25 Intraspecific variation in inhibitory motor control in guppies, *Poecilia reticulata*

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27 Alessandro Macario[1*], Safi Darden[1], Frederick Verbruggen[2] and Darren P. Croft[1]

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30 [1] Centre for Research in Animal Behaviour, College of Life and Environmental Sciences,

31 University of Exeter, Exeter, EX4 4QG, UK

32 [2] Department of Experimental psychology, Faculty of Psychology and Educational Sciences,

33 Ghent University, Henri Dunantlaan 2, 9000 Gent, Belgium.

34

35 *Corresponding author:*

36 Dr Alessandro Macario

37 7, Clinton Avenue

38 EX4 7BA

39 Exeter, UK

40 alessandro_macario@hotmail.fr

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51 **<u>Abstract</u>**

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53   Inhibitory control (IC) is the ability to overcome impulsive or prepotent but ineffective

54   responses in favour of more appropriate behaviours. The ability to inhibit internal

55   predispositions or external temptations is key to cope with a complex and variable world.

56   Traditionally viewed as cognitively demanding and a main component of executive

57   functioning and self-control, IC was historically examined in only a few species of birds and

58   mammals but recently a growing number of studies has shown that a much wider range of

59   taxa rely on IC. Furthermore, there is growing evidence that inhibitory abilities may vary

60   within species at the population and individual levels owing to genetic and environmental

61   factors. Here we use a detour-reaching task, a standard paradigm to measure motor inhibition

62   in non-human animals to quantify patterns of inter-individual variation in IC in wild-

63   descendant female guppies, *Poecilia reticulata*. We found that female guppies displayed

64   inhibitory performances that were, on average, half as successful as the performances

65   reported previously for other strains of guppies tested in similar experimental conditions.

66   Moreover, we showed consistent individual variation in the ability to inhibit inappropriate

67   behaviours. Our results contribute to the understanding of the evolution of fish cognition and

68   suggest that IC may show considerable variation among populations within a species. Such

69   variation in IC abilities might contribute to individual differences in other cognitive functions

70   such as spatial learning, quantity discrimination, or reversal learning.

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72   Keywords: Detour task, Fish Cognition, Inhibitory control, Individual differences, Response

73   inhibition, Trinidadian guppy.

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75   Executive control refers to a set of cognitive functions required to monitor and

76   regulate behaviours when automatic, habitual, or conditioned responses are inadequate,

77   inefficient or impossible (Diamond, 2013; Gilbert and Burgess, 2008; Miyake and Friedman,

78   2012). Among those functions, inhibitory control (IC) is usually considered pivotal as it allows

79   an individual to restrain inappropriate prepotent responses and enables the realisation of

80   deliberate, goal-directed behaviours (Diamond, 2013). Without response inhibition (the

81   behavioural component of inhibitory control) strong internal predispositions or external

82   temptations and affordances may prevent or impede behaviour to be optimised to a variable

83   and complex environment. For example, animals require IC in social contexts when competing

84   for resources claimed by higher ranking individuals, when facing the choice between a small

85   immediate reward and a bigger delayed reward (a behaviour that has been historically

86   defined as "self-control" (Beran, 2015)), or to stop the urge to feed under the threat of

87   predation (Ryer and Olla, 1991). In humans, impulsivity (a lack of IC) has been linked to lower

88   academic achievement (Duckworth and Seligman, 2005), depression, and a whole range of

89   externalising disorders and behavioural problems, including substance abuse and criminal

90   tendencies (Moffitt et al., 2011). In non-human animals, IC abilities have been shown to

91   correlate with the song repertoire size of song sparrows, *Melospiza melodia*, (Boogert et al.,

92   2011, but see MacKinlay and Shaw 2019) and problem solving performances of various

93   mammalian species (dogs (*Canis lupus familiaris*) (Mueller et al., 2016), chimpanzees (*Pan*

94   *troglodytes*) (Vlamings et al., 2010) and cotton-top tamarins (*Saguinus oedipus*) (Hauser et al.,

95   2002)). Furthermore, IC has been associated with proxies for general cognitive abilities such

96   as absolute brain size (MacLean et al., 2014; Stevens, 2014) and complex social organisations

97   (Ashton et al., 2018; Amici et al., 2008).

98

99   Traditionally viewed as cognitively demanding (Anderson et al., 2000; Santos et al.,

100   1999), IC was first studied in mammals, mainly humans, non-human primates and a few bird

101   species (mostly pigeons)(Ainslie, 1974; Diamond, 1981; Köhler, 1925/1959; Logan and Cowan,

102   1984; Scholes, 1965; Tobin and Logue, 1994), but a growing interest in the ultimate causes

103   underpinning IC abilities has seen a surge in the range of species investigated within the

104   mammalian and avian classes (horses (Baragli et al., 2017), dogs (Bray et al., 2014; Brucks et

105   al., 2017a), wolves (Marshall-Pescini et al., 2015), sheep and goats (Knolle et al., 2017;

106   Langbein, 2018), rodents (MacLean et al., 2014; Mayse et al., 2014), primates (Amici et al.,

107   2008; MacLean et al., 2014) and birds (Kabadayi et al., 2016; MacLean et al., 2014; Meier et

108   al., 2017; van Horik et al., 2019)) and beyond showing that also arthropods (Mayack and Naug,

109   2015; Wendt and Czaczkes, 2017) and teleost fishes (Lucon-Xiccato and Bertolucci, 2019;

110   Lucon-Xiccato et al., 2017; Santaca et al., 2019a) rely on inhibitory processes. These studies

111   have revealed considerable variation in interspecific IC abilities, but the origin of such

112   variation remains unclear. Moreover, the extent to which variation in IC is the consequence

113   of specific ecological adaptations or phylogenetic constraints on the central nervous system

114   requires more in-depth analysis.

