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

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Abstract

Inhibitory control (IC) is the ability to overcome impulsive or prepotent but ineffective responses in favour of more appropriate behaviours. The ability to inhibit internal predispositions or external temptations is key to cope with a complex and variable world. Traditionally viewed as cognitively demanding and a main component of executive functioning and self-control, IC was historically examined in only a few species of birds and mammals but recently a growing number of studies has shown that a much wider range of taxa rely on IC. Furthermore, there is growing evidence that inhibitory abilities may vary within species at the population and individual levels owing to genetic and environmental factors. Here we use a detour-reaching task, a standard paradigm to measure motor inhibition in non-human animals to quantify patterns of inter-individual variation in IC in wild-descendant female guppies, *Poecilia reticulata*. We found that female guppies displayed inhibitory performances that were, on average, half as successful as the performances reported previously for other strains of guppies tested in similar experimental conditions. Moreover, we showed consistent individual variation in the ability to inhibit inappropriate behaviours. Our results contribute to the understanding of the evolution of fish cognition and suggest that IC may show considerable variation among populations within a species. Such variation in IC abilities might contribute to individual differences in other cognitive functions such as spatial learning, quantity discrimination, or reversal learning.

Keywords: Detour task, Fish Cognition, Inhibitory control, Individual differences, Response inhibition, Trinidadian guppy.

Executive control refers to a set of cognitive functions required to monitor and regulate behaviours when automatic, habitual, or conditioned responses are inadequate, inefficient or impossible (Diamond, 2013; Gilbert and Burgess, 2008; Miyake and Friedman, 2012). Among those functions, inhibitory control (IC) is usually considered pivotal as it allows an individual to restrain inappropriate prepotent responses and enables the realisation of deliberate, goal-directed behaviours (Diamond, 2013). Without response inhibition (the behavioural component of inhibitory control) strong internal predispositions or external temptations and affordances may prevent or impede behaviour to be optimised to a variable and complex environment. For example, animals require IC in social contexts when competing for resources claimed by higher ranking individuals, when facing the choice between a small immediate reward and a bigger delayed reward (a behaviour that has been historically defined as “self-control” (Beran, 2015)), or to stop the urge to feed under the threat of predation (Ryer and Olla, 1991). In humans, impulsivity (a lack of IC) has been linked to lower academic achievement (Duckworth and Seligman, 2005), depression, and a whole range of externalising disorders and behavioural problems, including substance abuse and criminal tendencies (Moffitt et al., 2011). In non-human animals, IC abilities have been shown to correlate with the song repertoire size of song sparrows, *Melospiza melodia*, (Boogert et al., 2011, but see MacKinlay and Shaw 2019) and problem solving performances of various mammalian species (dogs (*Canis lupus familiaris*) (Mueller et al., 2016), chimpanzees (*Pan troglodytes*) (Vlamings et al., 2010) and cotton-top tamarins (*Saguinus oedipus*) (Hauser et al., 2002)). Furthermore, IC has been associated with proxies for general cognitive abilities such as absolute brain size (MacLean et al., 2014; Stevens, 2014) and complex social organisations (Ashton et al., 2018; Amici et al., 2008).

Traditionally viewed as cognitively demanding (Anderson et al., 2000; Santos et al., 1999), IC was first studied in mammals, mainly humans, non-human primates and a few bird species (mostly pigeons)(Ainslie, 1974; Diamond, 1981; Köhler, 1925/1959; Logan and Cowan, 1984; Scholes, 1965; Tobin and Logue, 1994), but a growing interest in the ultimate causes underpinning IC abilities has seen a surge in the range of species investigated within the mammalian and avian classes (horses (Baragli et al., 2017), dogs (Bray et al., 2014; Brucks et al., 2017a), wolves (Marshall-Pescini et al., 2015), sheep and goats (Knolle et al., 2017; Langbein, 2018), rodents (MacLean et al., 2014; Mayse et al., 2014), primates (Amici et al., 2008; MacLean et al., 2014) and birds (Kabadayi et al., 2016; MacLean et al., 2014; Meier et al., 2017; van Horik et al., 2019)) and beyond showing that also arthropods (Mayack and Naug, 2015; Wendt and Czaczkes, 2017) and teleost fishes (Lucon-Xiccato and Bertolucci, 2019; Lucon-Xiccato et al., 2017; Santaca et al., 2019a) rely on inhibitory processes. These studies have revealed considerable variation in interspecific IC abilities, but the origin of such variation remains unclear. Moreover, the extent to which variation in IC is the consequence of specific ecological adaptations or phylogenetic constraints on the central nervous system requires more in-depth analysis.

