

## University of Groningen

### The missing link

Berlinghieri, Flavia

DOI:  
[10.33612/diss.929760767](https://doi.org/10.33612/diss.929760767)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2024

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Berlinghieri, F. (2024). *The missing link: Exploring laterality and personality development in two fishes*. [Thesis fully internal (DIV), University of Groningen]. University of Groningen.  
<https://doi.org/10.33612/diss.929760767>

#### Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

#### Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

# Chapter 7

## General Discussion



The four data chapters of this PhD thesis had the following aims: Firstly, by manipulating the early (including prenatal) environment in fish, I investigated developmental plasticity and determined whether there is a mechanistic link between the development of behavioural laterality and personality traits (Chapter 2 and 3). Secondly, I investigated the differences in laterality in two phenotypes of three-spined sticklebacks (marine migrants, freshwater residents and their reciprocal hybrids), reared in standard conditions, to search for possible genetic effects; Chapter 4). Third, I determined if differences in laterality and personality traits, known to be related to cognitive processes, result in differences in cognitive bias (chapter 5). Lastly, I explored the relevance of laterality for the concept of welfare in fish (Chapter 6). Overall, I did not find strong support for the hypothesis that behaviour laterality and a personality trait correlate. However, I have demonstrated; 1: that ecologically relevant environmental factors in the form of light and predation pressure can affect, even in the prenatal stage, the development of laterality and personality, 2: that apart from these maternally shaped environmental effects maternal genes also affect differences in laterality, and 3: that understanding behavioural laterality can be applied to animal welfare.

In the first data chapter (Chapter 2), my intention was to manipulate visual laterality with the exposure to light or dark during early embryogenesis and investigate the effects not only on early lateralized behaviour, but also at personality. This might reveal to what extent both traits share a common causal factor. Moreover, I tested to what extent the effects might persist into adulthood as this was not yet undertaken in the literature. The laterality test revealed that fish reared under standard conditions (normal light regime) were more lateralized (measured as eye use towards a mirror simulating a conspecific) than those reared entirely in the dark which is consistent with previous studies on other species of fish and birds (Andrew et al., 2008a; Budaev & Andrew, 2009a, 2009b; Dadda & Bisazza, 2012; Jha & Kumar, 2017). However, the effect of rearing environment on laterality was only evident in the young fish and was lost by the time they reached sexually maturity. In addition, fish reared in the dark spent significantly more time in the inner part of the test arena (more exploratory) when young but there was no difference between age groups in the light-reared treatment. I also found no evidence that laterality and personality were correlated. Collectively the findings from this and other experiments suggest that rearing fish under normal conditions, where embryos had considerable and standard exposure to light, positively influences the development of lateralization. Exposure to light seems to stimulate the visual system which then activates the

development of lateralisation. That this effect was lost in older fish suggests that fish may possess significant neuroflexibility and months of exposure to natural light conditions may correct for the early exposure to darkness.

This study is important because, to our knowledge, it is the only one studying the long-term effect of manipulating the rearing environment across two different age groups. Previous studies examining the impacts of light on laterality in fishes examined reasonably young individuals, specifically at 7 and 10 days old (Budaev & Andrew, 2009a; Dadda & Bisazza, 2012). Similarly there is little evidence for prolonged effects in the chick as after 3 weeks of age the asymmetry in neural connections in the visual system disappear model (Andrew et al., 2008a; Rogers, 2010; Rogers & Deng, 2005).

It is important to recognise that the experiment had one limitation in that we could not track the development of individual fish so we lack individual data and our observations are limited to the population level. This limitation arises from the small size of the young fish, making tagging unfeasible. Future studies will require tagging larger fish species or waiting for the fish to grow to a sufficient size, enabling the collection of individual data to assess personality traits. Researchers can consider tagging the fish shortly after hatching and conducting follow-up tests at intervals, such as every two weeks, to provide a more comprehensive understanding.

