1 **ABSTRACT**

2 Animal species differ considerably in their ability to detour around a see-through obstacle to reach a

3 goal positioned behind it. This variation is commonly assumed to derive from interspecific

4 differences in the cognitive functions involved in the execution of the task, such as spatial abilities

5 and inhibitory motor control. A teleost fish, the guppy (*Poecilia reticulata*), has been recently found

6 to outperform many mammals and birds in this type of task. To determine whether this is a typical

7 condition in teleost fish or whether detour abilities vary among fish species as observed in

8 mammals and birds, we compared four distantly related teleosts in the transparent barrier task using

9 a group of conspecifics as goal. The scores of three species (*Poecilia reticulata*, *Xenotoca eiseni*,

10 *Oryzias sarasinorum*) were similar to those previously reported for fish. The remaining species, the

11 zebrafish (*Danio rerio*), showed a much higher performance, close to that of warm-blooded animals

12 with highest scores (e.g., corvids and monkeys). In comparative cognition studies, contextual

13 variables rather than differences in cognitive ability may be responsible for observed differences

14 between species. In a second experiment, we found that the four species were similarly gregarious,

15 excluding a different motivation to reach the target as an explanation for the different performance.

16 In another experiment, however, we provided evidence that zebrafish's higher detour performance

17 might be due to a sensory advantage. Zebrafish used olfactory cues (towards which the barrier was

18 opaque) to navigate to the social stimulus, whereas the guppy, which we used as a control species,

19 preferentially relied on visual information. This study highlights the importance of sensory

20 differences as a source of potential experimental confound in comparative cognition research.

21

22 **Keywords:** cognitive abilities, comparative cognition, detour, fish cognition, sensory differences

INTRODUCTION

For many animal species, survival and reproductive success may hinge on the ability to efficiently

find the way to resources such as food, social groups, mating partners and refuge. Animals that live

in complex environments frequently face situations in which they must bypass an obstacle, such as

a gap in the route or thick vegetation, to reach a resource located behind it (Eloff, 1951; Tarsitano &

Andrew, 1999; Zeil & Layne, 2002). This behaviour, often referred to as detour behaviour, requires

the animal to temporarily move away from the goal in order to find an indirect route to it.

Several cognitive functions are thought to influence the ability to accomplish the detour behaviour,

including spatial learning abilities, reasoning and inhibitory motor control (Kabadayi, Bobrowicz, &

Osvath, 2018). For the past century, laboratory studies have investigated these abilities using the

detour task (e.g. Kabadayi et al., 2018; Köhler & Winter, 1927; Regolin, Vallortigara, & Zanforlin,

1994; Thorndike, 1911; Zucca, Antonelli, & Vallortigara, 2005). Typically, a barrier is placed

between the subject and the goal, a biologically relevant stimulus. The performance is generally

scored in terms of latency to reach the goal or the number of successful attempts, namely reaching

the goal without touching the barrier (Kabadayi et al., 2018). Using variations of the detour task, in

terms of number of trials and type of barrier, it is possible to investigate different cognitive abilities

underlying the detour behaviour. For example, by testing subjects in a single trial it is possible to

assess whether they can solve the detour problem the first time they face it, which is considered an

indication of capacities for insight or spatial reasoning (Tarsitano & Andrew, 1999; Köhler &

Winter, 1927). By testing subjects in repeated trials, it is possible to assess their learning ability,

indicated by performance improvement over trials (Gatto, Lucon-Xiccato, & Bisazza, 2018;

Kabadayi, Krasheninnikova, O'neill, van de Weijer, Osvath, & von Bayern, 2017; van Horik,

Langley, Whiteside, Laker, Beardsworth, & Madden, 2018).

More recently, two variants of this paradigm, the transparent barrier detour task and the transparent

cylinder task, have been used to study inhibitory motor control (Kabadayi, Taylor, von Bayern, &

Osvath, 2016; MacLean et al., 2014; Lucon-Xiccato, Gatto, & Bisazza, 2017; van Horik et al.,

2018). In both variants, animals could see a reward (e.g. food or conspecifics) behind a transparent

barrier or inside a transparent cylinder, which creates a strong lure for a direct reach. Inhibiting such

prepotent direct response is necessary for successful detour. To accomplish this inhibition, animals

are expected to rely on inhibitory control, a cognitive process that allows an individual to override

an automatic or compelling response to adopt behaviour more appropriate to the specific

circumstance (Chudasama, 2011; Diamond, 2013; Gilbert & Burgess, 2008). Comparative research

on inhibitory control with the detour task has revealed compelling performance differences across

species. For example, MacLean and colleagues (2014) found that some great apes, such as

chimpanzees and Bornean orangutans, achieved a mean performance of 95% of correct responses,

while some prosimians and Old World monkeys, such as Coquerel's sifakas and golden snub-nosed

monkeys, achieved far below 50% correct responses. In this investigation, a correct response

consisted in reaching a food portion inserted in a transparent cylinder without touching the cylinder;

instead a response was considered as incorrect if a subject touched the transparent cylinder before

reaching the food. According to this study, the best predictor of detour task performance was

absolute brain size of a species, suggesting that large brained animals are capable of higher levels of

inhibitory control (MacLean et al., 2014). Several studies have also suggested that other factors,

related to the evolutionary history and ecological adaptation of each species, may have shaped the

cognitive abilities at the basis of detour task solution (Amici, Aureli, & Call, 2008).

