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Laterality Influences Cognitive Performance in Rainbowfish *Melanotaenia duboulayi*

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KEYWORDS

conditioning, cognition, cerebral, lateralization, fitness, rearing environment, hatchery

ABSTRACT

*Cerebral lateralization has been suggested to convey a selective advantage to individuals by enhancing their cognitive abilities. Few, however, have explicitly compared the cognitive ability of animals with strongly contrasting laterality. Here, we examined the influence of laterality on learning performance in the crimson spotted rainbowfish, *Melanotaenia duboulayi*, using a classical conditioning paradigm. We also compared the learning ability of wild caught and captive-reared fish to examine the influence of rearing environment on cognitive performance. Laterality was established by observing which eye fish preferred to use while viewing their mirror image. Subjects were then conditioned to associate the appearance of a red light with a food reward over 7 days. Our results revealed that left-lateralized fish learned the conditioning task faster than right-lateralized. These results provide further evidence that cerebral lateralization can play important roles in cognitive function which likely have diverse fitness consequences for animals in their natural environments.*

Introduction

Brain lateralization is a common trait among vertebrate and invertebrate animals (Rogers and Andrew 2002). Each brain hemisphere tends to specialize in analyzing specific sources of information and is differentially involved in mediating responses. In species with laterally placed eyes, the right hemisphere of the brain processes input from the left eye and controls emotions such as fear and aggression, whereas the left hemisphere processes input from the right eye and controls discrimination between stimuli and manipulation of objects (Vallortigara and Rogers 2005).

The ubiquitous nature of laterality suggests that it conveys fitness benefits. In terms of cognitive function, it has been hypothesized that brain lateralization enhances cognitive abilities by partitioning different types of information into the two separate brain hemispheres, thereby enabling separate and parallel processing, thus maximizing processing efficiency (Rogers 2000, 2002). One advantage of laterality is that it enables individuals to cope with divided attention. For instance, it may allow animals with a lateralized brain to process two tasks at the same time (Dadda and Bisazza 2006) in contexts such as foraging (Güntürkün et al. 2000) or schooling (Bisazza and Dadda 2005; Bibost and Brown 2013). Rogers (2000) suggested that brain lateralization evolved at the population level in order to maintain coordination among social groups. Despite the apparent benefits of laterality, however, remarkable variation in

laterality occurs among species (Bisazza et al. 1997, 2000), populations and individuals (Brown et al. 2007; Brown and Magat 2011). Emerging evidence suggest that this occurs because laterality may also incur costs that balance the many benefits (Rogers 2000; Dadda et al. 2009).

There is some evidence that having a lateralized brain confers a direct advantage while learning. Fruitfly, *Drosophila melanogaster*, with an asymmetrical brain structure develop longer memories than individuals with symmetrical brains when required to associate an odor with an electric shock (Pascual et al. 2004). Moreover, strongly lateralized birds tend perform better in a pebble-seed discrimination test than non-lateralized individuals (Güntürkün et al. 2000; Rogers et al. 2004; Magat and Brown 2009). In the context of a spatial learning, strongly lateralized Goldbelly topminnows (*Girardinus falcatus*) were better in spatial learning using visual geometrical cues than non-lateralized fish (Sovrano et al. 2005). Conversely, Brown and Braithwaite (2005) found that lateralized poeciliid fish (*Brachyraphis episcopi*) took longer to find the reward location in a radial maze than non-lateralized individuals and suggested that the natural turning bias of lateralized individuals prevented them from heading directly to the reward room. Few, however, have compared the cognitive performance of strongly left- and right-biased animals.

