Factors affecting the measure of inhibitory control in a fish (*Poecilia reticulata*)

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Abstract

Inhibitory control allows an individual to block automatic responses as well as to control behaviour and attention. There is growing evidence that many species possess this ability, although the difference in performance among species is great. Inhibitory control has been frequently measured using the detour task: a desired reward is placed behind a transparent barrier, and the animal has to inhibit the tendency to directly move toward the goal, instead making a detour around the barrier. Mammals' and birds' inhibitory performance varies according to several factors, such as the distance from the reward and its value, and in dogs, the breed also affects it. We investigated whether these factors affected performance in a fish, the guppy (*Poecilia reticulata*), by using the detour task, with reaching a social group as goal. We found that guppies were more proficient in making a detour around the barrier when the goal was far, but the value of the reward (i.e., the size of the social group) had no effect. We also found a clear effect of strain, with the guppies that descended from a wild population performing better than the domesticated guppies. Our study revealed that some of the factors affecting inhibitory control in warm-blooded vertebrates also modulate the performance of fish. These factors should be taken into account when comparing this function across species.

Keyword: detour task, inhibitory control, fish cognition, *Poecilia reticulata*

Introduction

In various situations, animals have to modify or block automatic responses, and eventually switch to diverse, more appropriate responses to achieve certain goals. For example, chum salmon (*Oncorhynchus keta*) inhibit foraging activity when exposed to predation risk (Ryer and Olla, 1991); predators need to inhibit predatory attacks until the prey reaches a convenient position (Hugie, 2003). The cognitive function in charge of these and similar processes is often referred to as inhibitory control (Diamond, 2013).

Inhibitory control has been classically studied in humans (Diamond, 2013; Gottfredson and Hirschi, 1990; Konrad et al., 2000; Moffit et al., 2011; Schachar et al., 2000), but more studies aimed at understanding the evolution of inhibitory control have been recently conducted on other mammals as well as on birds (e.g., Kabadayi et al., 2016; MacLean et al., 2014). Most of the studies on non-human animals have exploited modified versions of the detour task originally developed to measure inhibitory control in infants (Diamond, 1981). In this task, study subjects have to make detours around a transparent obstacle, which require inhibiting the tendency to pass directly through it, to reach a goal placed behind the obstacle, such as a food reward (reviewed in Kabadayi et al., 2017a). There is not complete agreement among researchers on which abilities are measured by the detour task (Beran, 2015) and on whether non-cognitive factors affect performance in this task (van Horik et al., 2018); however, the detour task is generally considered to measure motor aspects of inhibitory control (Kabadayi et al., 2017a).

A common finding of research on animals' inhibitory control is that animals' performance varies widely across species, although the reasons for this variation remain unclear. For example, apes and ravens tested using the detour task were close to 100% correct trials (i.e., trials in which they reached the goal without touching the transparent obstacle), whereas parrots' and sparrows' performance was around 30% correct (Kabadayi et al., 2016;

Kabadayi et al., 2017b; MacLean et al., 2014). The aforementioned performance differences might be due to differences in inhibitory control capacities. However, part of this variation might be due to other, non-cognitive factors that affect task performance. For example, several studies indicated that the greater the distance between the subjects and the goal, the greater the ability to make a detour around the barrier (Diamond and Gilbert, 1989; Junghans et al., 2016; Regolin et al., 1994). Other studies suggested that the value of the goal has an impact on the ability to inhibit a behaviour (Auersperg et al., 2013; Brucks et al., 2017b; Bugnyar et al., 2012; Hilleman et al., 2014; Rosati et al., 2007). For example, humans show reduced inhibition when the reward has a high value, i.e. money versus food (Estle et al., 2007; Odum and Rainaud, 2003; Odum et al., 2006; Rosati et al., 2007), and dogs show reduced inhibition with a higher amount of food as a reward (Brucks et al., 2017a, b).

