Vegetation cover induces developmental plasticity of lateralisation in tadpoles

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Abstract

Lateralization of cognitive functions influences a large number of fitness-related behaviours and shows, in most species, a large variation in both strength and direction. Laboratory work and field data have suggested that this variation is often due to adaptive phenotypic plasticity. Strong lateralisation should be favoured in some ecological conditions, for example under high risk of predation. For anuran tadpoles, the presence of cover affects predation risk, with tadpoles being more exposed to predators in environments with reduced cover. We tested the hypothesis that the amount of cover experienced early in life affects lateralisation in edible frog, \textit{Pelophylax esculentus}, tadpoles. We exposed embryos and larvae to high or low vegetation cover environments. For half of the subjects, the treatment was constant whereas the remaining subjects were switched to the opposite treatment after hatching. In agreement with theoretical expectation, tadpoles exposed to low-vegetation cover for the entire development were more laterised and showed a stronger directionality alignment in lateralisation compared to tadpoles exposed to high-vegetation cover. This indicates a possible role of natural variation in vegetation abundance as a determinant of between-population differences in lateralisation via developmental plasticity. We also found that shifting from high- to low-vegetation cover treatments and vice versa disrupted lateralisation alignment, suggesting that developmental trajectories for this trait are determined at the embryonic stage and need environmental stability to be fully expressed.

Keywords: lateralisation; light exposure; \textit{Pelophylax esculentus}; phenotypic plasticity.

In many animals, specific cognitive functions such as individual recognition, acoustic communication, prey catching or predator recognition are preferentially performed by one brain hemisphere, either the left or the right (Bisazza and Brown 2011; Rogers and Vallortigara 2017; Vallortigara et al. 2011). This causes left-right differences in the perception and elaboration of stimuli associated with these functions, and asymmetries in the resulting motor responses (e.g., Bisazza et al. 1996; Deckel 1995; Vallortigara et al. 1998).

In both humans and non-human species, one aspect of lateralisation is the presence of consistent variation in both strength and direction; individuals might differ in the preferential use of either their left or right cerebral hemisphere and with regards to how strongly a specific function is linked to one hemisphere (Knecht et al. 2000; Reddon and Hurd...
The pattern of cerebral lateralization can have important effects on fitness. For example, in the goldbelly topminnow, *Girardinus falcatus*, strongly lateralized individuals were better at schooling and were more efficient in performing two simultaneous cognitive tasks such as foraging while avoiding unsolicited males’ mating attempts (Bisazza and Dadda 2005; Dadda and Bisazza 2006a). On the other hand, strong lateralisation can cause pseudoneglect, i.e. the failure to properly respond to a significant stimulus when it appears on the side of the body that transfers information to the hemisphere not specialised for its processing (Chiandetti 2011). Prey-catching behaviour, for example, is highly lateralised in amphibians: toads are much more likely to strike at prey moving on their right than on their left visual hemi-field (Vallortigara et al. 1998). Conversely, anole lizards *Anolis* spp., and gelada baboons *Theropithecus gelada*, direct much less agonistic responses to rivals seen on their right side (Deckel 1995; Casperd and Dunbar 1996).

Because the advantages and disadvantages of lateralisation often vary in time and space, a possible explanation for lateralization variability is differential selection (Levins 1968). Laboratory studies have revealed that strongly lateralized fish and birds exhibit faster predator detection and higher escape reactivity (Rogers et al. 2004; Dadda et al. 2010). In addition, in some circumstances, alignment of lateralization at the population level (i.e., individuals showing similar directionality of lateralization) enhances coordination during collective antipredator behaviour such as schooling in fish (Bisazza and Dadda 2005; Bibost and Brown 2013). In other cases, having a specific direction of lateralisation might confer advantages, such as improved escape performance (Chivers et al. 2016) and greater predator recognition ability (Lucon-Xiccato et al. 2017). Along with these direct advantages of lateralization in dealing with predators, other studies indicate the presence of indirect advantages: lateralized individuals were more efficient in capture live preys while monitoring for a predator compared to non-lateralized individuals (Dadda and Bisazza 2006b; Rogers et al. 2004). Collectively, these findings suggest that strongly lateralized individuals, in some cases with a specific directionally of lateralisation, should be positively selected in high-predation risk environments while poorly lateralized individuals should be favoured in low-predation risk environments. Support for this hypothesis is provided by field data on the distribution of lateralised individuals in wild-caught fish from high and low predation sites (Brown et al. 2007). A limit of this hypothesis is that, despite lateralization is affected by genes in some species (*Brachyraphis episcopi*; Brown et al. 2007; goldbelly topminnow: Bisazza et al. 2000; *Pan troglodytes*, chimpanzee: Hopkins et al. 1994; mouse: Collins 1985), genetic factors account for only a fraction of the observed variation.