The aforementioned interpretations of studies on detour behaviour rely on the assumption that

differences in performance between species are due to variability in the cognitive functions

involved in the solution of the task. However, the observed interspecific differences may also be

due to non-cognitive contextual variables that affect the execution of the detour task (Macphail,

1987; Shettleworth, 2010). For example, a more attractive goal is expected to create a stronger lure

for a direct approach, making it harder to correctly execute the detour. Animals presented with a

3

more desirable target, such as a greater amount of reward or a closer goal, decrease their capacity to execute the detour task (e.g., Gatto et al., 2018; Regolin et al, 1994). Even when the same goal is placed behind a barrier, the value assigned to it and the consequent motivation to reach can vary among species (and individuals), thus creating a potential experimental confound.

Interspecific differences in the detour task could also emerge as a consequence of variation in sensory systems. In the comparative study by MacLean and colleagues (2014), macrosmatic species, such as canids and rodents, showed performances higher than most microsmatic species and not dissimilar from that of great apes. This result might be related to the different way a transparent barrier is perceived by a species that relies on olfaction rather than vision: while the vision of the goal creates a strong lure through the barrier, the odour from the stimulus follows the same pathway that the animal has to take to correctly solve the detour task.

A tiny teleost fish, the guppy (*Poecilia reticulata*), demonstrated performances in detour tasks that exceeded those of many mammals and birds (Gatto et al., 2018; Lucon-Xiccato et al., 2017; Santacà, Busatta, Savaşçı, Lucon-Xiccato, & Bisazza, 2019). However, it is not clear whether the performance of guppies is representative of that of teleost fish. Detour performance might vary considerably among teleost species as observed among mammals and birds, and guppies might be a species exceptionally skilled because of ecological adaptations. Indeed, ecological adaptations often prompt the evolution of a remarkable cognitive capacity such as in the case of spatial memory in food storing corvids (Healy & Krebs, 1992).

In the first experiment of this study, we investigated interspecific differences in detour behaviour by testing four fish species: guppies (*Poecilia reticulata*), zebrafish (*Danio rerio*), red-tailed splitfin fish (*Xenotoca eiseni*) and Sarasins minnows (*Oryzias sarasinorum*). As the obstacle, we used a transparent barrier; thus, our task was expected to measure various cognitive skills including spatial and inhibitory abilities. As a goal, we used a shoal of conspecifics because the four species usually live in group. The four species tested in this study have evolved independently for a long time, more

98 than 100 million years in some cases. Given that mammalian species with less than half such

99 divergence time exhibited remarkable differences in detour performance (MacLean et al., 2014),

100 these fish species were expected to show some variation in detour performance. Moreover, there is

101 evidence that detour abilities might vary according to the habitat in which a species has evolved

102 (Zucca et al, 2005). Despite some similarities among the four species, such as size, lifespan, and

103 social behaviour, there are differences in their original habitats that may cause variation in detour

104 performance. Two species, guppies and zebrafish, occupy a variety of habitats from lowland slow

105 moving streams to fast running mountain brooks, which are often rich of vegetation, rapids, rocks

106 and other obstacles (Magurran, 2005; Roy & Bhat, 2018). The red-tailed splitfin fish live in similar

107 environments, and in some cases in lakes, although usually these habitats have less vegetation

108 (Piller, Kenway-Lynch, Camak, & Domínguez-Domínguez, 2015). Conversely, Sarasins minnows

109 are endemic of Poso lake, a large and deep basin in central Sulawesi and mainly show pelagic life

110 style (Kottelat, 1990; Parenti, 2008). The pelagic species has evolved in a habitat with few

111 obstacles, which may cause relaxed selection on detour abilities compared to the remaining species.

112 In the second and third experiments of this study, we investigated possible non-cognitive causes for

113 the differences observed in Experiment 1. In particular in Experiment 2, we studied whether the

114 four species differed in their sociality and therefore whether social reward could constitute a

115 different lure, making the detour task more or less difficult to solve. If a different motivation is the

116 cause of interspecific differences, highly gregarious species were expected to show the poorest

117 performance. In Experiment 3, we tried to understand whether the high detour performance of

118 zebrafish could be due to the use of a different sensory system. As observed in mammals, there is a

119 large variation among fishes in the development of the different sensory systems (Hara, 1975;

120 Kasumyan, 2004). This factor can give rise to interspecific differences in the relative importance of

121 vision and other senses (e.g., olfaction and lateral line sense) in solving the detour task. To address

5

122   this issue, we compared zebrafish and a control species, the guppy, in a detour task modified to

123   assess the role of lateral line information and olfactory cues in solving the task.

