1 **The contribution of executive functions to sex differences in animal**

2 **cognition**

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8   **Abstract**

9   Cognitive sex differences have been reported in several vertebrate species, mostly in

10   spatial abilities. Here, I review evidence of sex differences in a family of general cognitive

11   functions that control behaviour and cognition, i.e., executive functions such as cognitive

12   flexibility and inhibitory control. Most of this evidence derives from studies in teleost fish.

13   However, analysis of literature from other fields (e.g., biomedicine, genetic, ecology)

14   concerning mammals and birds reveals that more than 40% of species investigated exhibit

15   sex differences in executive functions. Among species, the direction and magnitude of these

16   sex differences vary greatly, even within the same family, suggesting sex-specific selection

17   due to species' reproductive systems and reproductive roles of males and females. Evidence

18   also suggests that sex differences in executive functions might provide males and females

19   highly differentiated cognitive phenotypes. To understand the evolution of cognitive sex

20   differences in vertebrates, future research should consider executive functions.

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22   **Keywords:** animal cognition; animal behaviour; comparative cognition; cognitive control;

23   cognitive ecology; individual differences; sexual dimorphism.

1. Introduction

Evidence of sex differences in cognitive task performance has been reported in several vertebrate clades. The largest collection of data on cognitive sex differences comes from psychological research in human species (reviewed in Halpern, 2000; Geary, 1996; Miller & Halpern, 2014; Spelke, 2005). A broad literature is also available on laboratory rodents (reviewed in Jonasson, 2005; Luine & Dohanich, 2008), especially in translational research on stress and brain disorders (reviewed in Barha et al., 2017; Leger & Neil, 2016; Luine et al., 2017), and teleost fish (reviewed in Cummings, 2018; Lucon-Xiccato & Bisazza, 2017a). Moreover, various investigations have been conducted among species belonging to other groups, such as birds (Guigueno et al., 2014), primates (Vannucchi et al., 2020), carnivorans (Perdue et al., 2011), and reptiles (Szabo et al., 2019).

The reasons for interest in cognitive sex differences vary across research disciplines. For example, in biomedical research, interest derives from the fact that many human cognitive diseases have sex-specific occurrence or aetiology (e.g., Li & Singh, 2014; Beatty & Aupperle, 2002), requiring sex-specific treatments. Moreover, translational model species often display sex differences that might hamper the results of behavioural tasks (e.g., Jonasson, 2005). For evolutionary biologists and comparative psychologists, cognitive sex differences are particularly interesting because they provide insight on the mechanisms of cognitive evolution. It is believed that cognitive abilities may evolve in response to selective pressures, as observed for other traits (Sherry, 2006). The same concept has been applied to sex differences: if a task has a different ecological relevance for the two sexes, selection is expected to determine an improvement in the performance of one sex (reviewed in Jones et al., 2003). In this light, the study of sex differences is capable of revealing how cognition responds to selective pressures, generating evolutionary changes within species.

48   Most of the evolutionary research on cognitive sex differences concerns spatial

49   abilities, such as learning new navigation routes or remembering the position of a resource

50   (reviewed in Jones et al., 2003). This is probably due to the fact that the two sexes often

51   differ in spatial ecology and spatial behaviour, thereby providing testable predictions and

52   interpretations for sex differences in spatial abilities. For example, Gaulin and Fitzgerald

53   (1986) observed that males of the polygamous voles *Microtus pennsylvanicus* made fewer

54   errors than females in a maze task. Because males of this species have a larger home-range

55   size compared to females, the effect observed was attributed to the evolution of a sex

56   difference in spatial abilities due to directional selection on males. Similarly, another study

57   detected enhanced performance of female shiny cowbirds, *Molothrus bonariensis*, in

58   memorising the position of a food reward in an array of cells; the sex difference was

59   associated with selection on spatial memory because in this species, the female (but not the

60   male) is required to memorise the position of the host nests (Astié et al., 1998). Similar sex

61   differences in spatial abilities have been reported for a range of vertebrates (e.g., Lacreuse et

62   al., 2005; Saucier et al., 2008; Wallace & Hofmann, 2021). However, in most cases, evidence

63   indicates that the evolutionary hypotheses proposed to explain these sex differences are not

64   substantially supported by empirical results (Jones et al., 2003). One of the causes of this

65   problem might be the fact that researchers have often focus on few very specific cognitive

66   tasks (e.g., spatial learning and memory tasks), while the cognitive phenotype of an

67   individual is determined by the interaction of multiple cognitive functions.

68   Here, I review literature on less-known cognitive sex differences that involve the so-

69   called executive functions (EFs). EFs are considered a family of top-down cognitive

70   functions involved in cognitive and behavioural control (reviewed in Diamond, 2013): EFs

71   are utilised when relying on automatic responses or previously learned behaviours is not

72   sufficient to reach a goal. Studies in humans, the species most studied in this respect,

typically identify three main EFs (reviewed in Diamond, 2013): cognitive flexibility that

permits to shift attention between different stimuli, and adapt behaviour to novel and

unexpected situations; inhibitory control that allows individuals to overrule internal

predispositions and external lures; and working memory that allows one to temporarily store

and manipulate the information necessary to complete a task (Baddeley, 1992). Several

studies suggest that EFs have a relatively general role in cognitive functioning, in the sense

that they affect the outcome of multiple tasks (Cain, 2006; Cragg & Gilmore, 2014; Shamosh

& Gray, 2008). This is usually considered evidence that EFs are activated in accord with

more specific functions to reach the solution of a task (Diamond, 2013). For some authors,

EFs should be regarded as domain-general cognitive mechanisms (Chiappe & MacDonald,

2005). The role of EFs implies that when an animal solves, for instance, a maze task, the

performance might be not only determined by a specific cognitive module that encodes new

spatial information, but also by EFs recruited for the task, such as working memory to store

information or inhibitory control to block impulsive wrong choices. The important role of

EFs makes it critical to understand whether they contribute to cognitive sex differences.

In this review, I first focussed on recent literature in teleost fish because most

experiments directly aimed at comparing EFs between males and females have been

performed in this group. Therefore, literature about teleost fish has provided the early

evidence of widespread sex differences in EFs and still offers the most complete picture of

the phenomenon. In the second part of this review, I looked for evidence of sex differences in

EFs in other vertebrate groups. Considering the numerous similarities observed between the

cognitive system of fish and that of other vertebrates (e.g., Bshary and Brown, 2014;

Oliveira, 2016; Salas et al., 2003), I hypothesise that sex differences in EFs might be

widespread among vertebrates, even if less studied. Because I found that literature on

tetrapods contains a limited number of works intended to study sex differences in EFs, I

98 expanded the search to review literature from other fields (e.g., neural disorders, biomedicine,

99 stress research). In the last part of the review, I analyse the putative mechanisms,

100 evolutionary explanations, and consequences of sex differences in EFs, with the aim to

101 suggest future research directions.

102

103 **2. Sex differences in executive functions in teleost fish**

104 This first review section focussed on teleost fish. Interest on sex differences in this

105 group has mostly arisen in the last decade but has rapidly become key in the field (Pouca &

106 Brown, 2017). Interestingly, several studies in fish have been specifically designed to detect

107 sex differences in EFs, a trend that is not observed in other vertebrate groups. For this reason,

108 literature in fish provides the most compelling analysis of sex differences in EFs available to

109 date.

110

111 2.1 Reversal learning tasks

112 A relatively extended line of research in fish has analysed the performance of males

113 and females in the discrimination reversal learning task (sensu Shettleworth, 2009). This task

114 requires the animal to choose a predetermined stimulus between two options via association

115 with a reward. After the animal learns this contingency, the food-reward association is

116 reversed requiring to select the previously unrewarded stimulus. Therefore, the reversal

117 learning task measures the ability to modify behaviour in response to the novel contingency,

118 which is mainly considered a form of cognitive flexibility (Boogert et al., 2010; Happel et al.,

119 2014).

120 The studies with the reversal learning involved several fish species, all but one

121 (discussed in section 2.3) belonging to the Poeciliidae family. The species with more

122 experimental data is the guppy, *Poecilia reticulata*. In this species, sex differences in the

123   discrimination reversal learning task were initially studied using red-yellow plastic discs as

124   the stimuli: the fish had to dislodge the disc with the correct colour to obtain a food rewarded

125   underneath. Results indicated that female guppies solved the task with approximately half as

126   many errors as males (Lucon-Xiccato & Bisazza, 2014; figure 1). Moreover, the study found

127   that the two sexes showed similar performance in the initial learning of the colour-reward

128   association. Therefore, the sex difference in the reversal phase was not likely due to general

129   learning or motivation.

130   A well-known problem is that animal cognition cannot be directly assessed, but it is

131   inferred from task performance (Boogert et al., 2018; Rowe & Healy, 2014). Consequently,

132   results of a single experiment should be considered carefully because it is difficult to ensure

133   which cognitive ability determined the performance. Replication with different tasks

134   designed to measure the same ability might confirm the involvement of the target ability.

135   This problem might apply also to the reversal learning task. In the specific case of guppies'

136   sex differences, a replication was also necessary to solve a theoretical problem. Considering

137   that female guppies display a highly flexible mate choice based on male red-orange spots

138   (Dugatkin & Godin, 1992; Gong & Gibson, 1996), one could hypothesise that female

139   guppies' greater cognitive flexibility was limited to colour discrimination due to a learning

140   predisposition (Shettleworth, 1972). To clarified these issues, in a follow-up study, Miletto

141   Petrazzini and colleagues (2017) compared male and female guppies in a spatial and in a

142   numerical reversal learning task, finding overall support for greater female performance

143   difference. The coherent results from three variants of the reversal learning task (i.e., colour,

144   spatial, and numerical discrimination) suggests that methodology and learning predispositions

145   did not explain the findings of the first study with the colour discrimination. Overall, the data

146   points towards the presence of a single EF that differs between the two sexes. Regarding the

147   evolutionary explanation, it is still possible that female guppies have evolved greater

148   cognitive flexibility in the context of mate choice (Briggs et al., 1996; Dugatkin & Godin,

149   1992); however, this evolutionary change has likely involved a general EF, thereby also

150   affecting performance in other contexts, like in the spatial and numerical reversal learning

151   tasks.

152   A colour discrimination reversal learning task with discs as stimuli has been also used

153   to study sex differences in three other poeciliid fish (Fuss & White, 2019). Interestingly, a sex

154   difference favouring males was found in *Poecilia mexicana*, whereas male and female

155   *Poecilia latipinna* demonstrated a similar performance (figure 1). Greater flexibility of males

156   in *P. mexicana* was also reported in a modified version of the task which required social

157   learning (Fuss et al., 2021); the target colour changed multiples times across the training, and

158   the subject could identify it by observing the choice of a trained demonstrator (Fuss et al.,

159   2021). As seen in guppies, results of the reversal learning task in *P. mexicana* are consistent

160   to small variations in methodological aspects, reinforcing the idea of a single EF (i.e.,

161   cognitive flexibility) that is recruited in multiple reversal learning tasks and varies between

162   the two sexes.

163   The whole set of data in poeciliids suggests that the pattern of sex differences in EFs

164   is highly variable across closely related species. Considering other species and other

165   cognitive abilities, a similar interspecific variability has been reported. For instance, *Microtus*

166   *pinetorum* does not show the greater male spatial performance described in the congeneric *M.*

167   *pennsylvanicus* (Gaulin & Fitzgerald, 1986). This interspecific variability has been associated

168   to the fact that the former species is monogamous, causing males and female to share the

169   same home range and determining relaxed selection for greater male spatial abilities.

170   Applying the same interpretation to the reversal learning data in poeciliid fish suggests the

171   presence of direct selection on cognitive flexibility that varies across species.

