

1 Exposure to predation risk reduces lateralization in fathead minnows

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14

15 Abstract

16 Lateralization of cognitive functions impacts many behaviours related to fitness and, in most

17 species, varies greatly among individuals. Laboratory and field studies have suggested that

18 within-species variation in lateralization is partly due to phenotypic plasticity. For example,

19 in fish, prey that have experienced predation risk during early ontogeny develop highly

20 lateralized phenotypes, and this lateralization often favours prey in evading predators. In

21 contexts other than predation, plasticity of lateralization has also been reported for adult fish.

22 Therefore, we asked whether adult fathead minnows, *Pimephales promelas*, exposed to high

23 predation risk would also show plasticity linked to increase lateralization. We exposed

24 minnows to conspecific alarm cues for up to 8 days to simulate predation risk, and tested

25 their lateralization with a standard detour test. The treatment affected lateralization but in an

26 unexpected direction: individuals exposed to high predation risk showed lower lateralization
27 scores compared to control fish. In addition, fish within groups exposed to risk reduced the
28 variability in their directionality of lateralization, i.e. they showed a similar turning
29 preference in the detour task. Our study suggests that lateralization can vary in response to
30 predation risk in adult fish.

31

32 **Keywords:** antipredator behaviour; behavioural plasticity; fish cognition; laterality.

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33 **Significance statement**

34 In individuals of many species, including humans, one brain hemisphere, either the
35 left or the right, preferentially performs specific cognitive functions. We showed that fish
36 exposed to predation risk were less likely to show this cognitive lateralization. This suggests
37 that lateralization is plastic and varies according to the individual's experience.

38

39 **Introduction**

40 Several cognitive functions, including predator recognition, prey catching, acoustic
41 communication, spatial reorientation, and individual recognition are preferentially executed
42 by either the left or the right brain hemisphere in humans and other animals (Bisazza &
43 Brown, 2011; Vallortigara et al., 2011). Consequently, left-right differences in detecting and
44 processing stimuli associated with these functions can develop, which may lead to
45 asymmetrical motor responses. For example, fish often move in the environment and turn
46 their body in specific directions to observe stimuli such as predators or conspecifics with the
47 eye contralateral to the hemisphere processing such information (Bisazza et al., 1997; Dadda
48 et al., 2012).

49 A puzzling characteristic of lateralization is its within-species variation: individuals
50 often differ in which hemisphere they exploit for certain cognitive functions and in how
51 strongly they rely on that hemisphere (Knecht et al., 2000; Reddon & Hurd, 2008). It has
52 been hypothesized that lateralization has genetic basis and its variability could be due to
53 fluctuating selection on alleles (Levins, 1968). Indeed, empirical studies detected genetic
54 heritability of lateralization (goldbelly topminnow: Bisazza et al., 2000; chimpanzee:
55 Hopkins et al., 1994; mouse: Collins, 1985) and advantages of lateralization are often
56 associated to selective pressures that fluctuate widely across space and time, such as
57 predation risk. Strongly lateralized individuals are faster at detecting, and better at responding

58 to, predators (Bisazza & Dadda, 2005; Chivers et al., 2016; Dadda et al., 2010; Rogers et al.,
59 2004), and individuals with a specific direction of lateralization showed greater ability to
60 recognize predators (Lucon-Xiccato et al., 2017). However, because genes explain only a
61 fraction of the total phenotypic variability in lateralization, fluctuating selection cannot
62 entirely account for this variability.

63 An alternative, non-mutually exclusive hypothesis is that variability in lateralization is
64 also due to adaptive phenotypic plasticity. Fish and anuran populations experimentally
65 exposed to predation risk during development showed a higher proportion of lateralized
66 individuals (Broder & Angeloni, 2014; Ferrari et al., 2015; Lucon-Xiccato et al., 2017). In the
67 edible frog, *Pelophylax esculentus*, increased occurrence of lateralized individuals was also
68 observed after embryonic exposure to environments with low vegetation cover (Lucon-
69 Xiccato et al., 2019). Low vegetation confers less protection from predators (Babbitt &
70 Tanner, 1997), although the effect could also be due to increased exposure to light (Rogers,
71 1982).

