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The influence of early experience on, and inheritance of, cerebral lateralization

CULUM BROWN*†, JAC WESTERN* & VICTORIA A. BRAITHWAITE*
*Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh
†Department of Biological Sciences, Macquarie University

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Cerebral lateralization refers to the lateralized partitioning of cognitive function in either hemisphere of the brain. Using a standard detour test, we investigated lateralized behaviour in wild-caught, female poeciliid fish, *Brachyraphis* (=*Brachyrhaphis*) *episcopi*, from high- and low-predation areas. Wild fish were bred and their offspring reared under controlled laboratory conditions. These laboratory-reared fish were screened in the same laterality assays as their parents. We observed differences between wild-caught females and their laboratory-reared female offspring in the pattern of lateralization (tendency to use one hemisphere over the other to process information). Conversely, the strength of lateralization (consistency of hemispherical bias) was largely conserved between generations, consistent with it being a heritable character. Both wild-caught females from high-predation sites and their laboratory-reared offspring showed stronger lateralized behaviour than their counterparts from low-predation sites. This difference in strength of lateralization is likely to provide fitness benefits to fish that occur in high-predation areas by enabling them to school and watch for predators simultaneously (dual processing). We hypothesized that the differences in the pattern of lateralization observed between species, and populations within species, are due to the manner in which they perceive and classify stimuli in the world around them. In particular, the perceived emotive content or context of a scene is likely to vary between individuals that have had different life experiences.

Keywords: *Brachyraphis episcopi*; cerebral lateralization; experience; heritability; ontogeny; poeciliid

Cerebral lateralization is widespread among the vertebrates and may even be common among the invertebrates (Vallortigara 2000; Byrne et al. 2002). In terms of cognitive function, it is often overtly revealed behaviourally by such things as hand biases (i.e. handedness), but more subtly is seen as a preference to use one eye over the other while viewing objects, or as turn biases while moving through novel terrain (Rogers & Andrew 2002). Such behavioural observations provide an indication of the way in which the functions of brain activities are partitioned in each hemisphere. It is apparent that such biases affect many aspects of the day-to-day behaviour of animals, ranging from their social interactions to predator avoidance and foraging behaviour (Casperd & Dunbar 1996; Bisazza et al. 1997a; Robins & Rogers 2004). While most research has concentrated on the mechanisms underlying cerebral lateralization, recent work is beginning to focus on its function and its potential fitness consequences (Brown et al. 2004; Rogers et al. 2004; Bisazza & Dadda 2005).

Based on studies of a relatively limited number of species, it appears that a common pattern of lateralization is emerging among the vertebrates, suggesting a common evolutionary origin (Rogers 2002; Rogers & Andrew 2002). Generally, the right side of the brain initiates rapidly executed responses, it processes information about new objects and, it is used to recognize conspecifics in species as disparate as fish and humans (Sovrano et al. 1999; Rogers 2002; Rogers & Andrew 2002). In contrast, the left hemisphere is involved in discriminating between

Correspondence: C. Brown, Department of Biological Sciences, Macquarie University, Sydney, 2109, Australia (email: cbrown@bio.mq.edu.au). J. Western and V. A. Braithwaite are at the Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, U.K.

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alternative categories of previously encountered objects (Rogers et al. 2004). However, as more data are collected on a greater number of taxa in a variety of contexts, this general pattern is becoming increasingly complex. For example, some species of birds forage with one eye and look for predators with the other, while other species show no preferences at all (Franklin & Lima 2001; Ventolini et al. 2005). Similarly, the cognitive function of left-handed humans for language control can be the mirror image of their right-handed counterparts but this is not always the case (Levy 1979). Barth et al. (2005) found that some but not all behavioural traits are reversed in the reverse frequent-situs-inversus line of zebrafish, *Danio rerio*, suggesting some degree of disassociation between neural and behavioural asymmetries. In some instances this variation in behavioural symmetry is due to variance in the underlying neurological architecture, but in others it may be caused by variation in which hemisphere individuals bring to bear on a certain task and the corresponding control of motor coordination. This latter point may be related to how an animal perceives the situation or context in which an individual finds itself, including the emotive context which may vary with individual experience during ontogeny.