Besides the large difference in IC performances found across species, some evidence also suggests that inhibition varies within species, that is, between individuals and between populations (Fagnani et al., 2016; Kralik et al., 2002; Lucon-Xiccato et al., 2020). For example, Fagnani et al. (2016) showed that pet dogs had better IC skills compared to shelter dogs, probably because of the differences in social experience among them; and a study comparing wolves and dogs demonstrated that the former had significantly poorer IC performances, emphasising the effect of domestication on the evolution of cognitive skills (Marshall-Pescini et al., 2015). It has also been shown that, in spotted hyaenas, IC varied as a function of the social ranking and the size of the group in which juveniles grew up (Johnson-Ulrich and Holekamp, 2019). Hence within the same species, behavioural inhibition may differ depending on the genetic or environmental background in which it is expressed (or has developed).

In the current study we use the Trinidadian guppy (*Poecilia reticulata*) to quantify patterns of intraspecific variation in IC. This species is rapidly emerging as a model system to study IC. In 2017, Lucon-Xiccato et al. demonstrated that guppies displayed inhibitory performances equivalent to the average score of mammals and birds despite a much smaller nervous system, which contradicted the strong positive correlation between brain size and IC abilities established by MacLean et al. (2014) and highlight the importance of other neurobiological measures such as neuronal density to account for animal intelligence (Kabadayi et al., 2016; Olkowicz et al. 2016). However, to date the majority of the work exploring IC in guppies has been made using ornamental strains (see Table 1 for a summary of similarities and differences between our study and previous works examining inhibition in guppies). Thus, previous studies may not describe the full cognitive potential of the species as artificial selection (e.g. domestication) can drive correlated responses in animal morphology, physiology and behaviour (Larson and Fuller, 2014), which might affect the evolution and expression of cognitive function.

Here we use the detour paradigm, which is a standard method used in animal cognition research to investigate IC skills (see Kabadayi et al. (2018) for a comprehensive review of the detour paradigm in Animal Cognition). In this paradigm the experimental subject is required to detour around a transparent obstacle to reach a reward and in the process suppress a strong prepotent tendency to approach directly (and thus hit the obstacle) the visible target. There are different versions of the detour task in which the obstacle can be a hollow cylinder (i.e. the “cylinder task” where the reward is placed inside) or a barrier (i.e. “the barrier task”) and there are some debates about the extent to which these tasks also involve different cognitive and non-cognitive factors (Kabadayi et al., 2017; van Horik et al., 2018). Furthermore, even though the barrier and cylinder tasks are supposedly both measuring the motoric aspect of inhibition, prior studies in other species has shown that inhibitory performances may not be consistent across these procedures (van Horik et al., 2018). Previous work that has looked at IC in wild-descendant guppies (but from a different river system than our population, hence presenting different ecological conditions potentially affecting the evolution of IC) consistently used the barrier task, so the performance of wild-descendant guppies using the cylinder task has not been quantified. Therefore, in the present study, we quantify patterns of individual variation in IC in a wild-descendant population of guppies using the cylinder task and compare the performance of this population to previously published values of IC for guppies and other species using the same task.

Methods

Study Subjects:

Guppies are small livebearing freshwater fish native to the coastal streams of the north eastern part of South America. We used adult female descendants of individuals collected in the lower part of the Aripo River on the island of Trinidad. Our laboratory population had been kept in mixed-sex groups within large tanks (300 x 120 x 70cm) since 2008 and regularly transferred across them to avoid inbreeding. Fish were fed *ad libitum* and kept at similar density across the pools minimising differences in life-history traits. Experimental subjects of similar size (25mm±1.4mm) were collected from these large tanks and housed in groups of six in maintenance tanks (15 x 26 x 16 cm). The controlled conditions across pools reduced variation in individual growth rate which in turn allowed us to use size as an indicator of age. They were provided with gravel bottoms and plastic plants to ensure physical enrichment. They were kept at 24±1°C on a 12h light:dark photoperiod cycle and were fed twice daily with commercial food flakes in the mornings and brine shrimp (*Artemia salina* nauplii) in the afternoon. Females were marked to allow the experimenters to identify them individually (guppy females do not have individual marking that would allow a human eye to distinguish among them). To do so they were anaesthetised for a short time with a tricane methane sulfonate solution (MS222) and given a within group individual identifying mark using Visible Implant Fluorescent Elastomer (VIE, Northwest Marine Technology). A unique dorsal green mark was sufficient to distinguish among the females kept within the same maintenance tank. We chose to use only females because in guppies they show better learning capabilities (Lucon-Xiccato and Bisazza, 2014; Lucon-Xiccato and Bisazza, 2017).