72 Adult fish also show lateralisation plasticity in response to various stressors.
73 Parasitized fish are more lateralized than controls (Roche et al., 2013) and lateralization
74 variations have been reported in fish exposed to hypoxia or elevated CO₂ (Lucon-Xiccato et
75 al. 2014; Sundin & Jutfelt, 2018). We investigated whether exposure to predation risk
76 similarly modifies lateralisation in adult fish using fathead minnows, *Pimephales promelas*.
77 To simulate predation risk, we exposed minnows to conspecific skin extract (alarm cue). In
78 nature, alarm cues are released upon skin damage due to predation (Ferrari et al., 2010).
79 Therefore, aquatic organisms, including minnows, use alarm cue as a signal of predation risk
80 (Ferrari et al., 2010). Prior studies highlighted strong and reliable behavioural plasticity of
81 adult minnows and other teleost species due to exposure to alarm-cue mediated predation risk
82 (Crane & Ferrari, 2015; Ferrari et al., 2005; Meuthen et al., 2019). In our experiment, we

83 exposed minnows to risk for either 2, 4 or 8 days and compared their lateralization to that of
84 control minnows. Following prior studies on plasticity in fish (e.g., Domenici et al., 2011;
85 Ferrari et al., 2015; Roche et al., 2013), we assessed lateralization using a detour test,
86 whereby the turning direction of fish in front of an opaque barrier is recorded. The turning
87 directions indicate how an individual splits information processing between the two
88 hemispheres, with particular reference to processing of visual stimuli (Facchin et al., 1999).
89 A highly lateralized individual is expected to turn consistently toward the same direction and
90 individuals with the same left-right hemispheric lateralization are expected to show the same
91 left-right turning bias. According to some authors, in this test fish turn to observe behind
92 them with a specific eye (Bisazza et al., 1997). A left turn, for example, indicates the left eye
93 dominance and right hemisphere dominance in information processing. At least in part, fish
94 turning decisions may be affected by the eye used to observe behind the barrier and by
95 lateralization of motor control (Dadda et al., 2012).

96

97 **Materials and methods**

98 **Subjects**

99 We collected 235 minnows with Gee's Improved Minnow traps in a pond in central
100 Saskatchewan in April 2015. Immediately after collection, we transferred minnows to two
101 laboratory pools (~ 2500 L) provided with filtered flow-through water and aeration. Twice
102 per day, we fed the fish with commercial flakes. We allowed the fish to acclimate to
103 laboratory conditions for 2 months before the start of the experiment. After the experiment,
104 we anesthetized the minnows in MS-222, and we measured their standard length ($M \pm SD =$
105 5.2 ± 0.4 cm). Both sexes were assigned haphazardly to the experimental treatments, but it
106 was not possible to analyse sex differences in the behavioural test because the sex could not
107 be recognised in some individuals (Flickinger, 1969).

108

109 Predation risk treatment

110 We obtained alarm cues using a standard protocol where we euthanized 5 minnows
111 with a blow to the head and homogenized their skin. We diluted skin extract in water at the
112 concentration of 1 cm² skin per 40 L, which is known to cause the antipredator response in
113 minnows (Crane & Ferrari, 2015; Meuthen et al., 2019).

114 We performed the treatment in 62 37-L aquaria provided with filtered water, aeration,
115 gravel, and shelters (halved plastic pipes). We introduced 4 minnows into each aquarium the
116 day before the beginning of the treatment. Each aquarium was randomly assigned to either
117 the treatment with alarm cue or the control treatment with water, and to the different
118 treatment lengths. This between-subjects experimental design was adopted because prior
119 studies indicated that fish habituate to the apparatus used in the behavioural testing (Bisazza
120 et al., 1997), potentially affecting lateralization assessment in case of repeated measurements
121 of the same fish. We randomized the onset of treatment in the different tanks to allow us to
122 test fish from all treatments on the same testing days. The number of aquaria per treatment
123 was as follows: 2 days predation risk = 10; 4 days predation risk = 9; 8 days predation risk =
124 10; 2 days water control = 10; 4 days water control = 12; 8 days water control = 11.