Behaviour is generally influenced by direct effects of genes and the environment but may also be shaped by indirect effects via so called parental effects. In the second data chapter (Chapter 3) I examined if parental effects generated differences in the offspring behaviour potentially via maternal cortisol concentration deposited in the eggs. Predation is one of the most studied environmental factors that influences the behaviour, here we focussed specifically on laterality and personality traits and their possible correlation. In this experiment I exposed the parents to predation cues or not. First of all, I analysed the parents' behaviour to confirm that the predation exposure was effective. Parents exposed to predation and later confronted with a model of a predator turned out to be relatively bold as they spent more time in the predator inspection zone than those that had not been exposed to predation. Concerning their offspring, the predation exposure of the parents caused the offspring to be bolder too, and also smaller, with more lateralized individuals. I assumed that the most likely mechanism would be via cortisol deposited in the eggs by stressed mothers. However, we failed to find any evidence of cortisol in the eggs. It remains a possibility that other hormones and / or their byproducts (metabolites) may be

responsible, this remains a key area for future investigation. Also in this chapter, as with the previous chapter, we did not find any correlation between laterality and personality.

As a complementary to Chapter 3, Chapter 4 focussed on the potential influence of genes on laterality, making use of sticklebacks from different heritage groups that are adapted to differences in predation exposure; Marine migrants that spend only the reproductive period in fresh water but then migrate to the sea, freshwater residents, and their hybrids from reciprocal crosses. It is well known that there are large differences in behaviour and morphology between marine and freshwater morphs largely due to variation in predation exposure (Reimchen 1995; Huntingford, 1982; Wark et al., 2011) and many of these traits having a genetic basis (Colosimo et al., 2004) We hypothesised that fish from low predation areas (freshwater residents) would be less strongly lateralised in their visual system than those from high predation areas (marine migrants). We also predicted that fish from marine parents would show population level bias in laterality to facilitate schooling. We expected that hybrids would be intermediate and that there may be variation depending on whether the mother or father had marine origins. While pure marine fish were not significantly more strongly lateralised nor were they consistently biased at the population level as predicted, I did find that fish with marine mothers tended to be right biased compared to fish with freshwater mothers. There was no apparent influence from the father on the laterality index. Hybrid fish with freshwater resident fathers and marine mothers were the only line that had a significant bias (to the right) in their social behaviour at the population level.

The results I observed in this chapter are consistent with the known influences of predation pressure on the evolution and development of laterality in fishes (Brown, Western, et al., 2007; Dale Broder & Angeloni, 2014; Hulthén et al., 2021; Lucon-Xiccato et al., 2017). That the marine mothers seem to have a large impact on the laterality of their offspring is particularly intriguing. Given the tremendous molecular resources available for sticklebacks, they likely offer a unique opportunity to identify the genes associated with laterality in fish.

Research into laterality and personality not only may tell us about how behaviour is organized, but may also impact cognition and welfare, the topic of the last two research chapters. The fourth data chapter (Chapter 5) explored the possibility that personality and laterality influences cognitive bias. To investigate this, I used a judgement bias test with the go/no-go procedure, taught the fish to obtain a food reward with one of two stimuli,