Apparatus and Procedure

We used the cylinder task that is a well-established procedure to investigate IC in animals (Kabadayi et al., 2018) and was used recently to research and compare inhibitory performances across mammals, birds (Kabadayi et al., 2016; MacLean et al., 2014) and teleost fishes (Lucon-Xiccato et al., 2017). In the cylinder task subjects are initially trained to find food put inside an opaque cylinder. Once the task has been learned, the opaque cylinder is swapped for a transparent one. With transparent cylinders, IC is required: the subject has to suppress the tendency to go directly towards the visible food and instead detour the cylinder to enter from the open sides (as learned in the training phase with opaque cylinders).

Apparatus

The experimental arenas consisted of 2 identical tanks covered with translucent sheets. Each tank was divided in to two compartments, a start zone (16 x 15.5 x 20 cm) and a test zone (31 x 15.5 x 20 cm), separated by a transparent guillotine door operated by a draw string (Fig.1). Each trial started with an acclimatisation period taking place in the start zone followed by the cylinder test occurring in the test zone after the guillotine door was lifted by the experimenter. We used two types of plastic cylinder (acrylic glass) of equal size (8 cm in length and 5 cm in diameter) in the different phases of the procedure. In the habituation and training phase the cylinder was opaque (wrapped with speckled self-adhesive plastic film) whereas in the test phase the cylinder was transparent. Two 2 x 0.5cm wedges were glued to the bottom of the tank to help stabilising the cylinder.

The subjects were rewarded with dried bloodworm (King British, bloodworm). For each trial a tiny quantity of bloodworm was crushed and attached with Vaseline to a 1cm red plastic square, which was then affixed to a metallic ring hold vertically at the back of the cylinder (Fig.1). The metallic ring was held by 2 magnets positioned outside the cylinder and faced the subject acclimatising in the start zone (Fig.1). Video recordings were used to ensure accurate data collection.

Habituation - Shaping phase

Guppies live in groups and establish complex and long-lasting social relationships which confer numerous benefits such as improved food acquisition or increased vigilance (Magurran, 2005). To diminish the adverse effects of stress associated with social isolation (Culbert et al., 2019; Shams et al., 2017) and a new physical environment (Stevens et al., 2017) the subjects were habituated to their novel experimental conditions during five days and underwent a step-by-step procedure to reinforce the target behaviour. On day one, two groups of four fish were randomly selected from the maintenance tanks and released in the start zone of the two experimental tanks in which we had added an opaque cylinder with the food ring positioned at one of the entrances of the cylinder. After two minutes the door was opened, and the fish were given one hour to explore their environment. Throughout the next four days the shaping phase continued during multiple 20-minute sessions in which the number of fish in each session was reduced and the food ring was gradually moved towards the middle of the cylinder. The experimental subjects proceeded to the training phase as soon as, alone in the tank, they managed to enter the cylinder. After 5 days of habituation and shaping, the fish that did not enter the cylinder while being solitary were removed from the study and substituted with new subjects.

Training phase

To learn to feed inside the opaque cylinder the experimental subjects performed three trials per day two hours apart starting at 10am. Before each trial they were placed in the start compartment for five minutes to acclimatise while the experimenter inserted in the middle of the test zone the cylinder equipped with the food ring (Fig.1). After five minutes the video recording started; the (transparent) guillotine door was opened, and the fish was given a maximum of 30 minutes to reach the food. Once the reward was found the fish was allowed five minutes to consume it before the cylinder was removed and the subject returned to its maintenance tank. Any subject that did not feed within 30 min received additional training trials within that day to ensure 3 trials in which they reached the food. We trained two fish simultaneously in adjacent tanks; the camera was positioned in order to capture both testing arenas. The adopted learning criterion to continue to the test phase was to reach the food (without touching the cylinder) within 90 seconds during two out of the three daily trials for which the females reached the food. In total twenty-seven females were transferred to the test phase reaching the learning criterion within a maximum of eight days.

