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Individual differences in cerebral lateralization are associated with shy–bold variation in the convict cichlid

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Cerebral lateralization, the preferential use of one hemisphere of the brain to perform certain cognitive functions, is a widespread and evolutionarily ancient adaptation. Lateralization appears to enhance cognitive capacity, yet substantial individual variation in the strength cerebral lateralization is apparent in all species studied so far. It is puzzling that cerebral lateralization, a seemingly advantageous trait, has not been driven to fixation. It has been suggested that variation in lateralization may be linked to individual variation in behaviour, which itself may be subject to disruptive selection. We examined the relation between cerebral lateralization and individual variation in boldness in the convict cichlid, *Archocentrus nigrofasciatus*. We show that convict cichlids that are more strongly lateralized when exploring a familiar environment, but not a novel one, are quicker to emerge from a shelter in a test for boldness. The possibility that cerebral lateralization is linked to life history strategy is discussed.

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Cerebral lateralization was long thought to be a unique adaptation of the human central nervous system (Rogers 2002) and has even been described as a key speciation event in human evolution (Corballis 2008). Research over the past three decades has revealed that this is not the case. Cerebral lateralization appears to be ubiquitous among the vertebrates (Vallortigara & Rogers 2005) and probably predates their evolution (Pascual et al. 2004; Letzkus et al. 2006; Letzkus et al. 2008; Rogers & Vallortigara 2008).

Fish have proven to be a useful system in the study of cerebral lateralization from an evolutionary perspective. Fish have no overlap in their visual fields; each eye projects almost entirely to the contralateral hemisphere. Cerebral lateralization can be tested in fish by assessing asymmetries in eye use (Facchin et al. 1999; Sovrano et al. 1999; De Santi et al. 2001; Sovrano & Andrew 2006; Andrew et al., in press).

Recent research effort has focused on understanding the costs and benefits of cerebral lateralization from a functional perspective (Rogers 2000; Vallortigara & Rogers 2005; Vallortigara 2006). It has been suggested that cerebral lateralization has been selected for because it provides a cognitive-processing advantage (Rogers 2000). Empirical research using both embryological manipulations (Rogers et al. 2004) and artificial selection (Dadda & Bisazza 2006)

on the strength of lateralization has supported this hypothesis. Animals with stronger lateralization appear to have an increased ability to attend to multiple stimuli simultaneously compared to those with a weaker hemispheric specialization.

Despite the described advantages of possessing a lateralized brain, most species studied so far show substantial variation at the individual level in both the strength and direction of lateralization (Vallortigara & Bisazza 2002). The frequency-dependent benefits model of Ghirlanda & Vallortigara (2004) appears to provide a reasonable explanation for the maintenance of variation in the direction of lateralization; there is some empirical evidence to suggest that the direction of lateralization is under frequency-dependent selection (Hori 1993; Billiard et al. 2005; Takeuchi & Hori 2008). The observed individual variation in the strength of lateralization however, remains difficult to explain.

Evidence suggests that cerebral lateralization is related to individual differences in behaviour. Nervousness and boldness are associated with handedness in chimpanzees (Hopkins & Bennett 1994) and macaques (Westergaard et al. 2003). Lateralization is related to emotionality in horses (Larose et al. 2006). Extroversion and emotionality are associated with greater cerebral asymmetry in humans (Howard et al. 1992; Hagemann et al. 1999). Nonlateralized chicks give more distress calls and take longer to resume foraging after exposure to a simulated predator than do lateralized chicks (Dharmaretnam & Rogers 2005). Different populations of the same fish species may differ in both boldness (Brown et al. 2005) and cerebral lateralization (Brown et al. 2004, 2007a). Reddon & Hurd

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(2008) found that the strength of cerebral lateralization in convict cichlids is related to individual differences in aggressiveness. The relationship between individual differences in behaviour and cerebral lateralization may be an important factor in understanding the maintenance of their variability.