black or white cards, and subsequently tested the bias by assessing their propensity to approach an ambiguous grey stimulus. Individuals with positive cognitive judgement bias (optimistic fish) have a high expectation of reward when faced with an ambiguous stimulus (d’Ettorre et al., 2017), and should approach the ambiguous stimulus faster than pessimistic fish. For example, depressed humans tend to have a pessimistic outlook and tend to react to ambiguous stimulus more negatively than people not affected by depression (Eysenck, 1991; Richards et al., 2002, 2007). Fish were tested with an emergence test where we scored the time to exit a shelter (personality – boldness) and their laterality scores in response to their reflection in a mirror. I found that the cognitive bias was influenced by the strength of laterality, sex and the interaction between boldness and sex. As we hypothesised, more strongly lateralised fish were also more optimistic as evidenced by their faster approach to the ambiguous stimulus. In addition, sex is clearly an important predictor of affective states. We observed that male sticklebacks generally displayed higher levels of optimism compared to the females, although this was moderated by their boldness levels. This is consistent with a meta-analysis led by Lagisz (2020), primarily comprising studies on mammals, that discovered that environmental manipulations were more likely to have a pronounced effect on judgment bias in males than in females (Lagisz et al., 2020). In a study conducted by Barker et al., (2016), the impact of different housing conditions, such as metabolic or standard housing, on the emotional states of laboratory rats was investigated using the novel judgment bias paradigm ((Barker et al., 2016)). However, their results indicated that males housed in metabolic cages exhibited a pessimistic judgment bias, while females in those cages displayed a more optimistic outlook. Nevertheless, it is evident that gender can significantly influence the outcomes of judgment bias tests.

Several studies in mammals have shown a correlation between personality traits and judgment bias. For example, social dogs, extroverted humans, proactive pigs, and less exploratory house mice all tend to exhibit a more optimistic outlook (Asher et al., 2016; Barnard et al., 2018; Clegg, 2018; Marshall et al., 1992; Verjat et al., 2021). Nowadays, assessing the affective state of animals on farms has become important as welfare is of a significant concern, and cognitive biases and personality traits are frequently used as indicators of these states (Bučková et al., 2019; Douglas et al., 2012; Kramer et al., 2021; Luo et al., 2019) . Consider, for instance, that pigs housed in enriched environments exhibited a higher degree of optimism compared to those living in barren conditions

(Douglas et al., 2012). Likewise, calves housed in pairs demonstrated a greater level of optimism than their counterparts raised individually (Bučková et al., 2019).

This optimistic outlook by more strongly lateralised fishes might be yet another way by which laterality enhances cognition. To our knowledge, this study is the first to evaluating the link between personality traits, laterality and cognitive bias in fish. Future studies should focus on fish cognitive bias to better understand their cognitive abilities and help facilitate improvements in welfare. The finding that the interaction between personality traits and cognitive bias is shaped by the sex of the subject is particularly intriguing and deserves further study. Moreover, optimistic or pessimistic perceptions may have considerable as yet unexplored fitness implications for fishes (Espigares et al., 2022). The fact that the strength of laterality is positively related to the degree of optimism opens a new avenue for testing functional cognitive consequences of laterality.

In the last chapter (Chapter 6), I discussed how an understanding of fish laterality can aid in the development of welfare indicators. Since the 1960s, there has been an increasing demand from the general public to prioritize animal welfare in various domains, including food production systems, as well as the treatment of companion animals and their use in scientific research. Fish kept in captivity often encounter stressors due to factors like overcrowding, handling, grading, and transportation (Eissa & Wang, 2016; Wilkinson et al., 2006). Unfortunately, it is noteworthy that fish have seldom been incorporated into our moral circle, as indicated by their frequent exclusion from animal welfare regulations on a global scale (Brown, 2015; Brown & Dorey, 2019). Therefore, it is necessary to find an easy and low-cost way to assess the affective state of fish, for example in aquaculture, to improve their welfare. For this reason, my sixth chapter reviewed our current knowledge of laterality and how it might be applied to animal welfare science. Cognitive bias has been used to assess welfare in farm and companion animals for some time where it is assumed that the animals may be suffering. There is a growing enthusiasm for employing cognitive bias tests as a means to evaluate fish welfare (Krzysztof et al., 2015). As I demonstrated with the results linking cognitive bias to laterality and personality, laterality may be a useful indicator of welfare status and that laterality and associated behaviour may be manipulated by shifting environmental conditions.