Test phase

The procedure in the test phase differed slightly from the training phase as the opaque cylinder was replaced with the transparent one and the 10 trials that the subjects received over a four-day period lasted 10 minutes each. Based on the video recordings, we quantified for each trial the performance of the females: whether the response was correct or incorrect and the time it took to obtain the reward. A trial was considered correct if the subject retrieved the food entering the cylinder from the open lateral sides and incorrect if it tried to cross through the transparent material. To score the time to solve the task, we measured the latency between the moment the fish left the start zone and the moment it started eating. If in any given trial a female did not enter the cylinder, a score of 600 (60 sec x 10 minutes) was given for the time needed to reach the reward and the trial was not repeated.

Statistical analysis

Analyses were carried out in R version 3.6.2 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). We analysed the performance of guppy females in the cylinder task (correct versus incorrect trial) using a generalized linear mixed model (GLMMs, “glmer” function of the “lme4” R package (v1.1.23)) with a binomial error structure and logit-link function with trial number included as a covariate and individuals’ ID as a random effect.

A Cochran’s Q test was used to test for differences in the ability to reach the reward independently of the outcome (i.e. collapsed across correct and incorrect attempts) across trials and among individual females.

We analysed time performance (the latency to reach the reward independently of the outcome of the trial) fitting a linear mixed-effects model (‘lmer’ function of the ‘lme4’ R package (v1.1.23)) with trial number as a covariate and individual ID as random effect. Due to a right-skewed distribution, the response variable was log-transformed and the females that did not get the food during the 10 minutes of a trial were removed from the analysis.

Individual differences were analysed using the “rptGaussian” and the “rptBinary” functions of the “rptR” R package (v0.9.22), which estimates repeatability from GLMM fitted by restricted maximum likelihood. The “rptGaussian” and the “rptBinary” functions estimate whether the latency to reach the reward and the percentage of correct attempts were significantly repeatable across trials respectively. The repeatability analysis was run for all the trials.

Processed data for the test phase and the R script used to analyse them can be found at https://osf.io/vy3s2/?view_only=ca4dcf67faef431897337c140fc8b8f3

Ethical Note

The study adheres to the ASAB/ABS guidelines for the Use of Animals in Research. The fish were tagged under the Home Office license PPL 30/3308 (UK). Following the marking procedure, they were allowed a 30-minute recovery period from the anaesthetic during which they were monitored for any ill effects and placed back in their experimental home tanks. None of the fish showed signs of injuries or pain potentially induced by the tagging procedure.

Results

In the training phase female guppies needed on average 14.4 ± 4.83 trials (mean±SD) to reach the learning criterion. On average during the test phase, individuals detoured around the transparent cylinder to reach the reward in 28.5% ± 18.8 (mean±SD) of the trials. Across females, correct trials ranged between 10-60% but 11.1% of them (3 out 27) failed to inhibit the urge to swim directly on all trials (Fig.2B).

The likelihood of successful trials did not change significantly across the test phase (GLMM: $\chi^2{}_1 = 0.1$, p=0.75; Fig. 2A, 2C) but the time to reach the food marginally decreased over time (LMM: $\chi^2{}_1 = 3.52$, p=0.06, Fig, 2E). The overall probability to obtain the reward (whether or not subjects successfully suppressed the initial urge to swim directly toward the visible target) did not change across trials (Q(9)=9.9, p=0.36, Fig. 2A, 2C); by contrast, we did observe differences between females in their tendency to reach the food during the task (again collapsed across correct and incorrect trials; Q(26)=85.6, p<0.0001, Fig.2B, 2D).

Female guppies showed significant individual differences in the percentage of correct attempts (R=0.075, CI=[0, 0.17], p=0.008) and latency to get the reward (R=0.206, CI=[0.07, 0.35], p<0.001) across the entire experiment.

Discussion

In this experiment we investigated IC abilities of wild-descendant female guppies evaluated in the cylinder version of the detour task. We showed that they successfully inhibited the urge to approach the food directly on 28.5% of the trials in total. We did not notice any improvement in females' inhibitory performance during the test phase, but the relatively small number of trials did not allow us to rule out an effect of training if the individuals had been tested for longer. On the contrary, they became faster in detouring the transparent cylinder to obtain the reward (independently of the outcome in the task), which suggests that a potential learning process could have taken place. Interestingly there is also consistent individual variation in females' performance to detour the transparent cylinder, reflecting differences in individuals' ability to efficiently inhibit prepotent behaviours.