Individual side biases influence fish cognitive ability particularly in a spatial navigation context (Brown and Braithwaite 2005). In order to avoid such confounding effects, one can turn to classical conditioning paradigms that lack a left/right spatial component and thus should not hamper the response of strongly lateralized individuals. For example, Nilsson et al. (2008) employed a classical conditioning approach to investigate fish learning capacity. The subject learned to associate a flashing light (Conditioned Stimulus, CS) with the arrival of food (Unconditioned Stimulus, US). Similar studies using a range of CS have been conducted in sharks (Guttridge and Brown 2013). These types of experiments are excellent for studying the relationship between brain lateralization and learning in fish as the subject associates temporal and spatial relationships to predict the time and place the food will be delivered. Moreover, the task involves multiple senses, combining both gustatory and visual elements. Individual responses can vary between sexes even when presented with the same cue or context because of variation in motivation (Reddon and Hurd 2008). In the classical conditioning paradigm where food is the US, we would expect females to outperform males since it is well-known that female fish are highly driven to find food compared with males (Griffiths 1996).

The complexity of the rearing environment is another important factor to take into consideration when examining cognition as it may influence brain evolution and development. The brain structure of fish reflects their lifestyles and the environment in which they live, and thus greatly differs between fish species or between populations occupying divergent habitats (Kotrschal et al. 1998). For instance, cichlids occupying a rocky substrate have a larger telencephalon than those occupying a sandy or muddy substrate (Huber et al. 1997), and the telencephalon has been implicated in spatial learning (Broglio et al. 2003). We have previously shown that habitat complexity can also influence the development of laterality. Differences in laterality were observed between rainbowfish reared in enriched and impoverished habitats with opposing effects between sexes (Bibost et al. 2013). Other environmental factors such as the level of predation and the amount of light exposure during embryogenesis can cause differences in behavioral laterality between species and among populations of the same species (Andrew et al. 2009; Bisazza et al. 2000; Brown et al. 2004; Dadda and Bisazza 2012). The pattern of laterality of fish from high predation locations can also change when they are reared in captivity (Brown et al. 2007).

Early rearing environment can not only influence the pattern of lateralization and brain development but also cognitive ability. Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks (Brydges et al. 2008). Similarly, sticklebacks from marine and freshwater habitats show variation both in learning and forgetting foraging related information (Mackney and Hughes 1995). There is widespread evidence that captive-bred fish that experience a stable,

mundane habitat possess restricted learning and memory skills compared with wild fish, but this can be overcome by environmental enrichment (Brown and Day 2002; Brown et al. 2003; Salvanes et al. 2013).

Rainbowfish, *Melanotaenia spp.*, provide an excellent model for examining the influence of rearing environment and laterality on cognitive performance. Firstly, they are widespread, occupy a large number of contrasting habitats and are very simple to rear in captivity (Tappin 2010) making them ideal for comparative studies. Some species are threatened or endangered, and there has been attempted to rear fish in captivity in order to supplement wild populations (Brown and Warburton 1997). They are also a model family for studying laterality (Bibost et al. 2013; Bibost and Brown 2013), cognition (Brown 2001) and the effects of rearing environments on behavior (Kydd and Brown 2009). Males are larger and more colorful than females and spend most of their time either fighting other males or courting females. Females, in contrast, tend to form schools and spend most of their time foraging.

Here, we examined the influence of laterality, sex and rearing environment of the cognitive ability of rainbowfish, *Melanotaenia duboulayi*, using a classical conditioning paradigm. Based on the theory developed above, we hypothesized that (1) the pattern of laterality would directly affect learning ability, (2) wild fish would learn faster than captive-bred individuals and (3) females would perform better than males.

Methods

Experimental subjects

Melanotaenia duboulayi is an abundant, robust species and found in a wide variety of coastal aquatic environments in eastern Australia from Coffs Harbour to Bundaberg, Australia. Here, we tested captive-bred and wild *M. duboulayi* (20 females and 20 males from each population). Captive-bred *M. duboulayi* were derived from a population established in 1990 (see Kydd and Brown 2009 for details). These fish were reared in nursery tanks (100 × 175 × 100) for 2 months and then housed in a large aquarium (120 × 45 × 45) with overhead fluorescent light but with no substrate until 12 months of age. Just prior to the experiment, 40 test fish were selected from the stock tanks and rehoused in shoals of eight fish in five aquaria (120 × 45 × 45 cm). Forty wild *M. duboulayi* were captured from the Orara River in Coffs Harbor, NSW (30°15'27.460'' S, 153°00'42.33'' E) using standard bait traps, bagged and airfreighted to Macquarie University. Once in the laboratory, wild fish were separated into five large aquaria (120 × 45 × 45 cm) furnished with river gravel, rocks, driftwood and a filter. Generally, we attempted to recreate their wild environment as closely as possible so as to not influence their laterality prior to testing. Given that we were testing adult fish, it is highly unlikely that the brief exposure to the captive environment influenced their laterality scores. All aquaria were lit with overhead fluorescent lighting. For all aquaria, the water temperature was maintained at 26 °C and pH ranged between a range of 7–7.5. All fish were tagged with a Visible Elastomer Implant (VIE) to aid individual recognition a week before the start of the experiment. Experiments began 2 months after the wild fish were brought into the lab allowing time to adjust to life in captivity.