Recently, interest in the evolution of lateralization has stimulated a number of studies of different species of fish. When tested under controlled conditions, it is clear that different species show broadly different patterns of lateralization (Bisazza et al. 1997b, 2000a; but see Sovrano et al. 1999 for similarities). The same cognitive function can be partitioned on the left or the right hemisphere depending on the species or individual under consideration, and at least part of this variation occurs at the neurological level (Barth et al. 2005). Rogers (1989) suggested that at the population level, lateralization might evolve in response to the need for maintaining coordination among individuals living in social groups. Heuts (1999) hypothesized that differential exposure to predators owing to the occupation of different habitats (benthic versus limnetic) may explain interspecific variation in lateralized escape responses in fish. Benthic species that rely on hiding to escape predators do not require coordinated responses at the population level, whereas those that shoal in open waters do. Examination of the pattern of lateralization observed in 16 species of poeciliids generally supported this view (Bisazza et al. 2000a). Bisazza et al. (2000a) found that closely related species are more likely to have similar patterns of lateralization in terms of the eye that they use to view a predator. Furthermore, independent tests of shoaling tendencies found that all gregarious species show high levels of lateralization compared to only 40% of the nongregarious species (Bisazza et al. 2000a). Nevertheless, the specific eye preference (left or right) still varies between species. It appears that selection acts on the strength of lateralization rather than the pattern or direction of cognitive asymmetry (Collins 1991). In those situations where group coordination is essential for survival, such selection should be acting in a frequency-dependent manner across the entire population, selecting for compatible behavioural asymmetries across all group members (Billiard et al. 2005; Brown 2005; Vallortigara & Rogers 2005). Theoretically, the direction of behavioural bias could evolve independently in every species because the pattern of lateralization is largely irrelevant, since the benefits associated with cerebral lateralization are apparent regardless of directional bias at the individual level, but may be vital at the population level (Rogers et al. 2004; Bisazza & Dadda 2005).

In an initial study, Brown et al. (2004) found that differential exposure to predation pressure was associated with differences in both the strength and direction of lateralized responses of a single poeciliid species collected from regions of high- and low-predation pressure, providing the first evidence that predation pressure influences the development and evolution of lateralization in vertebrates. More recently, Bisazza & Dadda (2005) found that strongly lateralized fish form more cohesive shoals than nonlateralized fish thus providing significant antipredator benefits during schooling manoeuvres (Pitcher 1986). It would seem, therefore, that improved shoaling behaviour, which is under very strong selection pressure in fish, is just one of many important functions influenced by cerebral lateralization.

Here we used an approach developed by Bisazza et al. (1997a) to examine the behavioural manifestation of cerebral lateralization in the poeciliid *Brachyraphis* (=*Brachrhaphis*) *episcopi* collected from high- and low-predation areas and their laboratory-reared offspring. The fish were required to swim down a corridor and detour to the left or right while observing stimuli partly obscured behind a barrier. The principal aim was to determine the relative contributions of experience during ontogeny and heritability in determining the pattern and strength of lateralization observed in wild fish. While it is apparent that cerebral lateralization has a heritable component (Bisazza et al. 2000b), we do not know how heredity and early experience interact during development in wild populations derived from various environments.

METHODS

Subjects

Brachyraphis episcopi is a live-bearing poeciliid endemic to Panama and similar in many respects to the Trinidadian guppy, *Poecilia reticulata*. Eighty adult *B. episcopi* (60 females and 20 males) were collected with dip-nets from high- and low-predation regions in four rivers: the Quebrada Juan Grande, Aqua Salud, Rio Macho and Rio Limbo (20 from each of four locations, Autoridad Nacional del Ambiente permit). All these rivers run off an escarpment and cascade over a series of waterfalls before flowing independently to the Panama Canal. *Brachyraphis episcopi* is confined to the upper headwaters of all the streams and are the dominant species above the falls where they coexist with the killifish, *Rivulus brunneus*. A full complement of predators is present below the falls including several species of cichlid and the wolf fish, *Hoplias microlepsis*; nevertheless, *B. episcopi* can still be found in these high-predation regions (for further details on the fauna and the grid references for these locations see Brown &

Braithwaite 2004). *Brachyraphis episcopi* is gradually replaced by the sister species *B. cascajalensis* in the lower reaches of these rivers long before they reach the Panama Canal. The predation regime these fish live under has a substantial bearing on a number of traits including life history, spatial-learning abilities, boldness and stress responses (Jennions & Telford 2002; Brown & Braithwaite 2004, 2005; Brown et al. 2005a, b).