The investigation of inhibitory control in teleost fishes is relatively recent and unlike previous studies (Gatto et al., 2018; Lucon-Xiccato et al., 2017; Santaca et al., 2019b; see table 1 for an overview) reporting performances in guppies similar to the average performance of mammalian and avian species (~58% of correct responses in the cylinder task), we observed here much lower performances. However, such relatively low level of behavioural inhibition is comparable to the findings of other studies that involved either guppies (Gatto et al., 2018) or cichlids (Brandao et al. 2019). IC abilities vary widely across species and succeeding 28.5% of the time is a performance equivalent to the one displayed by parrots or sparrows and far from the almost perfect score displayed by apes and ravens (Kabadayi et al., 2017; Kabadayi et al., 2016; MacLean et al., 2014), positioning guppies at the lower end of the spectrum of the species investigated (MacLean et al., 2014).

Our study recorded significant individual repeatability in the outcome of the cylinder task and in time performance. Females differed in their ability to suppress the urge to reach directly the reward without detouring the obstacle as successful trials ranged between 0 and 60%. Likewise, they varied in the time they needed to get the food with some females being consistently quicker than others. This consistent individual variation in both behaviours was found across the 10 trials of the experiment. Our results are consistent with previous studies showing consistent individual differences in inhibition in zebrafish (Lucon-Xiccato et al. 2019) and guppies (Lucon-Xiccato et al. 2020). As inhibition might support other higher-level cognitive abilities (Diamond 2013), IC variability could contribute to individual differences found among vertebrates (Lucon-Xiccato et al. 2019) in processes such as spatial abilities, reversal learning or social learning. From an evolutionary perspective variability in IC could result from selection pressures acting on other traits. There is a growing number of studies showing a relationship between personality traits and cognitive individual differences (Brown et al. 2013, White et al. 2107, Lucon-Xiccato et al. 2019). Personality traits are maintained through frequency-dependent selection and spatio-temporal fluctuation in natural selection (Dingemanse et al. 2004; Dingemanse and Re´ale 2005) that in turn may generate variation in inhibitory performances. Alternatively, IC can be under direct selection (and contribute to personality traits) if it enhances survival for example when facing high predation risk or when living in, for example, a social group with strong hierarchical structure. Here inhibiting foraging or sexual behaviours could diminish the risk of being attacked by predators (Ryer and Olla, 1991) or more dominant group members. In Australian magpies, *Cracticus tibicen dorsalis*, higher inhibitory performances were linked to increased group size and higher females' reproductive success suggesting that the demands of social life drove cognitive evolution (Ashton et al., 2018). An important next step is to look at whether individual performances are consistent when tested in the wild versus in captivity.