Lesley Rogers theorised that matching of individual lateralization to actual environmental conditions can also be the consequence of adaptive phenotypic plasticity. In the early eighties, she discovered that light that passes through the egg shell influences the development of laterality in domestic chicks: chicks hatching from light incubated eggs are more strongly lateralized than dark incubated chicks (Rogers 1982). She suggested that this may be part of an adaptive mechanism that allows the mother to adjust the phenotype of chicks to the current ecological conditions. By spending more or less time at the nest or by choosing a particular nest site, the hen could produce a progeny that is better adapted to cope with high predator risk or with high levels of intraspecific competition (Adret and Rogers 1989).

In recent years, evidence of developmental plasticity of lateralization has continued to accumulate. For example, exposure to predation risk during development increased the occurrence of lateralised individuals in juvenile fish and anuran larvae (guppy *Poecilia reticulata*: Broder and Angeloni 2014; whitetail damselfish *Pomacentrus chrysurus*: Ferrari et al. 2015; wood frog *Lithobates sylvaticus*: Lucon-Xiccato et al. 2017). Early social environment affects lateralization in Rainbowfish *Melanotaenia duboulayi* (Bibost et al. 2012). Altered water conditions reduce lateralisation in several fish (Domenici et al. 2012; Domenici et al. 2014; Lucon-Xiccato et al. 2014). Beside in domestic chicks, early lighting conditions influence development of lateralisation in goldbelly topminnows and in zebrafish *Danio rerio* (Dadda and Bisazza 2012; Andrew et al. 2009; Sovrano et al. 2016). Environmental light
intensity can correlate with other important ecological factors. In guppies, for example, light intensity has a strong effect on vulnerability to predators and indirectly influences schooling and mating behaviour (Endler 1987).

In this study, we tested whether an environmental factor that is a predictor of predation risk affects lateralisation in tadpoles via developmental plasticity. Predation is a major source of mortality for many anuran species (Calef 1973; Heyer et al. 1975) and habitat complexity, i.e. the amount of vegetation cover, greatly affects the survival of larvae to predation from both vertebrates and invertebrates (Babbitt and Tanner 1997; Babbitt and Tanner 1998; Baber and Babbitt 2004; Figiel and Semlitsch 1991; Hartel et al. 2007; Kopp et al. 2006; Tarr and Babbitt 2002). The edible frogs *Pelophylax esculentus* lay eggs in habitats that vary considerably in the amount of vegetation cover (Ildos and Ancona 1994; Warren and Büttner 2008). We reasoned that this factor might affect the lateralisation of edible frogs and we tested our hypothesis by comparing behavioural lateralisation of tadpoles raised from eggs with high and low vegetation cover. Since the amount of cover affects predation, we expected that tadpoles raised with reduced vegetation cover - hence under potentially greater predation risk - will be more lateralised and more aligned compared to tadpoles raised with high vegetation cover. In other anurans, lateralisation plasticity may differ according to the developmental stage (embryonic or larval) in which the stimulation occurs (TLX, unpublished results). Soon after hatching, we reversed the condition in half of the subjects of each treatment, allowing us to measure the effects of cover amount on embryonic and larval stages separately.