The shy–bold continuum is the best studied personality-like characteristic in animals (Wilson et al. 1994). Many species show substantial individual variation in this dimension (Sih et al. 2004), and explaining this variation in terms of costs and benefits has been a major goal in the study of animal behaviour (Bell 2007). Variation on the shy–bold continuum appears to represent a trade-off between growth and mortality (Stamps 2007), with bolder animals growing faster but suffering a high mortality rate (Smith & Blumstein 2008). This trade-off may reflect a more general difference in life history strategies, in which boldness represents a focus on current reproduction at the expense of future reproduction (Wolf et al. 2007).

The experiment reported here examines the relationship between individual differences in cerebral lateralization when navigating novel and familiar environments and placement on the shy–bold continuum. The study species is the convict cichlid, *Archocentrus nigrofasciatus*, a highly territorial, monogamous and biparental freshwater fish.

METHODS

Subjects consisted of 100 adult convict cichlids, 56 females and 44 males that had never been tested for lateralization or boldness. Two males failed to complete all phases of testing and were excluded from the analysis. Prior to experimentation, animals were housed in 95-litre (75 × 31 × 41 cm) mixed-sex communal aquaria at densities of approximately 15 fish per aquarium. Aquaria were maintained on a 12:12 h light:dark cycle and water temperature was held constant at 25 ± 1 °C. Fish were fed daily on a variety of frozen or dried prepared fish foods. All protocols were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee (protocol number 544706).

Subjects were tested for lateralization when exploring a novel environment using a detour apparatus (Bisazza et al. 1997; Reddon & Hurd 2008). The apparatus consisted of a large aquarium (195 × 30 × 29 cm) constructed of opaque Plexiglas that was filled with water to a depth of 11 cm. The aquarium was divided into two equal compartments connected by a narrow channel (10 × 75 cm). A movable barrier made of alternating bars (0.75 cm) of clear and opaque Plexiglas, 15 cm across and extending up above the surface of the water was placed at the far end of the channel. Each fish was placed in one of the two compartments with an opaque Plexiglas barrier blocking the entrance at the near end of the runway. The animal was allowed to acclimate for 2 min before the onset of testing.

During testing, the opaque barrier was raised and the fish was gently coaxed towards the opening of the runway using a black dip net (13 × 10 cm). Upon reaching the start of the channel, the fish would swim towards the far end of the tank and detour around the bared barrier into the other compartment. As the fish went around the barrier, it could view the environment with only one eye, indicating which hemisphere it preferred to use to process the information. The detour decision was considered complete when the main axis of the fish's body was parallel to the barrier. Detour decisions were almost always unambiguous and in the rare instance where no clear decision could be determined, the trial was discarded. Each fish received 10 trials run towards alternating ends of the tank. After each trial, the fish was allowed to rest for 2 min while the barrier was repositioned at the opposite end of the tank.

Following the completion of 10 detour trials, the fish remained in the detour apparatus with all barriers removed for 24 h. After familiarizing itself with the environment for a 24 h period, each animal was run through the detour task a second time.

Detour task responses were scored for each animal in each of the two delay conditions by calculating a laterality index (LI; Bisazza et al. 1997) using the following formula:

$$\text{Laterality Index} = \frac{(\text{Right Turns} - \text{Left Turns})}{(\text{Right Turns} + \text{Left Turns})}$$

LI may obscure individual variation in the strength of lateralization because extreme scores in opposite directions will cancel each other out (Brown et al. 2007a; Clotfelter & Kuperberg 2007; Reddon & Hurd 2008). To investigate individual variation we analysed the absolute value of LI as a measure of the strength of lateralization.

After laterality testing, each fish was tested for placement on the boldness–shyness continuum. Boldness was scored based on the time to emerge from a shelter into a novel environment (Brown & Braithwaite 2004; Brown et al. 2005, 2007b). The boldness testing apparatus (Brown et al. 2007b) consisted of a 38-litre aquarium (50 × 27 × 30 cm) filled with water to a depth of 11 cm. At one end of the aquarium there was an opaque Plexiglas box (15 × 15 × 20 cm) with no ceiling and a removable door at one end. Subjects were placed inside the box and allowed to acclimate for 5 min. After the acclimation period, the door was raised and the fish was free to swim out of the box to explore the unfamiliar environment. Each trial was filmed from behind an opaque curtain. Fish were scored for their delay to emerge from the start box, which was counted when the fish stuck its head out of the box past the opercula. Eleven females and five males failed to emerge within 5 min and were excluded from further analysis; additionally, two males emerged from the shelter in less than 10 s and were excluded as outliers. The delay-to-emerge scores were log-transformed for normality.