The fish were air freighted to the University of Edinburgh (with permits from the Autoridad Nacional del Ambiente and Ministerio de Desarrollo Agropecuario, Panama, and the Environment and Rural Affairs Department, U.K.) in sealed plastic bags supplied with oxygen. The bags were secured inside polystyrene insulation boxes packed with newspaper. Despite the 24-h journey, mortality rates were less than 1%. Once at the university, the fish were housed in standard glass aquaria (90 × 30 cm and 30 cm deep). Fish from each river and predation regime were housed separately in four similar aquaria. The aquaria were equipped with a power filter, river gravel and assorted rocks and plastic plants. The fish were fed daily with a commercial flake food and sporadic live food supplements. The room in which they were housed was lit by overhead fluorescent tubes and was kept on a 12:12 h light:dark cycle and the room temperature was maintained at 26 ± 1°C.

Fish from up- and downstream sites in the Quebrada Juan Grande and Rio Limbo (four populations) were allowed to breed freely within their own population. Fry were collected and housed separately from their parents. When the fry reached 6 months of age (around 25 mm standard length), we selected 60 individuals for the lateralization assays: 13 males and 15 females from high-predation parents and 16 males and 16 females from low-predation parents (roughly half from each river). One of the high-predation males behaved erratically during the experiment and was eliminated from the data set. Thirty-seven wild-caught adult females from each of the four rivers (19 from high-predation and 18 from low-predation sites) were randomly selected from the captive stock as representatives of the wild populations. Wild males were not tested because of their low abundance. All fish were maintained for further breeding and experimental work after the study.

Apparatus

The experimental apparatus consisted of an aquarium (110 × 30 cm and 30 cm deep) with a plastic corridor running down the middle (10 × 47 cm) that opened out in a cone shape at either end (Fig. 1). The ends of the cones were capped with white plastic. Three different types of stimuli were presented to the fish: (1) a blank (or control) where no stimulus was present, (2) a novel object consisting of a yellow plastic cross attached to a red weighted base or (3) an unfamiliar conspecific of the same sex and generation as the test subject in a transparent plastic cylinder. The stimuli were placed behind a barrier made of transparent plastic with a series of black vertical bars (0.25 cm wide and spaced 0.25 cm apart) attached to a weighted base at either end of the corridor. The fish could see the stimulus, but could not pass through the barrier. The water in the experimental aquarium was 10 cm deep and lighting was provided by a fluorescent light mounted directly above the corridor 2 m overhead (Fig. 1). This design of apparatus is based on that used by Bisazza et al. (1997a).

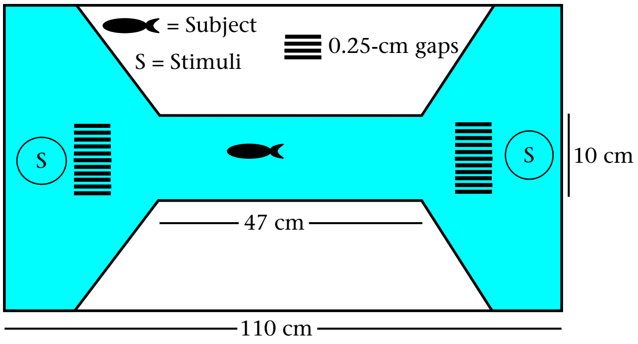

Figure 1. Diagrammatic representation of the experimental apparatus showing the runway with a conical end opening out to the slatted barrier around which the fish must detour while inspecting the stimulus partially obscured behind it.