Laterality test

In order to assay behavioral laterality, a flume was constructed measuring 110 cm × 30 cm × 30 cm (see Bibost and Brown 2013 for details). Briefly, a 32 L/min bilge pump generated lamina flow extending 10 cm from the left and right sides of the tank after passing through banks of straws (Fig. 1). Two mirrors were placed on either side to simulate the presence of shoal mates using the subject's reflection. The flow encouraged test subjects to maintain station with their mirror image by swimming against the current. The center area consisted of low flow refuge. Fish swimming on the left side of the flume use their left eye to

view their mirror image and visa versa. During observations, the flume was isolated from the rest of the laboratory using curtains and observations were made remotely via a web camera suspended above the apparatus.

Each fish was tested in isolation. Subjects were removed from their home tank and allowed to settle for 20 min in a large container adjacent to the flume. Each individual was then transferred to the flume and observed for 10 min using an overhead web camera. All precautions were taken to reduce stress from handling the fish. The position of the fish with respect to the mirrors on the lateral side of the tank was recorded every 10 s. A fish located in the center of the flume was recorded as non-lateralized and a fish located adjacent to either mirror was classified as left or right lateralized. The proportion of time spent in the right side of the tank ($R/R + L$) was calculated. Based on the frequency distribution of the fish's laterality scores, we categorized them into three classes: L 0–30 %, NL 30–70 % and R 70–100 %. Rainbowfish populations have strongly bimodal laterality distributions with very few NL individuals. Consequently, all NL fish were removed from the analysis ($n = 8$).

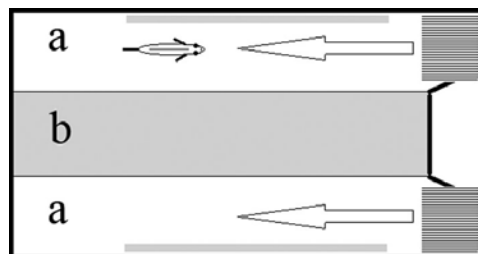


Fig. 1. A diagram of the laterality mirror test. A pump generates laminar flow down the left and right hand sides of the tank (a) after passing through a bank of straws. Fish can shoal with their mirror image by staying close to the mirrors on either side of the tank. A no flow refuge is available in the center of the apparatus (b)

Classical conditioning test

The classical conditioning tank (110 cm × 30 cm × 30 cm) was composed of a large room (90 cm long) with a small store room at one end (20 cm long). A trapdoor facilitated fish movement between the two rooms. A feeder was set up with a red flashing light (CS) and a pipe to deliver the food reward (blood worms; US) at the opposite end of the arena to the store room (see Fig. 2). The tank was covered with black paper in order to reduce any observer influence.

Fish were acclimatized to the testing arena in groups of eight (four males and four females) for a week prior to testing to minimize stress and to precondition the fish to feeding on blood worms. Trials were initiated by ushering all the fish into the stock room. A fish was chosen based on its tag and gently encouraged to leave the storage area and move through the trap door. Within 5 min of the fish entering the experimental arena, the red flashing light was turned on for 60 s and a bloodworm was then delivered 30 s later. The latency for each fish to catch the blood worm was recorded. After the fish ate the reward, it was gently ushered back into the storage area and another subject chosen. This was repeated until all eight subjects had been tested six times. Three trials were conducted in the morning and afternoon every day for 7 days (total 42 trials). Five wild males appeared to lose motivation during the training regime

(they were more interested in chasing the females behind the barrier) and consequently did not forage reliably. They were eventually removed from the experiment entirely.

