

# The Effect of Sex and Early Environment on the Lateralization of the Rainbowfish *Melanotaenia duboulayi*

Anne-Laurence Bibost, Erin Kydd and Culum Brown

**Abstract** The influence of environmental complexity on the development of brain lateralization during ontogeny was investigated using the rainbowfish, *Melanotaenia duboulayi*. Male and female fish reared in enriched and impoverished environments were swum in a flume where they schooled with their mirror image on the left- or right-hand side. Interestingly, rearing conditions influenced the development of laterality in each sex differently. Males were more strongly lateralized when reared in enriched conditions compared with those reared in impoverished conditions. In contrast, females tended to show the opposite pattern. This difference in response to enrichment was likely due to variation in life-history priorities between sexes that can provide alternative fitness benefits. Males and females respond to stimuli differently as male are motivated by agonistic interactions with one another and courting females, whereas females are motivated by foraging. These varying motivating factors likely interact with habitat complexity in different ways during development resulting in different developmental trajectories with respect to laterality. When we examined turning preferences of females in a radial maze, we found no differences between fish reared in different habitats with respect to the turn biases. However, we did find that the activity rates of enriched females tended to be higher across all time periods, whereas impoverished fish increased activity levels as they became familiar with the apparatus. In general, our results suggest that male fish laterality may be more responsive to changes in rearing conditions than females.

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## 1 Introduction

Cerebral lateralization is a common trait among vertebrates and perhaps even invertebrate species (see review by Vallortigara and Rogers 2005). Cerebral lateralization refers to the functional partitioning of information processing between the two hemispheres of the brain and is often expressed as lateralized behavioral traits such as handedness or turn preferences. This overt expression of cerebral lateralization is referred to as laterality and it can provide noninvasive insights into the hemispherical specialization of information processing by using traditional behavior observational approaches. The ubiquitous nature of laterality in the animal world suggests that it is an evolutionarily ancient trait, there is even some suggestion of its existence as far back as the Cambrian period (Babcock 1993), and conveys fitness benefits.

It is well known that the majority of humans are right handed when performing tasks that require a high degree of dexterity. However, strongly lateralized biases at the species level, similar to those observed in humans, appear to be relatively rare in non-human animals. Only some species of parrots show species level bias of a level similar to or exceeding human handedness (Magat and Brown 2009). The explanation for such biases at the population level remains something of an enigma in the laterality literature (Vallortigara and Rogers 2005; Brown 2005). If laterality does convey some kind of advantage, one would expect all individuals to be strongly lateralized. Nevertheless, one can observe a wide diversity of lateralized phenotypes at every taxonomic level. Those species that do not show population level biases often comprise individuals displaying a range of laterality biases. While Galahs (*Eolophus roseicapilla*) are handling food items, for example, individuals may show left or right biases or anything in between (Magat and Brown 2009). Populations of poeciliid fish (*Brachyraphis episcopi*) exposed to varying levels of predation pressure also differ in their laterality (Brown et al. 2004). Examination of the frequency distribution of foot preferences in Japanese jungle crow (*Corvus macrorhynchos*) reveals a bimodal distribution with a lack of ambidextrous individuals (Izawa et al. 2005). Bimodal or strongly skewed distributions suggest that there may be selective pressures acting in favor of strongly lateralized individuals in some contexts perhaps via frequency-dependent selection (Brown 2005).

There is mounting evidence that laterality may convey fitness advantages and this likely occurs at two levels; cognitive and motor. Chimpanzees (*Pan troglodytes*) fishing for termites may be left or right handed while manipulating the fishing stick, but strongly lateralized chimps are more efficient at extracting prey than those that repeatedly swap hands (McGrew and Marchant 1999). It is likely in these circumstances that repeatedly carrying out the same task using the same hand entrains the animal and thus enhances motor performance. This may result from enhanced dexterity through finer motor control and the recruitment of new neurons devoted to the task. However, laterality is also hypothesized to convey a cognitive advantage independently from motor entrainment. Strongly lateralized parrots are