METHODS

Experiment 1: Interspecific differences in detour task performance

Subjects

Four species of teleost fish (*Danio rerio*, *Oryzias sarasinorum*, *Poecilia reticulata*, *Xenotoca eiseni*) were tested in this study. Two previous studies have reported sex differences in detour performance in guppies (Lucon-Xiccato & Bisazza, 2017a; Lucon-Xiccato, Gatto & Bisazza, 2019). Therefore, we used only adult females to avoid the confound of sex differences. We tested 16 guppies, 16 zebrafish, 16 red-tailed splitfin fish and 16 Sarasins minnows. Guppies are the descendant of wild caught ancestors collected in the lower Tacarigua River (Trinidad) in 2002. They are maintained in a large (> 10000 individuals) self-sustaining population in an artificial pond. Twice a year guppies from the pond are collected and used as breeders for the laboratory population. Zebrafish originate from some stocks bought in pet shops in the nineties and maintained since then in the Zebrafish facility of University of Padova as a large stock (> 500 fish) and regularly outbred to avoid inbreeding. Zebrafish used in our experiments originated from many different spawnings. They were raised in petri dish for the larval period and then moved to large tanks and raised in the same conditions of the other fish. Red-tailed splitfin fish were bought from a local pet shop in 1996 and thereafter maintained in our laboratory in a large population (>300 fish). Sarasins minnows were caught at Lake Poso (Sulawesi, Indonesia) in 1996 and thereafter maintained in our laboratory in a large population (>300 fish). In our laboratory, each species was maintained in large social groups in opaque plastic tanks (400 L or 70 L) with abundant plants and gravel bottoms. A 30-w fluorescent lamp illuminated each tank according to a 12 h:12 h light/dark photoperiod. The water was constantly filtered and maintained at 26 ± 1 °C. Fish were fed twice a day, alternating between commercial food flakes (Aqua tropical, Padovan®) and live *Artemia salina* nauplii. In a recent study, we showed that experience with transparent surfaces does not alter fish performance in the detour task (Santacà et al., 2019). However, at the start of the present study, those results were not

available. Therefore, for all four species, we used subjects that had no experience of transparent

surfaces to avoid potential confounding effect of this factor.

Five days before the start of the experiment, subjects were moved in an 80 L habituation tank

provided with vegetation, gravel, and filter as described for the previous maintenance tanks. All

tanks were covered with thick grey net so that fish could not see through. Inside, we constructed a

grey plastic apparatus in the shape of an hourglass (Figure 1a), which was similar to the shape of

the experimental apparatus. In this way, subjects could habituate to swimming from one side to the

other of the tank passing through a central corridor as in the detour task (see below). One 15-w

fluorescent lamp was placed above each half of the tank.

Apparatus

The experimental apparatus (Figure 1b) consisted of three juxtaposed tanks: a central subject tank

and two lateral stimuli tanks. In the middle of the subject tank ($110 \times 42 \times 35$ cm), a runway (11×9

cm) allowed the fish, at both ends of the runway, to face a C-shaped barrier behind which a social

reward was located. The barrier was 15 x 10 cm in size and made of transparent plastic material.

Each barrier was displaced 25 cm from the runway that presented two semi-transparent guillotine

doors. Two lateral white plastic panels were attached to the barrier to prevent fish from accidentally

detouring by simply sliding along the barrier. Each short wall of the subject tank was adjacent to a

stimuli tank ($60 \times 40 \times 30$ cm) in which eight adult conspecific females were housed. The stimuli

tanks were provided with natural gravel bottom, vegetation, filters and two 18-w fluorescent lamps.

Inside these tanks, we built a green trapezoidal compartment ($15 \times 10 \times 14$ cm) adjacent to the short

wall of the subject tank. The background of the compartments was white to improve the visibility of

the stimuli. A green plastic sliding panel that could be inserted between the stimuli tanks and the

subject tank was used to regulate the sight of the conspecifics during the different phases of the

experiment (see below). The stimuli tanks and the subject tank were in olfactive communication by

174 means of a system of pumps. A water pump withdrew water from the stimuli tank and directed it in

175 a transparent tube the end of which was placed inside the subject tank. In the subject tank two water

176 pumps released the water in the two stimuli tanks. A video camera was placed above each subject

177 tank barrier to record the experiment.

178

179 *Procedure*

180 Thirty minutes before the start of the experiment six stimuli were confined in the front compartment

181 of both stimuli tanks. The stimuli were chosen from tanks different from that of the subjects to

182 avoid effects of familiarity (Griffiths & Magurran, 1999). We were not aware of the kin relationship

183 between subjects and stimulus fish. In adult guppies kinship seems to not affect schooling decisions

184 (Griffiths & Magurran, 1999). In zebrafish, kin recognition seems to occur as a consequence of

185 familiarity during early development and was therefore controlled using fish from different tanks

186 (Gerlach, Hodgins-Davis, Avolio, & Schunter, 2008). For the remaining two species, there is not

187 literature on the effects of kinship. However, since fish of the same brood were kept together in the

188 same tank, and subject and stimuli came from different tanks, kinship was not expected to cause

189 substantial effects in our test. During the experiment, subjects were observed in a series of 12

190 consecutive detour trials in which they had to reach one group of conspecifics. Each experiment

191 began with the transfer of a subject from the habituation tank to the runway of the subject tank. The

192 sliding panel prevented the subject from seeing one social reward and the corresponding guillotine

193 door was closed. The social reward visible in the first trial was randomized among subjects; this did

194 not affect fish performance (rm ANOVA, $F_{1,63} = 0.199$, $P = 0.657$. The subject was let free to reach

195 the visible group of conspecifics. Exiting from the runway, the subject had to detour the transparent