Procedure

We removed fish from their home tank the day before the experiment and placed them in individual floating compartments adjacent to the experimental aquarium. The aim of this was to reduce handling stress on the fish. On the day of the experiment, the test subject was gently transferred into the experimental tank, and left there for 15 min to allow it to become accustomed to its surroundings. At this stage no barriers were present in the test tank. The fish was then isolated at one end of the tank while the barrier and stimulus were placed at the other end. We used two symmetrically arranged fish nets to encourage the fish to enter the corridor. As the fish approached the barrier it had to make a decision to turn to the left or right. The direction the fish took to detour the barrier was recorded when its head was parallel to the barrier. Observations were conducted by a stationary observer standing directly behind the aquaria such that the subject was swimming away from the observer and could see only the observer's head. An observer-induced turning bias was therefore unlikely. The fish was confined at that end of the tank for 20 s while the stimulus was moved to the opposite end of the corridor. The fish was then encouraged back into the corridor and swam towards the stimulus once more, this time travelling in the opposite direction. We repeated this procedure 10 times for each of the three treatments: control, novel object and conspecific. Between each treatment the fish was restrained in a clear cylinder for 2 min while we changed the stimuli. The order of treatment was randomized for each individual. We screened the turn preferences in both the wild-caught females and their laboratory-reared offspring of both sexes.

Data Analysis

We converted the turn data for each individual to a laterality index (LI; Bisazza et al. 2000a): LI = (number of turns to the right − number of turns to the left)/total number of turns. LI is a continuous variable ranging from +1 to −1. Positive scores represent a right-turn bias, negative scores represent a left-turn bias and scores of 0 have no turn bias. We conducted three discrete analyses. The first examined the behaviour of the wild-caught female fish in response to the three treatments; the second examined the difference in LI between the wild-caught females and the female laboratory-reared offspring; and the third examined the differences between males and females in the laboartory-reared fish only. A repeated measures analysis of variance (ANOVA; Statview version 5.0, SAS Institute, Cary, NC, U.S.A.) was used in all instances to analyse the data, with LI as the response variable, treatment as the repeated variable and predation pressure and generation or sex as the independent variable for the second and third analyses, respectively.

In some instances differences in turn biases between individuals within a given population may mask any effect of predation regime (i.e. one individual consistently turning right and another always turning left would result in an overall LI of 0). To gauge whether there were strong turn biases (regardless of whether these were to the left or to the right) we also analysed the absolute value of LI. This provided a measure of the strength of the lateralized behaviour.

Finally, we calculated the proportion of strongly lateralized individuals (number of fish that turned either left or right in over 80% of trials) during any of the three treatments.

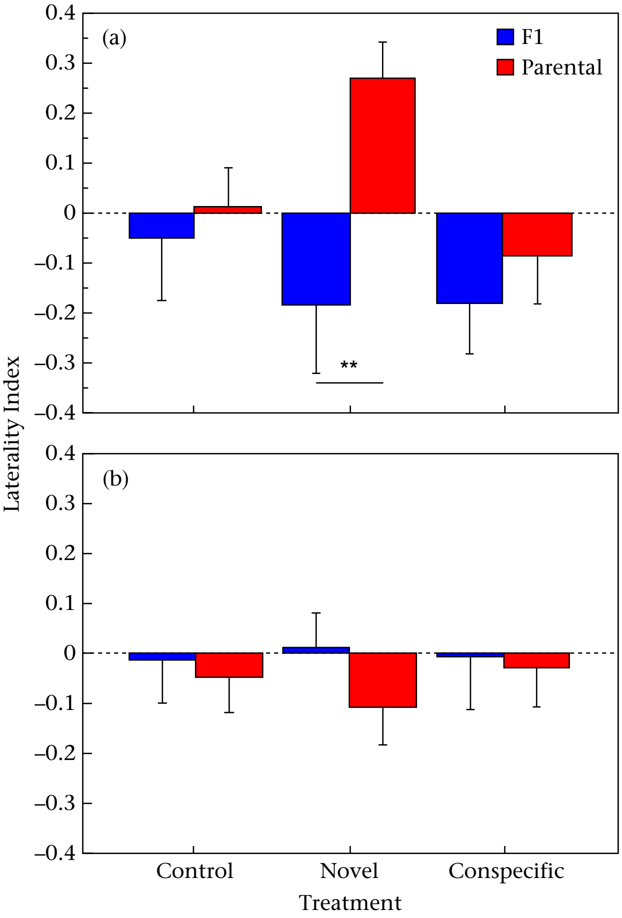

Figure 2. Mean + SE laterality index for parental wild-caught fish and their F1 laboratory-reared offspring from (a) high-predation areas and (b) low-predation areas. Positive scores represent right-turn biases and negative scores represent left-turn biases. Bars marked with asterisks represent results of *t* tests and signify turn biases that differed significantly from 0. Significant differences between groups are indicated by a solid line and accompanying asterisks. $*P < 0.05$; $**P < 0.01$.

