" group were tested with a modified version of the transparent cylinder provided with holes. In this way, the odour of bait spread in all directions to prevent directional cues regarding cylinder entrances. In the test phase, guppies received 20 trials, divided into five trials for four consecutive days. During this test phase, six guppies (one in the "Glass experience" group, two in the "Detour experience" group, and three in the "Odour control" group) ceased to participate and were substituted with new subjects.

Based on the video recordings, we scored the accuracy and the time it took to enter the cylinder in each test trial. To score the accuracy, we recorded whether the subject entered the cylinder directly via the lateral openings without touching the cylinder (correct trial) or whether it touched the transparent material (incorrect trial). To score the time to solve the task, we measured the time from when the subject exited the start box to when it entered the cylinder. All of the videos were analysed by two experimenters to assess the reliability. We calculated trial-by-trial interobserver agreement by dividing the number of trials in which experimenters agreed by the total number of trials and then converting the result to a percentage (the mean agreement for total performance was 98%). Even the time to solve the task indicated high inter-rater reliability (Spearman's rank correlation: $\rho = 0.981$, $P < 0.0001$); therefore, we conducted all of the analyses with the database of the first experimenter.

d. Statistical analysis

Analyses were performed in R version 3.4.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). We performed a two-step analysis: first, we analysed the performance of all of the experimental groups on both the training and the test phase with a pooled analysis to achieve greater statistical power; then, we specifically compared the groups useful for testing our main hypothesises (the effect of experience and effect of odour), focussing on the test phase with the transparent cylinder. In the pooled analysis, we initially compared the number of training trials necessary for each treatment to reach the learning criterion of four out of five daily correct trials with a Kruskal-Wallis test fitted with group as fixed factor. Then, we compared the proportion of correct trials (trials in which the subject did not touch the transparent cylinder) in the four days of the test phase; this variable was a repeated measure variable, and we thus used repeated measure analysis of variance (ANOVA) fitted with "day" as a within-subject factor and "group" as a between-subject factor. We similarly analysed the time to enter the cylinder in the four days of the test phase with repeated measures ANOVA.

The effect of experience was studied by comparing the proportion of correct responses and the time to enter the cylinder in the four days of the test phase of the groups "No experience", "Glass experience" and "Detour experience" using two repeated measures ANOVAs. The effect of odour was studied by comparing the proportion of correct responses and the time to enter the cylinder in the four days of the test phase of the groups “No experience” and “Odour control” using two repeated measures ANOVAs.

In the case of no significant support for our main hypothesis, it remains possible that the factors examined affected the performance, but our study was not able to detect this. To tackle this possibility, we used a Bayesian approach and calculated an approximate Bayes factor that allows for estimating the relative strength of the evidence for the two competing models even in the case of the small sample size and non-significant results (Dienes, 2014). We computed the Bayes factor from the Bayesian information criteria of linear models with and without the effect of “group” (Schwarz, 1978).

3. Results

a. Pooled analysis

During the training phase, the number of training trials necessary to meet the learning criterion did not significantly differ among experimental groups (trials for criterion: “No experience”: 12.33 ± 2.46; “Glass experience”: 12.42 ± 3.32; “Detour experience”: 11.25 ± 2.26; “Odour control”: 11.17 ± 2.74; Kruskal-Wallis: $\chi^2_3 = 2.618$, $P = 0.454$). This indicated that there was no difference in the ability to learn the task with the opaque cylinder in the subjects used in the different experimental groups.

During the test phase, “No experience” guppies performed 68.33 ± 23.14% correct trials in which they retrieved food without touching the transparent cylinder (correct trials), the “Glass experience” group performed 74.17 ± 22.00% correct trials, and the “Detour experience” guppies performed 73.33 ± 18.96% correct trials. The “Odour control” guppies performed 76.25 ± 24.28% correct trials. The analysis on the proportion of correct responses showed that the performance did not differ among the four groups (rmANOVA: $F_{3,44} = 1.048$, $P = 0.381$). There was a significant increase in the number of correct responses with test days (rmANOVA: $F_{1,140} = 12.819$, $P < 0.001$). The interaction between group and day was not significant (rmANOVA: $F_{3,140} = 0.986$, $P = 0.401$).