125 Twice per day (h 0900-1500), we injected 5 mL of alarm cues into the aquaria of the
126 predation risk treatment. To not disturb the fish, we injected the cues from a distance using a
127 1.5-m silicone hose connected to the syringe. For the water control aquaria, we injected the
128 same volume of water. Thirty minutes after injections, we flushed the aquaria with clean
129 water using a pump. During the treatment, we fed the minnows with flakes, but at least 2 h
130 before or after cue injections.

131

132 Lateralization test

133 The apparatus was a 100 × 60-cm tank filled with 10 cm of water (Figure 1) and was
134 placed in a room with the same conditions (illumination, temperature) of the room with the
135 treatment tanks. By using white plastic, we built a central runway (50 × 15 cm). Six cm ahead
136 of the end of the runway, we placed the plastic opaque barrier (25 × 15 cm) perpendicular to
137 the runway. The test was performed at the end of the predation risk treatment. The day before
138 testing, we assigned a number code to each treatment tank, to allow blind testing. The test
139 started by netting an individual minnow from the treatment tank, placing it into the apparatus,
140 behind one barrier, and providing 2 min for recovery from the transportation. Thereafter, the
141 experimenter used a pair of nets to encourage the subject to enter the runway. This procedure
142 was performed in a standardised way for all the subjects, inserting the nets behind the barrier
143 and moving them simultaneously around it from either side. Then, the nets were removed,
144 and the experimenter rested motionless to observe the behaviour of the subject. The minnow
145 usually swam through the corridor until facing the barrier. In front of the barrier, the minnow
146 made a turning decision either the right or the left side, which was recorded. Each individual
147 was tested 10 times separated by 2-min intervals. Some subjects did not swim through the
148 runway and showed freezing behaviour. These subjects were removed from the analysis. The
149 final sample size was as follows: 2 days predation risk = 37; 4 days predation risk = 39; 8
150 days predation risk = 36; 2 days water control = 39; 4 days water control = 42; 8 days water
151 control = 42. The lateralization test was performed across 10 days.

152 To analyse the data, we computed two indices that describe the lateralization pattern
153 of the groups of subjects, the absolute lateralization index (LA) and the relative lateralization
154 index (LR; Bisazza et al., 1997). LA indicated the absolute strength of lateralization,
155 independently from the directionality of the turning preference: $LA = |LR|$. LA ranged from 0,
156 no turning preference, to 100, maximum turning preference. LR indicated the relative
157 lateralization of the individuals in the population: $LR = [(right\ turns - left\ turns) / (right$

158 turns+left turns)]*100. LR ranged from -100, indicating complete preference for left turning,
159 to +100, indicating complete preference for right turning.

160

161 Statistical analysis

162 We analysed the LA and the LR index in R (version 3.4.0). We analysed the indices
163 using 2×3 ANOVAs fitted with treatment (alarm cue-predation risk versus water-control)
164 and treatment length (2, 4 or 8 days) as fixed effects, and treatment tank as random effect. We
165 calculated effect sizes using Hedges' *g* because the different treatments had slightly different
166 sample sizes. When necessary, we performed a comparison separated by treatment length
167 using one-sample *t* tests. We also used Pearson correlations to confirm that the size of the
168 subjects did not affect the indices. Then, For the LR index, we also calculated the variance
169 for each treatment tank and we performed an ANOVA on this variable, after log
170 transformation, to test for differences between treatments and treatment length. This was
171 done because alignment of lateralization might occur at the tank level rather than at the level
172 of the entire experimental population (Chivers et al., 2016).

173

174 Ethical Note

175 The present study was approved by the Committee on Animal Care of University of
176 Saskatchewan reviewed and approved all the experimental procedures (protocol no.
177 20130079). Fish collection was authorized by the Saskatchewan Ministry of Environment. At
178 the end of the experiments, subjects were kept in the laboratory as part of a stock colony.