Data analysis was conducted using the SPSS 15.0 statistical package (SPSS Inc., Chicago, IL, U.S.A.). One-sample *t* tests were used to test whether LI, or absolute LI, scores differed from zero. Analyses of covariance (with sex as the covariate) were used to test for correlation between absolute LI and boldness scores.

RESULTS

Right and left eye use was equally common in both the novel (one-sample *t* test: $t_{79} = -1.79$, $P = 0.08$; Fig. 1) and familiar ($t_{79} = -0.42$, $P = 0.68$; Fig. 1) contexts in this population. Eye use was not random at the individual level: each fish tended to favour either the right or left eye in both the novel (one-sample *t* test: $t_{79} = 10.74$, $P < 0.001$; Fig. 2) and familiar environments ($t_{79} = 12.27$, $P < 0.001$; Fig. 2). LI in the novel and familiar contexts was not significantly correlated ($R^2 = 0.013$, $F_{1,78} = 1.02$, $P = 0.32$).

There was no significant difference between males and females in lateralization in the novel ($t_{78} = 0.09$, $P = 0.93$; Fig. 1) or familiar ($t_{78} = 0.61$, $P = 0.55$; Fig. 1) contexts. The absolute value of LI also did not differ between the sexes in either the novel ($t_{78} = -1.04$, $P = 0.30$; Fig. 2) or familiar ($t_{78} = -0.60$, $P = 0.55$; Fig. 2) environments. Similarly, there was no difference between males and females in their boldness scores ($t_{78} = 0.55$, $P = 0.58$).

Analysis of covariance showed a significant correlation between absolute strength of laterality scores in the familiar environment and the latency to emerge from shelter in the boldness task ($R^2 = 0.131$, $F_{1,78} = 11.76$, $P = 0.001$; Fig. 3a), and no effect of the sex of the animal ($R^2 = 0.004$, $F_{1,78} = 0.31$, $P = 0.58$). No such relationship existed between boldness and laterality in the novel environment ($R^2 = 0.001$, $F_{1,78} = 0.05$, $P = 0.82$; Fig. 3b).

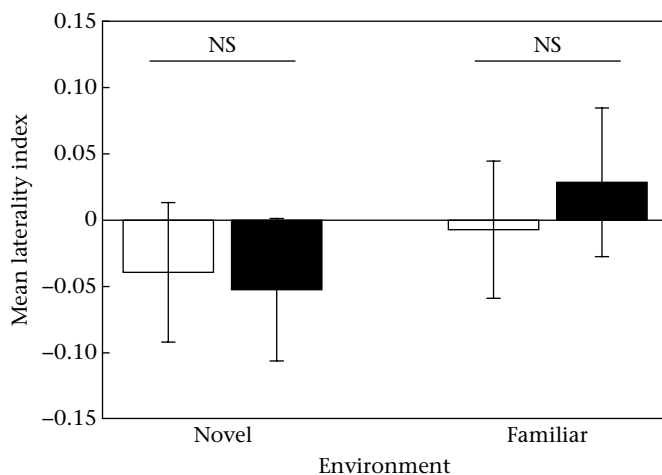


Figure 1. Mean \pm SE laterality index scores for convict cichlids in novel and familiar contexts. Positive scores are right-hemisphere biased; negative scores are left-hemisphere biased. Females: □; males: ■.

DISCUSSION

On average, convict cichlids appear to be lateralized at the individual level but not at the population level when exploring both novel and familiar environments, although there was a nonsignificant ($P = 0.08$) tendency towards left hemisphere use in the novel environment. This tendency was in the same direction as a similar effect in another freshwater fish, *Xenopoeilus sarsinorum*, which preferentially uses its left hemisphere to view novel objects (Sovrano 2004).