far better at problem solving in a foraging context (Magat and Brown 2009), strongly lateralized fish (*Girardinus falcatus*) show enhanced schooling behavior (Bisazza and Dadda 2005), and strongly lateralized fruit flies (*Drosophila melanogaster*) have better spatial memories (Pascual et al. 2004). The dual processing hypothesis proposes that lateralized individuals may be capable of processing different sources of information simultaneously in each hemisphere of the brain (Rogers et al. 2004). This could potentially enhance cognitive efficiency while keeping investment in brain tissue to a minimum and there is evidence that animals process different information in different brain hemispheres. Chicks (*Gallus gallus*), for example, categorize and learn the size and shape of food items using their left eye (right hemisphere of their brain) whereas the right eye (left hemisphere) is preferentially used to observe predators (Rogers et al. 1985). This asymmetry also allows them to better perform two tasks simultaneously, foraging and detecting predators, thus enhancing fitness (Rogers et al. 2004). In contrast, nonlateralized chicks are less efficient in foraging under predation risk, because they suffer from divided attention as they cease foraging to scan overhead for predators (Rogers et al. 2004). Similar lateralities for eye preferences exist in fish (see Bisazza and Brown 2011 for a review).

Interestingly, the hemispheres involved in analyzing certain sources of information can vary between the sexes, in terms of bias preference or strength of laterality. Male chicks learned to avoid potentially toxic prey items by observing a trained demonstrator when using the left eye (right hemisphere) but not the right eye (left hemisphere), whereas females learned this task using either eye (Rosa Salva et al. 2009). In poeciliid fish, only females show a right eye bias when looking at social stimuli of the same sex (Bisazza et al. 1998) and dogs (*Canis lupus familiaris*) also show sex differences in the lateralization when in a situation of novelty (Poyser et al. 2006). Similarly, male and female humans (*Homo sapiens*) vary in their laterality in a variety of ways, including their propensity for using the left hand (Papadatou-Pastou et al. 2008). Such differences between sexes could be explained by several mechanisms, the most prominent of which is variation in hormonal expression. A number of potential mechanisms have been proposed, that most probably relates the fact that early exposure to testosterone causes lateralized traits to become increasingly masculine (Hines and Shipley 1984). Despite this rather simple theory, empirical results from human subjects have been largely equivocal. To answer the question more directly, an experimental approach using animal subject is required. Such research has shown that variation in exposure to steroids affects the visual laterality of domestic chicks (Schwarz and Rogers 1992; Rogers and Rajendra 1993; Deng and Rogers 2002). In Cichlids fish (*Aequidens rivulatus*), females exposed to high doses of testosterone as eggs showed a significant change in their laterality scores, whereas no effect of the treatment was observed in males (Schaafsma and Groothuis 2012). These data suggest that hormones can influence sex differences in brain structure and behavior.

In addition to the hormone generated variation in laterality between the sexes, sex specific variation in lateralization may also be indicative of differences in

underlying motivational factors that likely relate to their underlying life-history priorities. For example, females are often highly motivated by food and potential food items, whereas males are more likely to be motivated by sex (Brown and Warburton 1997; Magurran and Garcia 2000). Thus males and females may assign different *values* to the same objects or contexts and therefore analyze the information using different hemispheres. When female fish were deprived of access to males for 2 months, for example, the strength of laterality while viewing males dramatically increased because they were unusually highly motivated to mate (Bisazza et al. 1998).

Within an individual, laterality can also vary with experience. For example, repeated exposure to a certain scene may result in habituation or recategorization of stimuli as the emotive content changes. The poeciliid (*Girardinus falcatus*) show an eye preference while viewing predators or neutral stimuli (Facchin et al. 1999) but the preference depends on the level of predation pressure experienced in the home stream (Brown et al. 2004). Common garden experiments, where fish from high and low predation streams were repeatedly exposed to simulated predator attacks, found enhanced laterality in both populations irrespective of population origin (Brown et al. 2007). These data suggest that prior experience with predators during development alters the emotive content of the encounter because the predator naïve fish learnt to fear the appearance of a predator which was formally a neutral or perhaps even an attractive stimulus (Brown and Warburton 1999). Similarly, rats (*Rattus norvegicus*) repeatedly exposed to a novel environment or handling during the early life stages show shifts in handedness in adulthood (Tang and Verstynen 2002; Cowell et al. 1997). Sarasins minnows (*Xenopoecilus sarasinorum*) show a preference for the left eye (right hemisphere) while facing an unfamiliar stimulus but this gradually switches to the opposite eye as the stimulus becomes increasingly familiar (Sovrano 2004). All of these examples illustrate that shifts in laterality during development may be triggered by a change in the psychological re-categorization of environmental stimuli via learning or habituation.

