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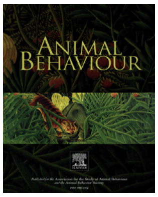

Predator-induced phenotypic plasticity of laterality

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Lateralized brain function, or partitioning of tasks to separate hemispheres of the brain, directly impacts behaviour and fitness. Highly lateralized individuals tend to outperform nonlateralized individuals in many survival-related behaviours, such as the ability to learn, escape predators and multitask. Despite these benefits to lateralization, there is a great deal of observed variation in this trait within and between populations that is likely determined by the balance between costs and benefits of laterality in a given environment. Laterality appears to be heritable, but it can also vary with the environment experienced during development. We investigated the role of evolutionary history and developmental plasticity in determining the degree of laterality in the Trinidadian guppy, *Poecilia reticulata*, a freshwater fish that experiences variable predation pressure in its native range. We compared pairs of closely related populations that experience either high or low levels of predation in the wild, and manipulated the perceived predation risk in the rearing environment using a common garden split-brood design. We assayed laterality in mature male guppies using a detour test. Fish reared with exposure to chemical predator cues were more lateralized than their brothers reared without predator cues. This plastic response is in the direction we would predict if lateralization is favoured in environments with high predation risk. However, unlike findings in related species, we did not detect repeatable differences in degree of laterality associated with historical predation regime, suggesting that predation risk experienced over evolutionary history does not shape laterality patterns in guppies. Thus, although it is currently underemphasized in the literature, plasticity is likely an important contributor to variation in laterality.

An animal's fitness is impacted by its degree of cerebral asymmetry, or laterality, which is the partitioning of tasks to separate hemispheres of the brain (Dadda, Bisazza, & Nepomnyashchikh, 2012; Rogers, 2000). Laterality is likely a very ancient adaptation in vertebrates, as it is found among birds, mammals, fish, reptiles and amphibians (Bisazza, Rogers, & Vallortigara, 1998; Vallortigara, Rogers, & Bisazza, 1999). Highly lateralized individuals outperform nonlateralized individuals in spatial orientation (Sovrano, Dadda, & Bizassa, 2005), shoaling in fish (Bisazza & Dadda, 2005), predator escape (Dadda, Koolhaas, & Domenici, 2010), learning (Bibost & Brown, 2014; Magat & Brown, 2009), foraging in the presence of predators (Dadda & Bisazza, 2006a) and foraging while avoiding harassment from conspecifics (Dadda & Bisazza, 2006b).

Because lateralized individuals tend to outperform nonlateralized individuals, it has been proposed that selection, particularly from predation (Rogers, Zucca, & Vallortigara, 2004), should consistently favour lateralization (Ghirlanda & Vallortigara, 2004; Rogers, 2000). Yet we observe incredible variation in the degree of laterality among species, populations and individuals (Bisazza, Pignatti, & Vallortigara, 1997a; Vallortigara et al., 1999), suggesting that there may be disadvantages and costs to being highly lateralized (Dadda, Zandona, Agrillo, & Bisazza, 2009). Lateralized individuals tend to respond differently to stimuli from the left and right side, which may create a disadvantage when stimuli appear at random in the environment (Vallortigara & Rogers, 2005), and they may perform poorly when tasks require coordination between hemispheres (Dadda et al., 2009). Additionally, the link between laterality and personality traits may be disadvantageous; lateralized individuals are consistently bolder (Reddon & Hurd, 2009) and more aggressive (Reddon & Hurd, 2008) than nonlateralized individuals, which may not be optimal in all situations and environments. The balance between costs and benefits of laterality likely determine the degree of asymmetry observed in any given species and environment (Corballis, 2006, 2008).

Laterality appears to be heritable (Bisazza, Facchin, & Vallortigara, 2000), allowing researchers to artificially select for lateralized and nonlateralized lines (Facchin, Argenton, & Bisazza, 2009). However, genetic differences cannot explain all of the variance in laterality (Bisazza et al., 2000), and furthermore, some lateralized functions cannot be artificially selected (Bisazza, Dadda, & Cantalupo, 2005), suggesting a potential role for the environment

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in shaping laterality (Rogers, 2006). Developmental plasticity, where the phenotype expressed by a given genotype can vary depending on the rearing environment, can influence laterality (Vallortigara & Rogers, 2005). For example, light exposure during development can affect the degree and direction of lateralization in pigeons (Güntürkün, 1993), chickens (Rogers, 1997), and a topminnow fish (Dadda & Bisazza, 2012). Hormones, particularly androgens like testosterone and corticosterone, have also been implicated, although this work is underemphasized (Rogers, 2006). Despite the recognized importance of genes, the environment, and their interaction in shaping phenotypes to a particular environment (West-Eberhard, 2003), theories about the roles of genes and the environment in shaping laterality have not been experimentally integrated (but see Rogers, 1995).