The four groups did not significantly differ in the time to enter the cylinder (rmANOVA: $F_{3,44}$ = 0.249, P = 0.861). The time to enter the cylinder significantly decreased over days (rmANOVA: $F_{1,140}$ = 6.132, P = 0.015). There was no group x days significant interaction (rmANOVA: $F_{3,140}$ = 0.948, P = 0.419).

b. Effect of experience

During the test phase, the proportion of correct responses did not differ among the three groups (rmANOVA: $F_{2,33}$ = 0.750, P = 0.480; Figure 2). There was a significant increase in the proportion of correct responses across days (rmANOVA: $F_{1,105}$ = 13.694, P < 0.001; Figure 2). The group x days interaction was not significant (rmANOVA: $F_{2,105}$ = 0.906, P = 0.408).

The three treatments did not significantly differ in the time to enter the cylinder in the test phase (rmANOVA: $F_{2,33}$ = 0.391, P = 0.680; Figure 2). The time to enter the cylinder significantly decreased over days (rmANOVA: $F_{1,105}$ = 8.528, P = 0.004; Figure 2); there was no significant group x days interaction (rmANOVA: $F_{2,105}$ = 0.339, P = 0.713).

The approximate Bayes factor indicated that the model without the effect of experience was 95 times more likely to explain the proportion of correct responses of the subjects than the model with the effect of experience. Considering the time to enter the cylinder, the model without the effect of experience was 65 times more likely to explain the data compared with the model with that effect.