We extracted the average foraging latency for each day for each fish over the 7 days. These data were analyzed using a repeated measures ANOVA, with laterality category, sex and rearing environment as independent variables. The data were normally distributed and did not need to be transformed.

All research here was conducted with clearance from the Macquarie University Animal Ethics Committee (ARA # 2010/028). Fish were collected under license from NSW Fisheries (P08/0010).

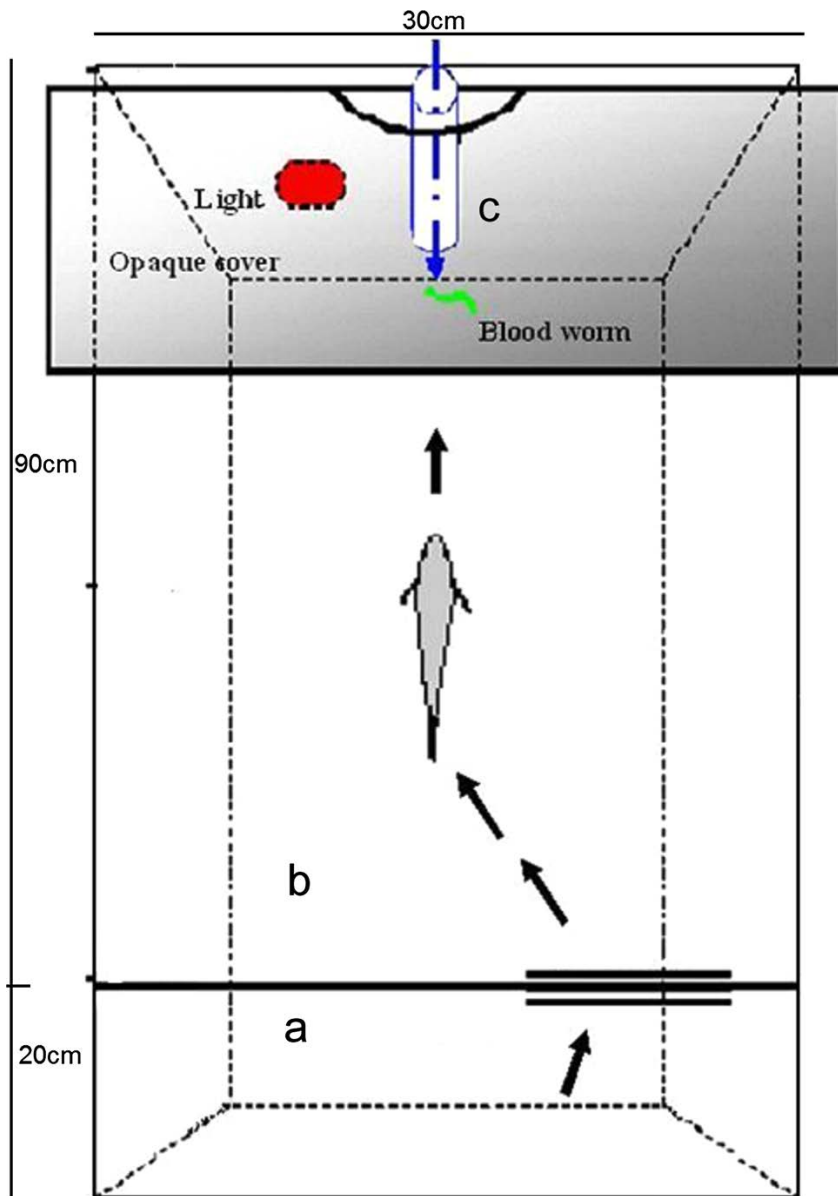


Fig. 2 Diagram of the classical conditioning experimental arena. Fish are ushered from the store room (a) into the experimental area (b) via a trapdoor. When the red light turns on, 30 s later the food reward is delivered down the feeder (c)

Results

Analysis of the laterality data showed that the distribution of left- and right-biased fish was reasonably evenly spread across sexes and rearing environments (Table 1).

