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The missing link

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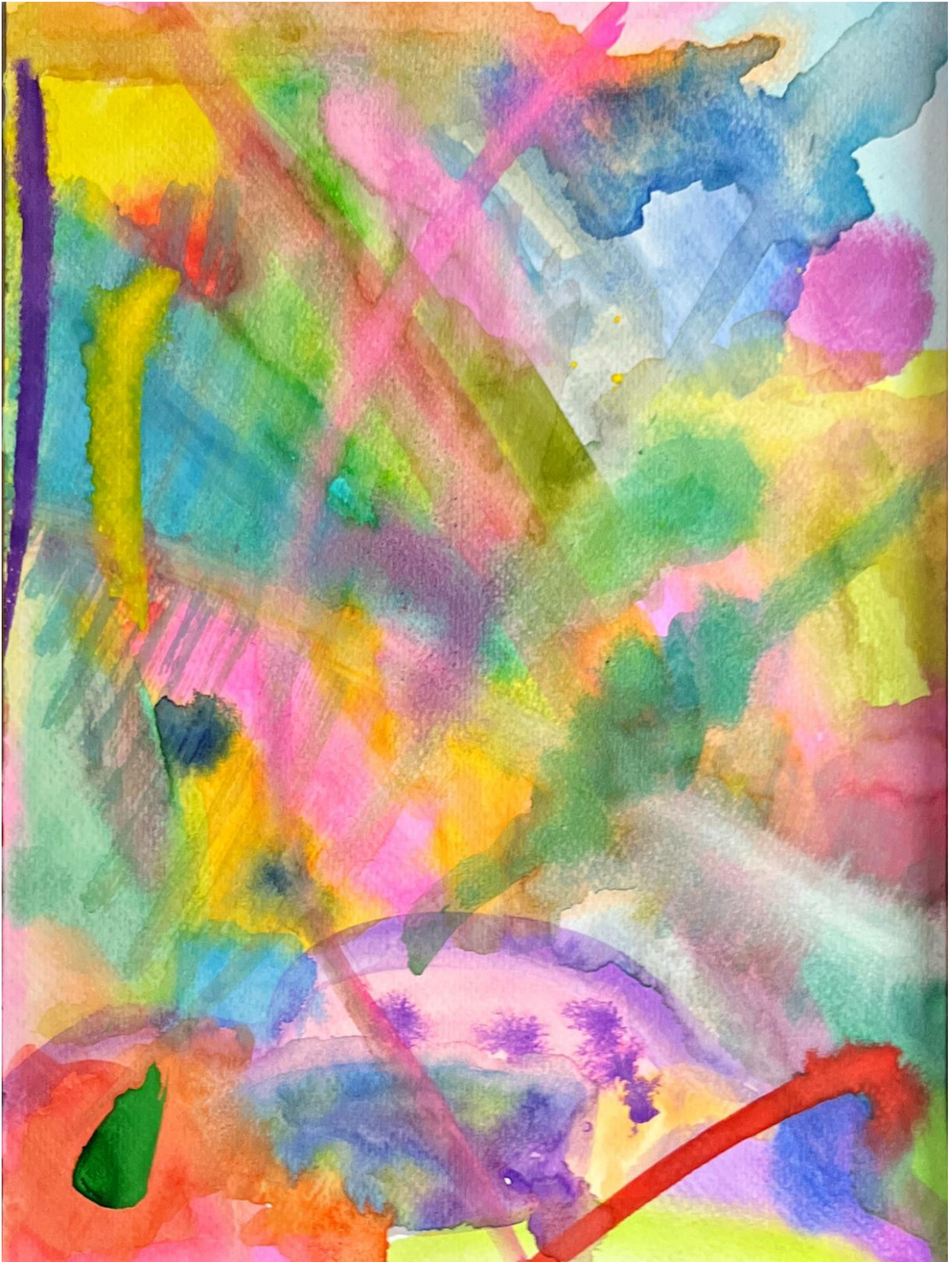
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“Life”

Chapter 1

General Introduction

Theoretical Background

Laterality

Brain lateralization or hemispheric specialization refers to the phenomenon whereby one brain hemisphere predominantly controls certain functions, processes, and behaviours relative to the other hemisphere. Motor and sensory control is predominantly crossed over from the contralateral hemisphere; the right hemisphere controls the left side of the body and vice versa, which means that cerebral lateralization often manifests itself as behavioural side biases. (Bisazza & Brown, 2011). These behavioural side biases are known as laterality (Bisazza et al., 1997; Schaafsma et al., 2008; Glick 2012) . Similarly, sensory information crosses over and is analysed in the opposite hemisphere. The study of laterality has a long history. In 1861 Broca, with his classical observation, discovered brain lateralization of language in humans and a century later Sperry and his collaborators extended this concept by studying split-brain patients in the 1960s. It was apparent that although each hemisphere of the brain looked superficially similar, they clearly performed different functions. While laterality was initially believed to be a unique human trait, nowadays, laterality in behaviour, sensory perception, and cognitive processes is considered ubiquitous among vertebrates (Leliveld et al., 2013; Rogers, 2014) and has also been identified in some invertebrate species (Frasnelli, 2013; Niven & Frasnelli, 2018) .