196 barrier to reach the conspecifics. Some studies used a pre-training with an opaque barrier that

197 improves subjects' detour performance (Vlamings, Hare, & Call, 2010) and might allow to

198 distinguish between the spatial abilities necessary to perform the detour behaviour and the

199 inhibitory abilities necessary to handle the transparent barrier. We did not perform such pre-training

200 because fish reached a similar performance with both procedures (Lucon-Xiccato et al., 2017) and

201 because the aim of our study was not to exclusively investigate inhibitory control. Three minutes

202 after the subject completed the task (i.e., it reached the conspecifics), the sliding panel between the

203 subject tank and the other stimulus tank was removed and the corresponding guillotine door was

204 opened. For the next two minutes, the subject was free to decide to move to the other side of the

205 tank in which the other conspecifics were visible. After that time, the sliding panel was placed

206 between the subject tank and the stimulus tank nearer to the subject; the subject was therefore

207 motivated to move to the other test sector. Once the subject passed through the corridor, the more

208 distant guillotine door was closed. The procedure was then repeated until the subject performed 12

209 trials. To eliminate potential directional chemical cues from the previously tested subject, the new

210 subject was tested after half an hour period during which pumps continued to exchange water

211 between the subject tank and the stimuli tanks. In addition half of the water of the apparatus was

212 changed after each trial adding new aged water. Two guppies ceased to participate after 10 trials;

213 their performance was analysed only up to that trial.

214 An experimenter observed all trials from a distant monitor connected to the video camera to control

215 the doors and the panels of the apparatus. Based on the video recordings, we scored the accuracy of

216 the subjects: we recorded whether the subject attempted to reach the social stimuli by touching the

217 barrier (incorrect trial) or detouring around it directly (correct trial). This measure of accuracy is

218 often used with the detour paradigm but in some cases might poorly describe subjects' performance

219 because it is a binomial variable with only two possible outcomes. For example, subjects that

220 persistently try to reach the goal and touch multiple times the barrier would have a score (incorrect

221 trial) that is equal to that of subjects that touch the barrier only once and then immediately correct

222 their behaviour. Therefore, we analysed a second measure of performance that was not binomial.

223 Because fish in the barrier tend to swim with the snout touching the transparency, it was not

224 possible to measure the number of attempts to reach the goal as in some recent studies (van Horik et

225 al., 2018). Following other studies on the detour behaviour (Kabadayi et al., 2017), we measured

226 the time that subjects spent trying to pass through the barrier. In all the species, we started to record

227 this time variable when the subject entered the area delimited by the wings of the barrier with its

228 snout. One third of the videos of each species were analysed by two different experimenters to

229 assess inter-rater reliability.

230

231 *Statistical Analysis*

232 Analyses were performed in R version 3.5.3 (The R Foundation for Statistical Computing, Vienna,

233 Austria, http://www.r-project.org). Initially, we assessed inter-rater reliability between the scores of

234 the two experimenters: for the accuracy, we calculated the mean agreement dividing the concordant

235 trials by the total number of trials; for the barrier time, we tested for a correlation between the two

236 scorers using Spearman's rank method. As inter-rater reliability was excellent, we conducted the

237 following analyses using the database of the first experimenter. We analysed the subjects' accuracy

238 in each trial (correct or incorrect) with generalized linear mixed-effects models for binomial

239 response distributions (GLMMs, 'glmer' function of the 'lme4' R package). To assess whether

240 accuracy increased trial after trial and whether the species differed, we fitted the models with the

241 trial number and the species as fixed effects. In addition, individual ID was fitted as random effect.

242 We also analysed the time (after log transformation due to right-skewed distribution) spent trying to

243 pass though the barrier using linear mixed-effects models (LMMs, 'lmer' function of the 'lme4' R

244 package) fitted with the trial and the species as fixed effects and individual ID as random effect.

245 Subsequently, all pairwise comparisons were performed with Tukey post-hoc tests. Intraspecific

246 differences in performance were investigated by estimating repeatability from GLMM fitted by

247 restricted maximum likelihood (Nakagawa & Schielzeth, 2010).

248

Experiment 2: Does sociality explain detour task performance?

Subjects, apparatus and procedure

We tested the same four species of teleost fish (*Poecilia reticulata*, *Danio rerio*, *Xenotoca eiseni*, *Oryzias sarasinorum*) as in the first experiment. All subjects were adult females and we tested 36 guppies, 36 zebrafish, 36 red-tailed splitfin fish and 36 Sarasins minnows overall. All subjects were experimentally naïve and none of them was used in the other two experiments. Fish were tested in groups of 3. The experiment was run in a square tank ($70 \times 70 \times 37$ cm) filled with 15 cm of water. Its base was covered by a green plastic panel in which twenty-five identical squares were drawn (14×14 cm). The lateral sides of the tank were covered by white plastic panels. The tank was illuminated by four 18-w fluorescent lamps at a distance of 25 cm from the water's surface and it was placed in a dark room. Three fish were inserted into a transparent cylinder (height: 15 cm; diameter: 12 cm) placed in the central square of the tank. After five minutes, we lifted the cylinder and began recording with a digital video camera fixed on the ceiling. Fish were recorded for thirty minutes, after which they were removed from the experimental tank, moved to apposite tanks and kept only for reproduction. Based on the video recordings, we scored two measures of sociality: the inter-individual distance and the number of squares occupied by each school. Videos were digitized using a computer at 12 frames per minute (for a total of 360 images for each group). To calculate the inter-individual distance, we used a computer program (written in Delphi5 Borland) that calculated for each school the average distance (snout to snout) between each pair of fish. To calculate the inter-rater reliability of the two measures of sociality, one third of the videos were reanalysed by another experimenter.