Our findings suggest significant differences exist among populations of guppies in IC which may reflect slight methodological differences across studies or adaptive variation among populations. To the best of our knowledge seven studies have investigated IC in guppies prior, but none of them implemented the exact same setting we used for ours (table 1). Previous work on guppies using the cylinder task has used domesticated strains (Lucon-Xiccato et al., 2017; Santaca et al., 2019b). In contrast, previous studies on wild-descendant guppies have used a different variant of the detour task – the barrier task (Gatto et al., 2018; Santaca et al., 2019a). Here we further extend our understanding of IC in guppies by testing wild-descendant guppies with the cylinder task. Differences in task variants and strains could contribute to the differences between studies. First, a growing number of studies show a lack of consistency in individual performances across IC tasks either because those tasks measured different aspects of inhibition within individuals (i.e. motor inhibition, self-control, cognitive inhibition) underpinned by different neural mechanisms or because of variation in non-cognitive factors such as motivation to acquire food that could affect the performance (Botvinick and Braver, 2015; Brucks et al., 2017a; Fagnani et al., 2016; van Horik et al., 2018). Even in tasks believed to capture the same aspect of inhibition such as the barrier task and the cylinder task, both detour-reach tasks supposedly evaluating motor inhibition abilities, dogs (Brucks et al., 2017a) and pheasants (van Horik et al., 2018) have shown inconsistent performances. Such findings highlight the context-specificity of IC in vertebrates and could account for the variable performances displayed by guppies. Second, independently of the detour task chosen the variation in performances found between different guppy populations might ensue differences in several non-cognitive factors known to affect the measure of IC in fish (Gatto et al., 2018) and, more generally, in animals, such as the distance between the subject and the goal (Junghans et al., 2016) or the value of the reward (Brucks et al., 2017b; Wascher et al., 2012). Several studies have indicated that with increasing goal distance it is easier for animals to detour around an obstacle (chicken (Regolin et al., 1995), dogs (Köhler, 1925/1959), long-tailed macaques (Junghans et al., 2016), guppy (Gatto et al., 2018), human infants (Diamond and Gilbert, 1989)). Gatto et al. (2018) specifically addressed this issue with guppies by varying the position of the reward (i.e. a group of conspecifics) with a transparent barrier and showed, as anticipated, that they were less able to suppress the urge to reach directly the social group when it was positioned nearer to (5cm) versus farther from (15cm) the barrier. Incidentally the fish that faced a close reward solved the task 28.3±28.8% of the time compared to fish more distant for which the likelihood of success was 50±25%. These numbers match respectively the outcome of our experiment in which the cylinder was positioned at 5 cm from the guillotine door (the food subsequently at 8 cm) and the performance of the subjects used by Lucon-Xiccato et al. (2017) who positioned the reward at 15 cm from the obstacle. Other non-cognitive factors such as the motivational and physiological state of the animal can affect the detour response (Kabadayi et al., 2018; van Horik et al., 2018) and be responsible for variation in IC abilities. A hungry individual might be less prone to block a prepotent tendency to reach food directly than a satiated individual. Hence, there is variation between but also within cognitive tasks, and these might all contribute to differences between studies. Such sources of variation are particularly important to account for when comparing different species or different populations. Third, differences between studies could also be caused by the use of wild-descendant vs. domesticated guppies. In fishes evidence of the effects of domestication on cognitive abilities remain scarce (Pasquet, 2019) but the main incentive for fish domestication is aquaculture (e.g. fish farming, ornamental fishes) for which traits relying upon inhibition are not the primary target of artificial selection. However, selection on a specific trait (e.g. a morphological trait such as fancy colour pattern or tail shape) could be sufficient to drive correlated physiological and behavioural changes characteristic of a phenomenon known as domestication syndrome (Belyaev, 1979; Darwin, 1868; Wheat et al., 2019). While the mechanistic basis of this phenomenon remains a source of controversy (Sanchez-Villagra et al., 2016), it could explain the difference observed between domesticated strains of guppy used in previous studies and their wild counterparts used here. Alternatively, the better performances displayed by domesticated guppies could result from selection for less aggressive individuals if, in fishes, aggressive behaviours are negatively related to IC abilities as it was shown in humans (Hsieh and Chen, 2017; Pawliczek et al., 2013; Vigil-Colet et al., 2004).

Trinidadian guppies vary drastically in morphology, life-history and behavioural traits due to variation in selection pressures such as predation levels (Devigili et al., 2019; Endler, 1980; Handelsman et al., 2013; Hasenjager and Dugatkin, 2017; Herbert-Read et al., 2017; Reznick, 1982), water turbidity (Borner et al., 2015) or ambient light (Endler, 1991, 1993; Gamble et al., 2003). Recently predation has also been linked to brain evolution in guppies (Kotrschal et al., 2017; Mitchell et al., 2020; Reddon et al., 2018) and killifish (*Rivulus hartii*) (Walsh et al., 2016) albeit showing contrasting effects for brain size or for brain anatomy. Reddon and colleagues (2018) found that exposure to predatory cues increased relative brain mass in guppies whereas killifish from sites with predators exhibited smaller brains than their counterparts living in predator-free habitats (Walsh et al., 2016). It is generally suggested that increased brain size is associated with better executive functions and increased learning abilities (Amiel et al., 2011; Benson-Amram et al., 2016; MacLean et al., 2014; Overington et al., 2009; Sol et al., 2008; Sol et al., 2007), which has also been found in guppies selected for relative brain size (Buechel et al., 2018; Corral-Lopez et al., 2017; Corral-Lopez et al., 2018; Kotrschal et al., 2015; Kotrschal et al., 2013a; van der Bijl et al., 2015). However large brains are energetically costly to develop and maintain and the cognitive benefits they provide might be overridden by the metabolic costs (and more generally fitness costs) (Kotrschal et al., 2013a; Laughlin et al., 1998) they entail. Assuming that the size of the brain is linked to cognitive abilities (Kotrschal et al., 2013b), the lower motor inhibition performance observed here could result from brain size variation between native populations or evolutionary changes that took place in the lab driven, for example, by an absence of predation pressure.