115

116   Besides the large difference in IC performances found across species, some evidence

117   also suggests that inhibition varies within species, that is, between individuals and between

118   populations (Fagnani et al., 2016; Kralik et al., 2002; Lucon-Xiccato et al., 2020). For example,

119   Fagnani et al. (2016) showed that pet dogs had better IC skills compared to shelter dogs,

120   probably because of the differences in social experience among them; and a study comparing

121   wolves and dogs demonstrated that the former had significantly poorer IC performances,

122   emphasising the effect of domestication on the evolution of cognitive skills (Marshall-Pescini

123   et al., 2015). It has also been shown that, in spotted hyaenas, IC varied as a function of the

124 social ranking and the size of the group in which juveniles grew up (Johnson-Ulrich and

125 Holekamp, 2019). Hence within the same species, behavioural inhibition may differ

126 depending on the genetic or environmental background in which it is expressed (or has

127 developed).

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129   In the current study we use the Trinidadian guppy (*Poecilia reticulata*) to quantify

130 patterns of intraspecific variation in IC. This species is rapidly emerging as a model system to

131 study IC. In 2017, Lucon-Xiccato et al. demonstrated that guppies displayed inhibitory

132 performances equivalent to the average score of mammals and birds despite a much smaller

133 nervous system, which contradicted the strong positive correlation between brain size and IC

134 abilities established by MacLean et al. (2014) and highlight the importance of other

135 neurobiological measures such as neuronal density to account for animal intelligence

136 (Kabadayi et al., 2016; Olkowicz et al. 2016). However, to date the majority of the work

137 exploring IC in guppies has been made using ornamental strains (see Table 1 for a summary

138 of similarities and differences between our study and previous works examining inhibition in

139 guppies). Thus, previous studies may not describe the full cognitive potential of the species

140 as artificial selection (e.g. domestication) can drive correlated responses in animal

141 morphology, physiology and behaviour (Larson and Fuller, 2014), which might affect the

142 evolution and expression of cognitive function.

143

144   Here we use the detour paradigm, which is a standard method used in animal

145 cognition research to investigate IC skills (see Kabadayi et al. (2018) for a comprehensive

146 review of the detour paradigm in Animal Cognition). In this paradigm the experimental

147 subject is required to detour around a transparent obstacle to reach a reward and in the

148 process suppress a strong prepotent tendency to approach directly (and thus hit the obstacle)

149   the visible target. There are different versions of the detour task in which the obstacle can be

150   a hollow cylinder (i.e. the "cylinder task" where the reward is placed inside) or a barrier (i.e.

151   "the barrier task") and there are some debates about the extent to which these tasks also

152   involve different cognitive and non-cognitive factors (Kabadayi et al., 2017; van Horik et al.,

153   2018). Furthermore, even though the barrier and cylinder tasks are supposedly both

154   measuring the motoric aspect of inhibition, prior studies in other species has shown that

155   inhibitory performances may not be consistent across these procedures (van Horik et al.,

156   2018). Previous work that has looked at IC in wild-descendant guppies (but from a different

157   river system than our population, hence presenting different ecological conditions potentially

158   affecting the evolution of IC) consistently used the barrier task, so the performance of wild-

159   descendant guppies using the cylinder task has not been quantified. Therefore, in the present

160   study, we quantify patterns of individual variation in IC in a wild-descendant population of

161   guppies using the cylinder task and compare the performance of this population to previously

162   published values of IC for guppies and other species using the same task.

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164

165   **Methods**

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167   <u>Study Subjects:</u>

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169   Guppies are small livebearing freshwater fish native to the coastal streams of the

170   north eastern part of South America. We used adult female descendants of individuals

171   collected in the lower part of the Aripo River on the island of Trinidad. Our laboratory

172   population had been kept in mixed-sex groups within large tanks (300 x 120 x 70cm) since

173   2008 and regularly transferred across them to avoid inbreeding. Fish were fed *ad libitum* and

174 kept at similar density across the pools minimising differences in life-history traits.

175 Experimental subjects of similar size (25mm±1.4mm) were collected from these large tanks

176 and housed in groups of six in maintenance tanks (15 x 26 x 16 cm). The controlled conditions

177 across pools reduced variation in individual growth rate which in turn allowed us to use size

178 as an indicator of age. They were provided with gravel bottoms and plastic plants to ensure

179 physical enrichment. They were kept at 24±1°C on a 12h light:dark photoperiod cycle and

180 were fed twice daily with commercial food flakes in the mornings and brine shrimp (*Artemia*

181 *salina* nauplii) in the afternoon. Females were marked to allow the experimenters to identify

182 them individually (guppy females do not have individual marking that would allow a human

183 eye to distinguish among them). To do so they were anaesthetised for a short time with a

184 tricane methane sulfonate solution (MS222) and given a within group individual identifying

185 mark using Visible Implant Fluorescent Elastomer (VIE, Northwest Marine Technology). A

186 unique dorsal green mark was sufficient to distinguish among the females kept within the

187 same maintenance tank. We chose to use only females because in guppies they show better

188 learning capabilities (Lucon-Xiccato and Bisazza, 2014; Lucon-Xiccato and Bisazza, 2017).

189

190 <u>Apparatus and Procedure</u>

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192 We used the cylinder task that is a well-established procedure to investigate IC in

193 animals (Kabadayi et al., 2018) and was used recently to research and compare inhibitory

194 performances across mammals, birds (Kabadayi et al., 2016; MacLean et al., 2014) and teleost

195 fishes (Lucon-Xiccato et al., 2017). In the cylinder task subjects are initially trained to find food

196 put inside an opaque cylinder. Once the task has been learned, the opaque cylinder is

197 swapped for a transparent one. With transparent cylinders, IC is required: the subject has to

198   suppress the tendency to go directly towards the visible food and instead detour the cylinder

199   to enter from the open sides (as learned in the training phase with opaque cylinders).