RESULTS

Wild-caught Females

Analysis of the LI for wild-caught females showed no differences between the four rivers (repeated measures ANOVA: $F_{3,47} = 0.901$, $P = 0.448$) so the data for each river were collapsed into high- and low-predation areas. Although there was no direct effect of predation regime ($F_{1,53} = 2.206$, $P = 0.143$) or treatment ($F_{2,106} = 2.354$, $P = 0.100$) on LI, respectively, there was a highly significant interaction between these two factors ($F_{2,106} = 5.747$, $P = 0.004$). Wild-caught females from high-predation areas showed no turn bias when confronted by a blank scene, showed a significant bias to turn right while approaching a novel object and a slight, but nonsignificant bias to turn left while viewing an unfamiliar female conspecific. This contrasted with the wild-caught females from low-predation areas which showed no turn biases while viewing a blank scene or conspecifics, although there was a statistically nonsignificant tendency to turn left while viewing a novel object (Fig. 2).

The results of the repeated measures ANOVA on the absolute value of the LI revealed no effect of treatment; however, a statistically nonsignificant trend suggested that high-predation fish were slightly more lateralized than low-predation fish ($F_{1,53} = 2.957$, $P = 0.091$). This is supported by the fact that 45% of fish from high-predation regions showed strongly lateralized responses (turn preference in one direction on more than 80% of occasions) during the experiment compared to only 15% of fish from low-predation areas (binomial test: $P = 0.023$).

Wild versus Laboratory-reared Females

As with the wild fish data, the LI of the laboratory-reared fish from different rivers did not differ (repeated measures ANOVA: $F_{1,29} = 0.061$, $P = 0.807$) so these data were collapsed into high- and low-predation regions. Repeated measures ANOVA of the LI revealed no differences between generations ($F_{1,82} = 0.967$, $P = 0.328$) and no influence of predation regime ($F_{1,82} = 0.012$, $P = 0.912$), although a statistically nonsignificant trend for an interaction was detected ($F_{1,82} = 3.303$, $P = 0.073$). There was no significant difference between the three treatments

($F_{2,164} = 1.023$, $P = 0.362$). A three-way interaction between treatment, predation regime and generation was detected ($F_{2,164} = 3.177$, $P = 0.044$). To interpret this complex interaction, we split these data by predation regime. No significant effects were detected in the low-predation fish; however, a significant interaction between generation and treatment was found in the high-predation fish ($F_{2,84} = 3.879$, $P = 0.025$; Fig. 2). High-predation fish collected from the wild and their laboratory-reared offspring showed no turn biases during the control treatment; however, they differed substantially during exposure to the novel object when wild fish showed a significant right-turn bias, whereas their laboratory-reared offspring showed a statistically nonsignificant tendency to turn left. Both generations tended to turn left in response to a conspecific, although this bias was statistically significant only in the laboratory-reared fish.

The results of the repeated measures ANOVA for the absolute value of LI (i.e. the strength of lateralization) revealed no differences between generations ($F_{1,82} = 0.078$, $P = 0.780$) and a significant influence of predation regime ($F_{1,82} = 5.840$, $P = 0.018$). High-predation fish were more strongly lateralized across all groups, but this effect was most evident in response to the novel object. However, the interaction between treatment and predation regime was not significant ($F_{2,164} = 2.522$, $P = 0.083$). The three-way interaction ($F_{2,164} = 2.734$, $P = 0.068$) was indicative of a trend such that the difference in lateralization strength between the high- and low-predation fish in response to the novel object was amplified in the laboratory-reared females. There were no differences between the three treatments ($F_{2,164} = 0.914$, $P = 0.403$).