When measuring laterality, researchers usually focus on two aspects: strength and direction. Strength indicates how far from parity (where there is no difference between left and right) an individual deviates irrespective of the direction of bias. Direction, on the other hand, indicates if the individual is right or left lateralized in behaviour (with the opposite direction in brain lateralization due to the contra-lateral control of hemispheres of motor control). It has been proposed that natural selection might act at on the strength of laterality rather than the direction of cognitive asymmetry in some contexts since the cognitive benefits are realized irrespective of direction (Collins, 1991) . This occurs because the processing power of the brain is enhanced by selectively dividing the processing of different types of information over the two specialized hemispheres thereby increasing cognitive capacity and facilitating multitasking (Magat & Brown, 2009; Rogers, 2000; Vallortigara & Rogers, 2005) . Being lateralized at the individual level can

be also advantageous because when one hemisphere is controlling a specific behaviour, it is not competing with the other hemisphere. This can lead to more rapid responses (Frasnelli & Vallortigara, 2018; Gülbetekin et al., 2009; Vallortigara et al., 2011). For example, if fish or birds are tested in a foraging task where they have to monitor a predator at the same time, lateralized individuals perform better (Dadda & Bisazza, 2006; Rogers et al., 2004). Today, modern computers emulate this benefit by using multiple CPUs.

It has also been argued that in social interactions, where behaviour can be aligned among group members, the direction of lateralization also has fitness consequences (Frasnelli & Vallortigara, 2018). Laterality at the population level has been explained as a consequence of selective social pressures where individuals coordinate with each other and align their biases in the same direction (Vallortigara & Rogers, 2005). It may also be under frequency dependent selection since the fitness consequences of being lateralized depends on the distribution of phenotypes within the group (C. Brown et al., 2005). For example, left-handed humans have an advantage during combat and competitive sports (Abrams & Panaggio, 2012). In contrast, schooling in fishes is a classic context where closely aligned responses are likely to be favoured by natural selection to counteract predatory attacks (Pitcher & Magurran, 1983; Pitcher & Wyche, 1983)

Personality

Personality is described as the consistency of an individual's behaviour over time and across contexts measured relative to other individuals of the same population (Castanheira et al., 2013; Koolhaas et al., 1999; Stamps & Groothuis, 2010). Personality has been identified in a wide range of animals (Carere and Mastroianni 2013), including invertebrates (Tariel et al., 2020a), teleost fish (Colléter & Brown, 2011), sharks (Byrnes & Brown, 2016), lizards (Barrett et al., 2022), birds (Groothuis & Carere, 2005a) and mammals (Mazza et al., 2019). In humans, the Five-Factor Model delineates the axes of variation in personality; researchers have proposed that analogous terminology could be employed for animals (Gosling & John, 1999), specifically aggressiveness, activity, exploration, boldness, and sociability (Réale et al., 2007a). Personality requires a linkage between several personality traits (Stamps & Groothuis, 2010) and indeed many studies have found a correlation between two behavioural traits, for example activity and boldness (Fraser et al., 2001, Dingemanse et al., 2007, Moretz et al., 2007). However, some of these correlations may arise through methodological issues, particularly when the traits in question are not well defined. Indeed, more active fish are more likely to explore a new environment or a novel object, just because they are active during the test.

Thus, there is some controversy as to the best assays for each of these personality traits. Therefore, it is necessary to implement a method to assess personality traits correctly. A well-defined single assay or a combination of measures is probably the best way to identify personality traits (Budeav & Brown 2011) .

The study of nonhuman personalities capitalizes on the fact that individuals behave in predictable, variable, and quantifiable ways. Recent studies have found that fitness consequences of personality traits differ according to variation in environmental conditions, such as predation pressure (Réale & Festa-Bianchet, 2003) and food availability (Dingemanse et al., 2004). A meta-analysis on personality and its fitness consequences discovered that bolder individuals had increased reproductive success, especially in males, but at a cost of having a shorter life span (Smith & Blumstein, 2008) . This may result in similar net fitness and co-existence of two types of personality, related to different paces of life (Smith & Blumstein, 2008).

Clearly, both laterality and personality are fundamental components of how brain and behaviour is organized throughout the animal kingdom.