To investigate the roles of evolutionary history and the rearing environment in shaping laterality, we used the Trinidadian guppy, *Poecilia reticulata*, a small freshwater fish. Previous studies have demonstrated cerebral lateralization in guppies (i.e. the use of the left side of the brain when viewing potential mates; Bisazza et al., 1997a) and in other poeciliids (Bisazza, Facchin, Pignatti, & Vallortigara, 1998; Bisazza et al., 1997a; Bisazza & de Santi, 2003; Brown, Gardner, & Braithwaite, 2004), although the direction and degree of lateralization varies across species, populations and contexts. Trinidadian guppies naturally occur in streams that vary in predation pressure because barrier waterfalls typically exclude predators, but not guppies, from upstream migration (Houde, 1997; Magurran, 2005). Thus, river drainages often contain populations of guppies exposed to high levels of predation (hereafter referred to as HP) and closely related upstream populations that exist with only one other fish, a minor guppy predator *Rivulus hartii* (Carvalho, Shaw, Magurran, & Seghers, 1991; Crispo, Bentzen, Reznick, Kinnison, & Hendry, 2006; Fajen & Breden, 1992). These low-predation (hereafter referred to as LP) populations have evolved unique phenotypes that differ from nearby high-predation populations across multiple traits, including colour, behaviour, morphology and life history strategy (Houde, 1997; Magurran, 2005). Although laterality has not been compared between high- and low-predation populations of *P. reticulata*, environments with high levels of predation risk are expected to favour lateralization because of its associated predator escape, multitasking and shoaling benefits (Brown, Western, & Braithwaite, 2007; Dadda et al., 2012; Rogers et al., 2004).

To measure the role of evolutionary history in shaping laterality, we compared two pairs of natural high- and low-predation populations of *P. reticulata* reared in a common garden environment. We predicted that guppies from high-predation sites would show greater lateralization than those from low-predation sites if predation risk selects for laterality. To experimentally integrate the role of developmental plasticity in shaping laterality, we used a split-brood design to rear brothers in an environment with or without chemical predator cues. We predicted that males exposed to predator cues during development would show greater lateralization than their brothers reared without predator cues if the trait exhibits adaptive plasticity in response to perceived risk.

METHODS

Collection and Husbandry

We collected juvenile *P. reticulata* from two HP rivers and two LP rivers (Aripo HP_1, Guanapo HP_2, Naranjo LP_1 and Tumbason LP_2) on the southern slope of the Northern Range Mountains in Trinidad, West Indies, in May 2011. The Aripo is a high-predation river that is downstream from the low-predation Naranjo River in one drainage. Similarly, the high-predation Guanapo is downstream of the low-predation Tumbason River in a neighbouring drainage. We collected 50 fish from each location, transported them to Colorado State University, and reared them for two generations under common garden conditions to minimize maternal and other environmental effects. Wild-caught guppies were housed in mixed-sex pairs (approximately 25 pairs per population) until females produced first-generation broods. We separated each brood by sex at 5 weeks of age when females could be distinguished from males by a patch of melanophores near the gonopore (following Reznick, 1982). We randomly selected one male and one female from each family line to rear to adulthood and randomly crossed unrelated pairs to produce a second generation. Within 24 h of birth, we divided each second-generation brood into two treatments that differed in exposure to predator cues (following Handelsman et al., 2013). Half of each brood was placed in a 1.5-litre tank that received recirculating water from a sump that housed a common guppy predator, the pike cichlid, *Crenicichla frenata*. Cichlids were fed two guppies daily so that experimental guppies were exposed to predator kairomones as well as alarm cues released by the epidermal club cells of consumed conspecifics. The other half of each brood was reared in an identical 1.5-litre tank that received recirculating water from a sump that did not house a predator. We sexed the second-generation fish at 5 weeks of age and continued to rear one male per family in an individual 1.5-litre tank in its respective treatment until we assayed its laterality; thus, at the time of the assays, males reared in the predator treatment were exposed to the chemical cues of predation their entire lives. We used males rather than females in this experiment because they were available as part of another study on male mating behaviour that utilized the same rearing design, and we lacked space to maintain females individually under these treatments. Fish were maintained at 24 °C on a 12:12 h light:dark cycle and were fed a specific quantity of food adjusted to their age twice daily (a paste made of TetraMin® Tropical Flakes (Spectrum Brands, Inc., Cincinnati, OH, U.S.A.) in the morning and brine shrimp nauplii, *Artemia* spp. (Brine Shrimp Direct, Inc., Ogden, UT, U.S.A.) in the evenings). Experimental fish were held in individual 1.5-litre clear plastic tanks that contained neutral gravel as well as a constant flow of water. Although fish had continuous visual access to guppies in neighbouring tanks, direct social experience was limited to 24 h of exposure to three females and a total of 2 h of experience with six other males from the same population and treatment. These controlled social interactions, which formed the basis of another study, were provided to each male systematically over the course of 4 weeks before the laterality assays.