## *Synthesis*

Collectively, the results of my thesis demonstrate that several factors, both environmental and genetic, influence the development of laterality during ontogeny. The environmental influences fine tune underlying heritable effects and likely allows animals to adapt to diverse fluctuating environmental circumstances while the genetic effects may allow local adaptation. The results from the comparisons of the different genetic lines (pure marine, pure freshwater and hybrids) indicate that there are potential genetic influences of marine mothers on laterality but not of fathers. This maternal genetic influence is further refined by environmental effects. The environmental effects start already with the prenatal environment which contributes to the increasing evidence that especially pre and perinatal effects play a crucial role in shaping the future life of offspring. As light exposure to eggs and predation pressure depend on the mothers habitat choice, these are maternal effects that lead to intergenerational epigenetics, indicating that environmental factors experienced by one generation can impact subsequent generations. Post hatch, further modifications can be induced even in the adult stage, such as via predation pressure, allowing the fish to adapt to changing local conditions. My results add to the considerable evidence that environmental factors and genetic factors influence laterality (Bisazza et al., 2000; Brown, Burgess, et al., 2007; Brown, Western, et al., 2007; Budaev & Andrew, 2009a; Dale Broder & Angeloni, 2014; De Santi et al., 2000; Freire et al., 2006; Ocklenburg et al., 2016; Rogers, 1981; Wiper, 2017; Zucca et al., 2011). In donkeys, for example, laterality occurs at the population level with a right forelimb bias while standing in a quadrupedal position, the opposite to horses (McGreevy & Rogers, 2005; Zucca et al., 2011) . It has been demonstrated that a reduction in available space influences the laterality bias in donkeys. This intriguing outcome reveals that the direction of laterality within a population can be reversed or nullified through the manipulation of a simple environmental variable. Once again, it suggests that laterality may also provide insight into the welfare of animals in our care.

Given the fact that we know that laterality is partially heritable and that environmental factors have a strong influence, the interplay between heritability and environmental factors in determining laterality is still an ongoing area of research, and the exact mechanisms remain a subject of study and debate. Future directions to continue my studies might be to understand the intricate relationship between epigenetics and



environmental influences. In species like the rainbowfish or zebrafish, where the mother lays eggs in a natural environment containing varying vegetation and rocks as substrate, mothers may make a deliberate choice in selecting the egg-laying location, influencing the laterality of the offspring. As I demonstrated in Chapter 2, in alignment with other studies (Andrew et al., 2008b; Budaev & Andrew, 2009a, 2009b; Dadda & Bisazza, 2012; Jha & Kumar, 2017), offspring raised in well-lit conditions exhibited stronger laterality than offspring raised in darkness. Therefore, the lighting conditions could be a crucial factor in the decision-making process for mothers when selecting the right spot to lay their eggs.

Throughout my thesis, I did not find a correlation between laterality and personality despite examining multiple personality traits and investigating the possible underlying mechanisms behind both. A possible explanation may be related to the fact that the sticklebacks in Chapter 3 were not in the reproductive season as they were still not sexually mature. In addition, they have seasonal changes in their morphology, so their behaviour may also be influenced. Therefore, the potential link between laterality and personality may not be clearly evaluated, as the study on laterality in sticklebacks (McLean & Morrell, 2021) found differences in their laterality scores when the fish were sexually matured. I thought hormones, particularly cortisol, might be a factor, as we know that hormones can influence laterality (Schaafsma & Groothuis, 2012) and personality (Giesing et al., 2011; Mehta & Prasad, 2015; Terburg et al., 2009). In my case, I investigated cortisol levels at the egg stage but I did not find a significant concentration in the stickleback eggs (Chapter 3) which contrasts with previous studies (Giesing et al., 2011; Mommer & Bell, 2013). It is worth noting that my method for detecting cortisol was far more specific than other approaches which may be why various studies have detected cortisol while others have not (Henriksen et al., 2011; Rettenbacher et al., 2013). This is perhaps one of the most puzzling outcomes of the thesis and it is apparent that much more work needs to be done in identifying which personality traits and what measures of laterality might be correlated and in what contexts. Identifying hormones or their byproducts that might link these important aspects of behaviour remains an outstanding goal.