There is also evidence that performance may vary within species (i.e., between individuals). For example, human children and cotton-top tamarins (*Sanguinus oedipus*) showed individual differences in their inhibitory control performance, suggesting that some individuals are more efficient in inhibiting a behaviour compared to others (Kralik et al., 2002; Moffitt et al., 2011). Evidences indicate that different breeds of dogs show differential inhibitory performance when tested using the same procedure (Fagnani et al., 2016; Marshall-Pescini et al., 2015). Understanding the role of these factors is important not only for understanding the mechanisms of inhibition but also for allowing a proper comparison across species and reducing confounds.

Fish have been investigated only recently regarding their inhibitory control. Guppies (*Poecilia reticulata*) have proved to be able to detour tasks with a performance similar to that of many warm-blooded vertebrates (Lucon-Xiccato et al., 2017b). However, information is still lacking regarding whether the same kinds of factors that affect performance in mammals and birds affect fish's inhibitory control performance. In the present study, we investigated in guppies the effect of three factors that are potentially important for inhibitory motor control performance in the detour task. As in a previous study, the subjects had to make detours around a transparent barrier to reach a social group as a reward (Lucon-Xiccato et al., 2017b)

In experiment 1, we studied the effect of the distance between the goal and the subject by varying the position of the social group (far from or close to the barrier). We expected that subjects will show greater difficulty in inhibiting the impulse to reach the goal when the goal is closer (Diamond, 1990). In experiment 2, we studied the effect of the reward value by presenting different numbers of conspecifics in the social group. Because protection against predators increases with increasing group size, larger social groups have greater value for guppies. Thus, we predicted that fish will show reduced inhibitory performance when the social group is larger. The last factor that we considered is strain. In the two experiments in this study, we used both domestic and wild-descendant guppies to compare the performance of the two strains.

Materials and Methods

Experimental subjects

The subjects were adult female guppies from two strains: an ornamental strain ('snakeskin cobra green') bred in the laboratory since 2012 and a wild strain descendant from guppies caught in a high predation–risk environment (Tacarigua River, Trinidad) in 2002. The wild strain is currently maintained in a semi-natural warm-water pond in Padova as a large (<10000) self-sustained population. Before the experiments were conducted, all fish were maintained in the laboratory in the Department of General Psychology (University of Padova) in large tanks (100 × 70 cm, 400 L). The tanks were provided with gravel bottoms, aquatic plants, water filters, and 36-W fluorescent lamps (12h:12h light/dark photoperiod). The water temperature was kept at 26 ± 1 °C, and the fish were fed with commercial food flakes (Aqua Tropical, Isola Vicentina, Italy) and *Artemia salina* nauplii two times per day.

We planned to test 48 guppies in experiment 1 (24 domestic guppies and 24 guppies from the wild population) and another 48 guppies in experiment 2 (24 domestic guppies and 24 guppies from the wild population). However, 23 subjects (16 subjects of the domestic strain and 7 subjects of the wild strain) did not complete the 5 trials of the experiment (see below). These guppies were discarded and substituted with new subjects of the same strain in order to maintain the predetermined sample size. The overall study included 96 guppies that completed the two experiments, plus 23 guppies that were discarded (total: 119 guppies). Each subject was tested once to ensure independence of the data of the different experiments and rule out the effects of experience (van Horik et al., 2018). Following the completion of the experiment, the subjects were released into a maintenance tank.