Genetic and environmental influences on personality and laterality

Both personality and laterality have heritable components (Bisazza et al., 2000; Ocklenburg et al., 2016a; Vukasović & Bratko, 2015) but they are also strongly influenced by experience during early ontogeny and later in life. Laterality is partially heritable (Bisazza et al., 2000; C. Brown, Western, et al., 2007; Ocklenburg et al., 2016a; Wiper, 2017), as shown by research using the poecilid, *G. falcatus*, which revealed that only two generations of artificial selection for a right or a left preference were enough to establish lines with evident lateral biases (Bisazza et al., 2007). As is the case in many traits, laterality is also affected by environmental factors (C. Brown, Western, et al., 2007; De Santi et al., 2000) of which the parents may be a pivotal part (C. Brown, Western, et al., 2007; Budaev & Andrew, 2009a; Dale Broder & Angeloni, 2014). A study on handedness in rats for example, investigated the influence of the early life environment exposing them to a novel environment daily during their first three weeks of life. Exposure to novelty caused a leftward shift in their paw preferences in comparison to the control group (Tang & Verstynen, 2002).

There is also evidence of a heritable component in personality (Réale et al., 2007b; Vukasović & Bratko, 2015). Generally, genetic heritability is defined as the relative amount of genetic variation in relation to the total phenotypic variation (Falconer &

Mackay, 1996). However, the term genetic does not entirely explain heritability, as epigenesis also play a role in the vertical transmission (Groothuis & Carere, 2005b) . In addition, animals with similar genotypes that are exposed to varying environments often develop, due to phenotypic plasticity, different phenotypes. The interplay between genotypic and environmental influences on phenotype can be complicated. Environmental influences that are common among relatives might also contribute to the diversity in personalities, and if not appropriately considered, could potentially distort estimates of heritability (Kruuk & Hadfield, 2007). Parental effects are a special case in point in which the environment provided by one or both parents results in similar offspring phenotypes (Mousseau et al., 2009; Mousseau & Fox, 1998), which can cause an overestimation of additive genetic effects when the influence of a common parental environment are not taken into account (Falconer & Mackay, 1996; Kruuk & Hadfield, 2007).

A human meta-analysis revealed that the average genetic contribution to individual differences in personality was approximately 40% (Vukasović & Bratko, 2015). A study of personality heritability in animals found that approximately 52% of the variation in personality was attributed to additive genetic variation (Dochtermann et al., 2015) . These findings suggest that the heritability of behaviour is often low or moderate while the heritability estimates for personality is often higher. These results may demonstrate that genetic variations are likely a significant factor contributing to the diversity in animal personality (Dochtermann et al., 2015). Clearly, variation in both laterality and personality have a genetic component, but account for only part of the variation, much of the remaining variation is due to environmental factors.

Environmental conditions during an individual's development also have consistent long-lasting effects on personality traits (Lindström, 1999) . Some of the key environmental variables that generate plasticity in both aspects of laterality and personality include predation, exposure to light during embryogenesis, and hormone exposure and parental effects. I discuss each of these below.

Predation

Exposure to predation threat plays a profound role in shaping both laterality and personality. Studies indicate that personality traits are affected by, or more likely to be expressed in, the presence of predation pressure (Bell & Sih, 2007; Dingemanse et al., 2009). Exposing sticklebacks to predation pressure generated a boldness–aggressiveness

behavioural correlation that did not emerge in non-exposed fish (Bell & Sih, 2007). Also, in sticklebacks, simulated predation risk generated repeatable behaviour for boldness and aggression (Edenbrow & Croft, 2012; Stein & Bell, 2014). Studies using the poeciliids demonstrate that fish from high predation zones emerged sooner from a shelter, were bolder, than fish from low predation zones (C. Brown et al., 2005; Harris et al., 2010). Personal experience with predation exposure can also influence personality traits, and within-individual variation (i.e. plasticity). Bucklaew and Dochtermann (2020) conducted tests on individual crickets, *Gryllodes sigillatus*, and found that individuals were less likely to emerge from shelters after exposure to predation cues but also exhibited increased activity (Bucklaew & Dochtermann, 2021).

Predation pressure can also alter lateralization and this influence has received much attention (C. Brown et al., 2004a; C. Brown, Western, et al., 2007; Dadda et al., 2020). Research has demonstrated that fish from high predation areas were more lateralized compared to those from low predation areas and tend to show population level laterality (C. Brown et al., 2004a). A possible explanation for this result is that a more strongly lateralized brain would be more efficient in a predation context because fish must pay attention to different stimuli at the same time for which they can use two different hemispheres for parallel processing, as well as to align laterality during escape responses (Vallortigara & Rogers, 2005). Indeed, this dual attention capacity has been demonstrated in both chicks and fish (Dadda & Bisazza, 2006; Rogers et al., 2004) where lateralized individuals more efficient at foraging in the presence of a model predator. For gregarious fish, such as sticklebacks (*Gasterosteus aculeatus*) and rainbowfish (*Melanotaenia australis*) for example, the advantage of schooling via the coordination of swimming exceeds the costs of being predictable for the predator (Ghirlanda & Vallortigara, 2004). A study by Chivers et al., (2016) on a schooling coral reef fish demonstrated that escape responses of fish that were coordinated with the majority of their school mates had improved escape performance than fishes that had contrasting laterality (Chivers et al., 2016). However, this is highly context-dependent because it only occurred when the school perceived high predation threat in the environment.