Statistical Analysis

A Spearman's rank correlation was used to assess inter-rater reliability between the two experimenters who scored the videos. A Pearson correlation test was used to assess the correlation

274 between the two measures of sociality, the inter-individual distance and the number of squares

275 occupied by the school. Then, we analysed the mean inter-individual distance (after log

276 transformation) and the mean number of squares occupied with multivariate analysis of variance

277 (MANOVA) fitted with the species as fixed effect. Subsequently, all pairwise comparisons were

278 performed with Tukey post-hoc tests.

279

280 **Experiment 3: Sensory information used in detour task**

281 *Subjects, apparatus and procedure*

282 In Experiment 3, we investigated the role of sensory information in the higher performance of

283 zebrafish observed in Experiment 1. We tested the zebrafish, which performance deviated from that

284 of the other three species. Because guppies, red-tailed splitfin fish and sarasins minnows showed a

285 similar performance in Experiment 1, in application of the Reduction principle (Russell, Burch, &

286 Hume, 1959; Sneddon, Halsey, & Bury, 2017) we decided to test only one of these species as a

287 reference to be compared with the zebrafish. Testing two more species was not expected to provide

288 further information on why zebrafish showed higher detour performance. We used the guppy as

289 reference species because this species is the most studied with this type of task (Gatto et al., 2018;

290 Lucon-Xiccato et al., 2017; Lucon-Xiccato & Bertolucci, 2019; Santacà et al., 2019). We tested

291 other 36 guppies and 36 zebrafish in the same apparatus and with the same procedure as in

292 Experiment 1. All 72 fish were experimentally naïve females. In particular, we tested 12 subjects

293 per species in an exact replication of Experiment 1 (Control condition). In a second condition

294 (Odour condition), 12 other subjects per species had to detour the same barrier of the Experiment 1

295 but the odour from the stimuli tank was released before the barrier by moving the end of the

296 transparent tube of the water pumps' system in front of the barrier itself. In a third condition (Net

297 barrier condition), 12 guppies and 12 zebrafish were tested using the same procedure of Experiment

298   1 but the transparent surface of the barrier was substituted with transparent net (mesh size: 0.35 cm;

299   wire thickness: 0.01 cm). As in Experiment 1, we scored accuracy and barrier time.

300

301   *Statistical Analysis*

302   Analyses were similar to those conducted for Experiment 1. To analyse the subjects' accuracy, we

303   fitted a GLMM with the condition (Control condition, Odour condition, Net barrier condition) and

304   the species as fixed effects and individual ID as random effect. We also analysed the time in front

305   of the barrier (after log transformation) using a LMMs fitted with the condition and the species as

306   fixed effects and individual ID as random effect. We did not include the trial as a fixed effect in

307   these analyses since, as emerged in the results of Experiment 1, it has no or little effect. In case of

308   significant interaction between fixed effects, we performed similar analyses of the three

309   experimental conditions separately.

RESULTS

Experiment 1: Interspecific differences in detour task performance

The analysis of fish detour behaviour was highly reliable between the two experimenter: the mean

agreement on accuracy excellent (99%) and the barrier was highly correlated (Spearman's rank

correlation: $\rho = 0.975$, $P < 0.001$).

The overall time required to complete the 12 trials was 111.35 ± 37.45 min (mean $\pm$ SD) for the 16

guppies, 96.75 ± 29.13 min for the 16 red-tailed splitfin fish, 89.16 ± 19.92 min for the 16 Sarasins

minnows and 62.96 ± 14.70 min for the 16 zebrafish. The four species showed a significant

difference in accuracy ($\chi^2_3 = 23.250$, $P < 0.05$; Figure 2a). A Tukey post-hoc test revealed that

zebrafish accuracy ($77.08 \pm 19.36\%$ correct trials, mean $\pm$ SD) was significantly higher than the

accuracy of the other three species (guppies: $49.90 \pm 18.18\%$; red-tailed splitfin fish: $50.52 \pm$

16.24%; Sarasins minnows: $59.90 \pm 15.28\%$; P values < 0.02); the accuracy of guppies, red-tailed

splitfin fish and Sarasins minnows did not significantly differ (all P values > 0.3). The accuracy of

the subjects did not significantly vary with the trial ($\chi^2_{11} = 17.483$, $P = 0.094$) and the interaction

trial x species was not significant ($\chi^2_{33} = 26.289$, $P = 0.790$).

The four species significantly differed in the time spent in front of the barrier (LMM: $F_{3,59} =$

28.339, $P < 0.001$; Figure 2b). A Tukey post-hoc test revealed the same pattern described for the

accuracy: zebrafish reached the conspecifics more rapidly than the other three species (guppies:

128.16 ± 56.43 s; red-tailed splitfin fish: 76.07 ± 29.35 s; Sarasins minnows: 74.16 ± 59.94 s;

zebrafish: 3.49 ± 2.64 s; all P values < 0.0001) while guppies, red-tailed splitfin fish and Sarasins

minnows did not differ (all P values > 0.2). The time spent in front of the barrier significantly

decreased over trials (LMM: $F_{11,655} = 3.606$, $P < 0.001$) and the trial x species interaction was not

significant (LMM: $F_{33,655} = 1.069$, $P = 0.366$).