Apparatus and procedure

The experiments followed a well-established procedure for studying detour behaviour in fish (Lucon-Xiccato and Bisazza, 2017a; Lucon-Xiccato et al., 2017b). Each subject underwent 5 trials in which it had to detour the transparent barrier to reach a social group. The apparatus was an 80 × 40 × 36 cm glass tank with walls covered with white plastic (Fig. 1). An 18-W fluorescent lamp placed above the stimuli illuminated the apparatus, and a video camera recorded the trials. On one of the short sides of the tank, we placed a white start box (15 × 10 × 20 cm). To start the first trial, we netted the subject from a maintenance tank and inserted it into the start box. From the start box, the subject could see the target: a social group confined in a transparent cylinder placed on the opposite extremity of the tank. These guppies were adult females from the same strain and were the same size as the subject. Outside the trials, we maintained stimulus guppies in a 60 × 40 × 38 tank provided with gravel bottom, plants, and water filters as described for maintenance tank. We inserted the stimuli into the cylinder 30 min before the beginning of the trial to habituate them to the experimental tank (Lucon-Xiccato et al., 2017a). After being inserted into the start box, the subject was free to exit and to swim towards the social group, but before reaching the group, the subject had to pass the barrier. The barrier (18 × 18 cm) was made from transparent plastic and was placed between the start box and the social group, at 30 cm from the start box (Fig. 1). The barrier was C-shaped by means of two white plastic wings (18 × 5 cm). This was done to prevent the guppies from making a detour accidentally while trying to pass through the barrier (Lucon-Xiccato and Bisazza, 2017a). A trial ended when the subject reached the social group. Subject that did not reach the social group within 20 min (because they did not exit from the start box or froze or swam along the wall) were discarded and substituted. After a subject joined the social group, we left it undisturbed for 5 min as a reward; then, we netted the subject again and repeated the procedure until the completion of the 5 trials. We tested 8 subjects per day divided into two sessions. At the end of a session, half of the water was removed from the apparatus and was substituted with clean water.

In experiment 1, we always used 4 stimulus fish as the social reward in the cylinder, and the subject guppies were tested with two different conditions regarding the position of the social group to study the effect of distance (Fig. 1a). In the first condition, the cylinder with the social group was placed at 5 cm from the barrier (N = 12 domestic guppies and 12 wild-descendant guppies); in the second condition, the cylinder with the social group was placed at 15 cm from the barrier (N = 12 domestic guppies and 12 wild-descendant guppies). A distance of 5 cm corresponds to 2 body lengths in this species, and it has been frequently observed as the inter-individual distance of shoaling guppies (Pitcher, 1986). Conversely, the distance of 15 cm corresponds to 6 body lengths and is larger than the normal inter-individual distance observed in guppies. We randomly assigned the subjects to the different conditions and tested alternately the subjects of the two conditions.

In experiment 2, the position of the stimuli was fixed, with the cylinder being placed at 10 cm from the barrier (Fig. 1b). The number of guppies of the social group in the cylinder varied to study the effect of the reward value: in the first condition, we used a 3-guppies social group (N = 12 domestic guppies and 12 wild-descendant guppies), whereas in the second condition, we used an 8-guppies social group (N = 12 domestic guppies and 12 wild-descendant guppies). Guppies have been proven to recognise the difference between two shoals made up of 4 and 5 conspecifics (Lucon-Xiccato et al., 2017a); the number of stimulus guppies used in the two conditions of the present experiment (3 versus 8) was therefore adequate for the subjects to notice the difference. Again, we randomly assigned the subjects to the conditions and randomized the condition between trials.

There were only three differences between the apparatuses used in the two experiments. First, the apparatus of experiment 1 was filled with 10 cm of water, whereas the apparatus of experiment 2 was filled with 20 cm of water. Second, the cylinder of experiment 1 had a diameter of 12 cm, whereas the cylinder of experiment 2 had a diameter of 14 cm. The larger amount of water and the larger cylinder in experiment 2 were necessary to accommodate a larger number of guppies. Considering both the cylinder diameter and the water level in the tank, the volume of water per stimulus fish in experiment 1 was approximately 300 cm^3 and the volume of water per fish in the 8 stimuli condition of experiment 2 was 400 cm^3. Thus, in the 8-stimuli condition of experiment 2, the density of stimulus fish in the cylinder was sufficient to ensure visibility of each stimulus at least as in experiment 1.

