

University of Alberta

**Sex, Personality and Individual Differences in Cerebral Lateralization in
the Convict Cichlid**

by

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Abstract

Cerebral lateralization was once thought to be unique to humans, but is now known to be widespread among the vertebrates. Lateralization appears to confer cognitive advantages upon those that possess it. Despite the taxonomic ubiquity and described advantages of lateralization, substantial individual variation exists in all species. Individual variation in cerebral lateralization may be tied to individual variation in behaviour and the selective forces that act to maintain variation in behaviour may also act to maintain variation in lateralization. Sex differences may also be an important source of variation in lateralization, as differences between males and females are often observed. Here, I present three papers that collectively deal with the interrelationships between sex, behaviour and cerebral lateralization in the convict cichlid. My results illustrate that lateralization is related to personality-like characteristics in the convict cichlid, and that there are important differences between the sexes in their pattern of lateralization.

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Introduction

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Cerebral lateralization

Cerebral lateralization is the partitioning of certain cognitive functions selectively into one hemisphere of the brain (Rogers & Andrew 2002; Vallortigara & Rogers 2005). The prominent lateralization of language functions and the conspicuous behavioural lateralization in the form of handedness in the human species led to the longstanding assumption that cerebral lateralization was a unique characteristic of *Homo sapiens* (Corballis 2006, 2008, 2009; Tommasi 2009). Some researchers have even postulated that the appearance of a lateralized brain was the key speciation event that gave rise to humans (Corballis 2006; Crow 2003, 2005). Over the last thirty years, cerebral lateralization has been demonstrated in a diverse array of vertebrate taxa (Facchin et al 1999; Bisazza et al 2002; Rogers & Andrew 2002; Vallortigara & Rogers 2005; Bonati et al 2008; Hook & Rogers 2008), and it is now widely accepted that lateralization is a widespread trait and perhaps a universal characteristic of the vertebrate nervous system (Rogers & Andrew 2002; Vallortigara & Rogers 2005; Vallortigara 2006b; Hopkins & Cantalupo 2008; Tommasi 2009). Furthermore, reports have begun to accumulate of lateralized behaviours in invertebrate taxa as well (Letzkus et al 2006, 2008; Girling et al 2007; Kight et al 2008; Rogers & Vallortigara 2008; Davison et al 2008; Takeuchi et al 2008). Collectively, these lines of research have resulted in most investigators who once believed lateralization to be a unique characteristic of the human species, to accept and embrace that lateralization is a far more ancient adaptation (Corballis 2006, 2008, 2009).

The advantages of being lateralized

Given that lateralization is a taxonomically widespread phenomenon, it is expected that it confers some evolutionary advantage upon those that possess it (Rogers 2000). Recently, substantial research effort has been dedicated to understanding what advantages a lateralized brain may provide an individual and the results suggest that a lateralized brain bestows cognitive advantages (*see* Vallortigara & Rogers 2005 for a general review and discussion; *also see* Hirnstein et al 2008 for contradictory results in humans). Strongly lateralized domestic cats show faster reaction times when tracking a moving spot of light (Fabre-Thrope et al 1993). McGrew and Marchant (1999) found that chimpanzees that favored one hand when termite fishing were more successful at the task than animals that used either hand interchangeably. Pigeons with a stronger visual lateralization have an advantage in visual discrimination tasks (Güntürkün et al 2000). Rogers (2000) found that domestic chicks that are more strongly lateralized because of a developmental manipulation detected a predator during a foraging task with shorter latency than did weakly lateralized chicks. Rogers et al (2004) showed that strongly lateralized chicks were proficient at discriminating food items from similarly shaped and coloured non-food items while also remaining vigilant for predators, whereas weakly lateralized chick's performance on the foraging task decreased under the threat of predation. A series of experiments conducted by Bisazza and collaborators illustrated the enhanced cognitive capabilities in a strain of the freshwater fish, *Girardinus falcatus* that had been selected for strong lateralization. Strongly lateralized *G. falcatus* form

more cohesive schools than do weakly lateralized fish (Bisazza & Dadda 2005). Sovranno et al (2005) found that strongly lateralized *G. falcatus* were better than weakly lateralized fish at using featural cues to reorient themselves. In the presence of a predator, strongly lateralized *G. falcatus* are faster at prey capture than are weakly lateralized fish, in the absence of a predator, however, there is no difference between the lines (Dadda & Bisazza 2006a). Strongly lateralized female *G. falcatus* retrieve food more quickly than weakly lateralized animals while being harassed by a male conspecific, and there is no difference between the lines in the absence of male harassment (Dadda & Bisazza 2006b). In general, it appears that strongly lateralized animals are superior at attending to multiple stimuli simultaneously when compared to their less-lateralized counterparts.