Light

Exposure to light during early development is an important environmental factor that affects laterality and personality. The presence or absence of light during the prenatal or perinatal development of the domestic chick and in fish larvae affects the degree of

individual lateralization (R. J. Andrew et al., 2008; Berlinghieri et al., 2023; Budaev & Andrew, 2009a, 2009b; Dadda & Bisazza, 2012; Rogers & Deng, 2005). In fish, eggs exposed to light were more lateralized compared to those that remained in the dark during development (R. J. Andrew et al., 2008; Berlinghieri et al., 2023; Budaev & Andrew, 2009a; Dadda & Bisazza, 2012). A possible explanation may be that the transparency of fish eggs allows direct exposure of light to the photosensitive regions in the epithalamus during egg development. This exposure may lead to the asymmetric development of certain structures, including the habenula, which play a role in regulating various behavioural responses (Budaev & Andrew, 2009a). While concerning personality, eggs developed in darkness during the first six days after fertilization increased shyness (Budaev & Andrew, 2009b). An hypothesis regarding these behavioural asymmetries may be mediated, as already mentioned, by the habenula. The habenula is a paired epithalamic structure, and in fish and other vertebrates is significant anatomical asymmetry (Concha et al., 2000). The connection between habenular and behavioural asymmetry gains additional support from the similarities in the functions of the principal habenular divisions in zebrafish and rats, despite the challenge of establishing homologies between habenular divisions in these phylogenetically distant species (Budaev & Andrew, 2009a). Similarly, a study on the circadian clock in zebra finches (*Taeniopygia guttata*) revealed that individuals exposed to constant light decreased their exploration (Jha & Kumar, 2017). This effect may be explained by the fact that the influence of light on circadian behaviour may depend on the intensity of light, as circadian rhythmicity is maintained in various songbird species under constant illumination (Aschoff & Paul, 1982). Chronic light exposure could indeed modulate behaviour controlled by the circadian clock.

Parental Effects and Hormones

Examining the effects of predation pressure on parents and the subsequent influence on offspring behaviour is one of the most well studied contexts of parental effects. While parental effects have been studied by manipulating both parents, it is more common to examine the influence of mothers (maternal effects instead of paternal effects). In several species, mothers exposed to predators generate offspring with enhanced antipredator behaviour (invertebrates: Storm & Lima, 2010, reptiles: Bestion et al., 2014; Shine & Downes, 1999; fish: Giesing et al., 2011, birds; Coslovsky et al., 2012; mammals: St-Cyr & McGowan, 2015). Parents may also adjust the offspring's personalities to enhance the alignment between their phenotype and the environment. Consequently, parental effects

can serve as a substantial mechanism for creating and maintaining behavioural diversity. Fathers can also influence the behaviour of their offspring. A study revealed that fathers exposed to predation pressure generate offspring with phenotypes associated with strong predation pressure (Stein & Bell, 2014). These offspring exhibited characteristics such as smaller size, reduced body condition, and reduced behavioural activity.

A study by Galuret et al. (2020) investigated the influence of maternal care on the laterality of non-brooded and brooded domestic chicks (*Gallus gallus domesticus*) (Galuret et al., 2020). The researchers examined and evaluated individual and population laterality, social behaviour, and emotional responses during the mothering period. Their findings indicated that non-brooded chicks displayed stronger lateralization also at the population level and were more consistent in their behaviours compared to brooded chicks. Consequently, in the absence of the mother, chicks may have learned from each other, which could explain why non-brooded chicks exhibited greater alignment. Maternal effects may also result from lateralized interactions between the mother and her offspring. For example, the chicks' positioning beneath the mother during the warming process, as well as their gentle or confrontational pecking behaviours, predominantly performed on one side, or the mother's preferred approach side to reach her chicks, might have influenced the lateralization of the chicks. This study highlights the postnatal impact of maternal care as a social environmental factor on the development of laterality in domestic chicks (Galuret et al., 2020; Schaafsma et al., 2008).

Early exposure to certain hormones can also influence the development of laterality as well as a personality. It has been demonstrated that early exposure of cichlid females to testosterone caused a significant shift in laterality while there was no effect in males (Schaafsma & Groothuis, 2012), perhaps because males are normally already exposed to elevated endogenous levels of the hormone. In the domestic chick prenatal exposure to cortisol enhanced visual laterality (Rogers & Deng, 2005). In birds, specifically chicks, when exposed to high level of androgen during development chicks become bolder, more aggressive and explorative adults compared to individuals exposed to lower androgens (Groothuis & Carere, 2005b)

The exposure to hormones during early development can be influenced by the mother. It is well known that in egg laying species mothers deposit maternal hormones in their eggs and that this varies depending on how she experiences the environment. For example, avian mothers may manipulate androgen levels within a clutch to enhance the diversity

of their chicks' personalities, thereby increasing the likelihood that at least some of them will be successful in the current environmental conditions (Eising et al., 2005).