In conclusion, this PhD thesis encompassed four chapters that explored the development of and potential connection between behavioural laterality and personality traits. While

the study did not yield strong support for the hypothesis correlating behaviour laterality and personality traits, it did shed light on how environmental factors, such as light and predation, in coordination with genetic and epigenetic factors, can impact the development of laterality and personality, using fish as model organisms.

## References

- Andrew, R. J., Osorio, D., & Budaev, S. (2008a). Light during embryonic development modulates patterns of lateralization strongly and similarly in both zebrafish and chick. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1519), 983–989. <https://doi.org/10.1098/RSTB.2008.0241>
- Andrew, R. J., Osorio, D., & Budaev, S. (2008b). Light during embryonic development modulates patterns of lateralization strongly and similarly in both zebrafish and chick. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1519), 983–989. <https://doi.org/10.1098/RSTB.2008.0241>
- Asher, L., Friel, M., Griffin, K., & Collins, L. M. (2016). Mood and personality interact to determine cognitive biases in pigs. *Biology Letters*, 12(11). <https://doi.org/10.1098/rsbl.2016.0402>
- Barker, T. H., Howarth, G. S., & Whittaker, A. L. (2016). The effects of metabolic cage housing and sex on cognitive bias expression in rats. *Applied Animal Behaviour Science*, 177, 70–76. <https://doi.org/10.1016/J.APPLANIM.2016.01.018>
- Barnard, S., Wells, D. L., Milligan, A. D. S., Arnott, G., & Hepper, P. G. (2018). Personality traits affecting judgement bias task performance in dogs (*Canis familiaris*). *Scientific Reports*, 8(1). <https://doi.org/10.1038/s41598-018-25224-y>
- Bisazza, A., Facchin, L., & Vallortigara, G. (2000). Heritability of lateralization in fish: concordance of right–left asymmetry between parents and offspring. *Neuropsychologia*, 38(7), 907–912. [https://doi.org/10.1016/S0028-3932\(00\)00018-X](https://doi.org/10.1016/S0028-3932(00)00018-X)
- Brown, C. (2015). Fish intelligence, sentience and ethics. *Animal Cognition*, 18(1), 1–17. <https://doi.org/10.1007/S10071-014-0761-0/METRICS>
- Brown, C., Burgess, F., & Braithwaite, V. A. (2007). Heritable and experiential effects on boldness in a tropical poeciliid. *Behavioral Ecology and Sociobiology*, 62(2), 237–243. <https://doi.org/10.1007/s00265-007-0458-3>
- Brown, C., & Dorey, C. (2019). Pain and Emotion in Fishes – Fish Welfare Implications for Fisheries and Aquaculture. *Animal Studies Journal*, 8(2), 175–201. <https://doi.org/10.14453/asj.v8i2.12>

Brown, C., Western, J., & Braithwaite, V. A. (2007). The influence of early experience on, and inheritance of, cerebral lateralization. *Animal Behaviour*, 74(2), 231–238. <https://doi.org/10.1016/J.ANBEHAV.2006.08.014>

Bučková, K., Špinková, M., & Hintze, S. (2019). Pair housing makes calves more optimistic. *Scientific Reports* 2019 9:1, 9(1), 1–9. <https://doi.org/10.1038/s41598-019-56798-w>

Budaev, S., & Andrew, R. J. (2009a). Patterns of early embryonic light exposure determine behavioural asymmetries in zebrafish: A habenular hypothesis. *Behavioural Brain Research*, 200(1), 91–94. <https://doi.org/10.1016/J.BBR.2008.12.030>

Budaev, S. V., & Andrew, R. J. (2009b). Shyness and Behavioural Asymmetries in Larval Zebrafish (*Brachydanio rerio*) Developed in Light and Dark. In *Source: Behaviour* (Vol. 146, Issue 8).