Male versus Female Laboratory-reared Fish

Analysis of the laboratory-reared juveniles' LI revealed a highly significant effect of treatment (repeated measures ANOVA: $F_{2,110} = 10.352$, $P < 0.001$) and a significant interaction between sex and treatment ($F_{2,110} = 6.861$, $P = 0.002$). Laboratory-reared fish showed no turn bias during the control and tended to turn left when observing a novel object. While males and females both tended to turn left when approaching a conspecific, males showed a far stronger and significant bias compared to females (Fig. 3). There were no significant differences between fish bred from parents captured in high- and low-predation areas. Overall, 33% of laboratory-reared fish with parents from high-predation areas showed strong lateralized responses during the experiment (turn preference in one direction on more than 80% of occasions) compared to 22% of low-predation laboratory-reared fish (binomial test: $P < 0.05$).

Analysis of the absolute value of LI using repeated measures ANOVA revealed a marginal difference between laboratory-reared fish bred from high- and low-predation parents ($F_{1,55} = 3.937$, $P = 0.052$). Laboratory-reared, high-predation fish were more strongly lateralized than low-predation fish. There was also a significant effect of treatment ($F_{2,110} = 6.830$, $P = 0.002$). The strength of lateralized responses increased from the control to the novel object to the conspecific in all laboratory-reared fish. However, a significant interaction with sex showed that this increase was almost entirely due to the males' response rather than the females'. Finally, there was a significant three-way interaction between treatment, sex and predation regime ($F_{2,110} = 5.745$, $P = 0.004$). Males and females from low-predation areas behaved very similarly, whereas there were significant differences between males and females with high-predation parents (Fig. 4). Males from

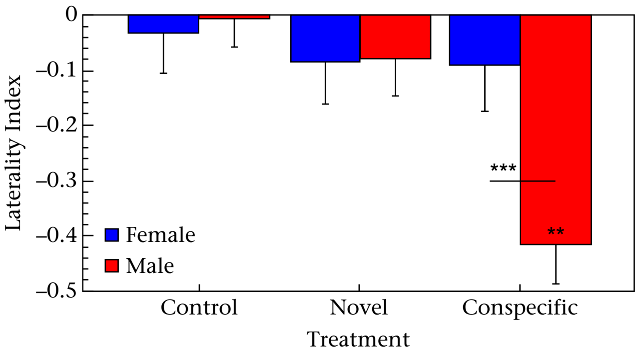

Figure 3. Mean + SE laterality index for female and male laboratory-reared F1 offspring during each of the three treatments: control, novel object, conspecific. Negative scores represent left-turn biases. Bars marked with asterisks represent results of *t* tests and signify turn biases that differed significantly from 0. Significant differences between groups are indicated by a solid line and accompanying asterisks. **$P < 0.01$; ***$P < 0.001$.

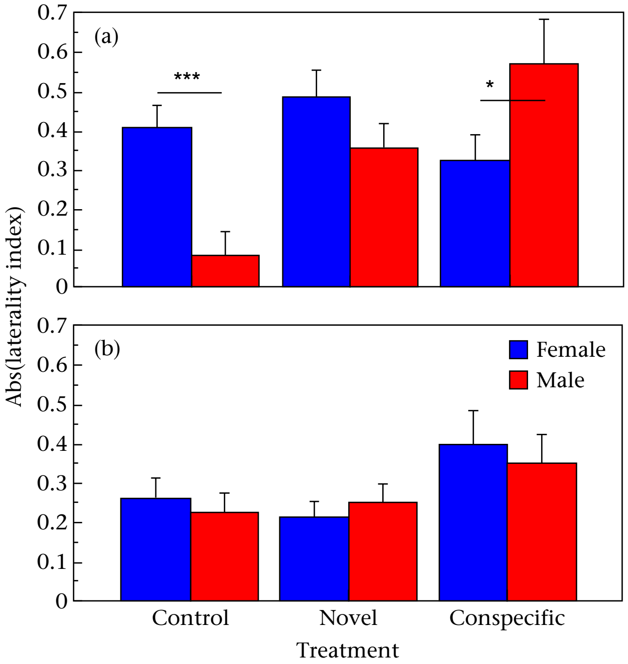

Figure 4. Mean + SE strength of lateralization for laboratory-reared males and females bred from (a) high-predation and (b) low-predation wild-caught parents for each of the three treatments: control, novel object, conspecific. High values represent more strongly lateralized responses. Significant differences between groups are indicated by a solid line and accompanying asterisks. *$P < 0.05$; ***$P < 0.001$.

high-predation areas showed the strongest change in the strength of lateralization across the three treatments of all fish (Fig. 4a). A similar percentage of males (26%) and females (29%) showed strongly lateralized responses.