In conclusion, our findings demonstrated individual variability in IC and highlight potential within-species population differences. Consistent individual variation in inhibition may explain the individual differences in other cognitive processes previously reported among teleost fishes. Moreover, our guppy population displayed on average lower inhibitory performances than domesticated guppies or guppies native to a different river. Future work using a comparative approach assessing inhibitory motor control in guppies found across and along the Trinidadian river system might shed light on the causes underpinning variation (at the group and individual level) in cognition in guppies and, more generally, in vertebrates facing similar environmental pressures.

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Author Contributions:

D.P.C., S.K.D and F.V. conceived the research program; A.M. designed and conducted the experiment, ran the analysis and wrote the manuscript. D.P.C., S.K.D and F.V. reviewed the manuscript.

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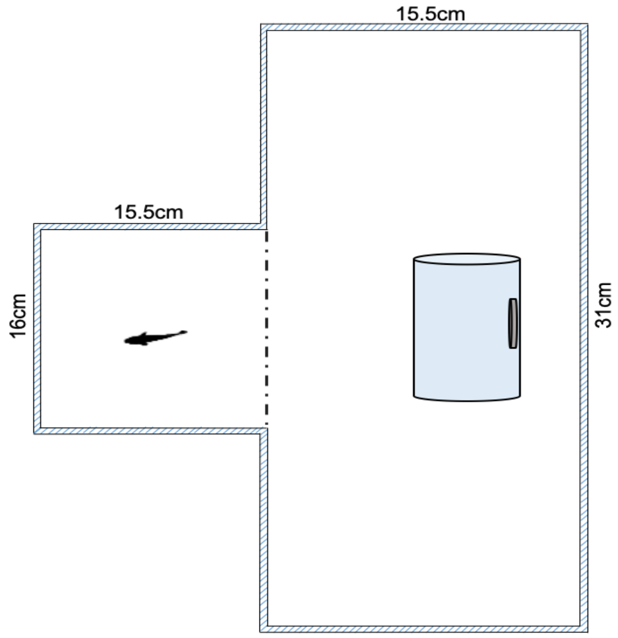
Figures

(a)



(b)

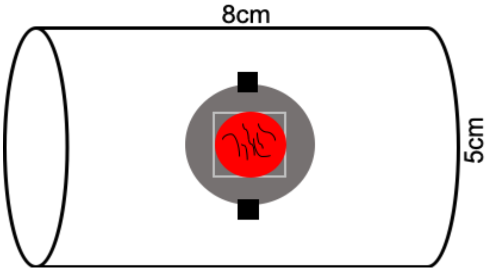


Figure 1: (a) Top view of the experimental apparatus. The left compartment is the start zone in which the subject acclimatized before the guillotine door was lifted, signalling the beginning of the trial. The right compartment is the test zone with the cylinder either wrapped during training or transparent during testing. (b) Side view of the transparent cylinder with the food reward attached inside on the posterior part of the cylinder.