200

201   *Apparatus*

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203   The experimental arenas consisted of 2 identical tanks covered with translucent

204   sheets. Each tank was divided in to two compartments, a start zone (16 x 15.5 x 20 cm) and a

205   test zone (31 x 15.5 x 20 cm), separated by a transparent guillotine door operated by a draw

206   string (Fig.1). Each trial started with an acclimatisation period taking place in the start zone

207   followed by the cylinder test occurring in the test zone after the guillotine door was lifted by

208   the experimenter. We used two types of plastic cylinder (acrylic glass) of equal size (8 cm in

209   length and 5 cm in diameter) in the different phases of the procedure. In the habituation and

210   training phase the cylinder was opaque (wrapped with speckled self-adhesive plastic film)

211   whereas in the test phase the cylinder was transparent. Two 2 x 0.5cm wedges were glued to

212   the bottom of the tank to help stabilising the cylinder.

213   The subjects were rewarded with dried bloodworm (King British, bloodworm). For

214   each trial a tiny quantity of bloodworm was crushed and attached with Vaseline to a 1cm red

215   plastic square, which was then affixed to a metallic ring hold vertically at the back of the

216   cylinder (Fig.1). The metallic ring was held by 2 magnets positioned outside the cylinder and

217   faced the subject acclimatising in the start zone (Fig.1). Video recordings were used to ensure

218   accurate data collection.

219

220   *Habituation - Shaping phase*

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222   Guppies live in groups and establish complex and long-lasting social relationships which

223   confer numerous benefits such as improved food acquisition or increased vigilance

224   (Magurran, 2005). To diminish the adverse effects of stress associated with social isolation

225   (Culbert et al., 2019; Shams et al., 2017) and a new physical environment (Stevens et al., 2017)

226   the subjects were habituated to their novel experimental conditions during five days and

227   underwent a step-by-step procedure to reinforce the target behaviour. On day one, two

228   groups of four fish were randomly selected from the maintenance tanks and released in the

229   start zone of the two experimental tanks in which we had added an opaque cylinder with the

230   food ring positioned at one of the entrances of the cylinder. After two minutes the door was

231   opened, and the fish were given one hour to explore their environment. Throughout the next

232   four days the shaping phase continued during multiple 20-minute sessions in which the

233   number of fish in each session was reduced and the food ring was gradually moved towards

234   the middle of the cylinder. The experimental subjects proceeded to the training phase as soon

235   as, alone in the tank, they managed to enter the cylinder. After 5 days of habituation and

236   shaping, the fish that did not enter the cylinder while being solitary were removed from the

237   study and substituted with new subjects.

238

239   _Training phase_

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241   To learn to feed inside the opaque cylinder the experimental subjects performed three trials

242   per day two hours apart starting at 10am. Before each trial they were placed in the start

243   compartment for five minutes to acclimatise while the experimenter inserted in the middle

244   of the test zone the cylinder equipped with the food ring (Fig.1). After five minutes the video

245   recording started; the (transparent) guillotine door was opened, and the fish was given a

246   maximum of 30 minutes to reach the food. Once the reward was found the fish was allowed

247   five minutes to consume it before the cylinder was removed and the subject returned to its

248   maintenance tank. Any subject that did not feed within 30 min received additional training

249   trials within that day to ensure 3 trials in which they reached the food. We trained two fish

250   simultaneously in adjacent tanks; the camera was positioned in order to capture both testing

251   arenas. The adopted learning criterion to continue to the test phase was to reach the food

252   (without touching the cylinder) within 90 seconds during two out of the three daily trials for

253   which the females reached the food. In total twenty-seven females were transferred to the

254   test phase reaching the learning criterion within a maximum of eight days.

255

256   *Test phase*

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258   The procedure in the test phase differed slightly from the training phase as the opaque

259   cylinder was replaced with the transparent one and the 10 trials that the subjects received

260   over a four-day period lasted 10 minutes each. Based on the video recordings, we quantified

261   for each trial the performance of the females: whether the response was correct or incorrect

262   and the time it took to obtain the reward. A trial was considered correct if the subject

263   retrieved the food entering the cylinder from the open lateral sides and incorrect if it tried to

264   cross through the transparent material. To score the time to solve the task, we measured the

265   latency between the moment the fish left the start zone and the moment it started eating. If

266   in any given trial a female did not enter the cylinder, a score of 600 (60 sec x 10 minutes) was

267   given for the time needed to reach the reward and the trial was not repeated.

268

269   Statistical analysis

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271   Analyses were carried out in R version 3.6.2 (The R Foundation for Statistical Computing,

272   Vienna, Austria, http://www.r-project.org). We analysed the performance of guppy females

273   in the cylinder task (correct versus incorrect trial) using a generalized linear mixed model

274   (GLMMs, "glmer" function of the "lme4" R package (v1.1.23)) with a binomial error structure

275   and logit-link function with trial number included as a covariate and individuals' ID as a

276   random effect.

277   A Cochran's Q test was used to test for differences in the ability to reach the reward

278   independently of the outcome (i.e. collapsed across correct and incorrect attempts) across

279   trials and among individual females.

280   We analysed time performance (the latency to reach the reward independently of the

281   outcome of the trial) fitting a linear mixed-effects model ('lmer' function of the 'lme4' R

282   package (v1.1.23)) with trial number as a covariate and individual ID as random effect. Due to

283   a right-skewed distribution, the response variable was log-transformed and the females that

284   did not get the food during the 10 minutes of a trial were removed from the analysis.