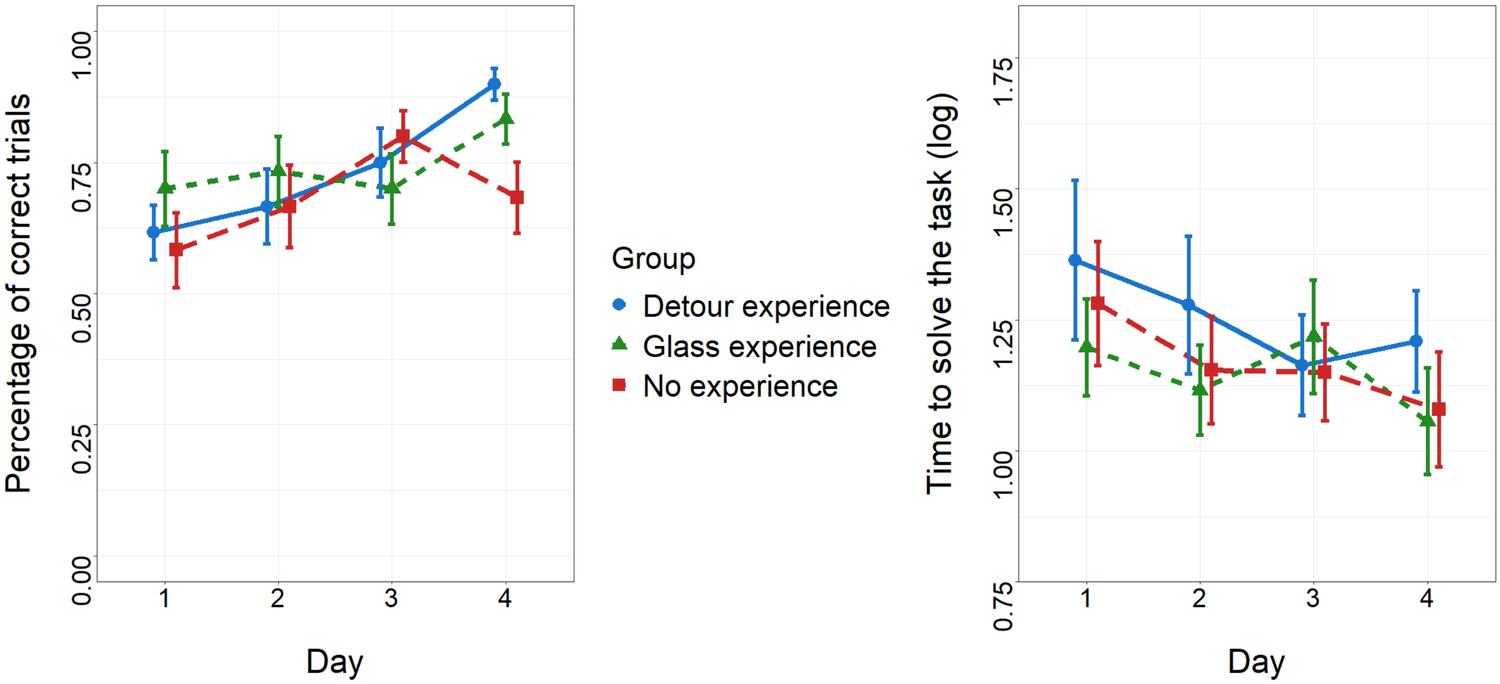

Figure 2. Comparison of mean percentage of correct trials in which guppies did not touch the cylinder (left) and mean time (log) to solve the task (right) for the three groups of the experience hypothesis.

c. Effect of odour

During the test phase, the proportion of correct responses did not differ among the three groups (rmANOVA: $F_{1,22} = 0.365$, $P = 0.552$; Figure 3). The there was an increase in the proportion of correct responses across days, but it did not reach the threshold for statistical significance (rmANOVA: $F_{1,70} = 2.940$, $P = 0.091$; Figure 3). The group x days interaction was not significant (rmANOVA: $F_{1,70} = 0.265$, $P = 0.609$).

The two treatments did not significantly differ in the time to enter the cylinder in the test phase (rmANOVA: $F_{1,22} = 0.329$, $P = 0.572$; Figure 3). The time to enter the cylinder did not significantly change over days (rmANOVA: $F_{1,70} = 0.414$, $P = 0.522$; Figure 3), and there was no significant group x days interaction (rmANOVA: $F_{1,70} = 0.488$, $P = 0.487$).

The approximate Bayes factor indicated that the model without the effect of odour was eight times more likely to explain the performance of the subjects compared with the model with this effect. Even considering the time to solve the task, the model without the effect of odour was eight times more likely to explain the data compared with the model with this effect.