172

2.2 Inhibitory tasks in fish

Several studies in teleost fish have addressed sex differences in inhibitory control. The performance of teleost fishes and other animals is usually measured with the detour task. The subject has to withhold the tendency to directly reach a desired stimulus placed behind a transparent barrier and rather detour the barrier (figure 2a). A simple version of the detour task developed for social fish exploits a group of conspecifics as the social stimulus (figure 2a). Guppies tested with this paradigm exhibited a remarkable sex difference: males persistently tried to swim through the transparent barrier and took five times more than females to detour it and reach the stimulus (Lucon-Xiccato & Bisazza, 2017b; figure 2d).

The validity of the detour task has been often criticised (e.g., van Horik et al., 2018). In particular, it might not provide a reliable indication of cognitive sex differences if the two sexes differ in one of the many factors that can affect performance, such as social motivation (Griffiths, Magurran, 1998), learning abilities (van Horik et al., 2020), or sensory capacities (Santancà et al., 2019). To control that motivation was not involved in the sex difference, the detour experiment in guppies was repeated deploying a barrier made visible with a mesh net (Lucon-Xiccato & Bisazza, 2017b). In this second version of the task, the sex difference in performance disappeared. Inhibitory control was arguably the cause of the heightened performance of females in the early version of the task because the effect was related to the presence of a transparent obstacle that made difficult to inhibit the tendency to swim directly towards the stimuli. Another confirmation was provided by a study with a different paradigm, which seems to measure the same underling inhibitory control ability (Montalbano et al., 2020) but does not involve issues related to social motivation or cues from different sensory modalities (Lucon-Xiccato & Bertolucci, 2019; Lucon-Xiccato et al., 2020b). In this task, the guppies were presented with live prey sealed inside a transparent tube to measure their capacity to progressively withhold their attack behaviour (figure 2b). Results confirmed the

two-fold sex difference favouring females (Lucon-Xiccato et al., 2020a; figure 2d). With a third inhibitory task, which required to enter a transparent cylinder to reach a food reward (figure 2c), the result observed was less clear as it varied according to the dependent variable analysed: females were faster in solving the task but less accurate compared to males (Lucon-Xiccato et al., 2020b; figure 2d).

Data on inhibitory control have been reported for other four teleost fish, including a hermaphroditic species (discussed in section 2.3). Another poeciliid fish, the mosquitofish, *Gambusia affinis*, was assayed in a detour task with a social reward (Wallace et al., 2020) and showed no effect of sex (figure 2d). Brandão and colleagues (2019) administered a detour task with food reward to an African cichlid, the Nile tilapia, *Oreochromis niloticus*. Both males and females learned the task, but females solved it faster than males (figure 2d). A modified version of the cylinder task, in which the cylinder was placed vertically, was used to study sticklebacks, *Gasterosteus aculeatus* (Keagy et al., 2019), resulting in males clearly outperforming females, with scores approximately three times higher (figure 2d). Interestingly, the higher inhibitory ability of female Nile tilapia and male sticklebacks was predicted based on the sex that provides parental care. Eggs and fry are highly preferred prey, but female Nile tilapia (Brandão et al., 2019) and male sticklebacks (Keagy et al., 2019) inhibit the behaviour of feeding on them to provide parental care.

Overall, evidence of sex differences in inhibitory control appears common in fish: it was detected in three out of four species investigated so far, and in all three families investigated (Poecilidae, Cichlidae, and Gasterosteidae). Studies on guppies are particularly interesting because of the replication with different paradigms. Three out of four measures of performance suggest that inhibitory capacities are greater in females of this species (figure 2d). One possible explanation for this sex difference might be the presence of selection acting on males for high persistence in trying to obtain mating (Rowe et al., 2005). Interestingly,

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223   results in guppies also suggest that the dependent variable collected might affect the outcome

224   of the experiments (see the variable 'correct responses' in Lucon-Xiccato et al., 2020b). This

225   is line with earlier reports on the importance of methodological aspects in fish cognition

226   research (Gatto et al., 2021; Gingins et al., 2018) and can limit our ability to compare the

227   results obtained in other species because each study used different paradigms.

228   Methodological replications and standardisation of experimental protocols are likely

229   important aspects to consider in future studies.

230

231   2.3 Sex differences in a hermaphroditic fish

232   Considering the studies in guppies analysed so far, it is interesting that females

233   showed in general much greater performance than males in both the discrimination reversal

234   learning and the detour task. This similarity may be due to two independent cognitive sex

235   differences or to a single cognitive sex difference that affects performance in both types of

236   task. For instance, one may argue that the reversal learning paradigm requires inhibition with

237   some extent, when the animal withholds the choice for the previously rewarded stimulus

238   (e.g., Tapp et al., 2003). While it is currently difficult to disentangle the two explanations

239   based on guppies' studies, a recent work with the cleaner fish, *Labroides dimidiatus*, has

240   provided interesting insights. *L. dimidiatus* is a protogynous hermaphroditic fish, in which the

241   males have previously been females. Triki and Bshary (2021) investigated sex differences in

242   this species with both the reversal learning task and the detour task with food reward.

243   Females showed enhanced performance compared with males in the detour task, but males

244   were better learners in the reversal learning task. This seems to support the idea that two EFs

245   are involved in the sex difference in discrimination reversal learning and the detour task.

246   Additionally, the results of this study support that selection on cognitive abilities that favour

247   one sex might determine intraspecific sexual conflict.

3. Do tetrapods display sex differences in executive functions?

Compared to fish literature, few studies in non-human tetrapods aimed at investigating sex differences in EFs. The cognitive literature in birds and mammals is, however, generally more extended compared to that of fish, encompassing many disciplines. Looking at this literature, I found EFs studies that analysed the effect of sex, even if this testing was not the primary goal of the experiment. In this section, I therefore discussed both studies aimed to test for sex differences and studies from other research fields.

3.1 Evidence in birds

A recent line of research by Lois-Milevicich and colleagues has focussed on sex differences in cognitive flexibility in cowbirds. In a first study on the shiny cowbird, *Molothrus bonariensis*, males and females were compared in the reversal learning using a shape discrimination and a left-right spatial discrimination task (Lois-Milevicich et al., 2021a). A sex difference favouring females was found in the former task, whereas the two sexes demonstrated similar performance in latter task (Lois-Milevicich et al., 2021a). In both cases, males and females did not show learning differences the initial association. In a second study, shiny cowbirds were tested along with a closely related species, the screaming cowbird, *Molothrus rufoaxillaris*, using a modified version of the reversal learning task (Lois-Milevicich et al., 2021b). The experimenters initially trained the subjects to retrieve a food reward indicated by both a colour and position cue; then, the colour cue was dissociated from the reward. Results confirmed greater cognitive flexibility in female shiny cowbirds, but no sex difference was found in the other species. Overall, the cowbird study system highlights both similarities and differences with the studies on reversal learning in poeciliid fish. As in poeciliids, congeneric species displayed variation in the sex difference, suggesting

the presence of species-specific selective pressures on cognitive flexibility of males and females. However, there was no result agreement between reversal learning variants in the species tested multiple times: *M. bonariensis* displayed sex differences only in two out of three reversal learning tasks. Notably, in the task with no sex differences (the spatial reversal learning), females' average performance was (non-significantly) higher compared to males (Lois-Milevicich et al., 2021a). Considering the low number of subjects tested (5 males and 6 females), it cannot be excluded that the experiments did not achieve sufficient power to detect a small sex difference. Before concluding that in this species the sex difference does not involve a cognitive flexibility function with general effects, it is important to conduct more experiments and possibly, analyse all the available data with a meta-analysis approach.

The literature in birds does not contain other studies performed to compare the two sexes in the reversal learning task. However, behavioural ecology studies have in some cases used this paradigm for other purposes and then included the effect of sex as predictor in the statistical analysis. Sex difference favouring males was found in zebra finches, *Taeniopygia guttata* (Brust et al., 2013) and no sex differences in six other avian species (*Aphelocoma coerulescens*, *Zenaida aurita*, *Amazona amazonica*, *Parus major*, *Nestor notabilis*, and *Corvus corax*; table 1). Therefore, sex differences in the reversal learning task in birds were reported in two out of nine species tested.

Considering inhibitory control, sex differences in birds were purposely investigated in one study on the effects of androgens by Rogers (1974). She found a greater performance of female chickens in a task in which subjects had to switch searching for food from an old to a novel location. Further data derives from other fields of cognitive research. In the pheasant *Phasianus colchicus*, two studies have reported contrasting results; one found no sex difference in the detour task (VanHorik et al., 2018) and the other found higher score of males in a task requiring to feed on a reward presented in changing locations (Meier et al.,

298   2017). In three other avian species, the sex was not a significant predictor of performance in

299   the cylinder task (Stow et al., 2018; Vernouillet et al., 2016).

300   Overall, birds displayed some evidence of sex differences in EFs, despite the low

301   number of studies focussing on this effect. It is worth noting that the absence of an effect in

302   great tits, *P. major*, and kea, *N. notabilis*, was confirmed by two independent studies,

303   strengthening the credibility of these null results.

304

305   3.2 Cognitive flexibility and inhibitory control in mammals

306   If we exclude humans (see Gaillard et al., 2021), literature in mammals contains only

307   a couple of studies aimed at searching sex differences in cognitive flexibility, and both were

308   performed in rodents. Guillamón and colleagues (1986) compared male and female

309   laboratory rats using a T-maze reversal learning task in which the two arms of the maze had

310   different colour. The two sexes showed no difference in the initial learning, but when the

311   reward contingency was reversed, females outperformed males. A study recently found no

312   sex differences in the bank vole, *Myodes glareolus* with a spatial reversal learning task

313   (Mazza et al., 2018).

314   As observed in birds, the lack of studies on sex differences in mammals can be

315   compensated by looking at the literature of other fields such as genetic and stress diseases

316   (table 1). In this literature, discrimination reversal learning studies evidenced sex differences

317   favouring females in pigs, *Sus domesticus,* and pigtailed macaque monkeys, *Macaca*

318   *nemestrina* (Ha et al., 2011; Roelofs et al., 2017). Conversely, reversal learning experiments

319   in other four mammalian species did not detect sex differences (dog: Brucks et al., 2017;

320   horse, *Equus ferus caballus*: Fiske & Potter, 1979; marmoset, *Callithrix jacchus*: LaClair &

321   Lacreuse, 2016; baboon, *Papio* sp.: Rodriguez et al., 2011).

322   Considering tasks aimed to study inhibition, a study reported difficulties in inhibit a

323   distraction in male rhesus monkeys, *Macaca mulatta*, compared to females (Loyant et al.,

324   2021). Studies on drugs abuse in laboratory rodents (mice and rats) have suggested that

325   generally males have more difficulties in inhibiting prepotent responses compared to females

326   (reviewed in Weafer & deWit, 2014). In the A-not-B task, in which subjects had to deal with

327   a stimulus that changed position across different trials, goats did not show sex differences

328   (Raoult et al., 2021). Last, studies on dogs' inhibitory control reported quite consistently a

329   similar performance in males and females with various tasks: cylinder task and A-not-B task

330   (Faganani et al., 2016); a task requiring to ignore a preferred, but unobtainable, food reward

331   (Bray et al., 2014); a battery of three inhibitory tasks (Brucks et al., 2017).

332   It is possible to conclude that literature in mammals provides evidence of sex

333   differences in cognitive flexibility and inhibitory control, possibly more often compared to

334   birds' literature. Also in this group, the number of studies with the aim of examining sex

335   differences is small.