Individual variation

Despite the taxonomic ubiquity and described advantages of cerebral asymmetry, substantial individual variation has been reported in all populations studied to date (Vallortigara & Bisazza 2002; Corballis 2009). This variation takes two forms: direction, with some members of the population being lateralized in one direction and others in the opposite direction, and strength, with some members of the population being more strongly lateralized than others.

Frequency-dependent selection has been advanced as a potential explanation for variation in direction (Vallortigara & Rogers 2005). Ghirlanda & Vallortigara (2004) have reported a model illustrating that left- and right-lateralized individuals may coexist in population in a ratio departing from 50:50, provided that cooperation is an important component of that species' biology and

that individuals that are lateralized in the same direction can coordinate their behaviours more effectively, for example, in schooling fishes. In this model, individuals with the opposite direction of lateralization are maintained in the population by virtue of the benefit of being rare. For example, if individuals with the uncommon lateralization have an advantage in avoiding predation because predators are less accustomed to handling them, then they may be maintained within the population despite their inferiority in cooperation (Ghirlanda & Vallortigara 2004). Recently, Ghirlanda et al (2009) have expanded upon this model to allow for the importance of antagonistic social interactions, where it may also be advantageous to possess the rare laterality type. If animals are accustomed to fighting with conspecifics of a particular laterality, then they may be less adept at combating individuals with the atypical pattern of lateralization. There are some empirical findings that provide support for the general predictions of these models. Scale-eating cichlids in Lake Tanganyika show a lateralization of their mouth opening direction, and variation in the direction of this asymmetry is maintained by frequency-dependent selection (Hori 1993). The shrimp-eating cichlid, *Neolamprologus fasciatus*, has a lateralization of its hunting behaviour and the relatively equal proportion of rightward and leftward hunting individuals appears to be maintained by frequency-dependent selection. Left-handedness in humans is more prevalent in cultures with higher frequencies of physical combat, and it has been suggested that frequency-dependent selection maintains left-handedness in humans because of the advantage of unfamiliarity in combative interactions (Billiard et al 2005).

Individual variation in the strength of lateralization is also a common feature of the lateralized brain (Hopkins & Cantalupo 2008). However, unlike variation in direction, variation in strength remains difficult to explain. If lateralization confers fitness advantages upon those that possess it, then one would expect natural selection to drive this trait to fixation. It has been noted numerous times that it is not necessary to align the direction of lateralization at the individual level within the population to confer its advantages upon the individual (Vallortigara & Rogers 2005, Vallortigara 2006a), therefore it is not unreasonable to expect that all individuals may not be lateralized in the same direction. The fact that a substantial number of individuals in all populations forgo the benefits of lateralization altogether requires some additional explanation.

It has been postulated that there are disadvantages to having a lateralized brain that may offset the apparent cognitive benefits (Rogers 2002; Rogers & Andrew 2002; Vallortigara & Rogers 2005; Vallortigara 2006a). For example, strongly lateralized animals may be more vulnerable to predation because of reduced sensory acuity on their non-preferred side, or because of an increase in the predictability of their behaviour that results from directional asymmetries in escape responses or other antipredator behaviours (Vallortigara & Rogers 2005; Vallortigara 2006a). An alternate way of thinking about this is to consider the fact that there are advantages to symmetry as well as asymmetry (Corballis 2006, 2008, 2009). The environment in general is indifferent as to right versus left, as events are equally likely to occur on either side in a three-dimensional world. It is

important to note that, when considering all the characteristics of a vertebrate, symmetry is overwhelmingly the predominant condition (Palmer 2004). As a result, there may be a trade-off between the advantages of symmetry and asymmetry (Corballis 2006, 2008, 2009) and not all animals may solve this trade-off in the same way.