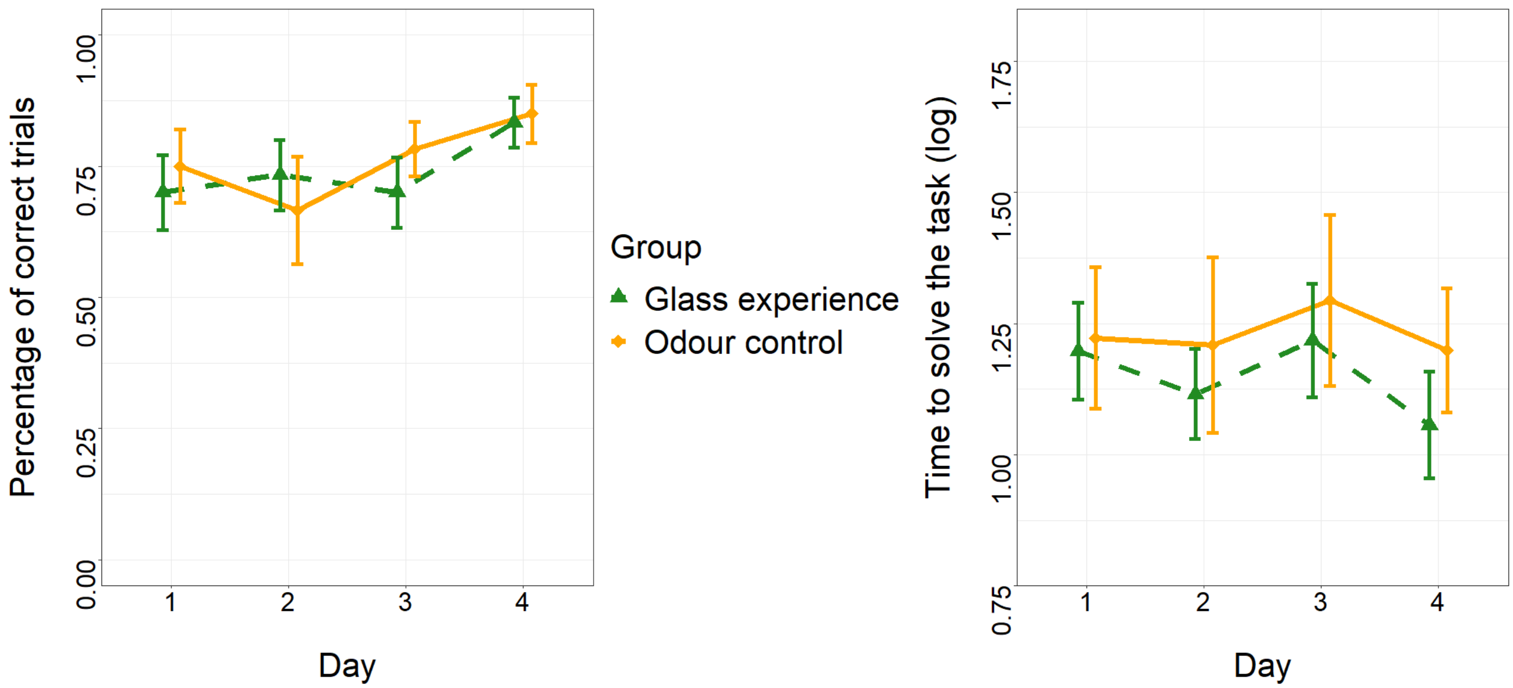

Figure 3. Comparison of mean percentage of correct trials in which guppies did not touch the cylinder (left) and mean time (log) to solve the task (right) for the two groups of the odour hypothesis.

4. Discussion

The cylinder task has been widely used to compare inhibitory control across species (e.g. Kabadayi et al., 2016; Lucon-Xiccato et al., 2017; MacLean et al., 2014; van Horik, Langley, Whiteside, Laker, Beardsworth, & Madden, 2018). Although the size of the brain appeared to be the main predictor of success in a recent study (MacLean et al., 2014), we cannot exclude the role of other factors in explaining interspecific differences. This study shows that previous experience with transparent surfaces and the presence of olfactory cues that could hint at the correct route did not enhance performance in the cylinder task of a fish species, the guppy.

To study the first factor, guppies were given three levels of experience with transparent surfaces. The experimental subjects were raised either without experience with transparent surfaces, in standard aquaria with glass walls (i.e., having experience with transparent surfaces but not having practiced detouring them), or with transparent panels inside their aquaria that could be detoured. The performance was high for all groups (73% trials without touching the transparency), and no difference in performance was found among guppies with these three levels of experience with transparency. The lack of the effect of experience is unlikely to be derived from a small sample size because the Bayes analysis strongly supported the absence of the effect of experience.

Our findings allow us to conclude that experience before the experiment with various types of transparent enclosures did not affect the guppies' cylinder performance. As a consequence, the results of previous study guppies, in which the fish reached the performance of many mammals and birds (Lucon-Xiccato et al., 2017), cannot be accounted for the rearing environment experienced by fish (i.e., glass aquaria) before the task. One is tempted to conclude that the differences observed between species in comparative studies involving "higher" vertebrates might not be affected by the type of enclosure experienced by the species before the test (MacLean et al., 2014). However, it is worth noting that fish often avoid entering clusters of filamentous vegetation, even if they are semi-transparent, to prevent the risk of getting caught. Evolution could thus have favoured fish cognitive mechanisms that predispose, even in the absence of specific experience, detouring obstacles even when they can see the target directly. These issues could be less important in other habitats, and our results do not exclude that the effect of experience does exist in other species.