Maternal effects can also be manifested in other ways. Dadda et al. (2020), exposed topminnows to simulated predation threats during pregnancy and found that predator exposure increased both visual and motor lateralization in their offspring (Dadda et al., 2020). A possible explanation can be found in prenatal hormone exposure of maternal origin, with cortisol being a potential candidate, as predator exposure often leads to an elevation of this hormone in adults (Deckel, 1998; Jutfelt et al., 2013; Ocklenburg et al., 2016; Raoult et al., 2012; Rogers & Deng, 2005; Westergaard et al., 2001). In mice, parental exposure to predator odour increased antipredator behaviour in their offspring (St-Cyr & McGowan, 2015). Specifically, offspring showed increased avoidance behaviour to the odour of predators and females also had a decreased locomotor activity and both are likely to be mediated by maternal cortisol (St-Cyr & McGowan, 2015).

Cognitive bias and welfare

The term cognitive bias is defined as the influence of emotions on cognition (Mathews & Macleod, 1994). This occurs because the positive or negative valence of an affective state can influence cognitive processes such as judgement, motivation, memory and attention (D'Ettorre et al., 2017; Novak et al., 2015) Individuals with positive cognitive judgement bias have a high expectation of reward when faced with an ambiguous stimulus (D'Ettorre et al., 2017). This state is commonly referred to as 'optimism' and operationally is observed when animals approach ambiguous stimulus quickly. In contrast, individuals with negative cognitive judgment bias have low expectation of reward (or punishment) when confronted with an ambiguous stimulus. This state is commonly known as 'pessimism', and operationally is observed when animals either avoid ambiguous stimuli or approach slowly (D'Ettorre et al., 2017; Douglas et al., 2012) Many studies based on the judgement of an ambiguous stimulus have been conducted in different animal species (Roelofs et al 2018). Laterality and personality may correlate with cognitive bias since both traits are known to have strong impacts on cognition and also cognitive bias.

Laterality is associated with enhanced cognitive abilities (Levy, 1977; Ocklenburg, Beste, et al., 2014; Ocklenburg, Hirnstein, et al., 2014). Many studies examined the specific advantages of being lateralized in terms of both strength and direction. For example, in parrots, highly lateralized individuals outperformed less lateralized individuals by being better able to distinguish between food and non-food items representing a higher foraging

fitness (Magat & Brown, 2009). Likewise, in fish, strongly lateralized guppies were more capable of distinguishing larger shoals from smaller shoals (Bisazza & Dadda, 2005a). It has been proposed that brain laterality improves cognitive abilities by dividing analysis of different types of information into the two cerebral hemispheres, allowing separate and parallel processing, thereby maximising processing efficiency (Rogers, 2000,2002) . Given that laterality can influence cognition, it may also affect cognitive bias.

Personality can also affect cognitive bias. In humans, certain personality traits have been found to correlate with cognitive processing of environmental stimuli, known as attention bias (Mathews et al., 1997). In humans, personality makes some individuals more susceptible to developing attention bias during times of stress (MacLeod et al., 2002) and there may be feedback loops on personality traits (Mathews et al., 1997). In animals, cognitive judgment bias is often tested using a simple go/no go procedure (Harding et al., 2004) which has a strong cognition element to it, particularly during the training phase. Several studies have suggested that personality traits may be linked to cognition assays. For example, bolder and more exploratory individuals are more likely to engage with and ultimately solve cognition assays (Sih & Del Giudice, 2012; Wolf et al., 2008). In three spine-sticklebacks, boldness affected information use, and consequently bold fish were better at perceiving and understanding environmental cues (Harcourt et al., 2010). There is also some evidence that personality traits can influence the outcome of judgement bias tests. In carpenter ants, for example, fast explorers showed a pessimistic bias towards an ambiguous cue while slow explorers were optimistic (D’Ettorre et al., 2017) Whereas more neurotic parrots showed greater attention bias for environmental stimuli (Cussen & Mench, 2014).

The (missing) link between laterality and personality

Specific emotions that can affect some personality traits are mainly processed by a specific hemisphere and are therefore lateralized (Rogers, 2010) Thus, it can be expected that some personality traits, such as boldness and aggression, may be expressed behaviourally in a lateralized fashion (C. Brown & Bibost, 2014; Byrnes, Pouca, et al., 2016; Irving & Brown, 2013; Reddon & Hurd, 2008, 2009). Previous studies have found such a link between laterality and personality traits: Black-lined rainbowfish (*Melanotaenia nigrans*) for example, non-lateralized fish were bolder than lateralized (Brown & Bibost, 2014). In contrast, Reddon & Hurd (2008) found that more lateralized

convict cichlids (*Archocentrus nigrofasciatus*) were bolder and more aggressive. A study on the feral guppy (*Poecilia reticulata*) found a link between laterality and personality depending on sex, where males were bold, active and antisocial compared to females (Irving & Brown, 2013). These examples highlight the variable associations between personality and laterality.