DISCUSSION

Wild female *B. episcopi* from regions of high- and low-predation pressure differed in their pattern of cerebral lateralization when viewing different types of stimuli. The choice of turn direction in the detour test is determined by the eye the fish prefer to use to focus on the stimulus partially obscured behind a barrier (Bisazza et al. 1997a). Our analysis of the laterality index found a significant interaction between predator regime and treatment. Whereas wild fish from both predation regimes showed similar responses while viewing the blank scene (control) and conspecific, fish from high-predation populations had a strong left-detour bias when viewing novel objects and fish from low-predation populations showed a nonsignificant tendency to turn to the right (Fig. 2). These results are consistent with our earlier findings where high- and low-predation fish differed in the eye used to investigate both predators and novel objects (Brown et al. 2004). When taken together, these experiments suggest that in the wild, high-predation *B. episcopi* use their right hemisphere to process information about novel objects and their left hemisphere to process information about predators and unfamiliar conspecifics. This differs from low-predation fish which have only marginal preferences for viewing various scenes.

The strength of lateralization was greater in high-predation fish with 45% of all fish tested showing strong turn biases compared to just 15% of low-predation fish. Fish were considered to be strongly lateralized if they showed a preference to turn in one direction than the other on more than 80% of occasions. Strong cerebral laterality is likely to have fitness benefits, in terms of both coordinated group antipredator responses and dual information processing in other contexts such as foraging. For example, strongly lateralized birds and fish both show improved ability to forage and remain vigilant for predators compared to nonlateralized individuals (Rogers et al. 2004; Bisazza & Dadda 2005).

Examination of the laterality index of the laboratory-reared generation bred from both high- and low-predation wild-caught parents revealed several interesting patterns. First, laboratory-reared and wild-caught females from low-predation areas did not differ in their pattern of lateralization. In contrast, the high-predation females and their offspring differed significantly, as revealed by a significant generation times treatment interaction. High-predation, wild females and their laboratory-reared female offspring showed opposing turn biases in response to the novel object, although the latter did not differ significantly from random. Furthermore, these results support a preference to use the right eye to view unfamiliar conspecifics but this was enhanced in the laboratory-reared offspring. It is evident that the pattern of expression of lateralized responses depends on experiences gained during ontogeny. It is uncertain if this expression of turn bias is a direct reflection of differences in the symmetry of the underlying neural architecture, or a reflection of which hemisphere is used to analyse and respond to the various scenes. Such large changes in the pattern of lateralization from one generation to the next are most likely to be the result of the latter which may influence motivation during inspection of various objects.

It is likely that experience, with predators for example, could make a substantial difference to how stimuli are processed. Crimson spotted rainbowfish, *Melanotaenia duboulayi*, that have had no experience with predators tend to approach them out of curiosity, whereas those that have experienced predators respond with avoidance behaviour (Brown & Warburton 1999). Laboratory-rearing could have significant effects on other traits such as boldness and stress responses, thus altering the manner in which laboratory-reared fish perceive the test situation. These traits are known to differ in the populations tested here (Brown et al. 2005a, b). Evidently the same stimuli can have different meanings to different individuals which may respond in their own unique way. Bisazza et al. (1997a) showed that it is possible to reverse the direction of laterality by manipulating fear during the test. Similarly, a change in laterality can be induced by manipulating sexual motivation (Bisazza et al. 1998) and chicks, *Gallus gallus domesticus*, switch between left and right hemispheres depending on whether a social partner is familiar or not (McKenzie et al. 1998). This variation in the perception of the environment could explain some of the differences observed between wild and laboratory-reared fish as well as the variation observed between high- and low-predation populations. It is apparent that the controlled laboratory conditions under which the laboratory-reared generation were reared are more similar to the low-predation environment in the wild than they are to the high-predation environment, the primary difference being the distinct lack of predators in the former.