Laterality Assays

We assessed laterality in sexually mature males (mean ± SE age = 130 ± 2.4 days, $N = 133$) from all four populations and both treatments using a detour test. Detour tests, frequently used to assay laterality in fish (Bisazza, Pignatti, & Vallortidara, 1997b), force the individual to turn either right or left to view an object directly in front of them, thus using one eye and the corresponding opposite side of the brain to process information about the object. We designed and constructed a testing apparatus that was circular to avoid having either choice yield a dead end, which could influence choices in subsequent tests; instead, fish could choose to view an object with either the left or right eye and then continue swimming indefinitely in that direction. The apparatus was made of acrylic and consisted of an acclimation chamber (8 × 12 cm) attached to a circular arena (30 cm diameter) that contained a semi-opaque circular barrier (15 cm diameter) with a target in its centre (Fig. 1). We used a target (an object for the fish to view with one eye) because it has been found that laterality may be

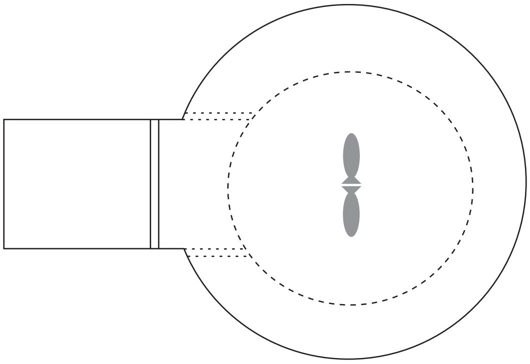

Figure 1. Schematic diagram of detour test apparatus. The square acclimation chamber was separated from the circular arena with a removable barrier (double solid line). The target was centred inside a semi-opaque barrier (dotted circle). Fish choice was recorded as left or right when the fish travelled past the bounds of the acclimation chamber (crossing one of the double dotted lines).

underestimated when assays are performed without one (Bisazza et al., 1997b; Brown et al., 2007). The target was a fish lure consisting of two identical generic fish models (3.5 cm long) facing opposite directions to avoid influencing the direction chosen by the test fish. Because the goal of this study was to measure the degree of lateralization and not to map the side of the brain that responds to a particular stimulus (e.g. a female or a predator), we used an arbitrary fish-shaped target that did not closely resemble either a guppy or a guppy predator.

Laterality assays were conducted during 21 May 2012–5 March 2013. Prior to assaying laterality, the testing apparatus was filled to a depth of 15 cm with water that did not contain predator cues. We used a net to transfer an individual fish to the acclimation chamber. After 2 min (following Reddon & Hurd, 2008, 2009), we slowly removed the barrier, allowing the fish to exit the acclimation chamber and enter the circular arena. If the fish remained in the acclimation chamber after 30 s and was not actively exploring (36% of tests), we directed the fish towards the arena with a small green dip net (following Bisazza et al., 1997b; Reddon & Hurd, 2008). For each laterality assay, we recorded whether the fish turned left or right after it swam past the walls of the acclimation chamber (double dashed lines in Fig. 1). After each test, the fish was returned to its individual tank. Each fish completed the detour test 10 times (following Bisazza et al., 2000) in 7 days with no more than two assays per day (separated by a minimum of 1 h). Because some guppies can learn to avoid negatively reinforced stimuli after fewer than 10 experiences in succession (Budaev & Zhuikov, 1998), we spaced the trials out over 1 week to minimize the possibility that handling after each trial might cause fish to turn a different direction in the subsequent trial. We also included three individuals that completed fewer than 10 trials: two that completed seven trials and one that completed nine trials.