Experience during ontogeny clearly shapes laterality but such environmental influences can also occur *in vivo*. For example, maternal stress during pregnancy influenced the laterality of newborn rats (Alonso et al. 1991) and exposure to prenatal testosterone can influence laterality in female cichlid fish (*Aequidens rivulatus*) (Schaafsma and Groothuis 2012). Rogers (1990) demonstrated that light during embryonic development of the chicken influences laterality, whereby rearing eggs in darkness produces nonlateralized chicks. Similarly, zebrafish (*Brachydanio rerio*) eggs and larvae developed in the dark showed decreased laterality during predator inspection (Budaev and Andrew 2009).

While the role of early rearing conditions on fish laterality traits is still far from resolved, the effect of rearing habitat on fish brains and behavior has received more attention. Rainbow trout (*Oncorhynchus mykiss*) reared in enriched environments have larger brains (Marchetti and Nevitt 2003), tend to show more natural behaviors, and greater behavioral flexibility (reviewed by Brown and Day 2002). When reared in an enriched environment, for example, guppies (*Poecilia reticulata*) exhibited a

greater learning ability (Burns et al. 2009) and Atlantic salmon (*Salmo salar*) are better able to generalize learned skills to new contexts (Brown et al. 2003). Some of this enhanced learning ability displayed by fish reared in enriched environments may be a manifestation of enhanced cerebral lateralization, because laterality may increase the capacity to deal with multiple sources of information emanating from complex environments.

Here, we examined the possibility that laterality might vary depending on the physical complexity of the rearing environment. In fishes, there are two possible scenarios regarding the influence of physical habitat complexity on laterality during development: the inclusion of physical complexity may increase laterality directly, because navigating in a complex environment may be more cognitively demanding. Thus, we predict that fish reared in enriched environments should display enhanced laterality. One might predict that this effect will be greater in females who prioritize searching for prey. Alternatively, it has been suggested that schooling species tend to be more strongly lateralized than non-schooling species (Bisazza et al. 2000a; Bisazza and Dadda 2005; Brown et al. 2007), thus enhanced structural complexity may act indirectly by breaking visual contact between individuals causing a loss of schooling behavior and, thereby, a reduction in laterality. In either case, one might envisage that differences between the sexes may emerge in response to the treatment. It is well known, for example, that female fish tend to form the core of schools to enhance protection from predators (Brown and Warburton 1997; Magurran and Garcia 2000). Thus, if enhanced complexity effects laterality via a loss of schooling behavior, this is most likely to be manifested in female fish. In contrast, enhanced contact with conspecifics in an open habitat might enhance laterality in males, as they are stimulated into increased conflicts with rivals and enhanced contact with potential mates.

## 2 Materials and Methods

### 2.1 Housing and Stock

Crimson-spotted rainbowfish (*Melanotaenia duboulayi*) derived from fish reared in captivity for multiple generations (see Kydd and Brown 2009 for details), were raised in either enriched or impoverished environments. Eggs from breeding individuals were collected from housing aquaria using spawning nets. To control for genetic background, half siblings from a single aquaria were divided between the two nursery environments. Upon hatching, the fry were housed in clear plastic  $21 \times 28 \times 38$  cm tanks. The water was kept at a temperature of  $23^\circ\text{C}$  ( $\pm 1^\circ\text{C}$ ). Half of these tanks were furnished with gravel on the base and artificial aquarium plants to form a complex habitat (enriched treatment). The remaining half had white Styrofoam wrapped around the walls and the underside of the tank. These aquaria were devoid of spatial cues within the tank with the exception of a small

black heater (impoverished treatment). The fry were initially fed using an alternate regime of micro-worms (*Anguillula silesiae*) and Fry Starter (Aquasonic Pty Ltd). Following this, period fish were fed once daily using finely crushed flake food.

Juvenile fish were transferred into the larger glass aquaria (92 × 35 × 50 cm) once they reached a size of 15 mm, at approximately 10 weeks post-hatch. Water depth was maintained at 35 cm and the temperature at 23 °C (± 1 °C). Tanks were lit by an overhead fluorescent bulb, providing a photoperiod of 12D:12L. Fish were fed once daily on a small quantity of commercially available flake food. Shoal sizes were kept at around 15 individuals of mixed sex. The larger aquaria were also furnished as either enriched or impoverished environments. The enriched aquaria contained similar artificial plantings as the initial rearing tank, with some additions including driftwood, large rocks, and spawning nets. Enriched aquaria were also open fronted allowing the fish to view the lab. The conditions in the impoverished tank were similar to the impoverished nursery environment with the exception of gravel substrate (to maintain bacterial colonies to stabilize water quality) and a filter. The fish were reared in their respective environments until they were 1 year of age prior to testing.