Although the pattern of lateralization appears to be influenced by experience, this may not be the case for the strength of lateralization. The absolute value of the laterality index provides an alternative means of examining the strength of lateralization as the data are not confounded by competing left and right individuals within each population. Analysis of wild-caught and laboratory-reared females revealed a significant effect of predation regime and no difference between generations. Both laboratory-reared and wild females from high-predation areas were more strongly lateralized than low-predation fish and this was most evident when the fish were viewing novel objects. Analysis of the data from male and female laboratory-reared fish also supports this position (Fig. 4). Furthermore, 33% of the high-predation, laboratory-reared fish were classified as having strong directional biases during the experiment (turning in one direction on more than 80% of occasions) compared to 22% of the low-predation offspring. As mentioned above, wild females from high-predation areas were more likely to be strongly lateralized than those from low-predation areas. Bisazza et al. (2000b, 2001) created laboratory-reared lines selected for left- and right-turn biases based on pet shop-purchased poeciliids (*Girardinus falcatus*). After several generations the heritability of lateralization was estimated to be greater than 0.5. Similar lines for paw preference have been established in mice, *Mus musculus*, and significant biases were observed after just three generations (Collins 1991). Although the estimates of heritability established from inbred lines are not applicable to wild populations, they do show that lateralization has a heritable component and thus is open to population shifts induced by natural selection caused by differential exposure to a variety of environments. Ideally such tests of heritability ought to be conducted on second-generation individuals to minimize the influence of maternal effects, which have been documented in live-bearing fish (Reznick et al. 1996). For example, stress hormones circulating through the body of the mother could influence the development of the young and may influence the manner in which juveniles respond to novelty. However, our fish were maintained in captivity for several months before breeding so maternal influences were probably minor and the consistency between generations is more likely to be caused by genetic factors.

Finally, the comparisons between our laboratory-reared males and females showed that the behavioural manifestation of lateralization varies with sex. Furthermore, the differences between the sexes in terms of the strength of lateralization were amplified in laboratory-reared fish originating from high-predation parents. Males and females differ in the manner in which they process information about unfamiliar conspecifics. In this experiment, males viewed other males, while females viewed females; therefore, the results could reflect general differences in response to either sex. There are many other potential combinations that could have been tested but we felt that this experience was likely to be the most similar for both sexes. Males and females of this species are generally very aggressive, males more so than females. In captivity, a pair of rival males will escalate fights until one of them is killed if they are kept in the same aquarium (personal observation). In low-predation areas females hold territories, with the biggest female usually occupying the territory at the head of the pool and thus securing the best access to drifting invertebrates. Males attempt to guard the females and one large male will normally dominate an entire pool. This domination is aided by the fact that males are relatively rare in all reaches of the river but the sex ratio is most heavily biased in low-predation areas where the densities of *B. episcopi* are very high (Brown et al., in press). Males approaching unfamiliar males analyse the information using their left hemisphere which matches that shown in wild, high-predation females inspecting potential predators and is consistent with studies conducted on three other poeciliid species (Bisazza & De Santi 2003). It is clear that males perceive one another as potential threats and process that information accordingly. These differences between male and female laterality are most prominent in fish bred from high-predation parents (Fig. 4).

Together, these results suggest that the strength of lateralization has a heritable component; however, the pattern is influenced by exposure to different experiences during ontogeny. It is likely that many of the differences we see between high- and low-predation fish exposed to different levels of predation are due to the manner in which they perceive the world around them. The emotive content of particular contexts or scenes is like to vary between individuals that have had different life experiences. For example, fish from low-predation areas are rarely confronted with predators and are likely to classify them in a manner similar to any novel object, whereas fish from high-predation areas immediately recognize the threat and process the information accordingly. There is no doubt that the display of lateralized behaviours can arise via a complex interaction of mechanisms both neurological and psychological. It is likely, therefore, that there is a strong interplay between learning, motivation and the hemisphere that animals use to classify and process information emanating from the world around them.

Acknowledgments

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