Analysis

To calculate a laterality score for each individual based on its 10 laterality assays, we used the following equation (Bisazza et al., 1997b): ((right turns − left turns)/(right turns + left turns)) × 100. Positive values indicate an individual's propensity to turn right, use the left eye to view the target, and thus use the right side of the brain to process the target. Conversely, negative values indicate an individual's tendency to turn left, use the right eye to view the target, and thus use the left side of the brain. Because we were particularly interested in measuring the degree of laterality, more so than direction (left or right), we took the absolute value of the laterality scores. Degree of laterality is a better measure of individual consistency in laterality since it ignores direction, whereas mean laterality scores include positive and negative values that may cancel each other out, resulting in a more conservative mean value that may not differ from zero even though a large portion of individuals may be highly lateralized (Brown et al., 2007). We then estimated differences in both the laterality score and the degree of laterality between predation regimes and treatments in two separate mixed-effects ANOVAs (following Bisazza, Facchin, et al., 1998) with predation regime (HP or LP), treatment (reared with or without cues), and their interaction included as fixed effects. We included family identity as a random effect to account for brothers across treatments. The age at which males were assayed did not differ across treatments ($F_{1,131} = 0.77$, $P > 0.1$), although the HP guppies were 10 days younger (mean ± SE = 125.90 ± 3.13, $N = 79$; $F_{1,131} = 4.09$, $P = 0.045$) than the LP guppies (mean ± SE = 135.92 ± 3.77, $N = 54$) because of their earlier maturation (consistent with Reznick, Shaw, Rodd, & Shaw, 1997). However, age was not predictive of laterality score or degree of laterality (both $F_{1,131} < 1.67$, $P > 0.1$) and hence was not included in our analysis. Similarly, laterality score and degree of laterality did not differ across drainages (both $t_{131} < 0.56$, $P > 0.1$); thus, we present results from both drainages combined. These analyses were conducted using JMP® version 11 (SAS Institute, Cary, NC, U.S.A.).

Ethical Note

To incorporate both conspecific alarm cues and predator kairomones in the predator rearing treatment, we fed live guppies to *C. frenata* predators housed in the sumps of our recirculating systems. Although other methods are available for extracting alarm cues (i.e. lacerating the skin of euthanized guppies), we used live guppies because the wild-caught predators required a live fish diet, and direct predation provided a way to administer realistic quantities of alarm cues. These methods were approved by Colorado State University's Institutional Animal Care and Use Committee (protocol number 11-3072A).

RESULTS

The laterality score of an individual can range from -100 (left side of brain dominant) to +100 (right side of brain dominant), and averages of these scores for a group of individuals can provide information about the consistency of directionality. We observed no difference between guppies from the HP and LP predation regimes in laterality score ($F_{1,129} = 0.99$, $P > 0.1$), in part because the average laterality scores were not strongly positive or negative for either of these groups (mean ± SE: HP: −10.21 ± 4.66, $N = 79$; LP: −2.94 ± 5.62, $N = 54$). We did observe a treatment effect ($F_{1,129} = 5.14$, $P = 0.03$); fish reared with predator cues were more negatively lateralized (mean ± SE = −14.40 ± 5.05, $N = 68$), tending to use the left side of the brain more than fish reared in the absence of predator cues (mean ± SE = 1.23 ± 4.99, $N = 65$). There was no interaction between predation regime and treatment ($F_{1,129} = 0.31$, $P > 0.1$).