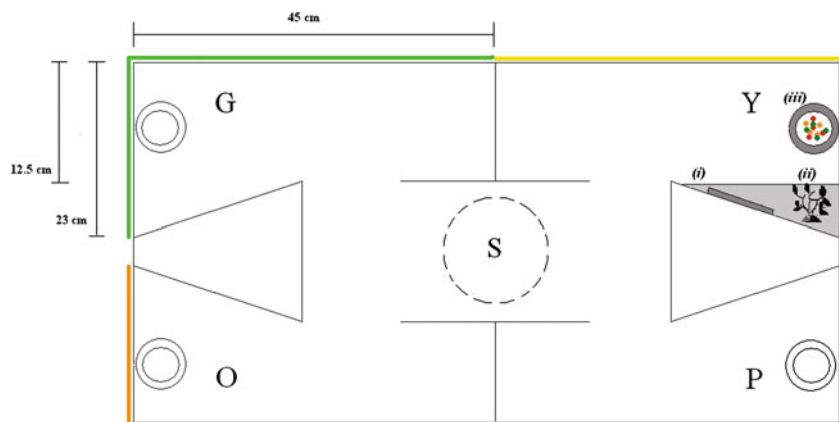
## 2.2 Protocol and Experimental Apparatus

### 2.2.1 Experiment 1: Radial Maze Task

The experimental task comprised a maze apparatus inspired by Brown and Braithwaite (2005). Juvenile females from the enriched and impoverished conditions ( $n = 16$  and 15 respectively) were selected as test subjects. The dimensions of the experimental tank measured 95 × 50 × 22 cm, and the water depth was maintained at 10 cm with a temperature of 23 °C (± 1 °C). The maze comprised a central compartment 43 × 25 cm with four doorways measuring 11 cm leading to four separate compartments (see Fig. 1). The outer walls of each compartment were lined with four different colors (orange, green, purple, and yellow). Many pelagic fish inhabiting clear shallow waters navigate the environment using visual cues and can perceive colors within the human visual spectrum (Reckel and Melzer 2003). These colors utilized here allowed the fish to differentiate between the rooms and locate the rewarded area.

The yellow reward room contained gravel, food, shelter, and a mirror. The mirror simulated the existence of a shoal mate. The reward stimuli were not visible to the fish until they had entered the room. Fish were not fed on the day of the procedure, thus the fish were provided with multiple incentives to locate the reward room.

Due to space constraints, the fish were tested in two batches. Experimental procedures were identical for both batches 1 and 2. Individual fish were transferred from their housing tank to a clear, plastic holding cylinder (18 cm diameter) located in the center of the maze. After an acclimatization period of 2 min, the holding cylinder was raised remotely. The fish was allowed 15 min to explore the maze. The movement of the fish within the maze was observed via a digital video



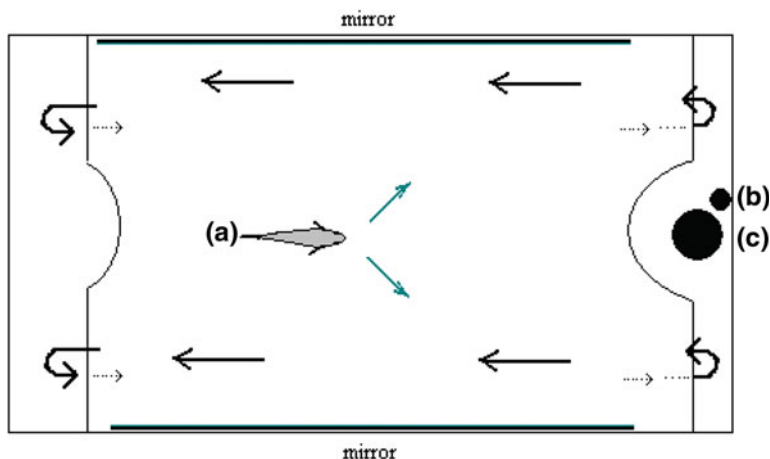
**Fig. 1** Radial maze apparatus used for testing turn biases; **S**: Starting area; **Y**: Reward area including: (i) mirror, (ii) plastic plant, and (iii) feeding ring; **G**: Green room, **O**: Orange room, **P**: Purple room

camera suspended overhead and data collected using Etholog 2.2 software. As the subject moved from room to room, the number of left and right turns was recorded. Individual fish were tested at approximately the same time each day for 12 days. All fish were fed at the end of each test day.