Clegg, I. L. K. (2018). Cognitive bias in zoo animals: An optimistic outlook for welfare assessment. In *Animals* (Vol. 8, Issue 7). MDPI AG. <https://doi.org/10.3390/ani8070104>

Colosimo, P. F., Peichel, C. L., Nereng, K., Blackman, B. K., Shapiro, M. D., Schluter, D., & Kingsley, D. M. (2004). The Genetic Architecture of Parallel Armor Plate Reduction in Threespine Sticklebacks. *PLOS Biology*, 2(5), e109. <https://doi.org/10.1371/JOURNAL.PBIO.0020109>

Dadda, M., & Bisazza, A. (2012). Prenatal light exposure affects development of behavioural lateralization in a livebearing fish. *Behavioural Processes*, 91(1), 115–118. <https://doi.org/10.1016/J.BEPROC.2012.06.008>

Dale Broder, E., & Angeloni, L. M. (2014). Predator-induced phenotypic plasticity of laterality. *Animal Behaviour*, 98, 125–130. <https://doi.org/10.1016/J.ANBEHAV.2014.09.033>

De Santi, A., Bisazza, A., Cappelletti, M., & Vallortigara, G. (2000). Prior exposure to a predator influences lateralization of cooperative predator inspection in the guppy, *Poecilia reticulata*. *Italian Journal of Zoology*, 67(2), 175–178. <https://doi.org/10.1080/11250000009356312>

d’Ettorre, P., Carere, C., Demora, L., Le Quinquis, P., Signorotti, L., & Bovet, D. (2017). Individual differences in exploratory activity relate to cognitive judgement bias in carpenter ants. *Behavioural Processes*, 134, 63–69. <https://doi.org/10.1016/j.beproc.2016.09.008>

- Douglas, C., Bateson, M., Walsh, C., Bédoué, A., & Edwards, S. A. (2012). Environmental enrichment induces optimistic cognitive biases in pigs. *Applied Animal Behaviour Science*, 139(1–2), 65–73. <https://doi.org/10.1016/j.applanim.2012.02.018>
- Eissa, N., & Wang, H. P. (2016). Transcriptional stress responses to environmental and husbandry stressors in aquaculture species. *Reviews in Aquaculture*, 8(1), 61–88. <https://doi.org/10.1111/RAQ.12081>
- Espigares, F., Alvarado, M. V., Faísca, P., Abad-Tortosa, D., & Oliveira, R. F. (2022). Pessimistic cognitive bias is associated with enhanced reproductive investment in female zebrafish. *Biology Letters*, 18(12). <https://doi.org/10.1098/rsbl.2022.0232>
- Eysenck, H. J. (1991). Neuroticism, Anxiety, and Depression. *Psychological Inquiry*, 2(1), 75–76. [https://doi.org/10.1207/s15327965pli0201\\_17](https://doi.org/10.1207/s15327965pli0201_17)
- Freire, R., Van Dort, S., & Rogers, L. J. (2006). Pre- and post-hatching effects of corticosterone treatment on behavior of the domestic chick. *Hormones and Behavior*, 49(2), 157–165. <https://doi.org/10.1016/J.YHBEH.2005.05.015>
- Giesing, E. R., Suski, C. D., Warner, R. E., & Bell, A. M. (2011). Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring. *Proceedings of the Royal Society B: Biological Sciences*, 278(1712), 1753–1759. <https://doi.org/10.1098/RSPB.2010.1819>
- Henriksen, R., Rettenbacher, S., & Groothuis, T. G. G. (2011). Prenatal stress in birds: Pathways, effects, function and perspectives. *Neuroscience & Biobehavioral Reviews*, 35(7), 1484–1501. <https://doi.org/10.1016/J.NEUBIOREV.2011.04.010>
- Hulthén, K., Heinen-Kay, J. L., Schmidt, D. A., & Langerhans, R. B. (2021). Predation shapes behavioral lateralization: insights from an adaptive radiation of livebearing fish. *Behavioral Ecology*, 32(6), 1321–1329. <https://doi.org/10.1093/BEHECO/ARAB098>
- Huntingford, F. A. (1982). Do inter- and intraspecific aggression vary in relation to predation pressure in sticklebacks? *Animal Behaviour*, 30(3), 909–916. [https://doi.org/10.1016/S0003-3472\(82\)80165-6](https://doi.org/10.1016/S0003-3472(82)80165-6)
- Jha, N. A., & Kumar, V. (2017). Effect of no-night light environment on behaviour, learning performance and personality in zebra finches. *Animal Behaviour*, 132, 29–47. <https://doi.org/10.1016/J.ANBEHAV.2017.07.017>