Third, in experiment 2, we equated the amount of conspecific's chemical cues experienced by the subjects in the two conditions. Indeed, during development of previous procedures, we observed that guppies show reduced activity and consistent freezing behaviour when inserted in a novel experimental tank with no or reduced olfactory cues from conspecifics. For this reason, we routinely provide experimental tanks with social cues by housing some conspecifics in separated compartments (e.g., Lucon-Xiccato et al., 2015; Lucon-Xiccato et al., 2017a). In experiment 2, the subjects would experience a different amount of chemical cues in the testing tank according to the experimental condition (3 or 8 stimulus fish); this might cause different activity of the subjects in the two experimental conditions and affect task performance. To deal with this confound, in experiment 2, we added an extra compartment (10 cm) behind the cylinder with the social group. In such compartment, we housed 5 guppies in the trials with the condition with the smaller social group. This small compartment communicated with the main experimental compartment by means of small holes, but the subject could not see the fish inside the compartment. With this setting, the subject guppies were exposed to the olfactory cues of an equal number of conspecifics in both experimental conditions. Further, our setting mimics the conditions of guppies' natural environment, where they could perceive the chemical cues of many conspecifics living in the area but they could see only few of them due to the windingness of the rivers and to the presence of stones and dense vegetation. In these conditions the number of fish seen rather than the amount of social odour perceived is likely to influence the decision about the social group to join.

Analysis of the video recordings

We analysed the performance of the subjects from the video recordings of the trials. We played back the recordings using a computer, and we scored whether the subjects reached the stimulus shoal by entering the area delimited by the wings of the barrier (incorrect trial) or not (correct trial). We also measured the time spent within this area. The experimenter was blind with respect to the experimental condition.

To test the reliability of our video analysis, a second observer blind to the aims of the experiments re-analysed the video recordings of 50 trials of 10 randomly chosen subjects in each experiment (100 trials overall). The binary measure of performance, correct versus incorrect trials, did not differ between the two scores. The time spent in front of the barrier was highly correlated between the two scores for both experiments (Spearman's rank correlation: experiment 1: *rho* = 0.997, $P < 0.001$; experiment 2: *rho* = 0.998, $P < 0.001$).

Statistical analysis

Analyses were performed in RStudio version 1.1.383 (RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/). For both experiments, we analysed the outcomes of the trials (correct or incorrect) with generalized linear mixed-effects models for binomial response distributions (GLMMs; 'glmer' function of the 'lme4' R package) fitted with the trial number as a covariate to examine whether the performance improved over trials, experimental condition and strain as fixed effects, and individual ID as random effect. To assess the significance of the models' parameters, we used the 'Anova' function of the 'CAR' package. We analysed the time performance (time spent trying to pass thought the barrier) by using linear mixed-effects models (LMMs; 'lmer' function of the 'lme4' R package) fitted as the GLMMs of the above. The time performance was log transformed due to the right-skewed distribution. Given the absence of a significant effect of the condition, in experiment 2, we used the Bayesian information criteria of the models with and without experimental conditions to approximate a Bayes factor (Wagenmakers, 2007). The Bayes factor allowed to test for similarity between the experimental conditions, providing an approach to interpret non-significant results which is robust to small sample size (Dienes, 2014). Data reported in the text are mean ± standard deviation.

Results

Experiment 1: Distance from the goal

In the analysis of the trials' outcomes, we found that the likelihood of a correct response significantly increased across the 5 trials administered (GLMM: $\chi^2_1 = 9.776$, $P < 0.002$; Fig. 2a,b), suggesting that the guppies' performance increased due to learning. We found a significant effect of the condition in the model (GLMM: $\chi^2_1 = 9.019$, $P < 0.003$; Fig. 2a), indicating that the guppies tested with the social group close to the barrier made fewer correct responses compared with the guppies tested with the social group far from the barrier (close: 28.33 ± 28.84 % correct trials; distant: 50.00 ± 25.02 % correct trials). We also found a significant effect of strain (GLMM: $\chi^2_1 = 9.019$, $P < 0.003$; Fig. 2b): the wild-descendent guppies made more correct responses than the domestic guppies did (wild: 50.00 ± 25.02 % correct trials; domestic: 28.33 ± 28.33 % correct trials).