### 2.2.2 Experiment 2: Flume Test

A flume measuring  $110 \times 30 \times 30$  cm was constructed to identify the laterality of each individual. The apparatus was designed with two levels to generate laminar flow on the top level to encourage the test subject to swim against the water current. A bilge pump was placed at the bottom level of the tank, generating circular flow along the left and right sides of the tank. Two mirrors were placed on either side to simulate the presence of shoal mates using the subject's reflection. During the observation, the flume was isolated from the rest of the laboratory using curtains and observations were made via a web-camera suspended above the apparatus Fig. 2.

Subjects were removed from their home tank and placed in a covered bucket to settle for 20 min. Each individual was then carefully transferred to the flume for a 10-min observation. *Melanotaenia duboulayi* are shoaling species, thus we expected them to school with a conspecific (i.e. their mirror image), on the left or right side of the flume, while maintain station against the current depending on the eye preference. The position of the subject with respect to the mirror was recorded every 10 s. Fish swimming within 2 body lengths of the mirror on the left- or right-hand side were scored as preferring the right or left eye to view conspecifics respectively. Fish located in the center of the flume were recorded as nonlateralized. At the end of the



**Fig. 2** The flume apparatus used for testing laterality preferences. *Arrows indicate water flow above (solid lines) and below (broken lines) the split layers of the flume. Blue lines represent the movement of the fish. a* Subject, *b* Location of heater, *c* Pump

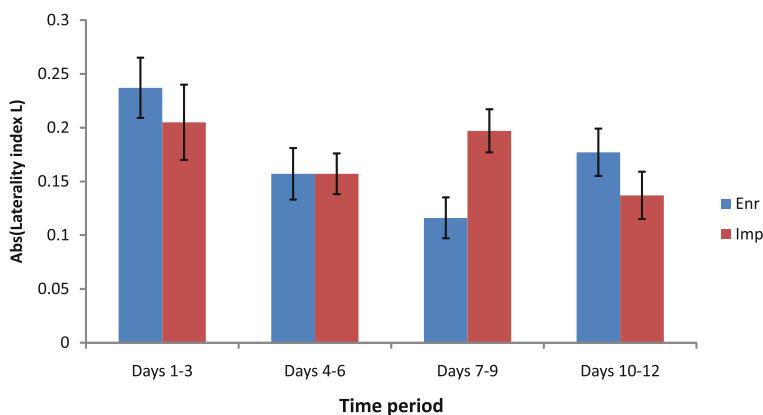
10-min observation period, the proportion of time spent schooling on the left or right side was calculated. A total of 7 males and 10 females were tested from the enriched environment and a total of 10 males and 7 females were tested from the impoverished environment.

### 2.3 Data Analysis

The number of left turns as a proportion of the total (left + right) turns while navigating through the maze was analyzed using a repeated measures ANOVA. The data were also transformed into an absolute laterality index:  $ALI = \text{absolute value of (laterality ratio} - 0.5)$  which is indicative of the strength of laterality irrespective of the direction. Fish crossing diagonally across the maze and u-turns were not included in the analysis. To reduce the complexity of the temporal component of the analysis, we grouped the data into 3-day lots. The data were arcsine- square root transformed to achieve a normal distribution prior to analysis in Statview version 5.0 (SAS Institute). The activity level of each fish (number of left, right, diagonal, and u-turns combined) was also analyzed using the repeated measures ANOVA.

The proportion of time spent on the left- or right-hand side of the flume was converted into a laterality ratio as in Experiment 1. The data were analyzed using ANOVA. The data were also transformed into an absolute laterality index. These data could not be adequately transformed, thus we used Mann–Whitney U-tests.





**Fig. 3** Mean  $\pm$  SE absolute laterality index of female laboratory fish reared in impoverished or enriched environments navigating in a radial maze