336

337   3.3 Working memory in mammals

338   In mammals, an extended literature has investigated working memory. This form of

339   memory is recruited to work with information that is no longer perceptually present

340   (Diamond, 2013). Although determining the presence of sex differences was often not the

341   primary aim of the studies on working memory, evidence of such effect has been reported. A

342   study found that male rhesus monkeys were more proficient than females in a task requiring

343   memorising a set of locations (Lacreuse et al., 2005). In another primate, the marmoset, no

344   sex differences were reported in a similar task (LaClair & Lacreuse, 2016). In laboratory

345   rodents, a larger amount of data on working memory is available, especially with a task

346   called the radial arm maze. The apparatus consists in a central platform with a series of

347   (usually eight) radial arms containing a food reward. Working memory errors are recorded

348   when the subject enters a previously visited, and thus not baited anymore, arm. Sex

349   differences have been often reported with the radial maze (reviewed Jonasson, 2005) but

350   variability in the experimental protocol and rearing environment have produced results that

351   are difficult to interpret (reviewed Jonasson, 2005). For instance, Seymoure and colleagues

352   (1996) found greater performance of male rats in the radial arm maze. Conversely, Bimonte

353   and Denenberg (2000) analysed other task parameters and concluded that aspects of

354   performance different from working memory were involved in the sex difference. This

355   literature on working memory suggests that tetrapods might show sex differences in EFs

356   other than cognitive flexibility and inhibitory control. Research on working memory is

357   however restricted to very few taxa compared with that on cognitive flexibility and inhibitory

358   control.

359

360   3.4 Reptiles and amphibians

361   Data on sex differences in EFs are essentially absent in two main tetrapod groups

362   (figure 3). In reptiles, only one study analysed sex differences in discrimination reversal

363   learning, finding greater male performance (Szabo et al., 2018). In amphibians, no results on

364   sex differences in EFs have been published, to the best of my knowledge.

365

366   3.5 Comparison between tetrapods and teleost fish

367   Overall, sex differences in inhibition and flexibility were found in 40% mammalian

368   species and in almost 30% avian species investigated (figure 3). This occurrence is lower

369   compared to that observed in teleost fish (~70%). Evidently, these numbers might be affected

370   by variability in the number of species studies across taxa, which is reported in figure 3a. The

371   difference between fish and other groups might be also affected by the fact that few studies

were directly aimed at investigating sex differences in tetrapods. Lack of intentionality might have artefactually increase the occurrence of null findings by inflating type II errors. A few species of mammals and birds have been tested multiple times, usually finding consistent results in sex differences, such as for inhibitory control in dogs and reversal learning in mice and great tits. This suggests that at least part of the null results might be reliable. On the other hand, for some species, inconsistencies between studies associated with methodology have been detected, such as for pheasants. It is currently unclear whether this interspecific variability is due to methodological issues or involvement of different cognitive abilities to solve the two tasks. At the current stage, it is also difficult to exclude that the high occurrence of sex differences in fish was due to a publication bias towards significant results. Regarding data collected in guppies in my laboratory, this does not apply because we routinely publish also 'negative' results on sex differences (e.g., Lucon-Xiccato & Bisazza, 2016; Lucon-Xiccato & Bisazza, 2017b; Lucon-Xiccato & Dadda, 2016). A formal analysis of publication bias including other studies was not possible due to a restricted range in the studies' sample size (all the experiment but one tested between 10 to 15 subjects per sex).

Despite the uncertainties about the exact occurrence and difference between taxonomic lineages, this literature review clearly demonstrates that sex differences in EFs are potentially common in vertebrates including tetrapods.

4. Current challenges and future directions

The aforementioned records reveal several aspects of the literature that deserve attention in future research: studies show marked gaps in the taxonomy of the species and in the EFs investigated; the evolutionary causes and mechanisms have not been addressed; the consequences of sex differences in EFs are not clear. The present section of the review is intended to provide a starting point for future research aimed at addressing these aspects.

397

4.1 Literature gaps

The first literature gap highlighted by the review is related to taxonomic distribution of the species investigated. Most of the relevant research on EF sex differences has been conducted in teleost fish; the reason for this is unclear. Fish might have greater sex differences in EFs, perhaps because of their large sexual variability in ecology, mating system, brain and behaviour (Kotrschal et al., 2012; Magurran & Garcia, 2000). If this is true, it might have facilitated the discovery of EF sex differences in fish. Another explanation could be simply that this group has grown in importance concerning cognitive research in recent years (Brown et al., 2011; Bshary and Brown, 2014). This expansion might have prompted researchers to explore and develop new lines of investigation, including that of sex differences in EFs. Notably, within the teleost fish taxonomic gaps are also evident, with no data available for many important orders. The absence of data on the zebrafish, *Danio rerio*, is particularly unexpected given that this species is commonly used as model in behavioural research. Developing research in the zebrafish would be advantageous given the unique genetic and brain imaging tools available for this model.

In mammals and birds, part of the literature gap was filled with data retrieved in studies from other disciplines. This allowed the present review to detect evidence of sex differences in EFs even in the absence of studies with such goals. However, the question is open as to whether these studies allow one to deduct robust conclusions. If a study was intended to address the effect of a certain factor on an EF, testing males and females was probably an indirect consequence of random subjects' selection. Hence, the researchers might have not chosen a sample size adapted to statistically detect sex differences, inflating type II errors. It also worth noting that more data on this phenomenon might be present in the literature of other disciplines: many studies might have tested males and females in EF tasks

422   without then adding the sex as predictor in the statistical analysis. For both these reasons, the

423   literature on birds and mammals reported in this review likely underestimates the actual

424   presence of sex differences. The most evident literature gap regards amphibians and reptiles,

425   for which studies of sex differences are basically absent. The reason for this gap is probably

426   that cognitive research in these groups is still relatively scarce compared mammals, birds and

427   fish. Yet, knowledge in amphibians and reptiles remains important to unravel the evolution of

428   sex differences (Matsubara et al., 2017). Evidently, a priority for future research is to expand

429   the taxonomic coverage of data with studies specifically designed to test for sex differences

430   in EFs. This is also true for invertebrates. While they were not on the focus of this review,

431   they will undeniably provide interesting insights in the evolution of cognition. Some

432   invertebrate species can be tested with EF tasks (Hadar & Menzel, 2010) and have been

433   already studied for sex differences in learning (Tierney & Andrews, 2013).

434   The second main literature gap concerns the EFs investigated. Most of the studies

435   have measured cognitive flexibility and inhibitory control, and this bias cannot be entirely

436   explained by methodological limits. Appropriate paradigms to measure other EFs are indeed

437   available. For example, data on sex differences in working memory are absent in fish, despite

438   the development of aquatic versions of the radial maze (Hughes & Blight, 1999). It is also

439   striking that most research has focussed on discrimination reversal learning and detour tasks,

440   whereas paradigms commonly used in other research fields have not been deployed. For

441   instance, a large amount of the literature on inhibitory control exploits the A-not-B task (e.g.,

442   MacLean et al., 2014) or the delayed gratification task (Koepke et al., 2015; Aellen et al.,

443   2021). Increasing the number of EFs investigated and the number of tasks used per each EF is

444   paramount to obtain more reliable conclusions, particularly considering the potential

445   methodological inconsistencies between studies highlighted in this review. When more data

446   is available, a meta-analysis approach might be useful to evaluate the presence of the sex

447 differences (Miletto-Petrazzini et al., 2017). Cognitive differences within species, such as

448 between the two sexes, are expected to be small, thereby increasing the chance of type II

449 errors. A meta-analysis based on effect size should be more sensitive in detecting small

450 effects than the results of a single test with the conventional statistical approach.

451

452 4.2 Evolutionary causes of sex differences in executive functions

453   Because the literature is mostly descriptive, the evolutionary causes of sex differences

454 in EFs have not been addressed. However, current knowledge on cognitive evolution permits

455 speculation on various hypotheses, which require formal testing once the literature

456 encompasses more species. A first hypothesis derives from the observation of a conspicuous

457 variation in the presence and direction of EFs sex differences, including between closely

458 related species. Remarkably, the poeciliid family displayed all possible scenarios of sex

459 differences in the reversal learning task (*P. reticulata*: female > male; *P. mexicana:* female <

460 male; *P. latipinna*: female = male; figure 1). The observed variability is consistent with the

461 role of direct selection due to species-specific requirements. In the absence of such selection,

462 we would expect closely related species to display the same sex difference due to

463 phylogenetic signals, in disagreement with the observed data. Therefore, in some species, an

464 EF might be involved in the solution of a task that is more relevant for one of the two sexes,

465 causing direct selection for sex difference in such EF.

466   Sexual selection is perhaps the main candidate source for sex-specific requirements in

467 EFs (Cummings, 2018; Jones et al., 2003; Lucon-Xiccato & Bisazza, 2017a). For example,

468 female guppies' greater cognitive flexibility and inhibitory control might be associated with

469 females' highly flexible mate choice (Dugatkin & Godin, 1992; Gong & Gibson, 1996)

470 and/or male persistence in trying to mate (Magurran & Seghers, 1994). Accordingly, *P.*

471 *mexicana*, in which males showed higher flexibility compared to females, almost entirely

472   lacks male courtship displays (Ptacek, 2002). Similar interpretations may apply to mammals,

473   in which sex differences in discrimination reversal learning tasks exclusively favour females

474   (table 1). Findings in Nile tilapia and stickleback suggest that selection might be also driven

475   by parental cares (Brandão et al., 2019; Keagy et al., 2019). Data on birds supports this

476   hypothesis; in the Passeriformes, a taxon of mostly monogamous species, four out of six

477   species showed no sex difference in reversal learning (table 1). Other types of selection

478   deserve consideration, at least for some species. Quite commonly, a species shows sexual

479   niche segregation (Catry et al., 2006; Kie & Bowyer, 1999; Wearmouth & Sims, 2008),

480   arguably determining different ecological requirements for the two sexes. These ecological

481   differences might provide selection for sexual dimorphic cognition. Future studies should

482   address these hypotheses by taking into account species ecology and phylogeny.

483   Selection for cognitive sex differences in EFs might be favoured if they have greater

484   evolvability compared to other cognitive functions. Under this circumstance, if solving a task

485   with sex-specific relevance requires an EF and another, more specific cognitive function, then

486   selection is expected to act preferentially on the EF. Evolvability is considered the capacity to

487   generate phenotypic variability that is heritable (Kirschner & Gerhart, 1998). Heritable

488   variability in EFs is commonly observed in humans (Carlson & Moses, 2001; Friedman et al.,

489   2008; Schachar et al., 2010; Vogel & Machizawa, 2004) and recently, evidence is growing to

490   the phenomenon in other vertebrates such as primates (Völter et al., 2018), rodents (Kearns et

491   al., 2006), dogs (Gnanadesikan et al., 2020), birds (Meier et al., 2017; vanHorik et al., 2018),

492   and teleost fish (Buechel et al., 2018; Lucon-Xiccato & Bertolucci, 2020; Lucon-Xiccato et

493   al., 2019; Lucon-Xiccato et al., 2020a; Lucon-Xiccato et al., 2020b; Macario et al., 2021).

494   Critically, data on a fish and a mammal species suggest that EFs' variability is greater

495   compared to that of other cognitive functions (Bray et al., 2021; Lucon-Xiccato et al., 2020a),

496   which may determine greater evolvability for EFs. It remains difficult to validate this

497 hypothesis due of lack of extended comparisons between variability and heritability across

498 cognitive abilities. Different evolvability of cognitive traits is certainly a promising research

499 field, not only for understanding sex differences.