In the analysis of the time spent trying to pass through the barrier, we found a significant effect of the trial (LMM: $\chi^2_1 = 12.653$, $P <0.001$; Fig. 2c,d), indicating that the guppies learned to solve the task faster as the training progressed. As in the previous model, we found a significant effect of the condition (LMM: $\chi^2_1 =15.799$, $P <0.001$; Fig. 2c) and a significant effect of the strain (LMM: $\chi^2_1 = 17.912$, $P < 0.001$; Fig. 2d). The guppies tested with the social group far to the barrier were faster in passing the barrier compared with the guppies tested with the social group close from the barrier (close: 78.42 ± 96.13 s; distant: 24.21 ± 21.21 s), and the wild-descendent guppies were faster than the domestic guppies were in passing the barrier (wild: 23.38 ± 28.28 s; domestic: 79.25 ± 93.79 s).

Experiment 2: Value of the reward

In the analysis on the trials' outcomes, we did not find a significant effect of the trial (GLMM: $\chi^2_1 = 0.519$, $P = 0.471$; Fig. 3a,b) or a significant effect of the condition (larger group: 35.00 ± 27.82 % correct trials; smaller group: 33.33 ± 25.48 % correct trials; GLMM: $\chi^2_1 = 0.070$, $P = 0.791$; Fig. 3a). The approximate Bayes factor indicated that the GLMM model without the effect of the experimental condition was 15 times more likely to explain the performance of the subjects compared with the model with the effect of the experimental condition. We found a significant effect of strain (GLMM: $\chi^2_1 = 9.446$, $P = 0.002$; Fig. 3b), indicating that the wild-descendent guppies made more correct responses than the domestic guppies did (wild: 45.00 ± 25.19 % correct trials; domestic: 23.33 ± 23.34 % correct trials).

In the analysis of the time spent trying to pass through the barrier, we did not find a significant effect of the trial (LMM: $\chi^2_1 = 0.168$, $P = 0.682$; Fig. 3c,d) or a significant effect of the condition (larger group: 69.96 ± 100.55 s; smaller group: 95.52 ± 79.37 s; LMM: $\chi^2_1 = 1.413$, $P = 0.235$; Fig. 3c). The approximate Bayes factor indicated that the LMM model without the effect of the experimental condition was 22 times more likely to explain the performance of the subjects compared with the model with the effect of the experimental condition. We found a significant effect of strain (LMM: $\chi^2_1 = 6.809$, $P < 0.009$; Fig. 3d), indicating that the wild-descendent guppies were faster than the domestic guppies were in passing the barrier wild: 79.59 ± 92.28 s; domestic: 85.88 ± 90.63 s).

Discussion

Several factors affect the inhibitory performance of mammals and birds (e.g., Marshall-Pescini et al., 2015; Junghans et al., 2016; Rosati et al., 2007). Recently, fish have been shown to perform similarly to warm-blooded vertebrates in standard inhibitory motor control tasks (Lucon-Xiccato et al., 2017b), but whether the same factors observed in warm-blooded vertebrates affect fish's performance remains to be investigated. We tested the hypotheses that the detour performance of a fish, the guppy, varies with the distance from the goal (experiment 1) and the value of the reward (experiment 2). The results of our experiments supported the former hypothesis but not the latter one, and they also evidenced a performance difference between the domestic and wild-descendant strains of guppies.