Cerebral lateralization and personality-like characteristics

It has been suggested that variation in cerebral lateralization may correlate with individual variation in other behavioural characteristics (Carlson & Glick 1989; Neveu 1996). In the human literature there is a long-standing interest in the correlation between lateralization of function in the brain and personality within individuals (Howard et al 1992). Although the patterns seem to be complex, there appears to be a relationship between cerebral lateralization and personality characteristics in humans (Howard et al 1992; Hagemann et al 1999). In the animal literature, examples of behavioural differences between animals with strong and weak lateralization have begun to accumulate. Rats differ in their response to stressors depending on their pattern of lateralization (Carlson & Glick 1989). Strongly lateralized marmosets in terms of hand preference show a more proactive stress coping style, mobbing predators rather than withdrawing from them (Rogers 2007, 2009). Strongly and weakly lateralized dairy ewes have different responses to stressful situations (Morgante et al 2007). Branson and Rogers (2006) found that strongly lateralized dogs show less anxiety in response to loud noises than do weakly lateralized animals. Strongly lateralized chicks give fewer alarm calls and are quicker to resume foraging after being disrupted with a

model predator than are weakly lateralized animals (Dharmaretnam & Rogers 2005). The strength of lateralization differs between populations of the freshwater fish, *Brachyraphis episcopi*, that are exposed to different predation regimes (Brown et al 2004, 2007a). These populations of fish also differ in their degree of boldness in novel environments (Brown et al 2005a, 2007b) and in their response to confinement stress (Brown et al 2005b).

It is now widely accepted that individual animals vary on a whole suite of behavioural characteristics including boldness, activity levels, stress responding and aggressiveness (Wilson et al 1994; Koolhaas et al 1999; Sih et al 2004a,b; Dingemanse & Réale 2005; Bell 2007; Réale et al 2007; Sih & Bell 2008). This variation exists independent of age, sex or other biological variables (Wilson et al 1994; Sih et al 2004a). Variation in personality characteristics may itself be adaptive (Muller & Chittka 2008) and this variation may be maintained by the forces of frequency- and/or habitat-dependent selection (Wilson et al 1994; Dingemanse et al 2004; Wolf et al 2007, 2008; Stamps 2007; Biro & Stamps 2008). If different patterns of lateralization, in particular different degrees of lateralization, correlate with different patterns of behaviour, this may help to explain why variation in the strength of lateralization is maintained in nature. It is possible that differences in the strength of lateralization are the cause of these behavioural differences, alternately it is conceivable that animals with different personalities may have different experiences early in life, leading to different patterns of lateralization (e.g. Denenberg 2005; Rogers 2002; Rogers & Andrew 2002; Andrew et al 2009). In either event, selective forces that maintain variation

in personality-like characteristics may act to maintain variation in the strength of lateralization.

Sex differences in lateralization

Sex differences in cerebral lateralization are another important source of variation in lateralized behaviour. In a seminal series of experiments, Bianki and his collaborators investigated the importance of sex on cerebral lateralization in laboratory rodents (reviewed in Bianki & Filippoava 2001). While the results vary to some degree between experimental protocols, in general, Bianki et al found that males are more strongly lateralized than females in a variety of functions. While sex differences have long been a focus of lateralization research on humans (Geschwind & Galaburda 1987) they have received much less attention in the animal literature. A noteworthy exception is the series of experiments conducted on domestic chicks by Vallortigara and his collaborators (Vallortigara & Andrew 1991; Vallortigara & Andrew 1994; Vallortigara et al 1994; Regolin & Vallortigara 1996). The work on chicks has generally supported the suggestion of Bianki and others that males seem, in general, to be more strongly lateralized than females, although some experiments seem to suggest that females are equally lateralized and this lateralization is merely masked in some testing situations. Existing evidence in fish suggests that sex differences in lateralization owe primarily to differences in motivation between males and females (Bisazza et al 1998). Given the apparent importance of sex in determining the pattern of lateralization within an individual, this topic deserves further attention, particularly in animal models.