500   Most of the above hypotheses on why EF sex differences exist assume some form of

501 direct selection. However, direct selection might be not required. EFs are often related to

502 other traits that undergo sex-specific selection, which might indirectly cause the evolution of

503 sex differences in EFs. One of these relationships involves personality (Carere & Locurto,

504 2011), namely individual variation in behaviours such as exploration, boldness, and

505 sociability. Personality has genetic bases (Dochtermann et al., 2015), and its variability is

506 maintained by frequency-dependent selection due to fluctuating environmental conditions

507 (Dingemanse & Réale, 2005). Correlational studies have reported a significant relationship

508 between EFs and personality at the individual level in various species (Ferland et al., 2015;

509 Gomes et al., 2020; Lucon-Xiccato et al., 2019). Critically, the two sexes differ regarding

510 personality (Buirski et al., 1978; Irving & Brown, 2013). Considering all these points, it is

511 possible to hypothesise that selection acting on sex differences in personality might indirectly

512 cause the two sexes to also differ in the covarying EFs. Personality and other traits that

513 covary with EFs should therefore be considered as potential indirect sources of selection,

514 provided that the covariation has genetic bases.

515

516 4.3 Proximate mechanisms of sex differences in executive functions

517   Another unanswered question is related to the proximate mechanisms that selection

518 has targeted determining sex differences in EFs. Hormonal mechanisms are perhaps the most

519 promising to investigate. Hormonal levels often vary between the two sexes and have broad

520 effects on cognition and behaviour (Gray, 1971; Mills et al., 1997). For example, circulating

521 testosterone predicts spatial abilities in men (Silverman et al., 1999), and experimental

administration of exogenous testosterone increases rats' performance in spatial learning and

memory tasks (Hawley et al., 2013; Spritzer et al., 2011). Some studies suggest that

hormones have similar effects on EFs (Sanman et al., 1973; Wallin & Wood, 2015). For

instance, Rogers (1974) demonstrated that male chickens treated with testosterone showed

decreased ability to inhibit a learned response whereas they showed the opposite change

when treated with antiandrogens. A study in rats found that sex differences in reversal

learning can be reversed by female androgenisation and male orchidectomy (Guillamón et al.,

1986). These studies convey that hormones might be a mechanism at the base of sex

differences in EFs. Notably, the hormonal action can be of two kinds. Circulating hormones

might have modulatory effects that alter brain functioning, which is in line with most

experimental evidence (e.g., Guillamón et al., 1986). However, hormones might also have

organisational effects that trigger long-term changes in the brain anatomy and the neural

circuitry, especially during development (Falter & Davis, 2006). These organisational

changes might determine sex differences in EFs, although a test of this hypothesis in humans

provided no support (Wierenga et al., 2019).

Interestingly, one study reported that African striped mice, *Rhabdomys pumilio*,

display sex differences in reversal learning in winter, but the effect disappears in summer

(Rochais et al., 2021). This suggests possible seasonal variability in sex differences in EFs, as

observed for various other cognitive functions (e.g., Galea et al., 1996; López-Olmeda et al.,

2021). It is conceivable that eventual sexual differences related to reproduction would be

plastic in those species that do not reproduce through the entire year. Regarding the

mechanisms, seasonal cognitive fluctuations have been typically associated with seasonal

fluctuations in sexual hormones (Kimura & Hampson, 1994), reinforcing the need to

investigate hormonal effects on EFs.

546   Brain substrates are an additional factor to consider as they can determine sex

547   differences in EFs via various mechanisms. In humans, functional neuroimaging studies

548   strongly support the idea that sex differences in EFs are associated with differential activation

549   of neural networks (reviewed in Gaillart et al., 2021). In other species, we know too little

550   about fine brain functioning to properly test this hypothesis, although EFs' brain substrates

551   are beginning to be analysed in a few species (monkeys: Puig & Miller, 2015; rats: Kesner &

552   Churchwell, 2011; guppies: Triki et al., 2022). Some results are however promising. Brain

553   lateralisation, which is often different between the two sexes (e.g., Reddon & Hurd, 2008),

554   has been show to affects individuals' inhibitory control in fish (Lucon-Xiccato et al., 2020c).

555   Moreover, in sticklebacks, the sex with greater performance in an EF task has much larger

556   relative brain size compared to the other sex (Kotrschal et al., 2012). These data suggest an

557   involved of brain activation and structure on sex differences in EFs that deserves further

558   attention.

559   Besides hormonal effects and brain substrates, some mechanisms for sex differences

560   might be less obvious. Among the others, recent studies suggest a potential role of

561   neuropeptides: orexin affects reversal learning in mice in a sex-dependent manner (Durairaja

562   & Fendt, 2021). Moreover, a study in mice has reported that sex chromosomes also determine

563   reversal learning performance (Aarde et al., 2021). Future studies should evaluate these and

564   other mechanisms with a comprehensive approach.

565

566   4.4 Potential impact of sex differences in executive functions on cognitive performance

567   Sex differences in EFs might have profound impact on a range of cognitive tasks and

568   complex behaviour. A key characteristic of EFs is that they are recruited as building blocks of

569   more complex cognitive processes (reviewed in Diamond, 2013). Consequently, when an

570   animal handles a certain cognitive task, at least one EF is likely involved, along with more

specific abilities. The impact of EFs in various cognitive tasks is well-established in humans (Cain, 2006; Cragg & Gilmore, 2014; Shamosh & Gray, 2008). For example, individuals with higher inhibitory control scores tend to perform better in mathematical tasks (Gilmore et al., 2013). Research on cognitive traits covariation is less developed in other animal species, but growing evidence seems to support a widespread effect of EFs on cognitive performance (Beran & Hopkins, 2018; Chandra et al., 2000; Chow et al., 2019; Hauser et al., 2002; Müller et al., 2016). For instance, Beran and Hopkins (2018)' study of 40 chimpanzees reported positive correlations between performance in an inhibitory control task and the scores in several other cognitive tasks measuring tool use, gaze/point comprehension, object permanence, rotation, transposition, gesture production, attention-getting behaviours, and numerical abilities.

The effects of EFs on various cognitive processes lead to a prediction related to sex differences: if the two sexes differ in terms of an EF, then their cognitive performance is expected to differ, in the same direction, in all the tasks in which such an EF is involved. To the best of my knowledge, there have been no direct tests of this prediction yet. I performed an exploratory review of the literature on the species with more data related to cognitive sex differences, the guppy. Results seems to support the prediction: females, which possess more efficient EFs (section 2.1 and 2.3), outperformed males in 8 out of the 9 (chi-squared test: $X^2{}_1=5.444$, $P=0.020$) sex differences observed in other cognitive tasks (table 2).

The example of guppies leads to the conclusion that evolution of differences in EFs between the two sexes likely allows selection to produce well-differentiated cognitive phenotypes for males and females. For instance, if one sex is selected for greater cognitive flexibility, it should outperform the other sex in all situations requiring switches between different behavioural responses, such as when a resource is depleted and the animal is required to find a new source. In extreme circumstances, one can hypothesise that a sex

596   differences in EFs might even favour niche divergence between the two sexes. Cognitive

597   differences might (at least in part) contribute to the evolution of sexual segregation by

598   increasing the fitness of one sex in a certain environment. It will be critical to investigate

599   cognitive sex differences in a broader framework that includes a species' ecology to fully

600   understand their evolutionary consequences.

601   A second consequence of the broad impact of sex differences in EFs is that we might

602   need to re-evaluate some of the previously discovered sex differences in other cognitive

603   abilities. Many cognitive tasks for which sex differences have been reported, such as spatial

604   mazes, might be indeed affected by EFs. If this occurs, then the differential performance of

605   males and females (previously attributed to a specific cognitive ability) might be rather due to

606   the sex difference in EFs. This has been observed for sex differences in human working

607   memory that have been shown to explain previously reported sex differences in spatial

608   abilities (Kaufman, 2007; Wang & Carr, 2014). With this in mind, it should not be assumed

609   that all the sex differences depend on EFs (Postma et al., 2004). The most likely possibility is

610   that sex-specific selection might act on various abilities, targeting either an EFs, causing

611   therefore widespread effects, or a more specific cognitive trait. Factors such as differences in

612   evolvability discussed before might favour one situation over the other.

613   From an empirical point of view, a more comprehensive collection of data on

614   cognitive traits will help to identify which option better applies to each species. Batteries of

615   cognitive tasks are currently available for a few species of mammals and birds (e.g., Arden &

616   Adams, 2016; Beran & Hopkins, 2018; Damerius et al., 2019; Shaw et al., 2015) and could

617   be used for this purpose. These batteries of tests allow one to measure potentially dozens of

618   traits and therefore study their covariance and relative interference in cognitive tasks. The

619   structure of covariance between traits should be carefully considered in developing this

620   research strategy. Some psychological theories assume that one latent factor, known as

26

621 general intelligence or *g*, explains a large deal of cognitive variance (Plomin & Spinath,

622 2002). According to some authors, this general intelligence factor is strictly related to or

623 perhaps actually is an EF (Convay et al., 2003). These aspects are still highly debated in

624 human psychology and little understood outside the human species, but they should be not

625 ignored when dealing with EFs.

626

5. Conclusions

628   The literature on teleosts, mammals, and birds reveals that at least 40% of vertebrate

629 species and almost two out of three orders investigated display sex differences in EFs. If

630 these data are plotted across the entire vertebrate clade, sex differences in EFs might be

631 extremely common. This family of cognitive functions is worth investigating in future studies

632 of sex differences, along with those traditionally investigated such as spatial abilities. The

633 magnitude and direction of sex differences in EFs is highly variable and potentially

634 associated with sexual selection during mate choice and parental care. It is therefore

635 important to implement the current research with hypothesis-driven studies in species chosen

636 based on their mating system and other ecological traits. Critically, the marked gaps in the

637 species investigated should be filled to allow generalised conclusions. This review has also

638 underlined that sex differences in EFs could affect the entire cognitive phenotypes of males

639 and females. Intriguingly, the sex differences previously described in various cognitive tasks

640 might be at least partially due to sex differences in EFs, although this does not rule out that

641 sex differences might also evolve outside EFs. Studies that investigate EFs and other

642 cognitive functions simultaneously, and thereby dissect the structure and components of

643 cognitive sex differences, are necessary. Research on sex differences is a rapidly growing

644 field of animal cognition. As our understanding of how cognition evolves remains limited,

645 sex differences may provide an invaluable ground for testing evolutionary hypothesis and

646 unravelling selective mechanisms that cause two 'populations' of the same species to diverge.

647 In this line of research, it is paramount to start considering the role of EFs thoroughly, which

648 may account for a large portion of cognitive sex differences observed in a species.

649

656

657 **8. Declaration of interests**

658 None.

659

660 **9. References**

661 Aarde S.M., Genner R.M., Hrncir H., Arnold, A.P., Jentsch, J.D., 2021. Sex chromosome

662 complement affects multiple aspects of reversal-learning task performance in mice. Gen.

663 Brain Behav. 20, e12685.

664

665 Aellen M., Dufour V., Bshary R., 2021. Cleaner fish and other wrasse match primates in their

666 ability to delay gratification. Anim. Behav. 176, 125–143.

667

668 Arden R., Adams M.J., 2016. A general intelligence factor in dogs. Intelligence 55, 79–85.

669

670 Astié A.A., Kacelnik A., Reboreda J.C., 1998. Sexual differences in memory in shiny

671 cowbirds. Anim. Cogn. 1, 77–82.

672

673 Baddeley A., 1992. Working memory. Science 255, 556–559.

674

675 Barha C.K., Falck R. S. Davis J.C., Nagamatsu L. S., Liu-Ambrose T., 2017. Sex differences

676 in aerobic exercise efficacy to improve cognition: a systematic review and meta-analysis of

677 studies in older rodents. Front. Neuroendocrinol. 46, 86–105.

678

679 Bebus S.E., Small T.W., Jones B.C., Elderbrock E.K., Schoech S.J., 2016. Associative

680 learning is inversely related to reversal learning and varies with nestling corticosterone

681 exposure. Anim. Behav. 111, 251–260.