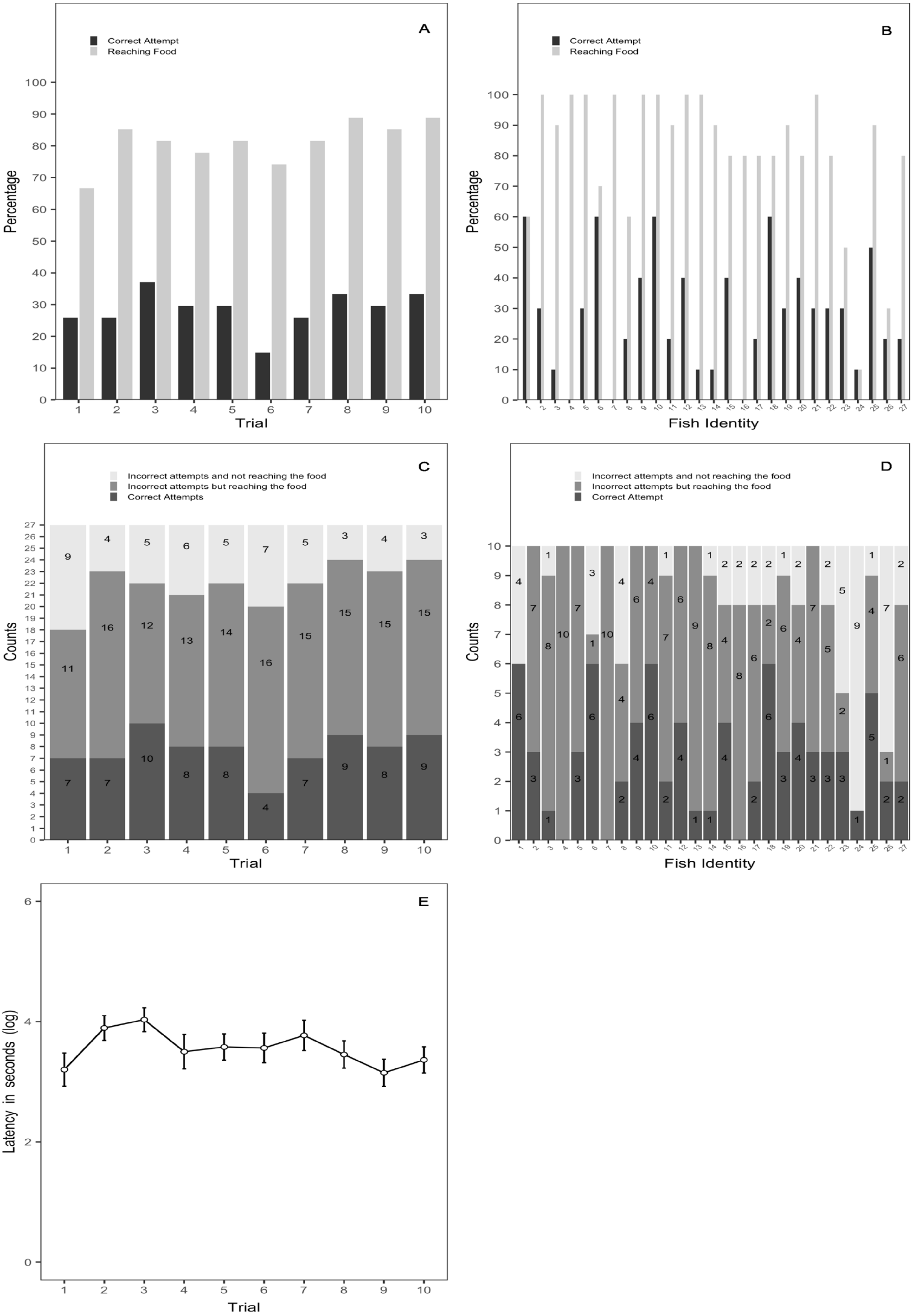

A
Correct Attempt
Reaching Food
Percentage
Trial
B
Correct Attempt
Reaching Food
Percentage
Fish Identity
C
Incorrect attempts and not reaching the food
Incorrect attempts but reaching the food
Correct Attempts
Counts
Trial
9 11 7
4 16 7
5 12 10
6 13 8
5 14 8
7 16 4
5 15 7
3 15 9
4 15 8
3 15 9
D
Incorrect attempts and not reaching the food
Incorrect attempts but reaching the food
Correct Attempt
Counts
Fish Identity
4 6
7 3
1 8 1
10
7 3
3 1 6
10
4 4 2
6 4
4 6
1 7 2
6 4
9 1
1 8 1
2 4 4
2 8
2 6 2
2 2 6
1 6 3
2 4 4
7 3
2 5 3
5 2 3
9 1
1 4 5
7 1 2
2 6 2
E
Latency in seconds (log)
Trial

Figure 2: **A/** In dark grey, percentage of correct attempts performed by the 27 females partaking in the experiment for each of the ten trials of the test phase. A trial is considered correct when a female detours around the cylinder without touching it to reach the reward. In light grey, percentage of females entering the cylinder and getting the reward across the 10 trials of the test phase including both correct and incorrect trials. **B/** In dark grey**,** percentage of successful trials performed by each female across the ten trials of the test phase. In light grey, percentage of trials in which each female entered the cylinder and reached the reward including both correct and incorrect trials. **C/** Count of females performing correct attempts, incorrect attempts but reaching the food and incorrect attempts and not reaching the food for each trial (dark, medium and light grey bars respectively; note: a female not suppressing the urge to directly reach the food (i.e. incorrect attempt) can either retrieve the food during a trial (i.e. incorrect attempt but reaching the food) or not retrieve it (i.e. incorrect attempt and not reaching the food). **D/** Number of correct attempts, incorrect attempts but reaching the reward and incorrect attempts and not reaching the reward (dark, medium and light grey bars respectively) for each female across the 10 trials. **E/** Time to the reach the food inside the cylinder over the ten trials both including correct and incorrect trials (Mean ±SEM).

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, 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.

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