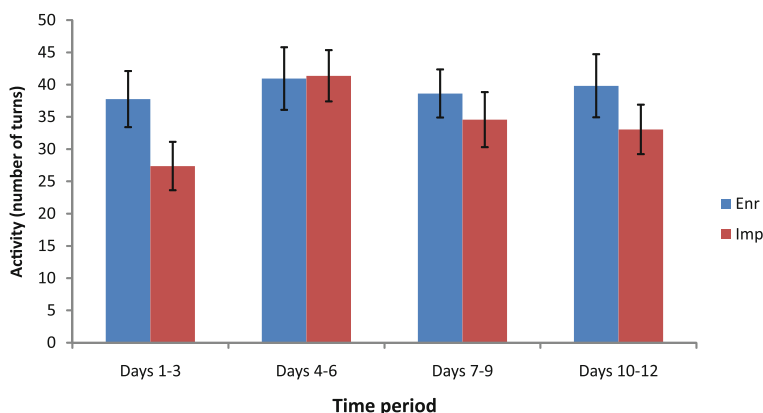
### 3 Results

#### 3.1 Experiment 1: Radial Maze Task

Analysis of the laterality data for turn preferences in the maze showed no significant main effects of rearing condition ( $F_{1, 30} = 0.165$ ,  $P = 0.687$ ), time ( $F_{3, 90} = 0.924$ ,  $P = 0.433$ ), or interaction between time and rearing condition ( $F_{3, 90} = 0.358$ ,  $P = 0.783$ ).

The results for the absolute value of turn preference in the maze revealed no significant effect of time ( $F_{3, 90} = 0.001$ ,  $P = 0.914$ ) but a significant treatment effect ( $F_{1, 30} = 3.519$ ,  $P = 0.018$ ) and a marginal interaction between time and environment ( $F_{3, 90} = 2.621$ ,  $P = 0.055$ ). Post hoc analysis found significant effect of time for the enriched fish ( $F_{3, 45} = 4.815$ ,  $P = 0.005$ ) but no effect existed for the impoverished fish ( $F_{3, 45} = 1.636$ ,  $P = 0.194$ ). Post hoc analysis found that enriched fish showed differences between days but with no obvious trend: Days 1–3 and 4–6 (Fishers PLSD:  $P = 0.018$ ) and between Days 1–3 and 7–9 (Fishers PLSD:  $P < 0.001$ ). In general, fish from both treatments showed a gradual reduction in the strength of laterality over repeated exposures (Fig. 3).

The activity results found no effect of rearing environment ( $F_{1, 30} = 0.903$ ,  $P = 0.350$ ) but there was a significant effect with time on activity levels ( $F_{3, 90} = 6.132$ ,  $P < 0.001$ ). While there was no significant interaction between time and rearing environment ( $F_{3, 90} = 2.575$ ,  $P = 0.059$ ), post hoc analysis found a strong effect of time in the impoverished fish ( $F_{3, 45} = 10.352$ ,  $P < 0.001$ ), but not in the enriched fish ( $F_{3, 45} = 0.398$ ,  $P = 0.755$ ). Over time, the activity level was consistently high for the enriched fish but tended to increase after the first 3 days in impoverished fish (Fig. 4).



**Fig. 4** Mean  $\pm$  SE of total turns (activity) of female fish reared in impoverished or enriched environments moving in the radial maze

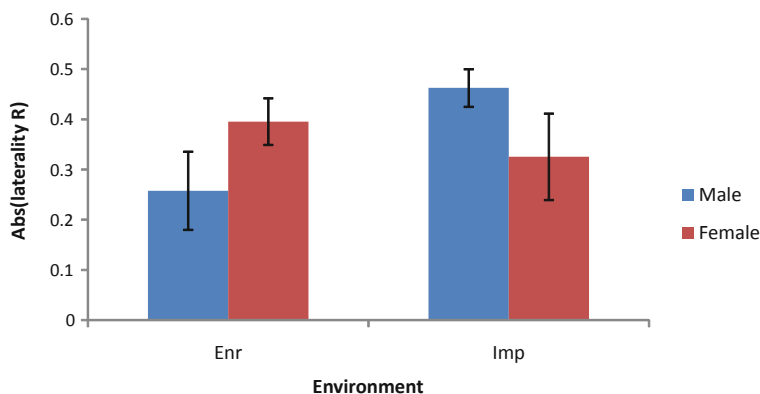
### 3.2 Experiment 2: Flume Test

Analysis of the lateralization index during the first 5-min observation in the flume showed no main effect of rearing environment or sex ( $P > 0.05$  in both cases). Nor was there a significant interaction between habitat and gender (ANOVA:  $F_{1,30} = 0.008$ ,  $P = 0.928$ ).

Mann–Whitney U-tests of the absolute laterality scores revealed no main differences between sex ( $Z = 0.177$ ,  $P = 0.859$ ) or rearing environment ( $Z = 1.359$ ,  $P = 0.174$ ). However, analysis of each sex independently (equivalent to an interaction in a 2-way ANOVA) found no differences in females reared in the two environments ( $Z = 0.546$ ,  $P = 0.585$ ) but a highly significant difference in males ( $Z = 2.398$ ,  $P = 0.016$ ). In general, the result of the flume test found that rearing habitat influenced the strength of laterality but the effect varied depending on the sex of the fish. Males were more strongly lateralized in the impoverished environment, whereas females tended to be more strongly lateralized in the enriched environment (Fig. 5).