Repeated measures ANOVA examining the average daily foraging time found no main effects of laterality, sex or rearing environment ($P > 0.05$ in all cases). However, a significant laterality*day interaction was revealed ($F_{6,354} = 2.598$, $P = 0.018$) as well as a marginal rearing environment*day interaction ($F_{6,354} = 2.070$, $P = 0.056$). Left-lateralized fish were faster learners than right-lateralized fish (Fig. 3), and wild fish tended to be faster learners than captive-bred fish (Fig. 4). Post-hoc tests showed that the differences between captive and wild fish were most evident in the first 4 days of training ($P < 0.05$ in all cases) but converged thereafter. The reverse pattern was true of strongly left- and right-lateralized fish such that no significant difference was observed in foraging latency for the first 4 days, but they diverged in the last 3 days of training ($P < 0.05$ in all cases).

Table 1. Distribution of laterality phenotypes by rearing environment and sex

Lat category	Captive female	Captive male	Wild female	Wild male
Left	10	5	10	6
NonLat	4	2	0	2
Right	6	13	10	7

Discussion

It is apparent that laterality directly influences learning performance in a classical conditioning test. Here, we found that strongly left lateralized fish out-performed strongly right lateralized fish. We also found that learning rate was marginally affected by the rearing condition of the fish. Wild fish tended to learn more quickly than captive-bred fish. Contrary to expectations, there were no differences in learning performance between the sexes.

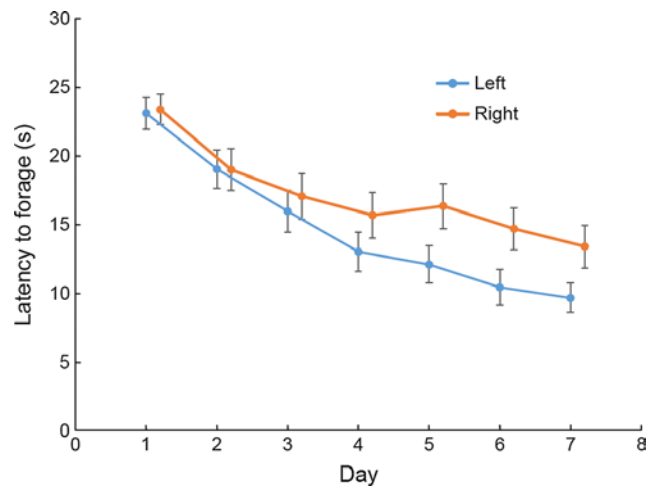


Fig. 3 Mean (SE) foraging latency of left (L) and right (R) lateralized rainbowfish over 7 days of classical conditioning

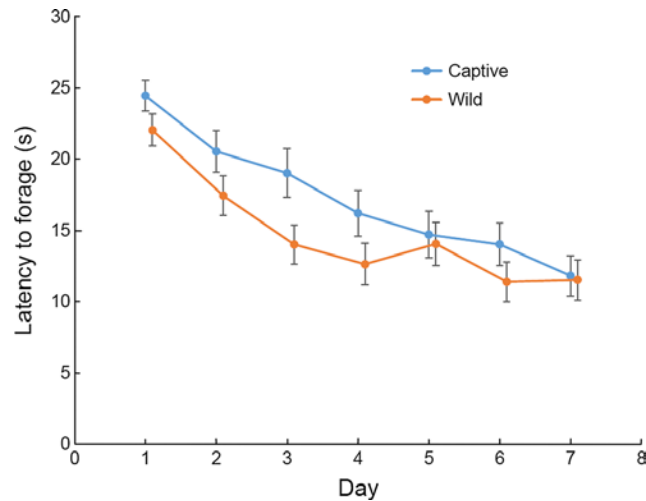


Fig. 4 Mean (SE) foraging latency of wild and captive-reared rainbowfish over 7 days of classical conditioning

The effects of laterality on learning have been studied in a number of species and have been found to both enhance and suppress learning rates. For example, in a radial maze, strongly lateralized fish struggle to overcome their inherent turning bias and thus perform worse than weakly lateralized fish (Brown and Braithwaite 2005). Similar observations have been made in rats (Kanit et al. 2005). While strongly lateralized parrots out-perform weakly lateralized parrots in a range of tasks, there was little evidence that the left- or right-biased birds performed differently (Magat and Brown 2009). Similarly, wild chimpanzees that preferentially use one hand fishing for termites out-perform those that are ambidextrous (McGrew and Marchant 1999). To our knowledge, this is the first example illustrating that there is a difference between left and right lateralized animals in a cognitive task.