Degree of laterality is measured as the absolute value of the individual's laterality score and can range from 0 to +100, and averages of these scores indicate the degree of lateralization of individuals within a group, regardless of the consistency in directionality. We observed no differences between predation regimes, HP or LP, in degree of lateralization ($F_{1,129} = 1.11$, $P > 0.1$; Fig. 2). We did observe a treatment effect ($F_{1,129} = 4.19$, $P = 0.04$); fish reared with predator cues were more highly lateralized than fish reared in

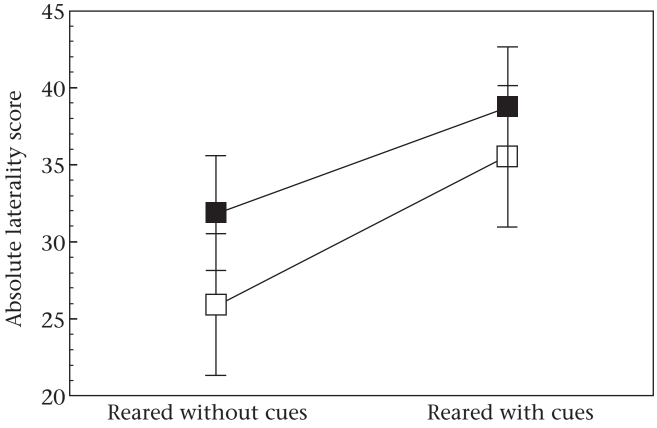

Figure 2. Reaction norms showing the degree of laterality, or the mean absolute laterality score ± SE for the high-predation (filed squares) and low-predation (open squares) populations across the two treatments, reared without and with predator cues.

the absence of predator cues (Fig. 2). There was no interaction between predation regime and treatment ($F_{1,129} = 0.14$, $P > 0.1$).

DISCUSSION

Much of the previous work on cerebral laterality has focused on its evolutionary origins and the selective pressures shaping the trait (e.g. Takahashi & Hori, 1994; Vallortigara et al., 1999), including the potential benefits for predator evasion (Dadda et al., 2012). However, studies investigating natural geographical variation in laterality across variable predation regimes have failed to evaluate environmental contributions to individual laterality. We used a common garden design to compare populations that evolved under low and high predation risk and we manipulated the perceived predation risk during development to simultaneously investigate the roles of evolutionary history and rearing environment on laterality in guppies. We did not find consistent differences in either laterality score or degree of laterality between populations that evolved under high and low predation risk. However, we did find that males reared in the presence of predator cues were more negatively lateralized, indicating greater use of the right side of the brain and the left eye to view the stimulus. Similarly, degree of laterality, or individual consistency ignoring direction, was greater for guppies reared with predator cues, supporting predictions.

Previous work by Brown et al. (2004, 2007) comparing poeciliid fish (*Brachyraphis episcopi*) from high- and low-predation environments found that HP populations were more highly lateralized than LP populations. Furthermore, the similarity in degree of laterality between wild-caught fish and first-generation laboratory-reared fish suggested that the pattern was heritable (Brown et al., 2007). Our findings suggest that some of the established geographical variation in laterality may be explained by developmental plasticity rather than evolutionary history. In our study, second-generation laboratory-born fish did not differ among populations in laterality score or degree of laterality, but fish reared in the presence of predator cues showed a higher degree of laterality than fish reared in the absence of predator cues. Note, however, that our power of inference was limited to two pairs of high- and low-predation populations, and thus our findings may not be generally representative of laterality patterns across predation gradients.

Differences between our findings and those of Brown et al. (2004, 2007) could be attributed to a number of factors. Laterality patterns are known to vary depending on the species (Bisazza et al., 1997a; Bisazza, Facchin, et al., 1998), the sex (Bisazza, Facchin, et al., 1998; Brown et al., 2007) and the target used in laterality assays (Bisazza, Facchin, et al., 1998; Brown et al., 2004, 2007), so our use of a different species, of males rather than females, and of a different target could explain some differences. Females are generally expected to show greater laterality than males in order to more efficiently multitask as they avoid forced copulations and predation while foraging (Dadda & Bisazza, 2006b). However, male–female comparisons have yielded mixed results (e.g. Bisazza, Facchin, et al., 1998), finding sex differences only in certain populations and treatments (Brown et al., 2007). It would be interesting to repeat our study, testing both male and female responses to multiple targets, to estimate sex differences in the strength and direction of laterality. Another difference between our study and Brown et al. (2004, 2007) is that our fish were reared in individual tanks rather than in large group tanks. If laterality facilitates social interactions and shoaling (Bisazza & Dadda, 2005; Brown et al., 2007), it is possible that direct social contact promotes the development of laterality and that our simple rearing environment led to lower laterality scores. However, if this lack of social complexity affected all fish similarly, it would have been unlikely to influence our population and treatment comparisons. Finally, an important difference between our study and Brown et al. (2004, 2007) is that we used second-generation laboratory-reared fish, rather than wild-caught or first-generation fish, which likely allowed us to reduce maternal and other environmental effects more fully in our population comparisons.