We found that variation in the strength of cerebral lateralization when exploring a familiar space was related to variation in a personality-like characteristic, boldness. Animals with stronger hemispheric bias when exploring a familiar environment behaved more boldly in a novel one.

It is puzzling that lateralization when navigating in a familiar space was related to boldness, while lateralization when navigating in a novel environment was not. It would seem, a priori, that lateralization in a novel environment would be more closely related to the boldness task. This unexpected finding may owe to the fact that convict cichlids are extremely territorial. Animals that are new to the detour apparatus may be primarily concerned with surveying

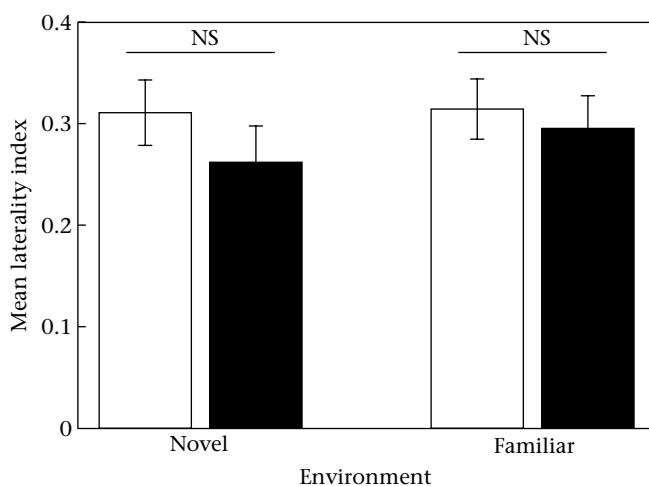


Figure 2. Mean \pm SE absolute laterality index scores for convict cichlids in novel and familiar contexts. Females: □; males: ■.

for dangers and seeking shelter. After the fish has had access to the apparatus overnight, its territorial tendencies might take precedence when navigating in that space. Variation in hemisphere use may be more closely related to the personality-like characteristic of boldness during territory patrol than during initial inspection.

The overall pattern of lateralization in convict cichlids that we observed in this study was similar to what we had observed in a previous study (Reddon & Hurd 2008). However, unlike our previous findings on the relationship between lateralization and aggressiveness (Reddon & Hurd 2008), we did not find evidence for a mediating effect of sex on the relationship between laterality and behaviour. This difference may reflect different fitness consequences of individual variation in boldness compared to aggressiveness, and how these factors interact with sex in this species.

There is good reason to believe that cerebral lateralization may be linked to personality through underlying neural mechanisms (Andrew 2006). Barth et al. (2005) found that at least two neural mechanisms underlie lateralized behaviour, and that those mechanisms may assort independently of one and other. *Frequent-situs-inversus* (*fsi*) are a strain of zebrafish that show a complete reversal of viscera and neuroanatomy. These *fsi* individuals show a concordant reversal of some but not all lateralized behaviours (Barth et al. 2005). Furthermore, *fsi* zebrafish tend to be more bold in novel environments than wild-type animals, possibly because behaviours that are often lateralized to opposite hemispheres tend to co-occur in the same hemisphere more often in *fsi* fish (Barth et al. 2005). Different lateralized abilities can also assort independently within individuals (Rogers 2002; Andrew et al. 2004; McGreevy & Rogers 2005).

Cerebral lateralization may itself be a trade-off between the cognitive advantages of cerebral asymmetry (Rogers 2000) and some other benefits of cerebral symmetry (Corballis 2006, 2008). For instance, strongly lateralized individuals may be at a disadvantage because biologically relevant stimuli are equally likely to appear on either side (Vallortigara & Rogers 2005) and the cognitive-processing advantages of strong lateral biases may be counteracted by the pitfalls of reduced sensory or cognitive acuity on one side of the body. Both lateralized chicks (Dharmaretnam & Rogers 2005) and toads (Lippolis et al. 2002) take longer to detect a predator in their nonpreferred visual field. The prevalence of lateralization within a species ought to depend on the relative advantages of symmetry and asymmetry in that species (Corballis 2008).