Kramer, A. C., Neubauer, A. B., Scott, S. B., Schmiedek, F., Sliwinski, M. J., & Smyth, J. M. (2021). Stressor Anticipation and Subsequent Affective Well-Being: A Link Potentially Explained by Perseverative Cognitions. *Emotion*, 22(8), 1787–1800. <https://doi.org/10.1037/EMO0000954>

Krzysztof, W., Przemyslaw, P. C., & Roman, K. (2015). Cognitive bias test as a tool for accessing fish welfare. *Frontiers in Marine Science*, 2. [https://doi.org/10.3389/CONF.FMARS.2015.03.00200/EVENT\\_](https://doi.org/10.3389/CONF.FMARS.2015.03.00200/EVENT_)

Lagisz, M., Zidar, J., Nakagawa, S., Neville, V., Sorato, E., Paul, E. S., Bateson, M., Mendl, M., & Løvlie, H. (2020). Optimism, pessimism and judgement bias in animals: A systematic review and meta-analysis. *Neuroscience & Biobehavioral Reviews*, 118, 3–17. <https://doi.org/10.1016/J.NEUBIOREV.2020.07.012>

Lucon-Xiccato, T., Chivers, D. P., Mitchell, M. D., & Ferrari, M. C. O. (2017). Prenatal exposure to predation affects predator recognition learning via lateralization plasticity. *Behavioral Ecology*, 28(1), 253–259. <https://doi.org/10.1093/BEHECO/ARW155>

Luo, L., Reimert, I., de Haas, E. N., Kemp, B., & Bolhuis, J. E. (2019). Effects of early and later life environmental enrichment and personality on attention bias in pigs (*Sus scrofa domesticus*). *Animal Cognition*, 22(6), 959–972. <https://doi.org/10.1007/S10071-019-01287-W/FIGURES/5>

Marshall, G. N., Wortman, C. B., Kusulas, J. W., Hervig, L. K., & Vickers, R. R. (1992). Distinguishing Optimism From Pessimism: Relations to Fundamental Dimensions of Mood and Personality. *Journal of Personality and Social Psychology*, 62(6), 1067–1074. <https://doi.org/10.1037/0022-3514.62.6.1067>

McGreevy, P. D., & Rogers, L. J. (2005). Motor and sensory laterality in thoroughbred horses. *Applied Animal Behaviour Science*, 92(4), 337–352. <https://doi.org/10.1016/J.APPLANIM.2004.11.012>

McLean, S., & Morrell, L. J. (2021). Sex Differences in Laterality Are Associated with Reproduction in Threespine Stickleback. <https://doi.org/10.1086/714138>, 197(6), 708–718. <https://doi.org/10.1086/714138>

Mehta, P. H., & Prasad, S. (2015). The dual-hormone hypothesis: a brief review and future research agenda. *Current Opinion in Behavioral Sciences*, 3, 163–168. <https://doi.org/10.1016/J.COBEHA.2015.04.008>