In experiment 1, guppies were tested for their ability to make a detour around a transparent barrier to join a social group placed at two different distances from the barrier. For half of the subjects, the social group was close to the barrier (5 cm), whereas for the remaining half of the subjects, the social group was farther, at 15 cm from the barrier. In both conditions, the guppies showed a steady decrease in the number of errors and in the time spent trying to pass through the barrier across the 5 trials administered. This effect was previously reported in guppies using this procedure, but not using a different procedure whereby the subjects had to make detours around a transparent cylinder instead of a barrier (Lucon-Xiccato et al., 2017b). This effect has also been found in cotton-top tamarins (*Saguinus oedipus oedipus*: Santos et al., 1999), orangutans (*Pongo pygmaeus*: Vlamings et al., 2010) and several bird species (*Taeniopygia guttata*; *Melospiza melodia*; *Melospiza georgiana*, *Amazona amazonica;* Maclean et al., 2014) but not in other primates and birds (primates: *Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*; Vlamings et al., 2010; birds: *Corvus sp.*, *Corvus moneduloides*, *Coloeus monedula*; Kabadayi et al., 2016). Performance improvement is usually interpreted as evidence that the subjects learn to handle the transparency of the barrier trial after trial, and that they obtain increasing ability in inhibiting their tendency to pass directly through the barrier.

The comparison between the guppies tested in the two conditions clearly indicated that the performance increased when the distance between the barrier and the goal was greater. In other words, when the guppies were close to the goal, it was more difficult to inhibit the tendency to reach it. Similar effects have been found in other species: sevenmonth-old human infants and long tailed macaques (*Macaca fascicularis*) failed to retrieve a toy and a food item, respectively, placed just behind a transparent barrier (Diamond and Gilbert, 1989; Junghans et al., 2016). Two-day-old chicks (*Gallus gallus domesticus*) take longer time to reach a proximal conspecific group (Regolin et al., 1994). It has been suggested that in humans and monkeys, the response inhibition depends upon the working memory load required to solve the task (reviewed in Ridderinkhof et al., 2011). In particular, motor activation seems to be dominant with respect to the inhibitory response when the internal impulse is stronger. A similar mechanism might explain the effect observed in guppies.

In experiment 2, guppies were tested using two rewards with different values. In one condition, the reward was a group of 3 fish, whereas in the other condition, the reward was a group of 8 fish. Joining large shoals is an effective antipredator mechanism of social fish species, as an individual in a large shoal has a reduced probability of being predated in the event of an attack (Hager and Helfman, 1991). Hence, we expected that guppies should be more attracted to the larger social group, thus resulting in greater difficulty with executing a detour when the social group is large. Contrary to our expectation, we found convincing evidence that the guppies performed similarly in the two conditions, both with regard to the number of trials in which the transparent barrier was not touched and the time spent trying to pass through the barrier. This result contrasts with that observed in other species (e.g., Brucks et al., 2017a; Rosati et al., 2007). One possible explanation for the absence of the expected effect is that the guppies did not perceive the differences between the two social groups. This appears unlikely because a large literature suggests that social fish are highly proficient in discriminating shoals of different sizes (Agrillo et al., 2017). Guppies can discriminate shoals that differ by one individual at least up to 4 versus 5 fish (Lucon-Xiccato et al., 2017a). Thus, guppies should have no problem with perceiving the difference between shoals differing by 5 individuals as in our experiment. An alternative interpretation is that the guppies perceived the difference between the two social groups but were not motivated differently. Although guppies consistently select the larger of two shoals when option is available (Agrillo et al., 2017; Lucon-Xiccato et al., 2017a), it is possible that when placed in a novel, potentially dangerous, environment with a single visible social group, they show a strong social attraction which is largely independent of group size. The fact that we equated the chemical cues of conspecifics in the two conditions might also have contributed to reduce the perceived difference in the value of the two groups. Before accepting the idea that the reward type does not affect guppies' inhibitory performance, it is necessary to test guppies using other kinds of lures, such as food, that allow a finer determination of the resource value.