285   Individual differences were analysed using the "rptGaussian" and the "rptBinary" functions

286   of the "rptR" R package (v0.9.22), which estimates repeatability from GLMM fitted by

287   restricted maximum likelihood. The "rptGaussian" and the "rptBinary" functions estimate

288   whether the latency to reach the reward and the percentage of correct attempts were

289   significantly repeatable across trials respectively. The repeatability analysis was run for all the

290   trials.

291   Processed data for the test phase and the R script used to analyse them can be found at

292   https://osf.io/vy3s2/?view_only=ca4dcf67faef431897337c140fc8b8f3

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294   <u>Ethical Note</u>

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296   The study adheres to the ASAB/ABS guidelines for the Use of Animals in Research. The fish

297   were tagged under the Home Office license PPL 30/3308 (UK). Following the marking

298   procedure, they were allowed a 30-minute recovery period from the anaesthetic during

299   which they were monitored for any ill effects and placed back in their experimental home

300   tanks. None of the fish showed signs of injuries or pain potentially induced by the tagging

301   procedure.

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305   **Results**

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307   In the training phase female guppies needed on average 14.4 ± 4.83 trials (mean$\pm$SD)

308   to reach the learning criterion. On average during the test phase, individuals detoured around

309   the transparent cylinder to reach the reward in $28.5\% \pm 18.8$ (mean$\pm$SD) of the trials. Across

310   females, correct trials ranged between 10-60% but 11.1% of them (3 out 27) failed to inhibit

311   the urge to swim directly on all trials (Fig.2B).

312   The likelihood of successful trials did not change significantly across the test phase

313   (GLMM: $\chi^2{}_1 = 0.1$, p=0.75; Fig. 2A, 2C) but the time to reach the food marginally decreased

314   over time (LMM: $\chi^2{}_1 = 3.52$, p=0.06, Fig, 2E). The overall probability to obtain the reward

315   (whether or not subjects successfully suppressed the initial urge to swim directly toward the

316   visible target) did not change across trials (Q(9)=9.9, p=0.36, Fig. 2A, 2C); by contrast, we did

317   observe differences between females in their tendency to reach the food during the task

318   (again collapsed across correct and incorrect trials; Q(26)=85.6, p<0.0001, Fig.2B, 2D).

319   Female guppies showed significant individual differences in the percentage of correct

320   attempts (R=0.075, CI=[0, 0.17], p=0.008) and latency to get the reward (R=0.206, CI=[0.07,

321   0.35], p<0.001) across the entire experiment.

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325   **Discussion**

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327   In this experiment we investigated IC abilities of wild-descendant female guppies

328   evaluated in the cylinder version of the detour task. We showed that they successfully

329   inhibited the urge to approach the food directly on 28.5% of the trials in total. We did not

330   notice any improvement in females' inhibitory performance during the test phase, but the

331   relatively small number of trials did not allow us to rule out an effect of training if the

332   individuals had been tested for longer. On the contrary, they became faster in detouring the

333   transparent cylinder to obtain the reward (independently of the outcome in the task), which

334   suggests that a potential learning process could have taken place. Interestingly there is also

335   consistent individual variation in females' performance to detour the transparent cylinder,

336   reflecting differences in individuals' ability to efficiently inhibit prepotent behaviours.

337

338   The investigation of inhibitory control in teleost fishes is relatively recent and unlike

339   previous studies (Gatto et al., 2018; Lucon-Xiccato et al., 2017; Santaca et al., 2019b; see table

340   1 for an overview) reporting performances in guppies similar to the average performance of

341   mammalian and avian species (~58% of correct responses in the cylinder task), we observed

342   here much lower performances. However, such relatively low level of behavioural inhibition

343   is comparable to the findings of other studies that involved either guppies (Gatto et al., 2018)

344 or cichlids (Brandao et al. 2019). IC abilities vary widely across species and succeeding 28.5%

345 of the time is a performance equivalent to the one displayed by parrots or sparrows and far

346 from the almost perfect score displayed by apes and ravens (Kabadayi et al., 2017; Kabadayi

347 et al., 2016; MacLean et al., 2014), positioning guppies at the lower end of the spectrum of

348 the species investigated (MacLean et al., 2014).

349

350   Our study recorded significant individual repeatability in the outcome of the cylinder

351 task and in time performance. Females differed in their ability to suppress the urge to reach

352 directly the reward without detouring the obstacle as successful trials ranged between 0 and

353 60%. Likewise, they varied in the time they needed to get the food with some females being

354 consistently quicker than others. This consistent individual variation in both behaviours was

355 found across the 10 trials of the experiment. Our results are consistent with previous studies

356 showing consistent individual differences in inhibition in zebrafish (Lucon-Xiccato et al. 2019)

357 and guppies (Lucon-Xiccato et al. 2020). As inhibition might support other higher-level

358 cognitive abilities (Diamond 2013), IC variability could contribute to individual differences

359 found among vertebrates (Lucon-Xiccato et al. 2019) in processes such as spatial abilities,

360 reversal learning or social learning. From an evolutionary perspective variability in IC could

361 result from selection pressures acting on other traits. There is a growing number of studies

362 showing a relationship between personality traits and cognitive individual differences (Brown

363 et al. 2013, White et al. 2107, Lucon-Xiccato et al. 2019). Personality traits are maintained

364 through frequency-dependent selection and spatio-temporal fluctuation in natural selection

365 (Dingemanse et al. 2004; Dingemanse and Re´ale 2005) that in turn may generate variation in

366 inhibitory performances. Alternatively, IC can be under direct selection (and contribute to

367 personality traits) if it enhances survival for example when facing high predation risk or when

368 living in, for example, a social group with strong hierarchical structure. Here inhibiting

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369   foraging or sexual behaviours could diminish the risk of being attacked by predators (Ryer and

370   Olla, 1991) or more dominant group members. In Australian magpies, *Cracticus tibicen*

371   *dorsalis*, higher inhibitory performances were linked to increased group size and higher

372   females' reproductive success suggesting that the demands of social life drove cognitive

373   evolution (Ashton et al., 2018). An important next step is to look at whether individual

374   performances are consistent when tested in the wild versus in captivity.