The plastic response we observed was similar in direction and strength for guppies from both high- and low-predation environments, as indicated by the similarity in slope and intercept of the reaction norms (Fig. 2). This plasticity is likely adaptive since a higher degree of laterality should increase fitness in environments with greater predation risk (Pitcher, 1986; Rogers et al., 2004). Laterality is thought to be a mechanism that facilitates social interactions, particularly shoaling (Bisazza & Dadda, 2005; Brown et al., 2007) and enhances cognitive ability (Magat & Brown, 2009), thus increasing survival in environments with high predation risk.

Here we suggest three possible explanations for the consistency of this adaptively plastic response across predation regimes. First, there could be strong selection for plasticity in environments with predators, and this plasticity persists even when guppies colonize locations without predators. Low-predation populations have been repeatedly founded from high-predation populations throughout Trinidad (Houde, 1997; Magurran, 2005), and plasticity in response to predator cues could persist in the absence of the selective force of predation if it is not costly to maintain. However, this may not be likely if plasticity is costly (DeWitt, Sih, & Wilson, 1998), or if lateralization is maladaptive in the absence of predation, for example because individuals respond inappropriately to stimuli from the right and left side (Vallortigara & Rogers, 2005) or if they perform poorly at tasks requiring coordination between hemispheres (Dadda et al., 2009). Second, selection on correlated traits may maintain plasticity. If there is selection on traits, like aggression, that are tightly and positively correlated with laterality (Reddon & Hurd, 2008, 2009), we might expect plasticity to persist. This is perhaps unlikely since Irving and Brown (2013) found only weak links between laterality and several plastic personality traits like boldness, activity level and sociability in a feral population of guppies. A third explanation is that low-predation environments contain enough predation risk to maintain the plastic response. The multipredator hypothesis suggests that different antipredator responses are pleiotropically linked such that removal of some, but not all, predators would result in the persistence of antipredator behaviour

(Blumstein, 2006). Guppies in low-predation environments still experience some predation through cannibalism and predation from *R. hartii*, which is known to prey on juvenile guppies.

In the future it will be interesting to explore the mechanisms during development that are responsible for the plastic response we observed. Hormones, specifically testosterone and corticosterone, are known to affect laterality in birds (Rogers, 2006; Vallortigara et al., 1999) and may act similarly in fish. Predator cues experienced by male guppies during development reduce the amount of glucocorticoid steroid hormone (cortisol) that fish release into the water (Fischer, Harris, Hofmann, & Hoke, 2014).

Finally, this work is germane to the recent conversation about behavioural responses to human-induced rapid environmental change (Sih, Stamps, Yang, McElreath, & Ramenofsky, 2010). The plasticity of laterality in response to predation may have consequences for the ways that animals respond to rapid changes in predation regime, particularly given that laterality is correlated with many other behaviours and traits that are intimately linked with fitness (e.g. Bisazza & Dadda, 2005; Dadda & Bisazza, 2006a, 2006b; Dadda et al., 2010). Thus, animals may be able to respond via lateralization to the introduction or removal of a novel predator in just one generation. However, a better understanding of the mosaic nature of traits is needed to predict responses to environmental change. Although laterality is positively correlated with a variety of antipredator behaviours like shoaling (Bisazza & Dadda, 2005) and multitasking (Dadda & Bisazza, 2006a), we still lack a general understanding for how groups of plastic and nonplastic traits respond to changes in the environment, for example whether they respond independently or in an integrated manner (Ghalambor, McKay, Carroll, & Reznick, 2007). Investigating behavioural and personality traits in conjunction with laterality (e.g. Irving & Brown, 2013) will improve our understanding of the potential role of cerebral laterality as an overarching mechanism for correlations among traits.

This study is one of the first to assess the roles of both evolutionary history and rearing environment on laterality and illustrates the importance of developmental plasticity. We suggest that developmental plasticity is currently underemphasized, and we encourage researchers investigating geographical variation of traits to consider its potential contribution.

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