It is not unusual to see strong effects of laterality on behavior in vertebrate and even invertebrate taxa. Castellano et al. (1987) report a right-turn bias in a T-maze with only 20 % of rats showing a left and 80 % showing a right-turn bias which was associated with a dominant dopaminergic system in the contralateral hemisphere. Mutant strains of mice that have unusual neural circuitry in their hippocampus showing no asymmetry perform poorly in both a spatial learning and delayed non-matching to position task compared with wild types (Goto et al. 2010). Spatial learning studies in humans and rodents often find laterality differences between males and females with the hippocampus being enlarged in the right hemisphere in males (Diamond et al. 1983; Tabibnia et al. 1999) which is responsible for their enhanced spatial learning abilities (Jacobs et al. 1990). Thus, in this context, one would predict that spatial learning would be enhanced in individuals that show a larger disparity in hippocampal size between the left and right hemispheres. In all of these examples, however, no comparison has been made between left- and right-biased individuals.

Gustatory learning can also be strongly lateralized in birds to the extent that the memory trace may only exist in one hemisphere and only one eye is used during learning and retrieval (Vallortigara 2000). In bees, the extent of laterality in the learning process is dependent on the senses involved. Tactile and olfactory stimuli tend to be unilateral, whereas visual stimuli are transferred between the two hemispheres (Sandoz and Menzel 2001). In the present study, one can assume that the pattern of laterality in the shoaling context (mirror image test) is indicative of the distribution of other lateralized functions in rainbowfish. It may be that the various cognitive functions and senses involved in learning the classical conditioning task are competing against one another or causing interference in right-biased individuals.

Alternatively, there may be poor communication between information stored in opposite hemispheres causing a reduction in conditioning efficacy. This could be happening either during the acquisition or retrieval phases of the conditioning process or perhaps as information is moved from short- to long-term memory. Recent studies using human subjects support this hypothesis and have revealed that the left hemisphere is more likely to interact with itself, whereas the right hemisphere tends to integrate with both hemispheres (Gotts et al. 2013; see Allen 1983 for a review). This variation in hemispherical interaction is not a general phenomenon and seems to be restricted to certain brain functions such as visuospatial attention. Moreover, the degree of lateralization in distinct systems also correlated with various measures of cognitive ability (Gotts et al. 2013).

An increasing number of studies have illustrated behavioral, physiological and anatomical differences between captive-reared and wild animals (Brown and Day 2002). The process of differentiation occurs via two, non-mutually exclusive routes. Firstly, rearing environment can dramatically change both the development of brains and behavior during an individual's life time via phenotypic plasticity. The mundane captive environment is not conducive to neural recruitment since the environment provides little sensory feedback. Secondly, differentiation between captive and wild fish can occur via natural and or artificial selection in just a few generations (Huntingford 2004). Traits that may be of value in the wild, such as high levels of aggression or territoriality, may not be adaptive in captivity. Thus, over multiple generations, a range of traits can shift to suit life in captivity. This is one of the major reasons that the post-release survival of hatchery-reared fish is so poor (Brown and Day 2002; Brown and Laland 2001). Thus, our findings that wild fish tended to out-perform captive-reared fish fits well with our current understanding of rearing environment of cognition and underlying brain development.

To conclude, the cognitive ability of animals is clearly influenced by the degree of laterality. While this is the first study to show that left-biased individuals out-performed right-biased individuals, it is highly likely that similar experiments in rodents or humans would yield similar results. It is surprising that such studies have yet to be conducted given the rich literature in this field.

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