682

683 Beran M.J., 2015. The comparative science of "self-control": what are we talking about?.

684 Front. Psychol. 6, 51.

685

686 Beran M.J, Hopkins W.D., 2018. Self-control in chimpanzees relates to general intelligence.

687 Curr. Biol. 28, 574–579.

688

689 Beran M.J, Menzel C.R., Parrish A.E., Perdue B.M., Sayers K., Smith J.D., Washburn D.A.,

690 2016. Primate cognition: attention, episodic memory, prospective memory, self-control, and

691 metacognition as examples of cognitive control in nonhuman primates. Wiley Interdiscip.

692 Rev. Cogn. Sci. 7, 294–316.

693

694   Beran M.J., Savage-Rumbaugh E.S., Pate J.L., Rumbaugh D.M., 1999. Delay of gratification

695   in chimpanzees (*Pan troglodytes*). Dev. Psychobiol. 34, 119–127.

696

697   Beatty W.W., Aupperle R.L., 2002. Sex differences in cognitive impairment in multiple

698   sclerosis. Clin. Neuropsychol. 16, 472–480.

699

700   Bimonte H.A., Denenberg V.H., 2000. Sex differences in vicarious trial-and-error behavior

701   during radial arm maze learning. Physiol. Behav. 68, 495–499.

702

703   Bond A.B, Kamil A.C, Balda R.P., 2007. Serial reversal learning and the evolution of

704   behavioral flexibility in three species of North American corvids (*Gymnorhinus*

705   *cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). J. Comp. Psychol. 121,

706   372–379.

707

708   Boogert N.J., Madden J.R., Morand-Ferron J., Thornton A., 2018. Measuring and

709   understanding individual differences in cognition. Phil. Trans. Roy. Soc. B: Biol. Sci. 373,

710   20170280.

711

712   Boogert N.J., Monceau K., Lefebvre L., 2010. A field test of behavioural flexibility in

713   Zenaida doves (*Zenaida aurita*). Behav. Process. 85, 135–141.

714

715   Bray E.E., Gruen M.E., Gnanadesikan G.E., Horschler D.J., Levy K.M., Kennedy B.S., Hare

716   B., MacLean E.L., 2021. Dog cognitive development: a longitudinal study across the first 2

717   years of life. Anim. Cogn. 24, 311–328.

718

719   Bray E., MacLean E.L., Hare B.A., 2014. Context specificity of inhibitory control in dogs.

720   Anim. Cogn. 17, 15–31.

721

722   Brandão M.L., de Almeida Fernandes A.M.T., Gonçalves-de-Freitas E., 2019. Male and

723   female cichlid fish show cognitive inhibitory control ability. Sci. Rep. 9, 15795.

724

725   Brigman J.L., Feyder M., Saksida L.M., Bussey T.J., Mishina M., Holmes A., 2008. Impaired

726   discrimination learning in mice lacking the NMDA receptor NR2A subunit. Learn. Mem. 15,

727   50–54.

728

729   Briggs S.E., Godin J.G.J., Dugatkin L.A., 1996. Mate-choice copying under predation risk in

730   the Trinigadian guppy (*Poecilia reticulata*). Behav. Ecol. 7, 151–157.

731

732   Brown C., Laland K., Krause J., 2011. Fish cognition and behavior. Hoboken, New Jersey:

733   John Wiley & Sons.

734

735   Brucks D., Marshall-Pescini S., Wallis L.J., Huber L., Range F., 2017. Measures of dogs'

736   inhibitory control abilities do not correlate across tasks. Front. Psychol. 8, 849.

737

738   Brust V., Wuerz Y., Krüger O., 2013. Behavioural flexibility and personality in zebra

739   finches. Ethology 119, 559–569.

740

741   Bshary R., Brown C., 2014. Fish cognition. Curr. Biol. 24, R947–R950.

742

743   Bshary R., Wickler W., Fricke H., 2002. Fish cognition: a primate's eye view. Anim. Cogn. 5,

744   1–13.

745

746   Buirski P., Plutchik R., Kellerman H., 1978. Sex differences, dominance, and personality in

747   the chimpanzee. Anim. Behav. 26, 123–129.

748

749   Cain K., 2006. Individual differences in children's memory and reading comprehension: An

750   investigation of semantic and inhibitory deficits. Memory 14, 553–569.

751

752   Cain R.E., Wasserman M.C., Waterhouse B.D., McGaughy J.A., 2011. Atomoxetine

753   facilitates attentional set shifting in adolescent rats. Dev. Cogn. Neurosci. 1, 552–559.

754

755   Carazo P., Noble D.W., Chandrasoma D., Whiting M.J., 2014. Sex and boldness explain

756   individual differences in spatial learning in a lizard. Proc. R. Soc. B-Biol. Sci. 281,

757   20133275.

758

759   Carere C., Locurto C., 2011. Interaction between animal personality and animal cognition.

760   Curr. Zool. 57, 491–498.

761

762   Carlson S.M., Moses L.J., 2001. Individual differences in inhibitory control and children's

763   theory of mind. Child Dev. 72, 1032–1053.

764

765   Ruckstuhl K., Neuhaus P., 2006. Sexual segregation in vertebrates: ecology of the two sexes.

766   Cambridge University Press, Cambridge.

767

768 Chandra S.B., Hosler J.S., Smith B.H., 2000. Heritable variation for latent inhibition and its

769 correlation with reversal learning in honeybees (*Apis mellifera*). J. Comp. Psychol. 114, 86–

770 97.

771

772 Chiappe D., MacDonald K., 2005. The evolution of domain-general mechanisms in

773 intelligence and learning. J. Gen. Psychol. 132, 5–40.

774

775 Chow P.K.Y., Lea S.E., de Ibarra N.H., Robert T., 2019. Inhibitory control and memory in

776 the search process for a modified problem in grey squirrels, *Sciurus carolinensis*. Anim.

777 Cogn. 22, 645–655.

778

779 Conradt L., Clutton-Brock T.H., Guinness F.E., 2000. Sex differences in weather sensitivity

780 can cause habitat segregation: red deer as an example. Anim. Behav. 59, 1049–1060.

781

782 Conway A.R., Kane M.J., Engle R.W., 2003. Working memory capacity and its relation to

783 general intelligence. Trend. Cogn. Sci. 7, 547–552.

784

785 Cook P.F., Spivak M., Berns G., 2016. Neurobehavioral evidence for individual differences

786 in canine cognitive control: An awake fMRI study. Anim. Cogn. 19, 867–878.

787

788 Cragg L., Gilmore C., 2014. Skills underlying mathematics: The role of executive function in

789 the development of mathematics proficiency. Trend. Neurosci. Ed. 3, 63–68.

790

791 Croston R., Branch C.L., Kozlovsky D.Y., Dukas R., Pravosudov V.V., 2015. Heritability

792 and the evolution of cognitive traits. Behav. Ecol. 26, 1447–1459.

793

794 Cuevas K., Bell M.A., 2010. Developmental progression of looking and reaching

795 performance on the A-not-B task. Dev. Psychol. 46, 1363–1371.

796

797 Cummings M.E., 2018. Sexual conflict and sexually dimorphic cognition—reviewing their

798 relationship in poeciliid fishes. Behav. Ecol. Sociobiol. 72, 73.

799

800 Cussen V.A., Mench J.A., 2014. Performance on the Hamilton search task, and the influence

801 of lateralization, in captive orange-winged Amazon parrots (*Amazona amazonica*). Anim.

802 Cogn. 17, 901–909.

803

804 Day L.B., Crews D., Wilczynski W., 1999. Spatial and reversal learning in congeneric lizards

805 with different foraging strategies. Anim. Behav. 57, 393–407.

806

807 Damerius L.A., Burkart J.M., van Noordwijk M.A., Haun D.B., Kosonen Z.K., Galdikas

808 B.M., Saraswati Y., Kurniawan D., van Schaik C.P., 2019. General cognitive abilities in

809 orangutans (*Pongo abelii* and *Pongo pygmaeus*). Intelligence, 74, 3–11.

810

811 Danisman E., Bshary R., Bergmüller R., 2010. Do cleaner fish learn to feed against their

812 preference in a reverse reward contingency task?. Anim. Cogn. 13, 41–49.

813

814 Diamond A., 1990. Developmental time course in human infants and infant monkeys, and the

815 neural bases of, inhibitory control in reaching a. Ann. New York Acad. Sci. 608, 637–676.

816

817 Diamond A., 2013. Executive functions. Ann. Rev. Psychol. 64, 135–168.

818

819   Dingemanse N.J., Réale D., 2005. Natural selection and animal personality. Behaviour 142,

820   1159–1184.

821

822   Dochtermann N.A., Schwab T., Sih A.., 2015. The contribution of additive genetic variation

823   to personality variation: heritability of personality. Proc. R. Soc. B-Biol. Sci. 282, 20142201.

824

825   Dugatkin L.A., Godin J.G.J., 1992. Reversal of female mate choice by copying in the guppy

826   (*Poecilia reticulata*). Proc. R. Soc. B-Biol. Sci. 249, 179–184.

827

828   Duff S.J., Hampson E., 2001. A sex difference on a novel spatial working memory task in

829   humans. Brain Cogn. 47, 470–493.

830

831   Durairaja A. Fendt M., 2021. Orexin deficiency modulates cognitive flexibility in a sex-

832   dependent manner. Gen. Brain Behav. 20, e12707.

833

834   Fagnani J., Barrera G., Carballo F., Bentosela M., 2016. Is previous experience important for

835   inhibitory control? A comparison between shelter and pet dogs in A-not-B and cylinder tasks.

836   Anim. Cogn. 19, 1165–1172.

837

838   Falter C.M., Arroyo M., Davis G., 2006. Testosterone: Activation or organization of spatial

839   cognition?. Biol. Psychol. 73, 132–140.

840

841   Faure J.B., Marques-Carneiro J.E., Akimana G., Cosquer B., Ferrandon A., Herbeaux K.,

842   Koning E., Barbelivien A., Nehlig A., Cassel J.B., 2014. Attention and executive functions in

843   a rat model of chronic epilepsy. Epilepsia 55, 644–653.

844

845   Ferland J.M.N., Zeeb F.D., Yu K., Kaur S., Taves M.D., Winstanley C.A., 2014. Greater

846   sensitivity to novelty in rats is associated with increased motor impulsivity following

847   repeated exposure to a stimulating environment: implications for the etiology of impulse

848   control deficits. Eur. J. Neurosci. 40, 3746–3756.

849

850   Fiske J.C, Potter G.D., 1979. Discrimination reversal learning in yearling horses. J. Anim.

851   Sci. 49, 583–588.

852

853   Friedman N.P., Miyake A., Young S.E., DeFries J.C., Corley R.P., Hewitt J.K., 2008.

854   Individual differences in executive functions are almost entirely genetic in origin. J. Exp.

855   Psychol. 137, 201–225.

856

857   Fuss T., Flöck S., Witte K., 2021. Sex-specific cognitive flexibility in Atlantic mollies when

858   learning from male demonstrators exploring a new food source. Anim. Behav. 173, 9–19.

859

860   Fuss T., Witte K., 2019. Sex differences in color discrimination and serial reversal learning in

861   mollies and guppies. Curr. Zool. 65, 323–332.

862

863   Gaillard A, Fehring D.J., Rossell S.L., 2021. Sex differences in executive control: A

864   systematic review of functional neuroimaging studies. Eur. J. Neurosci. 53, 2592–2611.

865

866   Galea L.A., Kavaliers M., Ossenkopp K.P., 1996. Sexually dimorphic spatial learning in

867   meadow voles *Microtus pennsylvanicus* and deer mice *Peromyscus maniculatus*. J. Exp. Biol.