179

180 **Results**

181 Absolute lateralization

182 The model on the LA index revealed that fish exposed to predation risk were less
183 lateralized than fish exposed to the no-predation risk treatment (predation risk LA: $27.14 \pm$
184 19.52 ; control LA: 34.31 ± 26.05 ; $F_{1,169} = 5.62$, $P = .02$, *Hedges' g* = .31; Figure 2a).
185 Treatment length (2, 4 or 8 days) and the interaction between treatment and treatment length
186 did not significantly affect subjects' absolute lateralization ($F_{2,169} = 1.63$, $P = .20$; and $F_{2,169} =$
187 $.74$, $P = .48$, respectively). A post-hoc analysis suggested that the difference between the risk
188 and the control treatment arose after 8 days of treatment (2 days: $t_{74} = .83$, $P = .41$; 4 days: t_{79}
189 $= .91$, $P = .36$; 8 days: $t_{76} = 2.47$, $P = .02$; Figure 2a). The size of the fish did not significantly
190 predict LA score ($r_{233} = -.02$, $P = .79$).

191

192 Relative lateralization

193 The LR index was not significantly affected by treatment (predation risk LR: $1.79 \pm$
194 33.48 ; control LR: 4.07 ± 43.00 ; $F_{1,169} = .20$, $P = .66$; Figure 2b), treatment length ($F_{2,169} =$
195 1.02 $P = .36$), and the interaction between these two factors ($F_{2,169} = .30$, $P = .74$). The size
196 of the fish did not significantly predict LR score ($r_{233} = .01$, $P = .84$).

197 The within-tank variance of LR was significantly affected by treatment (LR variance
198 scores: predation risk: 1363.33 ± 1494.16 ; control: 1934.38 ± 1087.05 ; $F_{1,56} = 7.11$, $P = .01$),
199 but not by treatment length ($F_{2,56} = 1.23$, $P = .30$). More importantly, the interaction between
200 treatment and treatment length was also significant ($F_{2,56} = 3.32$, $P = .04$; Figure 2c). A post-
201 hoc analysis suggested that the difference between the risk and the control treatment arose
202 after 8 days of treatment (2 days: $t_{18} = 1.12$, $P = .28$; 4 days: $t_{19} = .52$, $P = .61$; 8 days: $t_{19} =$
203 2.41 , $P = .03$; Figure 2c).

204

205 Discussion

206 Anamniotes exposed to predation risk during early ontogeny develop increased
207 lateralization (Broder & Angeloni, 2014; Ferrari et al., 2015; Lucon-Xiccato et al., 2017). We
208 demonstrated that exposure to predation risk during adulthood can also alter lateralization in
209 minnows, but in the reversed direction; minnows exposed to predation risk showed reduced
210 tendency to turn in a specific direction in the detour test, which indicates reduced
211 hemispheric dominance on behavioural control. Reduced lateralization has previously been
212 observed in fish as a consequence of several stressors (e.g., Domenici et al., 2011; Lucon-
213 Xiccato et al., 2014), but not predation risk. Plasticity in lateralization due to predation risk
214 may vary in the different species as observed for exposure to elevated carbon dioxide in two
215 damselfish species; the treatment reduced lateralization strength in *Neopomacentrus azysron*
216 (Domenici et al., 2011) whereas it altered directionality of lateralization in *Pomacentrus*
217 *wardi* (Domenici et al., 2014). Another aspect potentially relevant is that we treated adult
218 fish, and the plasticity of lateralization might vary according to developmental stage.
219 Interestingly, a study by De Santi and colleagues (2000) apparently contrasts the general
220 hypothesis of developmental differences. They found increased lateralization, measured as
221 eye preference for a predator versus a conspecific, in adult guppies, *Poecilia reticulata*, that
222 were previously exposed to the attacks of the predator compared to naïve guppies. This result,
223 however, was confounded because the predator-exposed guppies recognised the predator and
224 processed it with the hemisphere involved in antipredator behaviour, whereas predator-naïve
225 guppies likely expressed general exploratory behaviour towards the stimulus. Therefore, the
226 study by De Santi and colleagues involved different behaviours rather than plasticity and
227 cannot be considered evidence against the hypothesis of developmental variation. It is
228 important that future research does not overgeneralise the effect of predation risk on
229 lateralization and investigates the specific response in the study species at different
230 developmental stages.