Lateralization of emotion

The asymmetric representation of emotional functions in each of the cerebral hemispheres is one of the best known examples of lateralization (Rogers & Andrew 2002), and the production or inhibition of emotions selectively with each hemisphere has been advanced as one of the key functions of lateralization (Andrew & Rogers 2002). An extensive body of research in humans has suggested that emotional processing and responding is controlled by a single hemisphere, typically the right (Root et al. 2006). Alternately, the emotional valence hypothesis posits that negative or withdrawal emotions are controlled by one hemisphere (usually right) while positive or approach emotions are controlled by the other (usually left; *reviewed in* Davidson 1995). Animal studies provide some tentative support for this idea. In general, animals seem to use their right hemisphere to control attack and fear responses (withdrawal) while their left hemisphere controls inhibition of aggression, foraging, and exploratory responses (approach) (Rogers & Andrew 2002; Vallortigara & Rogers 2005). Domestic dogs wag their tails to the right, indicating left hemisphere activation when they see their owners and to the left, indicating right hemisphere activation, when they see an unfamiliar, dominant conspecific (Quaranta et al 2007). The degree to which animals vary in the lateralization of emotional processing, either individually or as a function of sex, remains poorly understood.

Fish as research animals in the study of lateralization

Along with birds (Rogers & Andrew 2002), fish have provided an invaluable model for understanding cerebral lateralization at the behavioural level

(Bisazza et al 1997; Bisazza et al 1998; Bisazza et al 2000; Vallortigara & Bisazza 2002). Most fish have laterally placed eyes with limited optic overlap and projections that decussate and travel almost entirely to the contralateral hemisphere (Bisazza et al 1997). As a result, cerebral lateralization can be measured in fish by measuring asymmetries in eye use while viewing certain stimuli or performing certain tasks (Facchin et al 1999; Sovrano et al 2001). A common method of measuring eye use in fish is the detour task, adapted from a similar task used to measure lateralization in birds (*reviewed in* Vallortigara & Regolin 2002) and first used in fish by Bisazza and his collaborators (Bisazza et al 1997). In this task (Fig. 1), the fish being tested swims down a narrow channel until it meets a barrier that it can see through but not swim through. In order to explore the environment or stimulus behind the barrier, the fish must detour around it, and as it does, it can maintain visual contact with the target using only one eye. Based on the direction of detour, it is possible to assess which eye, and hence, hemisphere of its brain the fish prefers to use to view the target. Typically, an animal performs a series of trials in this task (by convention, 10), and based on the detour direction in each trial, a single score, the laterality index (LI; Bisazza et al 1997) is assigned to the fish using the following formula: $LI = (\text{Right Detours} - \text{Left Detours}) / (\text{Total Detours})$, or some equivalent. It is often useful to also take the absolute value of LI as a measure of the overall strength of lateralization, as strongly positive and strongly negative LI scores will cancel each other out when averaging, thus obscuring the strength of lateralization (Brown et al 2007a; Clotfelter & Kuperberg 2007). The detour task has proven to be a useful measure

of lateralization in fish, and has seen extensive application (Bisazza et al 1997; Fachin et al 1999; Bisazza et al 2000; Brown et al 2007a; Sovrano et al 2001; Vallortigara & Bisazza 2002; Reddon et al 2009).

Purpose and study species

The purpose of this thesis is to explore the interrelationships between cerebral lateralization, personality-like characteristics, and emotion and how they may vary as a function of sex in a freshwater teleost fish. My study species for all three papers that comprise this thesis is the convict cichlid (*Archocentrus nigrofasciatus*), a biparental and monogamous Neotropical fish. The convict cichlid has proven to be a valuable research species that has been widely employed in the behavioural sciences. Convicts are a useful species because of their diverse behavioural repertoire and ease of use in the laboratory. Research on convict cichlids has advanced our knowledge of pair-bonding, parental care and aggressive behaviour among other topics (Keeley & Grant 1993a, b; Koops & Grant 1993; Wisenden 1995; Barlow 2000; Draud & Lynch 2002; Santangelo & Itzkowitz 2004; Richter et al 2005; Gagliardi-Seeley & Itzkowitz 2006; Gumm & Itzkowitz 2007; Bockelman & Itzkowitz 2008; Reddon & Hurd 2009). To my knowledge, the papers contained within this thesis are the first investigations of cerebral lateralization in the convict cichlid.