**Materials and Methods**

**Subjects**

We collected edible frogs as freshly laid eggs from a stream close to Padova, Italy (45° 32′ 30″ N, 11° 53′ 40″ E). Eggs were raised in 20 20-l plastic pails. Each pail contained approx. 50 eggs and was randomly assigned to the experimental treatments (see Experimental treatment). Embryos and larvae were kept outdoors, in semi-natural conditions, exposed to normal temperature and precipitation. After hatching, we fed rabbit pellets ad libitum to the larvae, to supplement the algae already present in the pails and to ensure no differences in nutrient availability across the treatments. Water used during the procedures derived from a pond filled with well water six weeks before the beginning of the experiments and enriched with the algae and plants from the sampling site. Each day, 80% pail water was substituted with new water from the pond. Tadpoles were returned to their natal stream after the experiments, in the same area where sampling occurred.

**Experimental treatments**

We followed prior studies that manipulated exposure to vegetation to study behavioural plasticity in this species (Lucon-Xiccato 2019a; Lucon-Xiccato 2019b). Ten pails were kept under high-vegetation cover conditions for the entire embryonic stage: water surface was completely covered by *Leman minor* collected from the near pond. The remaining ten pails were kept under low-vegetation cover conditions: less than 20% of water surface was covered by *L. minor*. One day after hatching, we split each group of pails in two. Half of the pails were kept under high-vegetation cover conditions, whereas the remaining pails were kept under low-vegetation cover conditions. This resulted in a 2 × 2 experimental design, having 5 pails with embryonic and larval high-vegetation cover conditions (HH); 5 pails with embryonic and larval low-vegetation cover conditions (LL); 5 pails with embryonic high-vegetation cover condition and larval low-vegetation cover condition (HL); and 5 pails with embryonic low-vegetation cover condition and larval
high-vegetation cover condition (LH). The amount of vegetation used in the treatments mirrored the variation in vegetation observed at the sampling site.

**Lateralisation test**

Fifteen days after hatching, we tested 8 tadpoles matched for size from each pail in the rotational preference test to assess lateralisation (overall $N = 160$; $N$ per treatment $= 40$). The rotational preference is used to assess lateralisation in tadpoles of different species and allows to measure preferential swimming direction (Blackiston and Levin 2013; Lucon-Xiccato et al. 2017). We placed the subject in a 0.5-l white cup filled with pond water. We started the assessment after a 15-min acclimation period. We noted the spontaneous swimming direction of the subject (clockwise or anticlockwise) 10 times, using scan sampling with a 2-min interval between observations. If the subject did not swim during one observation, we repeated the observation later. If the subject did not swim in 3 consecutive observations, we removed it from the experiment (~25% of subjects). Because of the discarded subjects, the final data set consisted in 29 HH tadpoles, 29 LL tadpoles, 27 HL tadpoles, and 30 LH tadpoles.

**Statistical analysis**

To analyse the data, we computed two commonly used lateralisation scores for each subject (Bisazza et al. 1997; Lucon-Xiccato et al. 2017). The relative lateralisation index accounted for directionality and strength of lateralisation: $(n. \text{ clockwise observations} – n. \text{ of anticlockwise observations}) \times 100 / n. \text{ of observations}$. On the basis of the relative lateralisation index, individuals were classified between the extreme values of ‘100’ (tadpoles that always swam clockwise) and ‘-100’ (tadpoles that always swam anticlockwise).

The absolute lateralisation index considered strength (intensity) of lateralisation irrespective of directionality and was computed as $|\text{relative lateralisation index}|$. The absolute lateralisation index thus range from 0 (tadpoles that swam in equal proportion clockwise and anticlockwise) to 100 (tadpoles that swam constantly in clockwise or anticlockwise direction).

Statistical tests were performed using R version 3.2.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). We used two tailed tests and we set the threshold for significance at $P = 0.05$. We analysed the two indexes with two-way ANOVAS fitted with larval (high-vegetation cover versus low-vegetation cover) and embryonic treatment (high-vegetation cover versus low-vegetation cover). For the relative lateralisation index, we also used one-sample $t$ tests to assess whether tadpoles of the four groups swam in anticlockwise direction more often than chance (chance level: relative lateralisation index $= 50$) and independent-sample $t$ test to compare LL and HH tadpoles.