868   199, 195–200.

869

870   Gatto E., Lucon-Xiccato T., Bisazza A., 2018. Factors affecting the measure of inhibitory

871   control in a fish (*Poecilia reticulata*). Behav. Process. 157, 11–17.

872

873   Gatto E., Santacà M., Verza I., Dadda M., Bisazza A., 2021. Automated operant conditioning

874   devices for fish. Do they work?. Animals 11, 1397.

875

876   Gaulin S.J., FitzGerald R.W., 1986. Sex differences in spatial ability: an evolutionary

877   hypothesis and test. Am. Nat. 127, 74–88.

878

879   Geary D.C., 1996. Sexual selection and sex differences in mathematical abilities. Behav.

880   Brain Sci. 19, 229–247.

881

882   Gilmore C., Attridge N., Clayton S., Cragg L., Johnson S., Marlow N., Simms V., Inglis M.,

883   2013. Individual differences in inhibitory control, not non-verbal number acuity, correlate

884   with mathematics achievement. PLoS One 8, e67374.

885

886   Gingins S., Marcadier F., Wismer S., Krattinger O., Quattrini F., Bshary R., Binning S.A.

887   2018. The performance of cleaner wrasse, *Labroides dimidiatus*, in a reversal learning task

888   varies across experimental paradigms. PeerJ 6, e4745.

889

890   Gnanadesikan G.E., Hare B., Snyder-Mackler N., MacLean E.L., 2020. Estimating the

891   heritability of cognitive traits across dog breeds reveals highly heritable inhibitory control

892   and communication factors. Anim. Cogn. 23, 953–964.

893

894   Gomes A.C.R., Guerra S., Silva P.A., Marques C.I., Trigo S., Boogert N.J., Cardoso G.C.,

895   2020. Proactive common waxbills make fewer mistakes in a cognitive assay, the detour-

896   reaching task. Behav. Ecol. Sociobiol. 74, 1–15.

897

898   Gong A., Gibson R.M., 1996. Reversal of a female preference after visual exposure to a

899   predator in the guppy, *Poecilia reticulata*. Anim. Behav. 52, 1007–1015.

900

901   Gray J.A., 1971. Sex differences in emotional behaviour in mammals including man:

902   endocrine bases. Acta Psychol. 35, 29–46.

903

904   Griffiths S.W., Magurran A.E., 1998. Sex and schooling behaviour in the Trinidadian guppy.

905   Anim. Behav. 5, 689–693.

906

907   Guigueno M.F., Snow D.A., MacDougall-Shackleton S.A., Sherry D.F., 2014. Female

908   cowbirds have more accurate spatial memory than males. Biol. Lett. 10, 20140026.

909

910   Guillamón A., Valencia A., Calés J., Segovia S., 1986. Effects of early postnatal gonadal

911   steroids on the successive conditional discrimination reversal learning in the rat. Physiol.

912   Behav. 38, 845–849.

913

914 Ha J.C., Mandell D.J., Gray J., 2011. Two-item discrimination and Hamilton search learning

915 in infant pigtailed macaque monkeys. Behav. Process. 86, 1–6.

916

917 Hadar R., Menzel R., 2010. Memory formation in reversal learning of the honeybee. Front.

918 Behav. Neurosci. 4, 186.

919

920 Halpern D.F., 2000. Sex differences in cognitive abilities. Psychology Press, New York.

921

922 Happel M.F., Niekisch H., Rivera L.L.C., Ohl F.W., Deliano M., Frischknecht R., 2014.

923 Enhanced cognitive flexibility in reversal learning induced by removal of the extracellular

924 matrix in auditory cortex. Proc. Nat. Acad. Sci. 111, 2800–2805.

925

926 Hauser M.D., Santos L.R., Spaepen G.M., Pearson H.E., 2002. Problem solving, inhibition

927 and domain-specific experience: experiments on cottontop tamarins, *Saguinus oedipus*.

928 Anim. Behav. 64, 387–396.

929

930 Hawley W.R., Grissom E.M., Martin R.C., Halmos M.B., Bart C.L., Dohanich G.P., 2013.

931 Testosterone modulates spatial recognition memory in male rats. Horm. Behav. 63, 559–565.

932

933 Healy S.D., Bacon I.E., Haggis O., Harris A.P., Kelley L.A., 2009. Explanations for variation

934 in cognitive ability: behavioural ecology meets comparative cognition. Behav. Proc. 80, 288–

935 294.

936

937 Hermer E., Cauchoix M., Chaine A.S., Morand-Ferron J., 2018. Elevation-related difference

938 in serial reversal learning ability in a nonscatter hoarding passerine. Behav. Ecol. 29, 840–

939 847.

940

941 Hughes R.N., Blight C.M., 1999. Algorithmic behaviour and spatial memory are used by two

942 intertidal fish species to solve the radial maze. Anim. Behav. 58, 601–613.

943

944 Irving E., Brown C., 2013. Examining the link between personality and laterality in a feral

945 guppy *Poecilia reticulata* population. J. Fish Biol. 83, 311–325.

946

947 Jonasson Z., 2005. Meta-analysis of sex differences in rodent models of learning and

948 memory: a review of behavioral and biological data. Neurosci. Biobehav. Rev. 28, 811–825.

949

950 Jones C.M., Braithwaite V.A., Healy S.D., 2003. The evolution of sex differences in spatial

951 ability. Behav. Neurosci. 117, 403–411.

952

953 Jonson K.M., Lyle J.G., Edwards M.J., Penny R.H., 1976. Effect of prenatal heat stress on

954 brain growth and serial discrimination reversal learning in the guinea pig. Brain Res. Bull. 1,

955 133–150.

956

957 Kaufman S.B., 2007. Sex differences in mental rotation and spatial visualization ability: Can

958 they be accounted for by differences in working memory capacity?. Intelligence 35, 211–223.

959

960 Keagy J., Minter R., Tinghitella R.M., 2019. Sex differences in cognition and their

961 relationship to male mate choice. Curr. Zool. 65, 285–293.

962

963   Kearns D.N., Gomez-Serrano M.A., Weiss S.J., Riley A.L., 2006. A comparison of Lewis

964   and Fischer rat strains on autoshaping (sign-tracking), discrimination reversal learning and

965   negative automaintenance. Behav. Brain Res. 169, 193–200.

966

967   Kesner R.P., Churchwell J.C., 2011. An analysis of rat prefrontal cortex in mediating

968   executive function. Neurobiol. Learn. Mem. 96, 417–431.

969

970   Kie J.G., Bowyer, R.T., 1999. Sexual segregation in white-tailed deer: density-dependent

971   changes in use of space, habitat selection, and dietary niche. J. Mammal. 80, 1004–1020.

972

973   Kimura D., Hampson E., 1994. Cognitive pattern in men and women is influenced by

974   fluctuations in sex hormones. Cur. Dir. Psychol. Sci. 3, 57–61.

975

976   Kirkish P.M., Fobes J.L., Richardson A.M., 1979. Spatial reversal learning in the lizard

977   *Coleonyx variegatus*. Bull. Psychon. Soc. 13, 265–267.

978

979   Kirschner M., Gerhart J., 1998. Evolvability. Proc. Nat. Acad. Sci. 95, 8420–8427.

980

981   Koepke A.E., Gray S.L., Pepperberg I.M., 2015. Delayed gratification: A grey parrot

982   (*Psittacus erithacus*) will wait for a better reward. J. Comp. Psychol. 129, 339–346.

983

984   Komischke B., Giurfa M., Lachnit H., Malun D., 2002. Successive olfactory reversal learning

985   in honeybees. Learn. Mem. 9, 122–129.

986

987 Kotrschal A., Räsänen K., Kristjansson B.K., Senn M., Kolm N., 2012. Extreme sexual brain

988 size dimorphism in sticklebacks: a consequence of the cognitive challenges of sex and

989 parenting?. PLoS One 7, e30055.

990

991 LaClair M., Lacreuse A., 2016. Reversal learning in gonadectomized marmosets with and

992 without hormone replacement: are males more sensitive to punishment?. Anim. Cogn. 19,

993 619–630.

994

995 Lacreuse A., Kim C.B., Rosene D.L., Killiany R.J., Moss M.B., Moore T.L., Chennareddi L.,

996 Herndon J.G., 2005. Sex, age, and training modulate spatial memory in the rhesus monkey

997 (*Macaca mulatta*). Behav. Neurosci. 119, 118.

998

999 Laland K.N., Reader S.M., 1999. Foraging innovation in the guppy. Anim. Behav. 57, 331–

1000 340.

1001

1002 Laschober M., Mundry R., Huber L., Schwing R., 2021. Kea (*Nestor notabilis*) show

1003 flexibility and individuality in within-session reversal learning tasks. Anim. Cogn. 24, 1339–

1004 1351.

1005

1006 Leger M., Neill J.C., 2016. A systematic review comparing sex differences in cognitive

1007 function in schizophrenia and in rodent models for schizophrenia, implications for improved

1008 therapeutic strategies. Neurosci. Biobehav. Rev. 68, 979–1000.

1009

1010 Li R., Singh M., 2014. Sex differences in cognitive impairment and Alzheimer's disease.

1011 Front. Neuroendocrinol. 35, 385–403.

1012

1013 Lois-Milevicich J., Cerrutti M., Kacelnik A., Reboreda J.C., 2021a. Sex differences in

1014 learning flexibility in an avian brood parasite, the shiny cowbird. Behav. Proc. 104438.

1015

1016 Lois-Milevicich J., Kacelnik A., Reboreda J.C., 2021b. Sex differences in the use of spatial

1017 cues in two avian brood parasites. Anim. Cogn. 24, 205–212.

1018

1019 Loyant L., Waller B.M., Micheletta J., Joly M., 2021. Heterogeneity of performances in

1020 several inhibitory control tasks: male rhesus macaques are more easily distracted than

1021 females. Roy. Soc. Open Sci. 8, 211564.

1022

1023 López-Olmeda J.F., Zhao H., Reischl M., Pylatiuk C., Lucon-Xiccato T., Loosli F., Foulkes

1024 N.S., 2021. Long photoperiod impairs learning in male but not female medaka. Iscience 24,

1025 102784.

1026

1027 Lucon-Xiccato T., Bertolucci C., 2019. Guppies show rapid and lasting inhibition of foraging

1028 behaviour. Behav. Process. 164, 91–99.

1029

1030 Lucon-Xiccato T., Bertolucci C., 2020. Inhibitory control in zebrafish, *Danio rerio*. J. Fish

1031 Biol. 97, 416–423.

1032

1033 Lucon-Xiccato T., Bisazza A., 2014. Discrimination reversal learning reveals greater female

1034 behavioural flexibility in guppies. Biol. Lett. 10, 20140206.

1035

1036   Lucon-Xiccato T, Bisazza A., 2016. Male and female guppies differ in speed but not in

1037   accuracy in visual discrimination learning. Anim. Cogn. 19, 733–744.

1038

1039   Lucon-Xiccato T., Bisazza A., 2017a. Individual differences in cognition among teleost

1040   fishes. Behav. Process. 141, 184–195.

1041

1042   Lucon-Xiccato T., Bisazza A., 2017b. Sex differences in spatial abilities and cognitive

1043   flexibility in the guppy. Anim. Behav. 123, 53–60.

1044

1045   Lucon-Xiccato T., Bisazza A., 2017c. Complex maze learning by fish. Anim. Behav. 125,

1046   69–75.

1047

1048   Lucon-Xiccato T., Bisazza A., Bertolucci C., 2020a. Guppies show sex and individual

1049   differences in the ability to inhibit behaviour. Anim. Cogn. 23, 535–543.

1050

1051   Lucon-Xiccato T., Dadda,M., 2016. Guppies show behavioural but not cognitive sex

1052   differences in a novel object recognition test. PLoS One 11, e0156589.