Paper I examines the relationship between sex, aggressive behaviour and cerebral lateralization in the convict cichlid. Paper II tests the relationship between lateralization of detour behaviour and boldness when exploring a novel environment. Finally, Paper III investigates how male and female convict cichlids

differ in their lateralized behaviour when viewing objects that have a conditioned association with either appetitive or aversive stimuli. Collectively, these papers illuminate the importance of individual variation and sex differences in cerebral lateralization in the convict cichlid.

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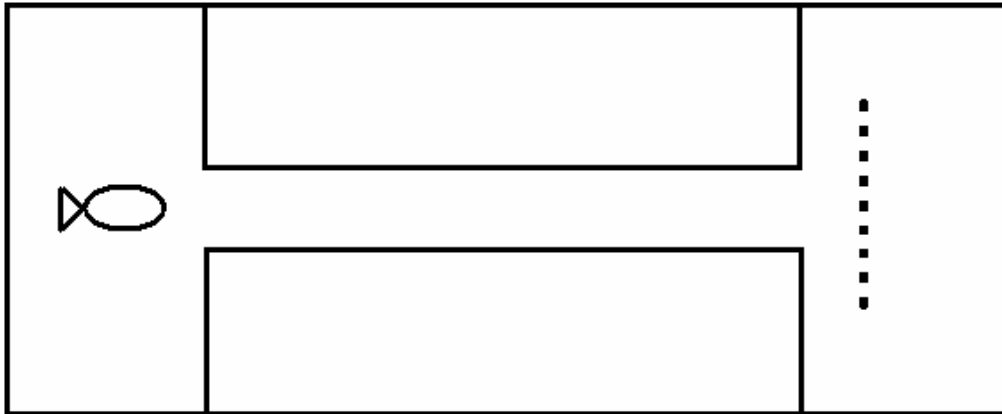


Figure 1. A schematic representation of a detour apparatus designed for measuring cerebral lateralization in fish (*based on* Bisazza et al 1997).

**Paper I: Aggression, sex and individual differences in cerebral
lateralization in a cichlid fish**

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Introduction

Cerebral lateralization is the partitioning of cognitive functioning into one hemisphere of the brain (Vallortigara & Rogers 2005). Once thought to be a unique property of the human brain, cerebral lateralization has now been demonstrated in a wide variety of vertebrate taxa, and appears to be an evolutionarily ancient adaptation (Vallortigara et al 1999). Recent research has focused on describing the evolutionary antecedents and ecological consequences of having a lateralized brain (Rogers et al 2004). Lateralization in fish is of particular interest because evolutionarily early patterns of vertebrate lateralization may have remained relatively unaltered in this taxon (Vallortigara & Bisazza 2002). Cerebral lateralization can be measured in fish by assessing asymmetries in eye use because fish don't have overlapping optic fields, and each eye projects almost entirely to the contralateral hemisphere (Facchin et al 1999).

Evidence from embryological manipulations (Rogers et al 2004) and artificial selection (Dadda & Bisazza 2006) on strength of lateralization suggests that individual animals with strongly lateralized brains enjoy cognitive advantages including an improved ability to multitask compared to those with weaker hemispheric specialization. Despite these advantages, substantial variability is seen in both direction and strength of lateralization at the individual level (Vallortigara & Bisazza 2002). Ghirlanda and Vallortigara (2004) have proposed a model based on frequency-dependence that appears to explain within-species variation in the direction of lateralization. It remains puzzling however, from an

adaptationist perspective, why some individuals should be less lateralized than others.

Sex differences are a known, but understudied, source of variation in cerebral lateralization. Sex differences appear to be important in the few animals systems in which they have been extensively investigated. Overall, males tend to be more strongly lateralized than females (Bianki & Filippova 2001).

Another potential source of variation, which has also received relatively little attention, is an individual level linkage between cerebral lateralization and behaviour. Animal personalities (temperaments, stress coping styles, behavioural syndromes) have garnered extensive theoretical and empirical treatment in recent years (Sih et al 2004). Variation in personality type may be selected for in a frequency dependent manner (Dall et al 2004), and could be linked to different life history strategies (Wolf et al 2007).

Few studies have investigated the relationship between personality-like behavioural traits and cerebral lateralization. Clotfelter and Kuperberg (2007) found no relationship between cerebral lateralization and individual differences in aggression in six species of anabantoid fishes. Brown et al (2004) have presented the most compelling evidence suggesting that variation in laterality may be linked to variation in behaviour. They have shown that two populations of a single species of poeciliid fish, which are exposed to different predation pressures, differ both in lateralization (Brown et al 2007) and personality (Brown et al 2005).