375

376   Our findings suggest significant differences exist among populations of guppies in IC

377   which may reflect slight methodological differences across studies or adaptive variation

378   among populations. To the best of our knowledge seven studies have investigated IC in

379   guppies prior, but none of them implemented the exact same setting we used for ours (table

380   1). Previous work on guppies using the cylinder task has used domesticated strains (Lucon-

381   Xiccato et al., 2017; Santaca et al., 2019b). In contrast, previous studies on wild-descendant

382   guppies have used a different variant of the detour task – the barrier task (Gatto et al., 2018;

383   Santaca et al., 2019a). Here we further extend our understanding of IC in guppies by testing

384   wild-descendant guppies with the cylinder task. Differences in task variants and strains could

385   contribute to the differences between studies. First, a growing number of studies show a lack

386   of consistency in individual performances across IC tasks either because those tasks measured

387   different aspects of inhibition within individuals (i.e. motor inhibition, self-control, cognitive

388   inhibition) underpinned by different neural mechanisms or because of variation in non-

389   cognitive factors such as motivation to acquire food that could affect the performance

390   (Botvinick and Braver, 2015; Brucks et al., 2017a; Fagnani et al., 2016; van Horik et al., 2018).

391   Even in tasks believed to capture the same aspect of inhibition such as the barrier task and

392   the cylinder task, both detour-reach tasks supposedly evaluating motor inhibition abilities,

393   dogs (Brucks et al., 2017a) and pheasants (van Horik et al., 2018) have shown inconsistent

394   performances. Such findings highlight the context-specificity of IC in vertebrates and could

395   account for the variable performances displayed by guppies. Second, independently of the

396   detour task chosen the variation in performances found between different guppy populations

397   might ensue differences in several non-cognitive factors known to affect the measure of IC in

398   fish (Gatto et al., 2018) and, more generally, in animals, such as the distance between the

399   subject and the goal (Junghans et al., 2016) or the value of the reward (Brucks et al., 2017b;

400   Wascher et al., 2012). Several studies have indicated that with increasing goal distance it is

401   easier for animals to detour around an obstacle (chicken (Regolin et al., 1995), dogs (Köhler,

402   1925/1959), long-tailed macaques (Junghans et al., 2016), guppy (Gatto et al., 2018), human

403   infants (Diamond and Gilbert, 1989)). Gatto et al. (2018) specifically addressed this issue with

404   guppies by varying the position of the reward (i.e. a group of conspecifics) with a transparent

405   barrier and showed, as anticipated, that they were less able to suppress the urge to reach

406   directly the social group when it was positioned nearer to (5cm) versus farther from (15cm)

407   the barrier. Incidentally the fish that faced a close reward solved the task 28.3±28.8% of the

408   time compared to fish more distant for which the likelihood of success was 50±25%. These

409   numbers match respectively the outcome of our experiment in which the cylinder was

410   positioned at 5 cm from the guillotine door (the food subsequently at 8 cm) and the

411   performance of the subjects used by Lucon-Xiccato et al. (2017) who positioned the reward

412   at 15 cm from the obstacle. Other non-cognitive factors such as the motivational and

413   physiological state of the animal can affect the detour response (Kabadayi et al., 2018; van

414   Horik et al., 2018) and be responsible for variation in IC abilities. A hungry individual might be

415   less prone to block a prepotent tendency to reach food directly than a satiated individual.

416   Hence, there is variation between but also within cognitive tasks, and these might all

417   contribute to differences between studies. Such sources of variation are particularly

418   important to account for when comparing different species or different populations. Third,

419   differences between studies could also be caused by the use of wild-descendant vs.

420   domesticated guppies. In fishes evidence of the effects of domestication on cognitive abilities

421   remain scarce (Pasquet, 2019) but the main incentive for fish domestication is aquaculture

422   (e.g. fish farming, ornamental fishes) for which traits relying upon inhibition are not the

423   primary target of artificial selection. However, selection on a specific trait (e.g. a

424   morphological trait such as fancy colour pattern or tail shape) could be sufficient to drive

425   correlated physiological and behavioural changes characteristic of a phenomenon known as

426   domestication syndrome (Belyaev, 1979; Darwin, 1868; Wheat et al., 2019). While the

427   mechanistic basis of this phenomenon remains a source of controversy (Sanchez-Villagra et

428   al., 2016), it could explain the difference observed between domesticated strains of guppy

429   used in previous studies and their wild counterparts used here. Alternatively, the better

430   performances displayed by domesticated guppies could result from selection for less

431   aggressive individuals if, in fishes, aggressive behaviours are negatively related to IC abilities

432   as it was shown in humans (Hsieh and Chen, 2017; Pawliczek et al., 2013; Vigil-Colet et al.,

433   2004).

434

435   Trinidadian guppies vary drastically in morphology, life-history and behavioural traits

436   due to variation in selection pressures such as predation levels (Devigili et al., 2019; Endler,

437   1980; Handelsman et al., 2013; Hasenjager and Dugatkin, 2017; Herbert-Read et al., 2017;

438   Reznick, 1982), water turbidity (Borner et al., 2015) or ambient light (Endler, 1991, 1993;

439   Gamble et al., 2003). Recently predation has also been linked to brain evolution in guppies

440   (Kotrschal et al., 2017; Mitchell et al., 2020; Reddon et al., 2018) and killifish (*Rivulus hartii*)

441   (Walsh et al., 2016) albeit showing contrasting effects for brain size or for brain anatomy.