1053

1054   Lucon-Xiccato T., Dadda M., Bisazza A., 2016. Sex differences in discrimination of shoal

1055   size in the guppy (*Poecilia reticulata*). Ethology 122, 481–491.

1056

1057   Lucon-Xiccato T., Gatto E., Bisazza A., 2020b. Male and female guppies differ in problem-

1058   solving abilities. Curr. Zool. 66, 83–90.

1059

1060   Lucon-Xiccato T., Montalbano G., Bertolucci C., 2019. Personality traits covary with

1061   individual differences in inhibitory abilities in 2 species of fish. Curr. Zool. 66, 187–195.

1062

1063   Lucon-Xiccato T., Montalbano G., Dadda M., Bertolucci C., 2020c. Lateralization correlates

1064   with individual differences in inhibitory control in zebrafish. Biol. Lett. 16, 20200296

1065

1066   Lucon-Xiccato T., Gatto E., Bisazza A., 2017. Fish perform like mammals and birds in

1067   inhibitory motor control tasks. Sci. Rep. 7, 13144.

1068

1069   Luine V.N., Dohanich G., 2008. Sex differences in cognitive function in rodents, in: Becker

1070   J.B., Berkley KJ., Geary N (Eds.), Sex differences in the brain: from genes to behavior.

1071   Oxford University Press, Oxford, pp. 227–252.

1072

1073   Luine V., Gomez J., Beck K., Bowman R., 2017. Sex differences in chronic stress effects on

1074   cognition in rodents. Pharmacol. Biochem. Behav. 152, 13–19.

1075

1076   Macario A., Darden S.K., Verbruggen F., Croft D.P., 2021. Intraspecific variation in

1077   inhibitory motor control in guppies, *Poecilia reticulata*. J. Fish Biol. 98, 317–328.

1078

1079   Mackintosh J., 1962. An investigation of reversal learning in *Octopus vulgaris* Lamarck. Q. J.

1080   Exp. Psychol. 14, 15–22.

1081

1082   MacLean E.L., Hare B., Nunn C.L., Addessi E., Amici F., et al., 2014. The evolution of self-

1083   control. Proc. Nat. Acad. Sci. 111, E2140–E2148.

1084

1085   Magurran A.E., Garcia C.M., 2000. Sex differences in behaviour as an indirect consequence

1086   of mating system. J. Fish Biol. 57, 839–857.

1087

1088   Magurran A.E., Seghers B.H., 1994. Sexual conflict as a consequence of ecology: evidence

1089   from guppy, *Poecilia reticulata*, populations in Trinidad. Proc. R. Soc. B-Biol. Sci. 255, 31–

1090   36.

1091

1092   Matsubara S., Deeming D.C., Wilkinson A., 2017. Cold-blooded cognition: new directions in

1093   reptile cognition. Curr. Op. Behav. Sci. 16, 126–130.

1094

1095   Mazza V., Eccard J.A., Zaccaroni M., Jacob J., Dammhahn M., 2018. The fast and the

1096   flexible: cognitive style drives individual variation in cognition in a small mammal. Anim.

1097   Behav. 137, 119–132.

1098

1099   Meier C., Pant S.R., van Horik J.O., Laker P.R., Langley E.J., Whiteside M.A., Verbruggen

1100   F., Madden J.R., 2017. A novel continuous inhibitory-control task: variation in individual

1101   performance by young pheasants (*Phasianus colchicus*). Anim. Cogn. 20, 1035–1047.

1102

1103   Miletto Petrazzini M.E., Bisazza A., Agrillo C., Lucon-Xiccato T., 2017. Sex differences in

1104   discrimination reversal learning in the guppy. Anim. Cogn. 20, 1081–1091.

1105

1106   Miletto Petrazzini M.E., Lucon-Xiccato T., Agrillo C., Bisazza A., 2015. Use of ordinal

1107   information by fish. Sci. Rep. 5, 15497.

1108

1109   Miller D.I., Halpern, D.F., 2014. The new science of cognitive sex differences. Trend. Cogn.

1110   Sci. 18, 37–45.

1111

1112   Mills A.D., Crawford L.L., Domjan M., Faure J.M., 1997. The behavior of the Japanese or

1113   domestic quail *Coturnix japonica*. Neurosci. Biobehav. Rev. 21, 261–281.

1114

1115   Montalbano G., Bertolucci C., Lucon-Xiccato T. 2020. Measures of inhibitory control

1116   correlate between different tasks but do not predict problem-solving success in a fish,

1117   *Poecilia reticulata*. Intelligence 82, 101486.

1118

1119   Müller C.A., Riemer S., Virányi Z., Huber L., Range F., 2016. Inhibitory control, but not

1120   prolonged object-related experience appears to affect physical problem-solving performance

1121   of pet dogs. PLoS One 11, e0147753.

1122

1123   O'Hara M., Huber L., Gajdon G.K., 2015. The advantage of objects over images in

1124   discrimination and reversal learning by kea, *Nestor notabilis*. Anim. Behav. 101, 51–60.

1125

1126   Oliveira R.F., 2013. Mind the fish: zebrafish as a model in cognitive social neuroscience.

1127   Front. Neur. Circ. 7, 131.

1128

1129   Perdue B.M., Snyder R.J., Zhihe Z., Marr M.J., Maple T.L., 2011. Sex differences in spatial

1130   ability: a test of the range size hypothesis in the order Carnivora. Biol. Lett. 7, 380–383.

1131

1132   Plomin R., Spinath F.M., 2002. Genetics and general cognitive ability (g). Trend. Cogn. Sci.

1133   6, 169–176.

1134

1135 Postma A., Jager G., Kessels R.P., Koppeschaar H.P., van Honk J., 2004. Sex differences for

1136 selective forms of spatial memory. Brain Cogn. 54, 24–34.

1137

1138 Pouca C.V., Brown C., 2017. Contemporary topics in fish cognition and behaviour. Curr. Op.

1139 Behav. Sci. 16, 46–52.

1140

1141 Ptacek M.B., 2002. Patterns of inheritance of mating signals in interspecific hybrids between

1142 sailfin and shortfin mollies (Poeciliidae: *Poecilia*: *Mollienesia*). Genetica 116, 329–342.

1143

1144 Puig M.V., Miller E.K., 2015. Neural substrates of dopamine D2 receptor modulated

1145 executive functions in the monkey prefrontal cortex. Cereb. Cort. 25, 2980–2987.

1146

1147 Range F., Bugnyar T., Schlögl C., Kotrschal K., 2006. Individual and sex differences in

1148 learning abilities of ravens. Behav. Process. 73, 100–106.

1149

1150 Raoult C.M.C., Osthaus B., Hildebrand A.C.G., McElligott A.G., Nawroth C., 2021. Goats

1151 show higher behavioural flexibility than sheep in a spatial detour task. Roy. Soc. Open Sci. 8,

1152 201627.

1153

1154 Reader S.M., Laland K.N., 2000. Diffusion of foraging innovations in the guppy. Anim.

1155 Behav. 60, 175–180.

1156

1157 Reddon A.R., Hurd P.L., 2008. Aggression, sex and individual differences in cerebral

1158 lateralization in a cichlid fish. Biol. Lett. 4, 338–340.

1159

Reynolds J.D., 1996. Animal breeding systems. Trend. Ecol. Evol. 11, 68–72.

1161

Rodriguez J.S., Paule M.G., 2009. Working memory delayed response tasks in monkeys. In

Methods of Behavior Analysis in Neuroscience. Boca Raton, Florida: CRC Press/Taylor &

Francis.

1165

Rodriguez J.S., Zürcher N.R., Keenan K.E., Bartlett T.Q., Nathanielsz P.W., Nijland M.J.,

2011. Prenatal betamethasone exposure has sex specific effects in reversal learning and

attention in juvenile baboons. Am. J. Obstet. Gynecol. 204, 545-e1.

1169

Roelofs S., Nordquist R.E., van der Staay F.J., 2017. Female and male pigs' performance in a

spatial holeboard and judgment bias task. App. Anim. Behav. Sci. 191, 5–16.

1172

Rogers L.J., 1974. Persistence and search influenced by natural levels of androgens in young

and adult chickens. Physiol. Behav. 12, 197–204.

1175

Rosati A.G., 2017. Foraging cognition: reviving the ecological intelligence hypothesis.

Trend. Cogn. Sci. 21, 691–702.

1178

Rowe L., Cameron E., Day T., 2005. Escalation, retreat, and female indifference as

alternative outcomes of sexually antagonistic coevolution. Am. Nat. 165, S5–S18.

1181

Rowe C., Healy S.D., 2014. Measuring variation in cognition. Behav. Ecol. 25, 1287–1292.

1183

1184   Salas C. Broglio C. Rodríguez F., 2003. Evolution of forebrain and spatial cognition in

1185   vertebrates: conservation across diversity. Brain Behav. Evol. 62, 72–82.

1186

1187   Sandman C.A., Alexander W.D., Kastin A.J., 1973. Neuroendocrine influences on visual

1188   discrimination and reversal learning in the albino and hooded rat. Physiol. Behav. 11, 613–

1189   617.

1190

1191   Santacà M., Busatta M., Lucon-Xiccato T., Bisazza A., 2019. Sensory differences mediate

1192   species variation in detour task performance. Anim. Behav. 155, 153–162.

1193

1194   Saucier D.M., Shultz S.R., Keller A.J., Cook C.M., Binsted G., 2008. Sex differences in

1195   object location memory and spatial navigation in Long-Evans rats. Anim. Cogn. 11, 129–137.

1196

1197   Schachar R.J., Forget-Dubois N., Dionne G., Boivin M., Robaey P., 2010. Heritability of

1198   response inhibition in children. J. Int. Neuropsychol. Soc. 17, 238–247.

1199

1200   Seymoure P., Dou H.U.I., Juraska J.M., 1996. Sex differences in radial maze performance:

1201   influence of rearing environment and room cues. Psychobiology 24, 33–37.

1202

1203   Shamosh N.A., Gray J.R., 2008. Delay discounting and intelligence: A meta-analysis.

1204   Intelligence 36, 289–305.

1205

1206   Shaw R.C., Boogert N.J., Clayton N.S., Burns K.C., 2015. Wild psychometrics: evidence for

1207   'general'cognitive performance in wild New Zealand robins, *Petroica longipes*. Anim.

1208   Behav. 109, 101–111.

1209

1210 Sherry D.F., 2006. Neuroecology. Annu. Rev. Psychol. 57, 167–197.

1211

1212 Shettleworth S.J., 1972. Constraints on learning. Adv. Stud. Behav. 4, 1–68.

1213

1214 Shettleworth S.J., 2009. Cognition, evolution, and behavior. Oxford, U.K.: Oxford University

1215 Press.

1216

1217 Silverman I., Kastuk D., Choi J., Phillips K., 1999. Testosterone levels and spatial ability in

1218 men. Psychoneuroendocrinol. 24, 813–822.

1219

1220 Spelke E.S., 2005. Sex differences in intrinsic aptitude for mathematics and science?: a

1221 critical review. Am. Psychol. 60, 950–958.

1222

1223 Spritzer M.D., Daviau E.D., Coneeny M.K., Engelman S.M., Prince W.T., Rodriguez-

1224 Wisdom K.N., 2011. Effects of testosterone on spatial learning and memory in adult male

1225 rats. Horm. Behav. 59, 484–496.

1226

1227 Stow M.K., Vernouillet A., Kelly D.M., 2018. Neophobia does not account for motoric self-

1228 regulation performance as measured during the detour-reaching cylinder task. Anim. Cogn.

1229 21, 565–574.