**Results**

**Absolute lateralisation index**

The ANOVA found a significant effect of embryonic treatment ($F_{1,111} = 7.554, P = 0.007$). There was no significant effect of larval treatment ($F_{1,111} = 1.571, P = 0.213$). The embryonic × larval treatment interaction was significant ($F_{1,111} = 4.342, P = 0.040$; Figure 1), indicating that LL tadpoles were more lateralised.
Relative lateralisation index

The ANOVA did not find significant main effect of the two treatments (embryonic treatment: $F_{1,111} = 1.173, P = 0.281$; larval treatment: $F_{1,111} = 2.708, P = 0.103$; Figure 2). The interaction between the two treatments was significant ($F_{1,111} = 14.156, P < 0.001$; Figure 2).

Both HH and LL tadpoles swam in anticlockwise direction more often than chance (one-sample $t$ test: HH: $t_{28} = 2.31, P = 0.028$; LL: $t_{28} = 4.097, P < 0.001$; Figure 3), indicating the presence of lateralisation. Lateralisation tended to be greater in LL than in HH tadpoles (independent samples $t$ test: $t_{56} = 1.821, P = 0.074$). Conversely, tadpoles that underwent a transition between the different treatments during the development (HL and LH) were not lateralised (one-sample $t$ test: HL: $t_{26} = 0.122, P = 0.904$; LH: $t_{29} = 0.496, P = 0.624$; Figure 3).

Discussion

It has been hypothesised that part of the variability in lateralisation commonly observed in natural populations might be due to adaptive plasticity in response to environmental conditions (Adret and Rogers 1989; Andrew et al. 2009; Broder and Angeloni 2014; Domenici et al. 2012). Since lateralisation allows coping with predators (e.g., Brown et al. 2007; Dadda et al. 2010; Rogers et al. 2004), individuals exposed to high predation risk should be more lateralised and, according some hypotheses, more aligned. For amphibian larvae, the amount of cover is an important determinant of predation risk (Babbitt and Tanner 1997; Figiel and Semlitsch 1991; Kopp et al. 2006). Here, we found that tadpoles raised with reduced vegetation cover, and thus exposed to higher perceived predation risk, were more lateralised and more aligned in the direction of asymmetry compared to tadpoles raised with high vegetation cover.

The analysis on the absolute lateralisation index, which did not consider directionality, showed that tadpoles constantly raised with low-vegetation cover (LL) were more lateralised when compared to tadpoles constantly raised with high-vegetation cover (HH) and to tadpoles raised with low-vegetation cover for only one developmental stage (embryonic stage: LH; larval stage: HL). When we looked at the directionality of lateralisation, we found that tadpoles of the LL group exhibited evidence of alignment of lateralisation at the population level causing a significant anticlockwise turning preference in the rotational test; tadpoles of the HH group also exhibited evidences of alignment but to a smaller extent. Tadpoles that were crossed between the two vegetation treatments after hatching (HL and LH) did not develop evident alignment of lateralisation.

Edible frogs likely perceived environmental cues signalling vegetation amount at the embryonic stage and thereafter undertook specific developmental trajectories for a lateralisation phenotype. Likewise, prior studies have reported that tadpoles’ cognitive phenotype changed according to the predation risk that they experienced as embryos, resulting in increased lateralisation and increased memory for novel predator identity (Ferrari 2014; Lucon-Xiccato et al. 2017). The major consequence of the differential amount of vegetation cover was that edible frogs were exposed to different amount of light during development. Thus, light exposure seems the best candidate as proximate mechanism for tadpoles’ lateralisation plasticity. In line with this hypothesis, our results resemble those obtained by laboratory studies that directly manipulated light exposure on fish (Andrew et al. 2009; Dadda and Bisazza 2012; Sovrano et al. 2016). Interestingly, the directionality of the effect on one of these fish species, *G. falcatus*, had the same direction of that observed in our tadpoles. *G. falcatus* exposed to high-light conditions (corresponding to our low-vegetation cover treatment) showed stronger anticlockwise swimming preference. Some of the mechanisms controlling lateralisation plasticity might be conserved within anamniotes. On the other hand, our experimental design did not allow us excluding the effect of other factors that covary with the amount of vegetation, such as the concentration of chemicals in the water,
as the signal for lateralisation plasticity. It is worth noting that a possible criticism to studies that investigated the effects of light on lateralisation: they have often failed to exclude alternative, non-adaptive responses to the experimental manipulation. For example, embryos might require a minimum amount of light for normal development of the nervous system and that the reduced lateralisation of individuals developed in reduced light might be a consequence of this unnatural treatment (Dadda and Bisazza 2012). The strength of our study is that our treatment closely mirrored natural situations; as thus, it is unlikely that the observed effect is an artefactual by-product of the experimental manipulation.

