



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

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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, *Brachyrhaphis* (= *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.

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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 (Casper & 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

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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 anti-predator 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 *Brachyrhaphis* (= *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

Brachyrhaphis 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. *Brachyrhaphis 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 microlepis*; 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 &

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