## 4 Discussion

This study has identified that enhancing habitat complexity during development influences brain lateralization. As predicted, we found that sex modifies the effect of environmental enrichment upon behavior and the expression of laterality. The effects of environmental enrichment on laterality were far greater in males than in females. Analysis of eye preferences while shoaling with a conspecific (mirror image) in the flume, revealed that males from impoverished habitats were more



**Fig. 5** Mean ( $\pm$  SE) absolute laterality index during the first 5 min of the flume for male and female fish reared in enriched or impoverished environments

strongly lateralized than males from enriched habitats and the reverse was true for females. While an effect of treatment was observed in the turn preferences of females in the radial maze, there was no consistent pattern. We did, however, find an effect of rearing environment on exploratory activity over time. Enriched females were highly active in the beginning of the experiment making more turns and entering more compartments, while females reared in impoverished environments gradually increased their activity levels over the course of the experiment.

Our results indicate that sex differences occurred in behavioral and brain asymmetry and suggest that rearing in different environments influences brain function or development during ontogeny. Importantly, the modification of laterality via environmental enrichment was most pronounced in males. Elliott and Grunberg (2005) have observed that rearing rats in an enriched environment influences the speed of information processing, and the observed effect was greater in males than females. In this study, males were also significantly more receptive to changes in their rearing environment than females, but the strength of lateralization was enhanced in the impoverished condition where contact between conspecifics is maximal. While females showed the expected pattern, enhanced laterality when reared under enriched conditions, the difference between treatments was not statistically significant. It is likely that these results highlight fundamental differences between male and female cognitive abilities and the manner in which the brain is structured with respect to analyzing specific information in each hemisphere. Male rats, for example, show greater performance in spatial navigation if their right hemisphere dominates the left hemisphere, while the opposite is true for females (Cowell et al. 1997) and our data suggest that similar functional differences in laterality may occur in fish (Reddon and Hurd 2008). Such a proposal requires further experimentation.

In fish, both genes and life experience can cause sex differences in the strength of laterality (Brown et al. 2007). From an evolutionary perspective, animals should evolve an asymmetrical brain in a manner that enhances the fitness benefits in their day-to-day lives and fitness optima are likely to differ between males and females. Thus, the response to specific stimuli by males and females differs due to the presence of varying underlying motivational factors which may be enhanced depending on the environmental context (Camp et al. 1984; Bisazza et al. 1998). In this study, females reared in enriched habitat might develop enhanced laterality because they are stimulated by the physical complexity of the habitat and must actively search for food. Conversely, males reared in an impoverished habitat might develop enhanced laterality because they are stimulated by the social interactions to engage in courtship behavior and agonistic interactions. This explanation is supported by the differing life-history priorities for male and female fish and is consistent with previous work on poeciliids (Bisazza et al. 1998). Females generally maximize fitness by concentrating on foraging so as to produce energetically costly eggs, whereas males maximize fitness by inseminating as many females as possible (Brown and Warburton 1997; Magurran and Garcia 2000).

We hypothesize that social stimulation in males may accentuate the laterality cognitive processing, as lateralized fish develop an eye preference for the recognition of conspecifics (Bisazza et al. 1998; Facchin et al. 1999). Rainbow fish are shoaling species which are known to use visual cues to distinguish between relatives and familiar conspecifics (Arnold 2000; Brown 2002). Therefore, it could be suggested that habitat complexity reduces visual contact between individuals and, as a result, decreases the interaction among conspecifics (Kadry and Baretto 2010). Fishes reared in an open, structurally impoverished habitat emphasize schooling behavior (Brown and Warburton 1997). More importantly, brain asymmetry has been found to enhance schooling performance (Bisazza and Dadda 2005). However, there is also evidence that schooling tendency varies between sexes, with females often forming the core of schools and lone males moving between schools to court them (Brown and Warburton 1997; Griffiths and Magurran 1998). Thus, it was somewhat surprising that the females did not enhance their laterality in open conditions in response to enhanced shoaling opportunities. Males tend to be more blasé about predators than females. However, one must bear in mind that we were working with a captive stock of fish that appear to have lost their strong shoaling motivation (Kydd and Brown 2009).