442   Reddon and colleagues (2018) found that exposure to predatory cues increased relative brain

443   mass in guppies whereas killifish from sites with predators exhibited smaller brains than their

444 counterparts living in predator-free habitats (Walsh et al., 2016). It is generally suggested that

445 increased brain size is associated with better executive functions and increased learning

446 abilities (Amiel et al., 2011; Benson-Amram et al., 2016; MacLean et al., 2014; Overington et

447 al., 2009; Sol et al., 2008; Sol et al., 2007), which has also been found in guppies selected for

448 relative brain size (Buechel et al., 2018; Corral-Lopez et al., 2017; Corral-Lopez et al., 2018;

449 Kotrschal et al., 2015; Kotrschal et al., 2013a; van der Bijl et al., 2015). However large brains

450 are energetically costly to develop and maintain and the cognitive benefits they provide might

451 be overridden by the metabolic costs (and more generally fitness costs) (Kotrschal et al.,

452 2013a; Laughlin et al., 1998) they entail. Assuming that the size of the brain is linked to

453 cognitive abilities (Kotrschal et al., 2013b), the lower motor inhibition performance observed

454 here could result from brain size variation between native populations or evolutionary

455 changes that took place in the lab driven, for example, by an absence of predation pressure.

456

457   In conclusion, our findings demonstrated individual variability in IC and highlight

458 potential within-species population differences. Consistent individual variation in inhibition

459 may explain the individual differences in other cognitive processes previously reported

460 among teleost fishes. Moreover, our guppy population displayed on average lower inhibitory

461 performances than domesticated guppies or guppies native to a different river. Future work

462 using a comparative approach assessing inhibitory motor control in guppies found across and

463 along the Trinidadian river system might shed light on the causes underpinning variation (at

464 the group and individual level) in cognition in guppies and, more generally, in vertebrates

465 facing similar environmental pressures.

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470
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476

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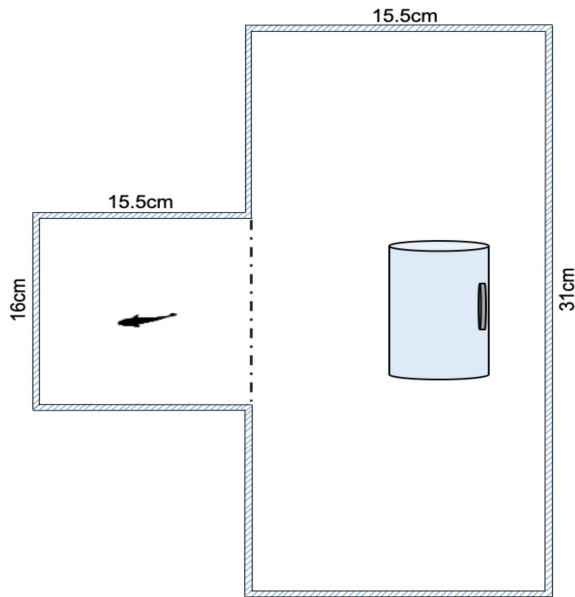
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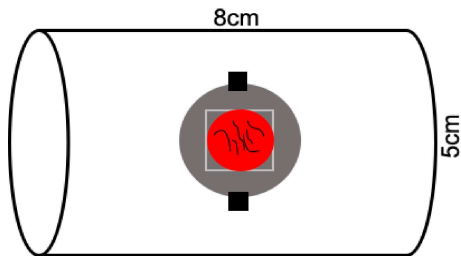
(a)

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(b)