1230

1231 Szabo B., Noble D.W., Byrne R.W., Tait D.S., Whiting M.J., 2018. Subproblem learning and

1232 reversal of a multidimensional visual cue in a lizard: evidence for behavioural flexibility?.

1233 Anim. Behav. 144, 17–26.

1234

1235 Szabo B., Noble D.W., Whiting M.J., 2019b. Context-specific response inhibition and

1236 differential impact of a learning bias in a lizard. Anim. Cogn. 22, 317–329.

1237

1238 Szabo B., Whiting M.J., Noble D.W., 2019a. Sex-dependent discrimination learning in

1239 lizards: a meta-analysis. Behav. Process. 164, 10–16.

1240

1241 Tapp P.D., Siwak C.T., Estrada J., Head E., Muggenburg B.A., Cotman C.W., Milgram

1242 N.W., 2003. Size and reversal learning in the beagle dog as a measure of executive function

1243 and inhibitory control in aging. Learn. Mem. 10, 64–73.

1244

1245 Tierney A.J., Andrews K., 2013. Spatial behavior in male and female crayfish (*Orconectes*

1246 *rusticus*): learning strategies and memory duration. Anim. Cogn. 16, 23–34.

1247

1248 Titulaer M., van Oers K., Naguib M., 2012. Personality affects learning performance in

1249 difficult tasks in a sex-dependent way. Anim. Behav. 83, 723–730.

1250

1251 Triki Z, Bshary R., 2021. Sex differences in the cognitive abilities of a sex-changing fish

1252 species *Labroides dimidiatus*. Roy. Soc. Open Sci. 8, 210239.

1253

1254 Triki Z., Fong S., Amcoff M., Kolm N., 2022. Artificial mosaic brain evolution of relative

1255 telencephalon size improves inhibitory control abilities in the guppy (*Poecilia reticulata*).

1256 Evolution 76, 128–138.

1257

1258 van Horik J.O., Langley E.J., Whiteside M.A., Laker P.R., Beardsworth C.E., Madden J.R.,

1259 2018. Do detour tasks provide accurate assays of inhibitory control?. Proc. R. Soc. B-Biol.

1260 Sci. 285, 20180150.

1261

1262 van Horik J.O., Beardsworth C.E., Laker P.R., Whiteside M.A., Madden J.R., 2020.

1263 Response learning confounds assays of inhibitory control on detour tasks. Anim. Cogn. 23,

1264 215–225.

1265

1266 Vannuchi C. R., Costa C.S., de Jesus F.M., Maior R.S., Barros M., 2020. Sex, diurnal

1267 variation and retention interval differently affect performance of marmoset monkeys in a

1268 recognition memory task for object location. Behav. Brain Res. 379, 112334.

1269

1270 Vernouillet A., Anderson J., Clary D., Kelly D.M., 2016. Inhibition in Clark's nutcrackers

1271 (*Nucifraga columbiana*): results of a detour-reaching test. Anim. Cogn. 19, 661–665.

1272

1273 Vogel E.K., Machizawa M.G., 2004. Neural activity predicts individual differences in visual

1274 working memory capacity. Nature 428, 748–751.

1275

1276 Voyer D., Voyer S.D., Saint-Aubin J., 2017. Sex differences in visual-spatial working

1277 memory: A meta-analysis. Psychon. Bull. Rev. 24, 307–334.

1278

1279 Völter C.J., Tinklenberg B., Call J., Seed A.M., 2018. Comparative psychometrics:

1280 establishing what differs is central to understanding what evolves. Philos. Trans. R. Soc. B-

1281 Biol. Sci. 373, 20170283.

1282

1283   Wallace K.J., Hofmann H.A., 2021. Equal performance but distinct behaviors: sex

1284   differences in a novel object recognition task and spatial maze in a highly social cichlid fish.

1285   Anim. Cogn. 24, 1057–1073.

1286

1287   Wallace K.J., Rausch R.T., Ramsey M.E., Cummings M.E., 2020. Sex differences in

1288   cognitive performance and style across domains in mosquitofish (*Gambusia affinis*). Anim.

1289   Cogn. 23, 655–669.

1290

1291   Wallin K.G., Wood R.I., 2015. Anabolic–androgenic steroids impair set-shifting and reversal

1292   learning in male rats. Eur. Neuropsychopharmacol. 25, 583–590.

1293

1294   Wang L., Carr M., 2014. Working memory and strategy use contribute to gender differences

1295   in spatial ability. Educ. Psychol. 49, 261–282.

1296

1297   Weafer J., de Wit H., 2014. Sex differences in impulsive action and impulsive choice. Addict.

1298   Behav. 39, 1573–1579.

1299

1300   Wearmouth V.J., Sims D.W., 2008. Sexual segregation in marine fish, reptiles, birds and

1301   mammals: behaviour patterns, mechanisms and conservation implications. Advan. Mar. Biol.

1302   54, 107–170.

1303

1304   Wierenga L.M., Bos M.G., van Rossenberg F., Crone E.A., 2019. Sex effects on development

1305   of brain structure and executive functions: greater variance than mean effects. J. Cogn.

1306   Neurosci. 31, 730–753.

1307

1308 Whitehouse C.M., Curry-Pochy L.S., Shafer R., Rudy J., Lewis M.H., 2017. Reversal

1309 learning in C58 mice: Modeling higher order repetitive behavior. Behav. Brain Res. 332,

1310 372–378.

1311

Figure captions

Fig. 1

Variability of cognitive sex differences in poeciliid fish: the colour discrimination reversal learning task. Data retrieved from Lucon-Xiccato and Bisazza (2014) and Fuss and Witte (2019). Bars represent a relative index based on the number of errors to the learning criterion: (mean female errors - mean male errors) / mean female errors. Negative and positive values indicate greater performance of males and of females, respectively.

Fig. 2

Sex differences in inhibitory control in teleost fish. Three paradigms adopted to study inhibitory control in dioecious species: (a) detour task, (b) cylinder task, and (c) tube task. (d) Results on sex differences in inhibitory control tasks in teleosts; bars represent a relative index calculated as (mean female performance - mean male performance) / mean female performance; negative and positive values indicate greater performance of males and of females, respectively.

Fig. 3

Distribution of sex differences in executive functions across vertebrates. (a) Number of taxa investigated. (b) Percentage of taxa with sex differences detected corrected for the number of taxa investigated; percentage was not calculated in reptiles due to the presence of a single study. Data are separated according to the main vertebrate groups and three taxonomic levels (indicated by bar colour). The two panels of the figure should be read together: due to binomial error sampling, the number of taxa investigated affects the calculation of the percentage of taxa showing sex differences.

1338   **Tables**

1339   Table 1

1340   Sex differences in discrimination reversal learning tasks in tetrapods. F > M, M > F, and =

1341   indicate greater performance of females, greater performance of males, and no sex

1342   differences, respectively.

Vertebrate group	Order / Family	Species	Result	Study
Mammals	Primates Cercopithecidae	Pigtailed macaque monkey, *Macaca nemestrina*	F > M	Ha et al., 2011
Mammals	Primates Cercopithecidae	Baboon, *Papio sp.*	=	Rodriguez et al., 2011
Mammals	Primates Callitrichidae	Marmoset, *Callithrix jacchus*	=	LaClair & Lacreuse, 2016
Mammals	Carnivora Canidae	Dog, *Canis lupus familiaris*	=	Brucks et al., 2017
Mammals	Perissodactyla Equidae	Horse, *Equus ferus caballus*	=	Fiske & Potter, 1979
Mammals	Artiodactyla Suidae	Pig	F > M	Roelofs et al., 2017
Mammals	Rodentia Muridae	Laboratory rat	F > M	Guillamón et al., 1986
Mammals	Rodentia Muridae	Laboratory mouse	=	Whitehouse et al., 2017
Mammals	Rodentia Muridae	Laboratory mouse	=	Brigman et al., 2008
Mammals	Rodentia Cricetidae	Bank vole, *Myodes glareolus*	=	Mazza et al., 2018
Mammals	Rodentia Caviidae	Guinea pig, *Cavia procellus*	=	Jonson et al., 1976
Birds	Psittaciformes Psittacidae	Amazon parrot, *Amazona amazonica*	=	Cussen & Mench, 2014
Birds	Psittaciformes Nestoridae	Kea, *Nestor notabilis*	=	O'Hara et al., 2015
Birds	Psittaciformes Nestoridae	Kea, *Nestor notabilis*	=	Laschober et al., 2021
Birds	Passeriformes Corvidae	Raven, *Corvus corax*	=	Range et al., 2006
Birds	Passeriformes Corvidae	Florida scrub-jay, *Aphelocoma coerulescens*	=	Bebus et al., 2010
Birds	Passeriformes Paridae	Great tit, *Parus major*	=	Hermer et al., 2018
Birds	Passeriformes Paridae	Great tit, *Parus major*	=	Titualer et al., 2012
Birds	Passeriformes Estrildidae	Zebra finch, *Taeniopygia guttata*	M > F	Brust et al., 2013
Birds	Passeriformes Icteridae	Shiny cowbirds, *Molothrus bonariensis*	F > M	Lois-Milevicich et al., 2021a

Birds	Passeriformes Icteridae	Screaming cowbirds, *Molothrus rufoaxillaris*		=	Lois-Milevicich et al., 2021b
Birds	Passeriformes Icteridae	Shiny cowbirds, *Molothrus bonariensis*	F > M		Lois-Milevicich et al., 2021b
Birds	Columbiformes Columbidae	Zenaida dove, *Zenaida aurita*		=	Boogert et al., 2010
Reptiles	Squamata Scincidae	Tree skink, *Egernia striolata*	M > F		Szabo et al., 2018

1343

1344   Table 2

1345   Studies reporting cognitive sex differences not involving executive functions in guppies, *P.*

1346   *reticulata*. F > M and M > F indicate greater performance of females and of males,

1347   respectively.

Cognitive ability	Task	Direction of the sex difference	Study
Innovation	Discovering food in a maze	F > M	Laland & Reader, 1999
Innovation	Discovering food in a maze	F > M	Reader & Laland, 2000
Social learning	Learning a foraging patch from conspecifics	F > M	Reader & Laland, 2000
Numerical abilities	Selecting the larger available social group	F > M	Lucon-Xiccato et al., 2016
Numerical abilities	Learning to select a stimulus with more dots	F > M	Miletto Petrazzini et al., 2017
Spatial abilities	Learning the route in a maze	M > F	Lucon-Xiccato & Bisazza, 2017b
Spatial abilities	Learning the route in a maze	F > M	Lucon-Xiccato & Bisazza, 2017c
Problem solving	Learning to dislodge a disc hiding food	F > M	Fuss & Witte, 2019
Problem solving	Learning to dislodge a disc hiding food	F > M	Lucon-Xiccato et al., 2020b

1348

(a)

(b)

(c)

(d)

Figure showing study; task; dependent variable on y-axis and Index of greater performance on x-axis.

Brandão et al., 2019;
barrier with food reward; correct responses

Brandão et al., 2019;
barrier with food reward; time to solve the task

Keagy et al., 2019;
vertical cylinder; correct responses

Keagy et al., 2019;
vertical cylinder; time to solve the task

Lucon-Xiccato & Bisazza, 2017b;
barrier with social reward; time to solve the task

Lucon-Xiccato et al., 2017;
cylinder; time to solve the task

Lucon-Xiccato et al., 2017;
cylinder; correct responses

Lucon-Xiccato et al., 2020a;
tube; number of attacks

Wallace et al., 2019;
barrier with social reward; successful fish

Study; task; dependent variable

-0.6   -0.3   0   0.3   0.6
Males   No sex difference   Females

Index of greater performance

Species

Gambusia affinis
Gasterosteus aculeatus
Oreochromis niloticus
Poecilia reticulata