- Mommer, B. C., & Bell, A. M. (2013). A test of maternal programming of offspring stress response to predation risk in threespine sticklebacks. *Physiology & Behavior*, 122, 222–227. <https://doi.org/10.1016/J.PHYSBEH.2013.04.004>
- Ocklenburg, S., Ströckens, F., Bless, J. J., Hugdahl, K., Westerhausen, R., & Manns, M. (2016). Investigating heritability of laterality and cognitive control in speech perception. *Brain and Cognition*, 109, 34–39. <https://doi.org/10.1016/J.BANDC.2016.09.003>
- Rettenbacher, S., Groothuis, T. G., Henriksen, R., & Möstl, E. (2013). Corticosterone in bird eggs: The importance of analytical validation. *Wiener Tierärztliche Monatsschrift-Veterinary Medicine Austria*, 100.
- Richards, A., Blanchette, I., & Munjiza, J. (2007). Contextual influences in the resolution of ambiguity in anxiety. *COGNITION AND EMOTION*, 21(4), 879–890. <https://doi.org/10.1080/02699930601054018>
- Richards, A., French, C. C., Calder, A. J., Webb, B., Fox, R., & Young, A. W. (2002). Anxiety-Related Bias in the Classification of Emotionally Ambiguous Facial Expressions. *Emotion*, 2(3), 273–287. <https://doi.org/10.1037/1528-3542.2.3.273>
- Rogers, L. J. (1981). Environmental influences on brain lateralization. *Behavioral and Brain Sciences*, 4(1), 35–36. <https://doi.org/10.1017/S0140525X00007500>
- Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science*, 127(1–2), 1–11. <https://doi.org/10.1016/J.APPLANIM.2010.06.008>
- Rogers, L. J., & Deng, C. (2005). Corticosterone treatment of the chick embryo affects light-stimulated development of the thalamofugal visual pathway. *Behavioural Brain Research*, 159(1), 63–71. <https://doi.org/10.1016/J.BBR.2004.10.003>
- Schaafsma, S. M., & Groothuis, T. G. G. (2012). Sex-specific effects of maternal testosterone on lateralization in a cichlid fish. *Animal Behaviour*, 83(2), 437–443. <https://doi.org/10.1016/J.ANBEHAV.2011.11.015>
- Terburg, D., Peper, J. S., Morgan, B., & van Honk, J. (2009). Sex differences in human aggression: The interaction between early developmental and later activational testosterone. *Behavioral and Brain Sciences*, 32(3–4), 290–290. <https://doi.org/10.1017/S0140525X09990367>

Verjat, A., Devienne, P., Rödel, H. G., & Féron, C. (2021). More exploratory house mice judge an ambiguous situation more negatively. *Animal Cognition*, 24(1), 53–64. <https://doi.org/10.1007/s10071-020-01414-y>

Wark, A. R., Greenwood, A. K., Taylor, E. M., Yoshida, K., & Peichel, C. L. (2011). Heritable Differences in Schooling Behavior among Threespine Stickleback Populations Revealed by a Novel Assay. *PLOS ONE*, 6(3), e18316. <https://doi.org/10.1371/JOURNAL.PONE.0018316>

Wilkinson, R. J., Porter, M., Woolcott, H., Longland, R., & Carragher, J. F. (2006). Effects of aquaculture related stressors and nutritional restriction on circulating growth factors (GH, IGF-I and IGF-II) in Atlantic salmon and rainbow trout. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 145(2), 214–224. <https://doi.org/10.1016/J.CBPA.2006.06.010>

Wiper, M. L. (2017). Evolutionary and mechanistic drivers of laterality: A review and new synthesis. *Laterality: Asymmetries of Body, Brain and Cognition*, 22(6), 740–770. <https://doi.org/10.1080/1357650X.2017.1291658>

Zucca, P., Cerri, F., Carluccio, A., & Baciadonna, L. (2011). Space availability influence laterality in donkeys (*Equus asinus*). *Behavioural Processes*, 88(1), 63–66. <https://doi.org/10.1016/J.BEPROC.2011.06.012>