Data of individual subjects are showed in Figure 2c. Intraspecific analysis revealed low but

significant repeatability in subjects' accuracy across trials in zebrafish ($R = 0.11$, $CI = [0, 0.26]$, $P =$

0.002). Graphical inspection of individual accuracy indicated that this effect could be due to two zebrafish that showed substantially low performance (Figure 2c). Removing these two subjects from the analysis resulted in non-significant repeatability of zebrafish' accuracy ($R < 0.01$, $CI = [0, 0.07]$, $P = 1$). None of the remaining species showed significant repeatability of individual performance (guppies: $R = 0.04$, $CI = [0, 0.13]$, $P = 0.122$; red-tailed splitfin fish: $R = 0.02$, $CI = [0, 0.09]$, $P = 0.306$; Sarasins minnows: $R = 0.01$, $CI = [0, 0.07]$, $P = 0.385$; Figure 2c).

Experiment 2: Does sociality explain detour task performance?

The inter-rater reliability was high for both measures of sociality were high (inter-individual distance, Spearman's rank correlation: $\rho = 0.971$, $P < 0.001$; mean number of squares occupied: $\rho = 0.995$, $P < 0.001$).

The two measures of sociality, inter-individual distance and number of squares occupied by the school, were positively correlated (Pearson correlation $r(58) = 0.785$, $P < 0.001$). The MANOVA revealed a significant effect of the species ($F_{6,112} = 20.427$, $P < 0.001$). A Tukey post-hoc test revealed a significant difference between Sarasins minnows and guppies ($P < 0.01$; Figure 3a) regarding the inter-individual distance; all other comparisons were nonsignificant (all P values > 0.5; Figure 3a). Regarding the number of squares occupied, a Tukey post-hoc test revealed that Sarasins minnows significantly differed compared to the other three species (all P values < 0.05; Figure 3b). Guppies, zebrafish and red-tailed splitfin fish did not differ (all P values > 0.4; Figure 3b).

Experiment 3: Sensory information used in detour task

The trial-by-trial inter-rater reliability on the accuracy was excellent (99%). Even regarding the barrier time, we found a high inter-observer reliability (Spearman's rank correlation: $\rho = 0.989$, $P < 0.001$).

360 The GLMM conducted on the accuracy revealed no significant effect of the condition ($\chi^2_2 = 4.633$,

361 $P = 0.099$) but revealed a significant effect of the species ($\chi^2_1 = 5.712$, $P < 0.05$). The interaction

362 condition x species was significant ($\chi^2_2 = 19.814$, $P < 0.001$), indicating that guppies and zebrafish

363 performed differently depending upon the condition. Considering only the Control condition, the

364 GLMM revealed a significant difference between the accuracy of the 12 guppies and the 12

365 zebrafish ($\chi^2_1 = 23.417$, $P < 0.001$; Figure 4a) confirming the results of Experiment 1. Considering

366 the Odour condition, the accuracy of the two species did not significantly differ ($\chi^2_1 = 1.229$, $P =$

367 0.268; Figure 4a). Also comparing the 12 guppies and the 12 zebrafish considering the Net barrier

368 condition, we found no significant difference between their accuracy ($\chi^2_1 = 0.690$, $P = 0.406$; Figure

369 4a).

370 Regarding the barrier time, we found a similar scenario: the LMM revealed no significant effect of

371 the condition ($F_{2,66} = 2.917$, $P = 0.061$) but revealed a significant effect of the species ($F_{1,66} =$

372 10.100, $P < 0.001$). The interaction condition x species was significant ($F_{2,66} = 4.199$, $P < 0.05$). In

373 the Control condition, guppies and zebrafish significantly differed (LMM: $F_{1,22} = 52.577$, $P <$

374 0.001; Figure 4b). The two species did not differ in the Odour condition (LMM: $F_{1,22} = 0.594$, $P =$

375 0.449; Figure 4b). A significant difference between guppies and zebrafish emerged in the Net

376 barrier condition (LMM: $F_{1,22} = 9.872$, $P < 0.01$; Figure 4b).

DISCUSSION

In Experiment 1, three out of four tested species (guppies, red-tailed splitfin fish and Sarasins minnows) showed a performance similar to that exhibited by guppies in the previous study (approx. 50% correct response; Lucon-Xiccato et al., 2017) and comparable to the average score of birds and mammals, excluding monkeys and great apes (MacLean et al., 2014). The fourth species, zebrafish, scored much higher in accuracy and spent less time on the barrier. In particular, the percentage of correct trials of zebrafish (77%) matches that of various species of corvids and monkeys (e.g., *Papio anubis*: 76%; *Macaca mulatta*: 80%; *Aphelocoma californica*: 77%; MacLean et al., 2014). It is interesting to note that 75% of zebrafish performed correctly on the first trial while in the other three fish species this proportion ranges between 25% and 50%.