Evidence is accumulating suggesting that variation in boldness reflects frequency-dependent variation in life history strategies (Wolf et al. 2007; Smith & Blumstein 2008). Bolder animals grow faster but also suffer higher mortality (Stamps 2007). Different patterns of cerebral lateralization may be connected to this trade-off. Strongly lateralized animals may have a cognitive advantage that allows them to process information about their environment more effectively but puts them at a greater risk of predation or other dangers. This hypothesis would predict that strongly lateralized individuals may favour current reproduction over future reproduction and behave in a bolder manner consistent with this frequency-dependent life history strategy. Of course, frequency-dependent effects are commonly advanced to explain the maintenance of both left and right directional lateralization in the same population (e.g. Hori 1993; Ghirlanda & Vallortigara 2004; Billiard et al. 2005). The relationship we have observed between the strength of the cerebral lateralization and placement on the shy-bold continuum may reflect different solutions to the trade-off between the benefits of symmetry and asymmetry. This association between strength of lateralization and life-history-associated personality suggests that frequency-dependent selection may exist not only in the left-right lateralization, but in the less considered more lateralized versus less lateralized trait dimension (Brown 2005).

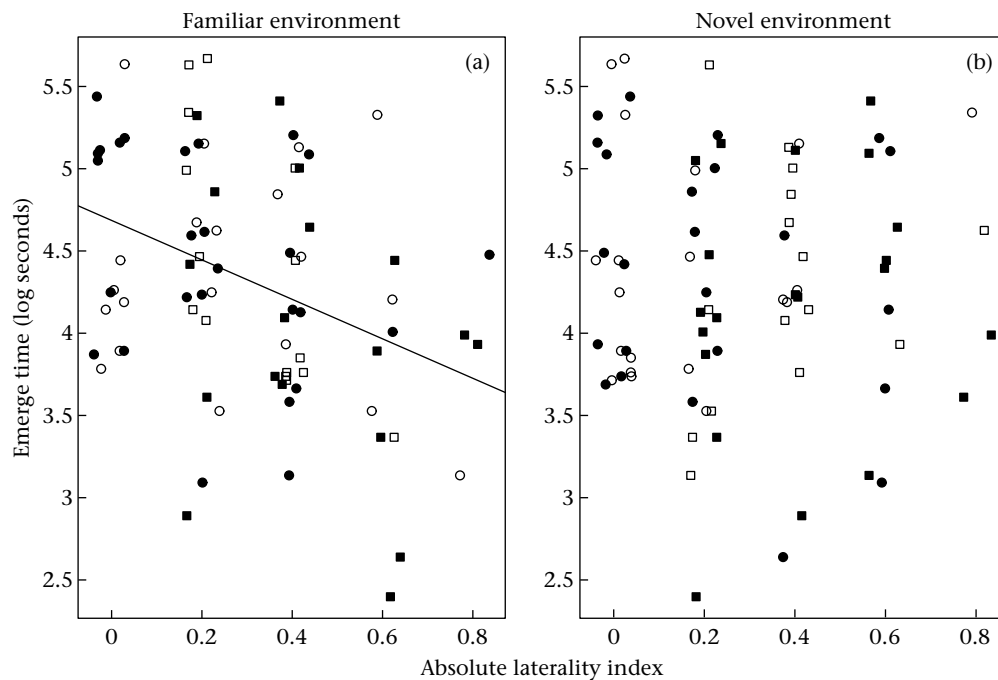


Figure 3. Linear relationship between latency to emerge from a shelter and absolute laterality index (LI) scores for convict cichlids in (a) familiar and (b) novel environments. Open symbols: males; filled symbols: females. Squares: negative (left-hemisphere biased) LI scores; Circles: positive (right-hemisphere biased) or neutral (unbiased) LI scores.

In conclusion, we have shown that individual variation in cerebral lateralization for the exploration of familiar environments is related to variation on the bold–shy continuum in the convict cichlid. There may be a common underlying neuroanatomical basis for the linkage between lateralization and personality. We suggest that the association between personality and lateralization may reflect the organization of adaptive variation in life history strategies.

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