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Figure 1: (a) Top view of the experimental apparatus. The left compartment is the start zone in which the subject acclimatized before the guillotine door was lifted, signalling the beginning of the trial. The right compartment is the test zone with the cylinder either wrapped during training or transparent during testing. (b) Side view of the transparent cylinder with the food reward attached inside on the posterior part of the cylinder.
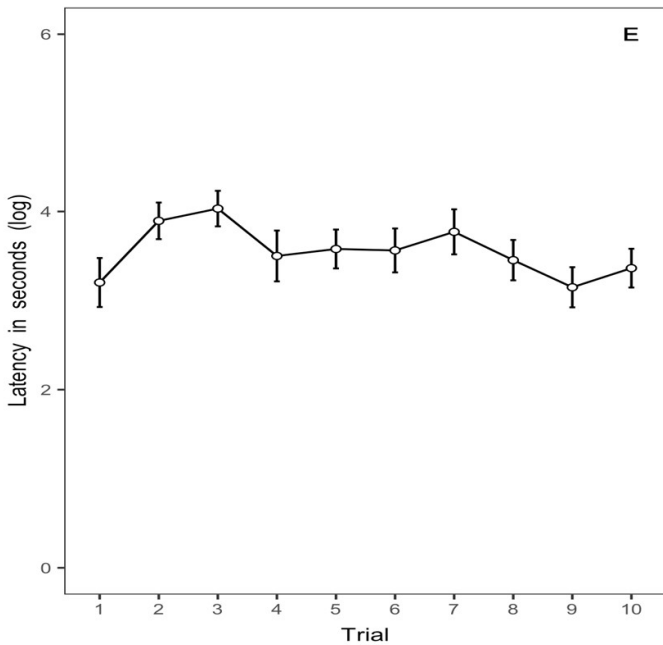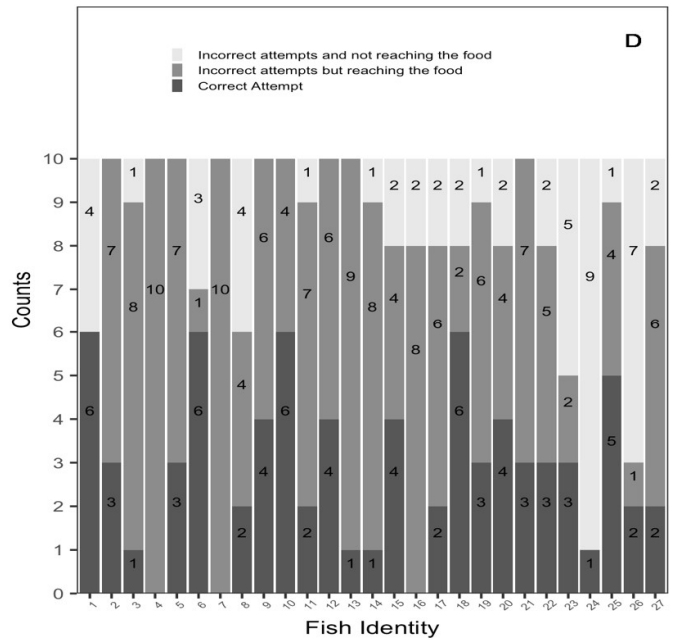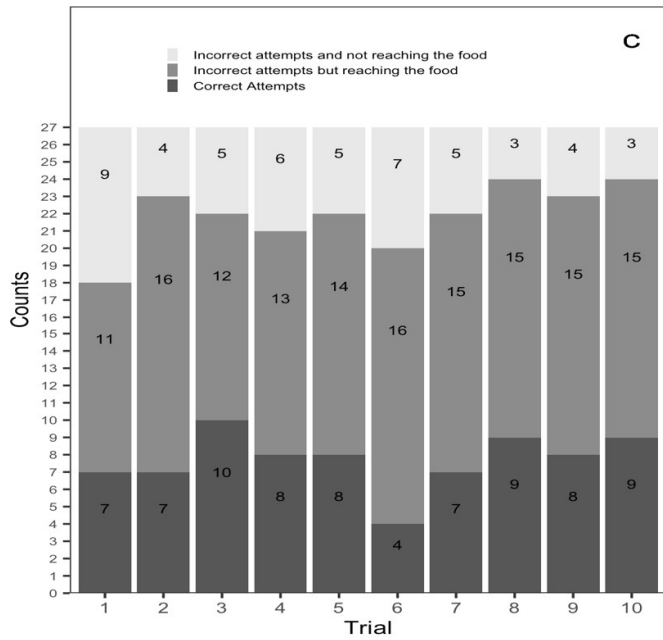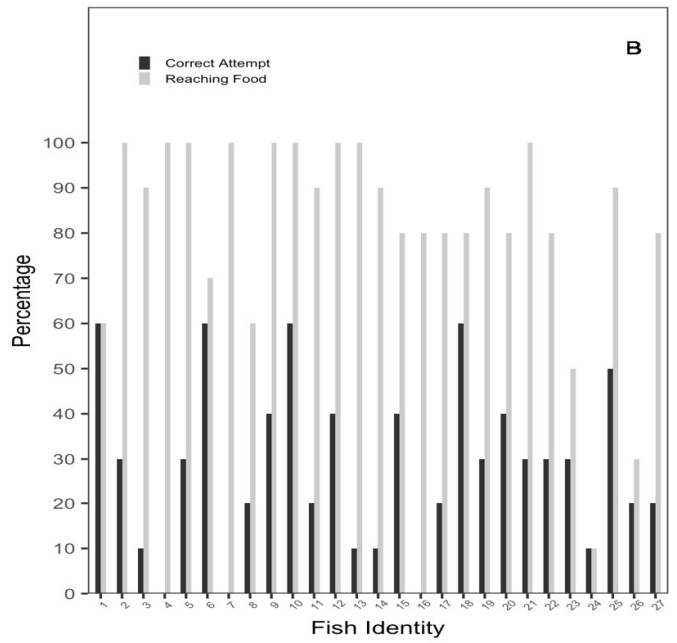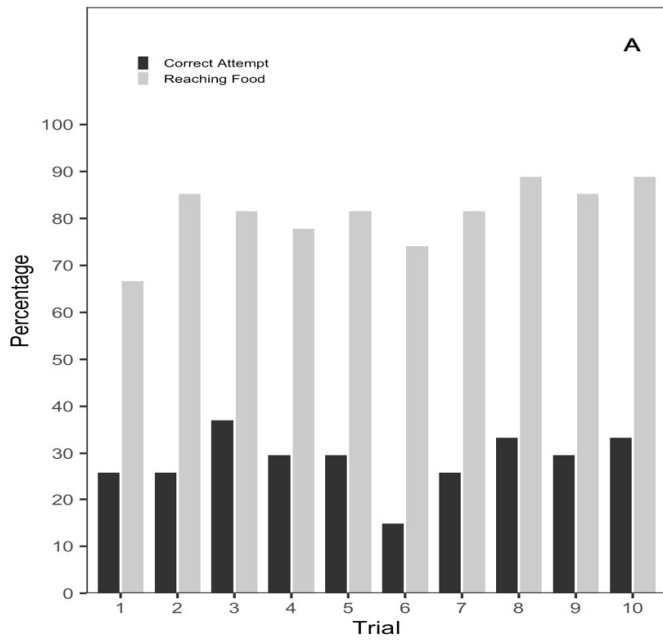
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774 <u>Figure 2</u>: **A/** In dark grey, percentage of correct attempts performed by the 27 females partaking in
775 the experiment for each of the ten trials of the test phase. A trial is considered correct when a female
776 detours around the cylinder without touching it to reach the reward. In light grey, percentage of
777 females entering the cylinder and getting the reward across the 10 trials of the test phase including
778 both correct and incorrect trials. **B/** In dark grey**,** percentage of successful trials performed by each
779 female across the ten trials of the test phase. In light grey, percentage of trials in which each female
780 entered the cylinder and reached the reward including both correct and incorrect trials. **C/** Count of
781 females performing correct attempts, incorrect attempts but reaching the food and incorrect
782 attempts and not reaching the food for each trial (dark, medium and light grey bars respectively; note:
783 a female not suppressing the urge to directly reach the food (i.e. incorrect attempt) can either retrieve
784 the food during a trial (i.e. incorrect attempt but reaching the food) or not retrieve it (i.e. incorrect
785 attempt and not reaching the food). **D/** Number of correct attempts, incorrect attempts but reaching
786 the reward and incorrect attempts and not reaching the reward (dark, medium and light grey bars
787 respectively) for each female across the 10 trials. **E/** Time to the reach the food inside the cylinder
788 over the ten trials both including correct and incorrect trials (Mean ±SEM).