In contrast to the difference between species, the individual subjects performed quite similarly within-species. This result seems to contrapose to the growing evidence of individual differences in cognition in fish (Lucon-Xiccato & Bisazza, 2017b) and to the fact that other species exhibit individual differences in detour tasks (Baragli, Vitale, Sighieri, Lanata, Palagi, & Reddon, 2017; Shaw, 2017). On the other hand, the low intraspecific variability in performance further increases our confidence in the results of the comparison between species. For example, 8 out 11 subjects that performed > 75% correct responses were zebrafish. Therefore, the higher performance of zebrafish was unlikely explained by individual differences and random fluctuations in the performance of few individuals.

There could be various explanations for the higher performance of zebrafish in Experiment 1. One is that the four species, because of their different ecology, differ in term of one or more of the cognitive skills that are involved to detour task solution. In particular, the differential presence of obstacles, which could block a direct path to a goal, in the natural habitat of a species is expected to cause diverse intensity of selection on its detour ability. However, this scenario does not appear compatible with our results. The presence of obstacles in the natural habitat of Sarasins minnows

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was likely very scarce in its evolutionary past, because this species is pelagic and endemic of a single large tropical lake (Kottelat, 1990; Parenti, 2008). Conversely, the other three species live in tropical rivers, often containing vegetation (although this factor may be scarce in some habitats of the red-tailed splitfin fish), rocks, rapids and other obstacles (Magurran, 2005; Piller et al., 2015; Roy & Bhat, 2018); these three latter species were expected to undergo convergent evolution for high detour capacities. Other things being equal, we expect Sarasins minnows to exhibit the lower detour performance, which did not occur in our experiment. One could hypothesise that other aspects of species ecology, such as the schooling behaviour, affect detour performance. However, to the best of our knowledge, the current literature does not provide indications with this respect. Excluding alternative ecological explanations would require more data on the natural behaviour of the species used in this study and data on the detour performance of many more species.

Other evidence is against the hypothesis that the observed differences in detour test performance were due to interspecific variation in cognitive skills. One could suggest, for example, that the four species differ in learning the properties of the transparent barrier (i.e., its impenetrability). Learning however, does not appear substantially involved in our task because we did not observe a significant improvement in accuracy over trials. Zebrafish could have more efficient spatial abilities, problem solving, or in inhibitory motor control skills than the other three species. The limited data in this regard seem to suggest that cognitive abilities of zebrafish are at best similar to those of the other three species examined. In a recent study, zebrafish performance did not differ from that of other fish species (including red-tailed splitfin fish) in a route planning task (Sovrano, Baratti, & Potrich, 2018). In a numerical abilities' study, zebrafish showed lower learning performance compared to guppy and red-tailed splitfin (Agrillo, Miletto Petrazzini, Tagliapietra, & Bisazza, 2012). In addition, recent studies tested zebrafish and guppies in a task designed to measure inhibition in which a food reward is placed inside a transparent tube and the subjects had to inhibit the tendency

426 to bite it; results indicate that zebrafish and guppies have similar capacity to learn to inhibit a

427 response (Lucon-Xiccato, Bisazza, & Bertolucci, 2019; Lucon-Xiccato & Bertolucci, 2019).

428 Alternatively, the differences observed in Experiment 1 could be due to non-cognitive factors.

429 Despite our attempt to maintain similar pre-test conditions (e.g., all the subjects experienced the

430 same rearing conditions, and they had no previous experience with transparent surfaces and with

431 detour tasks), other factors could have differentially affected the performance for the four species.

432 For example, all four species are social to some degree, but the importance of living in a group

433 could differ among them. In turn, a stronger attraction to social companions could have potentially

434 made it more difficult to inhibit the response of swimming through the barrier as observed with

435 food lures in other species (Brucks, Soliani, Range, & Marshall-Pescini, 2017; Auersperg, Laumer,

436 & Bugnyar, 2013). In Experiment 2 we measured the tendency of the four species to aggregate

437 when placed in a novel environment. We found a certain heterogeneity in their gregarious

438 tendencies, but a different degree of sociality does not seem to explain the results of Experiment 1

439 as zebrafish was not found to be more gregarious than the other species.

440 The results of Experiment 1 could also be explained by sensorial differences among the species

441 studied. Ostariophysi (the clade to which zebrafish belongs) and Acanthopterygii (to which the

442 other three species belong) evolved separately for approximately 220 million years ago (Steinke,

443 Salzburger, & Meyer, 2006). Beloniformes (the order to which the Sarasins minnow belongs)

444 diverged from Cyprinodontiformes (to which guppies and red-tailed splitfin fish belong)

445 approximately 150 million years ago, while the phylogenetic distance between guppies and red-

446 tailed splitfin fish is smaller, approximately 65 million years (Meyer & Lydeard, 1993; Pohl,

447 Milvertz, Meyer, & Vences, 2015; Reznick, Furness, Meredith, & Springer, 2017). Therefore, wide

448 differences in sensory systems could have reasonably evolved. For a fish species that relies more on

449 vision to navigate and find conspecifics, the transparent barrier could be almost imperceptible. On

450 the contrary, if a species uses other sensory modalities, for example, lateral line sense or olfaction, a

451 solid obstacle is perceived in the same way regardless of whether it is transparent or opaque. To test