When we compared the two strains of guppies, we found evidence of differential performance in both experiments. The wild-descendant guppies made fewer errors and made detours around the barrier more quickly compared with the domestic guppies. At the current stage of research, it is not clear what caused this difference between the strains. Previous studies comparing wild and domestic guppies did not find significant differences in cognitive performance (Lucon-Xiccato and Bisazza, 2017b), but they did find behavioural differences in sociability (Swaney et al., 2015). For foxes (*Vulpes vulpes*), researchers have reported the rapid evolution of their cognitive abilities following simulated domestication consisting of artificial selection for tame behaviours (Hare et al., 2005). It is possible that humans have selected domestic guppies for certain behaviours adapted to captivity conditions (i.e., sociability), and this, in turn, has affected their inhibitory control via genetic pleiotropy. Differential inhibitory performance has also been reported between dogs and wolfs, suggesting an effect of domestication (Marshall-Pescini et al., 2015); however, in this system, the results are less clear. One explanation for part of the results of Marshall-Pescini and colleagues is that selection for inhibitory control in dogs is relaxed, as they do not live in social groups as wolfs do (Amici et al., 2008). Similarly, it is possible that wild guppies undergo selection for inhibitory control, for example, to inhibit foraging tendencies in the presence of predators (Katz et al., 2010; Ryer and Olla, 1991); conversely, selection for the inhibitory control of domestic guppies might be relaxed. Whatever the evolutionary cause of the strain difference may be, these data are important for two reasons. First, they reveal the presence of significant intraspecific variation in inhibitory control. Future studies should investigate whether fish also show individual variation within population in inhibitory control similarly to humans and other primates (Carlson and Moses, 2001; Gilmore et al., 2013; Kralik et al., 2002; but see Bray et al., 2014) and similarly to what observed in fish for other cognitive abilities (Lucon-Xiccato & Bisazza, 2017c). Second, the difference between strains may be problematic when comparing experiments performed in different laboratories and it should be carefully considered in further studies.

Overall, our study provides evidence of mechanisms modulating inhibitory control that are similar across vertebrates. This may also have some methodological implications for comparative research on inhibitory control. Indeed, our findings align with previous research in suggesting that the commonly-used detour task may, at least to some extent, measure factors other than inhibitory control (Auersperg et al., 2013; Brucks et al., 2017b; Bugnyar et al., 2012; Diamond and Gilbert, 1989; Hilleman et al., 2014; Junghans et al., 2016; Regolin et al., 1994; Rosati et al., 2007; van Horik et al., 2018). For example, in pheasants, *Phasianus colchicus*, the detour task seems to be sensitive to the subjects' motivation to feed (van Horik et al., 2018). To date, it is not clear whether and to which extent the detour task measures inhibitory control in animals. Also, the present study and the early studies addressing the effects of different factors on the detour performance also suggest that, as for other cognitive abilities (Gatto et al., 2017; Lucon-Xiccato et al., 2017a; Prétôt et al., 2016; Salwiczek et al., 2012), small modifications to the apparatus and the procedure might bear different conclusions regarding the cognitive ability of a species. These potential confounds should be carefully taken into account when comparing performance across species.

Ethical statement

The experiments adhered to the current legislation of our country (Decreto Legislativo 4 Marzo 2014, n. 26) and were approved by the Ethical Committee of the Università di Padova (protocol n. 33/2015).

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Figure captions

Fig. 1 Apparatus adopted in our study. **(a)** In experiment 1, the position of the stimuli varied according to the experimental condition (close versus distant); **(b)** in experiment 2, the position of the stimuli was fixed, but the value of reward varied (3 versus 8-guppies social group).

Fig. 2 Performance of guppies in experiment 1. Percentage of successful guppies that made detours around the barrier without touching it divided according to the **(a)** two experimental conditions (close versus distant goal) and the **(b)** strain (wild-descendant versus domestic guppies); and mean time required to complete the task divided according to the **(c)** two experimental conditions and the **(d)** strain. Lines indicated the change in performance across trials as predicted from the model and shaded areas 95 % C.I..

Fig. 3 Performance of guppies in experiment 2. Percentage of successful guppies that made detours around the barrier without touching it divided according to the **(a)** two experimental conditions (3- versus 8-guppies social group) and the **(b)** strain (wild-descendant versus domestic guppies); and mean time required to complete the task divided according to the **(c)** two experimental conditions and the **(d)** strain. Lines indicated the change in performance across trials as predicted from the model and shaded areas 95 % C.I..