Interestingly, a recent study, investigating pheasants (*Phasianus colchicus*) in two detour-reaching tasks, apparently reached opposite conclusions regarding the role of experience (van Horik et al., 2018). Half of the pheasants were first tested in a transparent cylinder task, as in our study, and then, they were tested with a transparent barrier that they had to detour to reach food bait. The other half received the two tests in the reverse order. Prior experience with a detour test, either the cylinder or the barrier test, improved the inhibitory control score in the subsequent test, suggesting that pheasants had learned something about the task (e.g., the general properties of transparent obstacles). There is, however, an important difference between van Horik and colleagues' (2018) procedure and that used in both the present study and the study of Mclean and colleagues (2014). Accomplishing detour tasks requires several cognitive abilities, including the capacity of problem-solving via trial-and-error learning (Kabadayi, Bobrowicz, & Osvath, 2017). An important step for singling out the motor inhibitory control component is that the subjects have already learned to detour the obstacle to find food so that when the obstacle becomes transparent, the only variable that prevents the animal from reaching the food is the difficulty of suppressing the tendency to reach the food directly through the obstacle. Both guppies and the species studied by Mclean and colleagues (2014) received extensive training to find food in an opaque cylinder and were allowed to enter the transparent cylinder phase only after they had passed a strict criterion of four out of five consecutive successful trials. Conversely, in the study of van Horik and colleagues (2018), subjects initially received only four trials of familiarization with the opaque cylinder. Quite likely at the beginning of the phase with transparent obstacles, pheasants were still learning the task by trial and error, and this could be the main reason why a clear experience effect was evidenced in the experiment. Thus, it is likely that experience with the task itself, rather than with transparent objects, affected pheasants' cylinder performance. Although we did not observe guppies in two tasks, our study supported this idea. We found some evidence that the number of errors made by guppies decreased over the days of the test and that the time to accomplish the task decreased, indicating that experience with the task might improve guppies' performance as suggested by previous studies (Gatto, Lucon-Xiccato, & Bisazza, 2018; Lucon-Xiccato et al., 2017).

The second aim of this study was to investigate the influence of olfactory cues in the cylinder test. In the cylinder task, visual and chemical information conflict, as the latter appropriately indicates the correct route to food. If olfaction is stronger in guppies in comparison with terrestrial microsmatic species, they are expected to have worst performance when tested with a pierced transparent cylinder, a condition in which both sight and odour cues indicate the shortest route to food. We found no evidence of such an effect, and the Bayesian analysis indicated that this result is unlikely to be attributed to a too-small sample size.

Our finding is in line with previous experiments showing that guppies' behaviour during cognitive tasks exploiting food as reward is not affected by olfactory cues (Lucon-Xiccato & Bisazza, 2014; Miletto Petrazzini, Bisazza, Agrillo, & Lucon-Xiccato, 2017). Furthermore, microscopy studies have showed that guppies possess a simple olfactory organ, indicating that they rely on odours less than other fish species do (Lazzari, Bettini, Ciani, & Franceschini, 2007). Although our study excluded that guppies used chemical cues to detour the transparent cylinder, it is not known if our results could be generalised to other species. The possibility remains that macrosmatic fish and macrosmatic terrestrial species, such as dogs and rats, would exploit chemical cues and easily override the tendency to go directly to the food they see. Such a hypothesis can easily be evaluated by performing a similar manipulation of the cylinder task in macrosmatic terrestrial species or by comparing the performance of microsmatic and microsmatic fish species.

Data availability

All data generated or analysed during this study are included in the Supplementary Information file.

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