452 this possibility, in one of the conditions of Experiment 3 we compared zebrafish and guppies after

453 replacing the barrier of transparent plastic material with a barrier made with a thin monofilament

454 net. The obstacle was still invisible but here we minimized surface available to generate a pressure

455 gradient typically produced by an approaching object to substantially reduce its detectability by the

456 lateral line system. This experimental manipulation eliminated the performance advantage of

457 zebrafish over guppies suggesting a possible implication of the lateral line. However, the net barrier

458 was also transparent to the odours coming from social stimuli, so interspecific differences in the

459 importance of olfaction was also a candidate for explanation. In Experiment 1 in fact, the same

460 facilitation effect could have occurred if a fish located conspecifics primarily using olfaction. In our

461 experimental setup, due to the system of water pumps, there was a constant flow of water from the

462 shoal of conspecifics to the starting point in the central corridor. Because the transparent barrier was

463 opaque to odour, scent from the stimulus shoal followed the same pathway that the animal had to

464 take to solve the detour task. To unravel this point, in the second condition of Experiment 3 we

465 retained the original transparent barrier but the odour flow was released before the barrier to prevent

466 any directional odour hint from the stimuli. Even in this case the advantage of zebrafish over

467 guppies was nullified, suggesting that zebrafish were taking advantage of odour cues in the classical

468 detour condition of Experiment 1. An implication of odour cues could also explain why, in

469 zebrafish, the majority of subjects performed the detour task correctly even on the first trial, as

470 though they could perceive the invisible obstacle. The result of the odour manipulation condition

471 suggests that the olfactory factor could also be responsible for the result of the net barrier condition,

472 although the implication of the lateral line system in avoiding transparent obstacles is not ruled out

473 by our study.

474 As in other taxonomic groups such as mammals, among fish there are microsmatic and macrosmatic

475 species that prioritise cues from the visual system or the olfactory system, respectively, in relevant

contexts such as social, sexual, navigation, feeding and predatory behaviours (Hara, 1975;

Kasumyan, 2004). Traditionally, guppies are considered to be a microsmatic species that relies

mainly on vision while zebrafish, is typically macrosmatic one (Lazzari, Bettini, & Franceschini,

2014). The two distinctive groups present evident differences in the morphology of the olfactory

mucosa. For example, macrosmatic fish species have well developed multilamellar olfactory

rosettes with a behaviourally predominant olfactory ability. In contrast, microsmatic species possess

less developed, even unilamellar olfactory rosettes (Lazzari et al., 2014). It is interesting to note that

a recent work demonstrated that olfactory cues do not appear to affect guppy performance in

another type of detour task, the cylinder test in which a fish has to enter from the lateral opening of

a transparent cylinder to obtain food (Santacà et al., 2019). It remains to be assessed whether

microsmatic fish species such as zebrafish enjoy a sensorial advantage in this test as well.

Overall, our study provides evidence that large interspecific variation in performing the detour task

may be the consequence of non-cognitive confounding effects, rather than reflecting a difference in

one or more cognitive abilities important for carrying out the task. In particular, sensorial

differences were responsible for a two-fold difference in accuracy and three-fold difference in the

time spent in front of the barrier between macro- and microsmatic species. This has important

implications for the interpretation of recent attempts to reconstruct the evolution of complex

cognitive functions, such as inhibitory control, using detour-like tasks: the amount of variation due

to sensory differences found here appears in fact much wider than the average variation observed

among species (Kabadayi et al., 2016; Brucks et al., 2017; van Horik et al., 2018). There is a long-

standing debate in comparative cognition about the risk that observed differences in performance

may be due to contextual variables rather than species' differences in cognitive ability (MacPhail,

1987; Shettleworth, 2010). Our work further highlights the need to adopt an adequate approach to

address this important problem (Bitterman, 1975; Kamil, 1988).

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Figure 1.

Representation of the habituation tank (A) and representation of the experimental apparatus (B).
The experimental apparatus was composed of the subject tank (a) and two stimuli tanks (b). The
subject tank was composed of a central runaway (c), two transparent barriers (d), and two semi-
transparent guillotine doors (e). A green plastic sliding panel (f) regulated the sight of the
conspecifics; a system of pumps (g) allowed olfactory cues of the stimulus to permeate the subject
tank.

Figure 2.

Results of Experiment 1: mean accuracy (A) and mean barrier time (B) after log transformation
divided in the 12 trials, and overall accuracy of the individual subjects (C) for the four species of
teleost fish (*Poecilia reticulata*, *Danio rerio*, *Xenotoca eiseni*, *Oryzias sarasinorum*). Bars represent
the standard error.

Figure 3.

Results of Experiment 2: mean inter-individual distance (A) and mean number of squares occupied
by the school (B), for the four species of teleost fish (*Poecilia reticulata*, *Danio rerio*, *Xenotoca*
eiseni, *Oryzias sarasinorum*). Asterisks denote a significant departure from chance level ($P < 0.05$).
Bars represent the standard error.

Figure 4.

Results of Experiment 3: mean accuracy (A) and mean barrier time (B), after log transformation, for
the three conditions (Control condition, Odour condition, Net barrier condition) for guppies and
zebrafish. Asterisks denote a significant departure from chance level ($P < 0.05$). Bars represent the
standard error.