Our results fit the predictions based on variability of predation risk in environments with different amount of cover. In absence of vegetation cover, predation on tadpoles is much higher (e.g., Babbitt and Tanner 1997; Figiel and Semlitsch 1991; Kopp et al. 2006). Highly lateralised tadpoles that develop in environments with low vegetation amount (and thus high predation risk) might enjoy cognitive advantages in defence against predators. For example, lateralised tadpoles learn to recognise the olfactory cues of novel predators faster (Lucon-Xiccato et al. 2017). They might also show greater detection of and responsiveness to predators as shown in other species (Dadda et al. 2010; Rogers et al. 2004). Adaptive phenotypic plasticity in response to environmental factors that predict predation risk might therefore be one of the causes of lateralisation variability observed in many species.

Several other hypotheses have been proposed to explain the variability of lateralisation, most of them based on differential selection on genotypes in the different environments (Levins 1968; Ghirlanda and Vallortigara 2004; Vallortigara and Rogers 2005; Vallortigara et al. 1999). These hypotheses are supported by the observation of significant hereditability for lateralisation (Bisazza et al. 2000; Collins 1985; Hopkins et al. 1994). Our results do not necessarily conflict with the hypotheses of genetic differences. If there is genetic flow between different habitats or if selective factors vary rapidly in time, then an adaptive mechanism based only on genetic variability is likely to cause mismatches between the lateralisation phenotype selected in the previous generation and the most advantageous phenotype in the actual ecological situation. In this scenario, phenotypic plasticity might have been positively selected as a secondary mechanism to cope with environmental uncertainty.

An interesting consequence of the lack of lateralisation alignment in tadpoles crossed between the two vegetation treatments after hatching (HL and LH) is that the development of behavioural lateralisation at the population level might be not possible without a certain level of habitat stability. The instantaneous switch between environmental conditions (i.e., reduction or increase of vegetation cover) might resemble a natural phenomenon, for example in case of large floods. However, some freshwater environments inhabited by frogs also undergo repenting reduction in vegetation due to human activities, such as weed cutting or river bed cleaning to reduce hydraulic risk. It will be important to determine whether the disruption of lateralisation due to rapid changes in vegetation cover has consequences on tadpoles’ fitness in anthropogenic habitats.

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CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.
ETHICAL APPROVAL

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (University of Padova Animal Welfare Committee, permit number 51/2016).

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Figure 1. Absolute lateralisation index (mean ± SE) of tadpoles exposed to the four treatments assessed with the rotational preference test. Left bars represent tadpoles exposed to constant high (HH) or low (LL) vegetation cover. Right bars represent tadpoles exposed to changing conditions between embryonic and larval stage: from high to low vegetation cover (HL) and from low to high vegetation cover (LH).

Figure 2. Relative lateralisation index (mean ± SE) of tadpoles exposed to the four treatments assessed with the rotational preference test. Left bars represent tadpoles exposed to constant high (HH) or low (LL) vegetation cover. Right bars represent tadpoles exposed to changing conditions between embryonic and larval stage: from high to low vegetation cover (HL) and from low to high vegetation cover (LH). Positive values indicate clockwise swimming preference; negative values indicate anticlockwise swimming preference.
**Figure 3.** Frequency distribution of the relative lateralisation index of tadpoles exposed to the four treatments. Positive values indicate clockwise swimming preference; negative values indicate anticlockwise swimming preference.