231 Lateralization is considered an advantage when dealing with predators. For example,
232 in damselfish, lateralization increases predation recognition learning and survival in
233 mesocosms with predators (Chivers et al., 2017; Ferrari et al., 2015). Splitting cognitive
234 processes between the two hemispheres likely permits each hemisphere to achieve greater
235 specialization and greater cognitive performance in tasks involved in dealing with predators.
236 It is therefore surprising that in minnows, predation risk reduced the occurrence of
237 individuals with high turning preference and consequently, high hemispheric dominance. In
238 minnows, low lateralization might favour individuals in surviving under predation risk.
239 Alternatively, we do know that exposure to risk for extended periods of time may
240 dramatically change anti-predator responses in some prey (risk allocation, Lima &
241 Bednekoff, 1999), including minnows (Meuthen et al., 2019). In these situations, fish may
242 fail to respond with anti-predator behaviour to acute risks because they cannot afford to waste
243 valuable time and resources. Given that alarm cues may last for several hours (Wisenden et
244 al., 2009) our eight-day exposure may have been enough to induce risk allocation and
245 influence lateralization (Lima & Bednekoff, 1999). Although our study did not test for risk
246 allocation effect, we found that lateralization reduction was greater when the exposure to risk
247 was longer (8 days), which seems in line with the hypothesis.

248 The mechanism for lateralization change might be direct, with alarm cue exposure
249 activating brain plasticity. Likewise, in mammals and birds, environmental cues can
250 relatively rapidly cause neurogenesis and adaptive reorganization in cerebral structures, even
251 in the adult brain (Caveng et al., 2013; Goldman & Nottebohm, 1983). Alternatively, stress
252 hormones, which may notably affect asymmetric brain functioning and structures (Zach et al.,
253 2016), might be the proximate cause of minnows' lateralization plasticity. Indeed, exposure
254 to predation risk activates stress-induced hormonal responses (Barcellos et al., 2007). It is

255 worth noting that the effects of hormones on lateralization are not necessarily adaptive
256 (Barnard et al., 2003; Mazzotti & Boere, 2009; Rogers, 2010).

257 Evidence also suggests that the directionality of lateralization is involved in dealing
258 with predators, in particular for social species. For example, in yellow-and-blueback fusiliers,
259 *Caesio teres*, individuals with a directionality of lateralization different from that of their
260 school mates had reduced escape performance (Chivers et al., 2016). One could expect that
261 minnows exposed to predation risk would tend to show the same directionality of
262 lateralization at the population level. However, we did not find evidence of this alignment.
263 Although minnows have been reported to form schools (Magurran, 1990; Pitcher, 1973), their
264 behaviour might be less synchronized than that of fusiliers and therefore lateralization might
265 be less relevant in predator escaping. Magurran (1990) also reported that minnows from
266 populations exposed to piscine predators are more prone to rely on schooling for defence, and
267 our population lives in a pond without piscine predators. However, our data revealed that the
268 variance of directionality of lateralization within-tank was lower in fish exposed to predation
269 risk compared to control fish. It is not clear whether this effect was an indirect consequence
270 of absolute lateralization reduction, yet it is possible that alignment of directionality of
271 lateralization occurs at the level of each specific shoal (in our case, fish from the same
272 treatment tanks) rather than of the entire population.

273 In conclusion, it will be important to collect data in other species and in other
274 populations to improve our understanding of how cognitive lateralization affects prey-
275 predator interactions. Interesting questions for future studies are whether lateralization
276 plasticity differs between adults and juveniles of the same species, whether small shoals'
277 coordination balances the disadvantages of reduced lateralization in minnows, and whether
278 lateralization plasticity involves long-term organisational effects in the nervous system,

279 giving fish extended potential for neurogenesis even in the adult brain (Zupanc, 2006), or a
280 temporary heightened state of vigilance.

281

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285

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