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Table 1: Similarities and differences in the methodology implemented by studies that have investigated inhibition in guppies, *Poecilia reticulata*.
Due to greater general cognitive abilities females only were used as experimental subjects in all these studies.

Study	IC task	Strain	Reward	Familiarization phase	Training Phase	Test Phase
Lucon-Xiccato T, Gatto E, Bisazza A, 2017	†Cylinder task:	Domesticated/ornamental strain ("snakeskin cobra green")	Food positioned at 15cm of the focal subject (commercial flakes)	3 days with 4 social companions in testing apparatus. Fed 5 times a day with a Pasteur pipette	5 trials/day. Food inserted in the cylinder with a Pasteur pipette. Learning criterion = 4/5 correct trials in a day	5 trials per day for 10 days
	†Barrier task:	Domesticated/ornamental strain ("snakeskin cobra green")	Social (shoal of 4 stimulus females)	1 week with social companions in home tank	-	5 trials per day for 5 days
Gatto E, Lucon-Xiccato T, Bisazza A, 2018	Barrier task	Domesticated/ornamental strain ("snakeskin cobra green") & Wild strain descendant from high-predation zone in Tacarigua river	Social reward that varies in its value (3 vs. 8 ind. in stimulus shoal) and in its distance to the focal subject	-	-	5 trials
Santaca M, Busatta M, Lucon-Xiccato T, Bisazza A, 2019a	Barrier task	Wild strain descendant from high-predation zone in Tacarigua river	Social (shoal of 8 stimulus females)	5 days in a habituation tank similar to the experimental apparatus	-	12 consecutive trials
Santaca M, Busatta M, Lucon-Xiccato T, Savasci BB, Lucon-Xiccato T, Bisazza A, 2019b	Cylinder task	Domesticated/ornamental strain ("snakeskin cobra green")	Food (commercial flakes)	3 days with 4 social companions in adjacent compartment. Fed 5 times/day with a Pasteur pipette	5 trials/day. Food inserted in the cylinder with a Pasteur pipette. Learning criterion = 4/5 correct trials in a day	5 trials per day for 4 consecutive days
Lucon-Xiccato T, Bertolucci C, 2019	‡Tube task	Domesticated/ornamental strain	Live prey in a transparent tube	3 days in the experimental apparatus. Fed through a Pasteur pipette with commercial flakes twice, 4 and 6 times the 1st, 2nd and 3rd day respectively	-	1 or 2 trials of 20 min depending on the condition (control vs. experimental)
Lucon-Xiccato T, Montalbano G, Bertolucci C, 2019	Tube task	Domesticated/ornamental strain ("snakeskin cobra green")	Live prey in a transparent tube	*Same as above cell*	-	2 trials of 20 min
Lucon-Xiccato T, Bisazza A, Bertolucci C, 2020	Tube task	Domesticated/ornamental strain ("snakeskin cobra green")	Live prey in a transparent tube	*Same as above cell*	-	6 trials of 20 min

The present study	Cylinder task	Wild strain descendant from high-predation zone in Lower Aripo river	Food (dried bloodworm)	Throughout 5 days focal fish are habituated to enter the cylinder while being solitary	3 trials/day. Food attached in the cylinder. Learning criterion = 2/3 correct trials within 90sec in a day	10 trials in total (3 trials/day for 3 days and a last trial on the 4th day)

[†]Detour reaching task: The *cylinder task* and the *barrier task* are 2 variants of the detour reaching task. In order to reach a reward, the subject is required to detour around a transparent obstacle (i.e. cylinder or barrier). The ability of suppressing the strong prepotent tendency to go directly towards the visible reward and instead executing a detouring behaviour is a measure of inhibitory control (and more precisely of motor inhibition). In the cylinder task an initial training phase in which the subject learns to detour around an opaque cylinder to get the reward ensures that response inhibition is the only cognitive function responsible for the outcome of the test with the transparent cylinder. Without training the cylinder task would involve other cognitive abilities such as problem solving which would blur the interpretation of the inhibitory performances due to potential individual variation in other cognitive traits.

[‡]Tube task: Live prey are placed inside a transparent tube and the tested subjects are required to inhibit the response of attacking them. Inhibition is measured as a decrease in the number of attacks. In this task, the experimenter should control for neophilic response, habituation learning and the activity of live prey.

Gatto E, Lucon-Xiccato T, Bisazza A, 2018. Factors affecting the measure of inhibitory control in a fish (*Poecilia reticulata*). Behav Process 157:11-17.

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Lucon-Xiccato T, Bisazza A, Bertolucci C, 2020. Guppies show sex and individual differences in the ability to inhibit behaviour. Anim Cogn 23: 535-543

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Santaca M, Busatta M, Lucon-Xiccato T, Bisazza A, 2019a. Sensory differences mediate species variation in detour task performance. Anim Behav 155:153-162.

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