A few studies addressed the potential link between laterality and personality, and there is little consensus about the existence and nature of such a link. Moreover, most studies are correlative and to date only one study manipulated an environmental factor and studied how the potential link between laterality and personality changed, suggesting a more causal relationship. Only a single study investigated the effects of light on both laterality and personality traits in fish and found that rearing fish in the absence of light reduced behavioural laterality in response to a predator model and also reduced boldness (Budaev & Andrew, 2009b).

It is possible that a common causal factor connects laterality and personality. In such a scenario, the manipulation of laterality might also influence personality, and vice versa. Some studies have demonstrated that the testosterone-cortisol ratio can predict personality traits, including boldness, sociability, or aggressiveness in humans (Mehta & Prasad, 2015; Terburg et al., 2009). Moreover, additional studies have established a connection between stress and laterality in multiple species (Brüne et al., 2013; Byrnes, Vila-Pouca, et al., 2016; Fernández-Lázaro et al., 2019a; Morgante et al., 2007). Similarly in primates, an association has been observed between exploration, activity, aggressiveness, stress and the levels of cortisol metabolites, as well as laterality (Fernández-Lázaro et al., 2019). Considering previously mentioned evidence that has established the influence of steroid hormones on laterality, hormones may serve as part of the underlying mechanisms that link laterality and personality. However, whether these correlations are really causal is yet to be firmly established.

Gaps in the literature

In this PhD thesis I report on my investigations on the effects of environmental factors during early development on the development of laterality and personality, and the association between them, in fishes, specifically the effects of the presence or absence of light and the effects of predation pressure. In addition, I wanted to determine how long through development the environmental manipulation effects might last. In the scientific literature there are only a few studies investigating the effect of light on laterality and

personality but only in young individuals not in adults or sexually matured individuals (R. J. Andrew et al., 2008; Berlinghieri et al., 2023; Budaev & Andrew, 2009a, 2009b; Dadda & Bisazza, 2012; Rogers & Deng, 2005). It has been established that the neural connections in the domestic chick from the eyes to the brain under light conditions initially develop asymmetrically (Rogers, 2008), but that this appeared after a few weeks of life. How visual laterality develops after that period has not yet been established. Therefore, to fill the knowledge gap, I explored if the effect of light (and also the absence thereof) on laterality during embryonic development lasted until fish became sexually mature (3 months old).

The environment for developing embryos is partly determined by both parents, therefore both personality and laterality might also be influenced by the parents very early during development perhaps via the exposure to maternal hormones, such as cortisol. In the literature there are many studies on parental effects, which report especially on changes in offspring morphology, physiology and behaviour (Eising et al., 2005; Moisiadis & Matthews, 2014; Rakers et al., 2020). The effect of predation pressure on parents and the subsequent influence on offspring behaviour is one of the most well studied contexts of parental effects. From literature findings one can draw the conclusion that personality traits can be affected by predation pressure (Bell & Sih, 2007; Edenbrow & Croft, 2012; Stein & Bell, 2014). To date, however, there are no studies that have determined whether the possible link between laterality and personality traits is affected by the same mechanism caused by parental factors in a single study system, indicating a causal link between them. Given that laterality and personality may be correlated through underlying common mechanisms, I tested the hypothesis that altering one trait through various environmental manipulations results in a shift in the other.

Laterality has been studied in many animal species, including fish (Bisazza & Brown, 2011). However, there are only two studies on sticklebacks which is somewhat astonishing. Given the known ecological impacts on laterality, particularly with respect to variation in predation, and the huge literature on sticklebacks, there is a clear gap in our knowledge here. In addition, the variation in behaviour and morphology between marine and freshwater sticklebacks is well documented (Mäkinen et al., 2006; Seebacher et al., 2016; Wang et al., 2020) but no one has as yet attempted to measure differences in laterality between these populations. Importantly, many of the traits that differ between marine and freshwater sticklebacks are known to have a genetic basis and variation in predation pressure seems to be the principal driver of diversification (Jiang et al., 2022;

Meyer & Kassen, 2007; Zu et al., 2015). By examining pure marine, pure freshwater and reciprocal hybrid lines I wanted to determine if the genetic background of fish contributes to variation in laterality.

Finally, given that laterality and personality are both known to influence cognition I wanted to determine if either trait might influence cognitive bias. Cognitive bias is increasingly used in welfare contexts as a means to determine an animal's affective state but has been rarely applied to fishes. Studies in the literature assess cognitive and judgmental biases in animals, with a particular focus on mammals, especially in the context of welfare (Lagisz et al., 2020). Also, regarding the personality field, there is a theoretical connection between the response to an ambiguous stimulus (judgmental bias) and personality (D'Ettorre et al., 2017). Indeed, individuals could be inclined to develop positive or negative affective states relating to their personality traits, with consequent cognitive judgment bias (Mathews et al., 1997). Moreover, if we look into laterality studies, we find that having a lateralized brain can also be advantageous while learning and problem solving (Magat & Brown, 2009; Sovrano et al., 2005). However, to what extent lateralization is related to a cognitive bias is as yet unknown. To date, no study has evaluated the link between personality traits, laterality and cognitive bias.