It has been previously suggested that the development of an asymmetrical brain is accentuated by predation pressure mediated through shoaling (Brown et al. 2007). Thus, it seems reasonable to conclude that the social environment also plays a big role in shaping the development of laterality, but social interactions are also effected by a range of environmental factors, including predation pressure and habitat complexity. In general, the greater the importance of stimuli during development, the more we would expect the animal to develop enhanced hemispheric specialization when processing information relating to those stimuli (Denenberg 1981). Thus the major function of experience during development is to further modify an already lateralized brain.

Our results clearly demonstrate that exposure to different environments during development can influence laterality but there appears to be a wide range of contexts that can influence laterality development. For example, manipulating the light in the environment influences the development of symmetrical brain in zebrafish and chickens during ontogeny (Budaev and Andrew 2009; Rogers 1982). In this instance, we hypothesize that the development of the lateral visual pathway is related to environmental complexity specifically the manner in which the environment stimulates the visual pathway in the fish brain. In males, this stimulus likely took the form of interaction with conspecifics, but for females it was likely stimulus while searching for prey. Obviously, light, habitat complexity, and other environmental factors such as predation pressure can differ vastly in an aquatic environment and this could generate different patterns of laterality between populations (e.g Brown et al. 2007). In the wild, *Melanotaenia duboulayi* has been found to occupy a diverse range of habitats but in general, these species prefer inhabit vegetated areas, which offer high food availability and protection from predators when it is available (Hattori and Warburton 2003; Brown and Warburton 1997). When cover in the form of habitat complexity is not available, rainbowfish tend to school rather than hide to avoid predators (Brown and Warburton 1997). Thus the presence or absence of cover may also indirectly influence the development of laterality via the development of facultative schooling. We suspect that changes in laterality as a result of experience might be caused by a common phenomenon, whereby environmental stimuli differentially stimulate the nervous system during ontogeny, and the identity of the stimuli may vary substantially depending on the context.

Denenberg (1981) has suggested that low environmental pressure or a lack of stimulation found in impoverished habitats will still result in a symmetrical brain that is adequate to the survival requirements of the animal. Although there is some evidence that in the absence of selective pressure, laterality can be lost over time perhaps due to genetic drift (Brown and Magat 2011). Our results confirm that even individuals reared in an impoverished habitat composed only of gravel and conspecifics can still develop an asymmetrical brain suggesting that there is a conserved genetic component to the development of laterality (Bisazza et al. 2000b; Brown et al. 2007). In our study, we suggest that the impoverished environment enhanced social contact or chasing behavior between conspecifics, as it has been demonstrated in zebrafish (Basquill and Grant 1998). It would be interesting to examine the development of lateralization in the absence of contact with conspecifics.

In addition to the effect on laterality, we found that enriched female fish were significantly more active in the maze at the beginning of the test (Day 1–3) than impoverished fish. Likewise, rats reared in enriched or impoverished environments differ in their exploratory behavior (Klein et al. 1994; Elliott and Grunberg 2005). This is probably due to the fact that individuals reared in enriched environments are accustomed to being surrounded by complex physical structures and therefore are faster to process spatial information than impoverished fish. Moreover, the enriched fish could see into the lab and were accustomed to constant movements and changes in

their environment. Indeed, the impoverished fish were more cautious at the beginning of the test (days 1–3) as indicated by the relatively few movements they made in the radial maze, but became increasingly active as they familiarized with their novel surroundings. On the other hand, it could be also suggested that the activity rates for exploring an unfamiliar environment could be due to individual differences originated from early life experience (Brown et al. 2007). It has been demonstrated that in the context of a familiar environment, there is an association between personality and laterality. Individuals that are able to process information rapidly are able to habituate faster to a novel environment (Reddon and Hurd 2009).

In conclusion, the strength of laterality is likely to affect fitness in multiple contexts by improving the brain's neural capacity (Vallortigara and Rogers 2005). Increased neural capacity may be beneficial in many ways, such as in allowing individuals to process multiple tasks simultaneously (Rogers et al. 2004) or solve complex problems (Magat and Brown 2009). Thus, it is important for us to know what environmental factors shape the development of laterality in natural populations so that we can determine the likely fitness benefits. Enriched rearing environments are of paramount importance because it is known to promote normal cognitive development and behavior (Strand et al. 2010) and to affect the development of laterality, both due to social and physical factors. These factors likely affect each sex differently owing to their divergent life-history priorities.

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