Choice of species

In order to evaluate laterality and personality and their link, I had to find an animal species that was easy to handle, test and maintain in an animal facility. Since my Ph.D. was a Cotutelle degree at the University of Groningen (Groningen, the Netherlands) and Macquarie University (Sydney, Australia), in principle I was supposed to spend half the time in Groningen and the rest in Sydney. As fish have been used for laterality and personality research for more than 25 years (Bell & Sih, 2007; Bisazza & Brown, 2011, Budaev & Brown 2011), and one of my supervisors (CB) had extensively studied rainbowfish, the initial aim was to assess laterality and personality in captive and wild populations of rainbowfish. Rainbowfish are also extremely popular in the aquarium trade and can be readily obtained in Europe. So, the idea was to start a series of experiments in Groningen using captive-bred rainbowfish and then switch to studying wild rainbowfish at Macquarie University. Unfortunately, this plan had to change, due to the Corona pandemic, so I used rainbowfish for one chapter and then switched to three-spined sticklebacks for the other three once it became clear I could not travel to and work in Australia. Three-spined sticklebacks are native to The Netherlands, can be studied both in the lab, in the field, and in semi-natural conditions. They have been widely used in

behavioural and ecological research (Bell & Stamps, 2004; Sih et al., 2004) and I could also team up with another group working on these sticklebacks that had built unique semi-natural housing facilities.

Rainbowfish

Rainbowfish are generally found with conspecifics in small shoals (C. Brown, 2002; Brown & Culum, 2000). Males are more brightly coloured and typically larger than females (see figure 1)(C. Brown, 2002; Young et al., 2010). Males court females and after finding a suitable mating partner, eggs are externally fertilized and deposited in the vegetation which serves as a shelter for the fry until they are large enough to fend for themselves. There is no parental care. Hatching time is temperature dependent but usually takes around 7 days post fertilization. Most rainbowfish reach sexual maturity in approximately 90 days (Humphrey et al., 2003) . The Western Rainbowfish is one of the most common and widespread freshwater fish in river systems of north-western Australia and are readily available from pet stores around the world.

Rainbowfish have previously been used as a model species to study laterality (A. L. Bibost & Brown, 2013; A.-L. Bibost et al., 2013; Brown & Bibost, 2014), social learning (C. Brown & Warburton, 1999a, 1999b), cognition (A. L. Bibost & Brown, 2014), animal personality (Colléter & Brown, 2011), stress responses (Zuberi et al., 2011), anti-predator behaviour (C. Brown, 2003; C. Brown & Warburton, 1997), and the effects of the rearing environment on behaviour (A.-L. Bibost et al., 2013b) . They are a preferred species for such studies because they are easy to rear in captivity and breed throughout the year under laboratory conditions (H. P. Reid & Holdway, 1995).



Fig1. Females and males of *Melanotaenia australis*, the Western Rainbowfish.

Sticklebacks

The Three-spined stickleback, *Gasterosteus aculeatus*, is a widespread freshwater and marine fish species found in the northern hemisphere (Pauly 2008; Fang et al., 2018). They

are arguably one of the most widely used species for studies in behaviour, physiology, evolution, ecology (Von Hippel, 2010) and, more recently, molecular biology (K. Reid et al., 2021). Sticklebacks are gregarious fish forming schools outside the reproductive season and are sexually dimorphic which is most pronounced in the breeding period from spring until summer. Males develop a red belly and are generally smaller than females (see figure 2). The male crafts a nest using plants material, and courts females. Females lay eggs inside the nest which are subsequently fertilised by the male. The male vigorously defends his nest and surrounding territory and takes care of the young (Fitzgerald, 1993).

Some populations inhabit freshwater environments across the year, while other migrate from the marine environment to freshwater for reproduction (Clavero et al., 2009). In the Netherlands barriers have been built in the last 50 years to maintain water level below the sea level and this created land locked water systems where sticklebacks became trapped and can no longer migrate. These populations became freshwater “residents” (Ramesh et al., 2022). During the 50 years of isolation, the resident sticklebacks have adapted to their environment developing differences in morphology and behaviour from their marine migratory ancestors. Residents are smaller and more poorly armoured, more active, exploratory, bolder and school less than migrants (Ramesh et al., 2022).

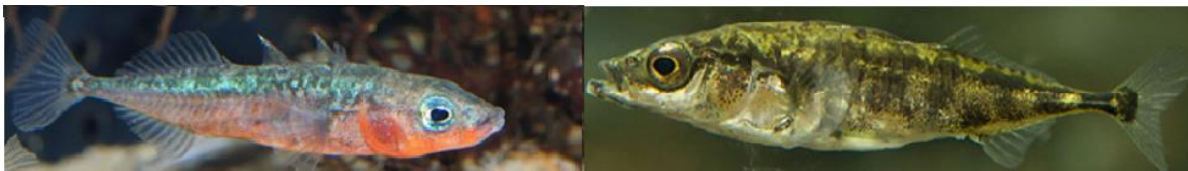


Fig 2. Male (left) and female (right) three-spined stickleback (*Gasterosteus aculeatus*).

Thesis overview

This PhD thesis has four data chapters (chapters 2-5), that explore different aspects of the relationship between laterality and personality as detailed below, a review on laterality and welfare implications, followed by a synthesis.

Chapter two: “The effect of light during embryonic development on laterality and exploration in Western Rainbowfish”.

Published in *Laterality* (<https://doi.org/10.1080/1357650X.2023.2252567>)

In this chapter I explored the effect of an essential ecological environmental factor on laterality and personality: light exposure during the egg phase of Western Rainbowfish.

In this experiment, I reared eggs in the total dark (<0.01 lux) and eggs under a tropical light/dark cycle (12/12h). When hatched, I moved the fry to a normal light/dark cycle (12/12h) and tested them at two different ages (10 to 17 days of age called “young” and at 42 to 60 days of age “mature”). I used a rotational mirror test and a novel object test to assess laterality scores, and a novel environment test for the exploration.

I expected, based on the literature presented earlier sections above, that offspring reared in the dark would be less lateralized and less explorative in a novel environment when tested soon after hatching. I also hypothesized that any effects of the rearing environment during embryogenesis would be lost by the time the fish matured, because other environmental factors will overrule the early effects.

Chapter three: “Parental predator exposure affects offspring boldness and laterality in the stickleback”.

In this chapter I switched animal species to the three-spined stickleback for logistical reasons (see above). In collaboration with another group (Weissing group) of my Institute (University of Groningen, GELIFES), I exposed parents of sticklebacks to perceived predator presence (or not) for about 5 months in a semi-natural system of ponds at the animal facility of the University of Groningen. I collected eggs soon after they were laid, let them hatch, and at the age of 3 months tested the offspring with a mirror test to establish laterality, predator inspection to estimate boldness and a schooling test to estimate sociality. I also analysed the level of cortisol in the eggs.

In line with the literature presented above I expected that offspring from parents exposed to predation would be consistently more strongly lateralized and bolder relative to offspring from the parents not exposed and that the treatment would induce a stronger correlation between both traits. I also hypothesised that mothers exposed to predation pressure would deposit more cortisol in their eggs which would correlate with the expected differences in offspring behaviour.

Chapter four:” Laterality the marine and freshwater three-spined stickleback (*Gasterosteus aculeatus*)

In this chapter I explored the laterality in the tree-spined sticklebacks (*Gasterosteus aculeatus*) derived from marine and freshwater populations and reciprocal crosses between them (hybrids). Individuals used in this study were previously used in another

experiment by Ramesh et al., (2021) They were the F1 generation of wild-caught individuals, obtained by artificial fertilization and all raised without paternal care under identical conditions. I hypothesize that in the marine population which forms large schools during migration and is supposed to be exposed to elevated levels of predation, will be more strongly lateralized than resident freshwater populations. I tested laterality by studying which eye was predominantly used during looking at a mirror. The use of different genotypes including hybrids enabled us to investigate the contribution of maternal and paternal genetic influences.

Chapter five: “Are lateralized and bold fish optimistic or pessimistic?”

This chapter has been submitted and is at the moment under review of the journal *Animal Cognition*.

In this chapter, I investigated the possibility that laterality and personality may correlate with cognitive bias. I analysed laterality and boldness of the three-spined sticklebacks and then performed a cognitive bias test using the classical go/no go paradigm followed by an ambiguous stimuli probe test to determine pessimism or optimism. Our aim was to determine if cognitive bias correlated with laterality, boldness and sex. I hypothesised, based on previous research, that bolder and more strongly lateralized fish would be more optimistic (approach the ambiguous stimuli faster) than shyer, less-lateralised fish. In addition, I also predicted that males would be more optimistic than females.

Chapter six: Laterality and fish welfare – A review

Published in *Applied Animal Behaviour Science*
(<https://doi.org/10.1016/j.applanim.2021.105239>)

This chapter is a review on how laterality may be used as a tool for welfare indicators in fish. The concern for fish welfare has significantly increased in recent years, prompting many countries to implement animal welfare regulations to protect fish welfare. A more comprehensive understanding of fish behaviour can lead to the development of better welfare indicators. In this context, we propose that laterality plays a crucial role in shaping fish behaviour, and gaining a better understanding of how laterality interacts with fish behaviour can offer opportunities to enhance fish welfare. Furthermore, assessing laterality through behavioural tests may itself serve as a valuable welfare indicator, given the apparent connection between laterality, personality, and stress reactivity. In this

review, we explore the current research on laterality in fish and emphasize instances where it could have significant implications for fish welfare.

In the last chapter (7. General Discussion) I synthesize the results of all the previous chapters, put them in a broader framework and suggest avenues for further research.

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