Several studies have demonstrated a link between cerebral lateralization and aggression, with many species showing a consistent population bias towards

right hemisphere control of aggressive responses (*reviewed in:* Rogers 2002). The evidence with regards to fish however, has shown individual but not population level biases (Cantalupo et al 1996; Clotfelter & Kuperberg 2007).

The present research investigates the relationship between sex, individual differences in aggression, and cerebral lateralization when navigating in a novel environment. The study species is the convict cichlid (*Archocentrus nigrofasciatus*), a highly territorial, bi-parental and monogamous freshwater fish.

Methods

Subjects consisted of 40 adult convict cichlids (*Archocentrus nigrofasciatus*), 20 of each sex, purchased from local suppliers. Fish were housed in 95l (75 x 31 x 41 cm) mixed sex communal aquaria prior to, and following experimentation. Aquaria were maintained at $25 \pm 1^\circ\text{C}$ on a 12:12h light:dark cycle. Fish were fed daily on a variety of dried or frozen prepared fish foods.

Subjects were tested for cerebral lateralization using a detour task, (Bisazza et al 1997). The apparatus (Fig. 1) consisted of a large aquarium (195 x 30 x 29cm) filled with water to a depth of 11 cm. The aquarium had two compartments joined by a narrow runway (10 x 75cm). A movable barrier (15 cm across and extending up above the surface of the water), consisting of alternating 0.75cm bars of opaque and transparent Plexiglas affixed to a weighted base, was placed at the distal end of the runway. Subjects were naive to this apparatus.

Each animal was placed in one end of the detour apparatus and allowed to acclimate for 2 minutes. An opaque door was inserted confining the animal to one

end of the tank. The barred barrier was placed at the far end of the runway. The door was then lifted and the subject was gently directed towards the starting point of the runway using a black dip net (13 x 10cm). Upon reaching the entrance, the fish swam down the runway and detoured around the barrier. When detouring, the fish could view the unfamiliar environment with only one eye indicating which hemisphere it preferred to use.

The detour decision was considered complete when the main axis of the fish's body was parallel to the barrier. The detour direction was almost always unambiguous. In the rare occasions in which the animal failed to make a clear decision, the trial was discarded. After each trial, the animal was isolated at that end of the aquarium using the opaque door. Successive trials were run towards opposite ends of the tank. The fish rested for two minutes after each trial while the barrier was repositioned. Each animal received 10 trials. Detour task responses were scored for each animal by computing the laterality index (LI; Bisazza et al 1997) using the following formula:

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

Absolute values of LI were also computed. Absolute LI values give an indication of the overall strength of lateralization. Directional scores may obscure variation in laterality strength because animals lateralized in opposite directions will cancel each other out (Brown et al 2007).

A mirror image simulation was used to assess propensity to aggression in each fish. The fish were isolated in a 57l aquarium (45 x 32 x 40cm) with a mirror at one end, behind an opaque door. A piece of opaque PVC tubing was placed in the aquarium to serve as a shelter for the fish. The fish was allowed to acclimate for 24h, following which, the opaque barrier was lifted and the fish interacted with its mirror image for 10 min. If the fish displayed aggressively to the mirror during the 10 min period, they were scored as an ‘aggressor’.

Results

Fourteen fish displayed at the mirror during the mirror image simulations while 26 fish did not. Of the 14 aggressors, five were females and nine were males. Of the 26 non-aggressors, 15 were female and 11 were males. There was no significant difference in the likelihood that males or females were aggressors (*Yates* $\chi^2 = .989$, $df = 1$, $p = .32$).

There was a significant association between detour direction and the interaction between aggressor status and sex ($R^2 = .156$, $F_{(1, 38)} = 7.05$, $p = .01$; Fig. 2a). Female non-aggressors and male aggressors tended to turn left (thus using their right visual field which projects to the left side of their brain), while female aggressors and male non-aggressors had slight tendency to turn right.

The strength of lateralization was significantly influenced by an interaction between sex and aggressor status ($R^2 = .234$, $F_{(1, 38)} = 11.58$, $p = .002$; Fig. 2b). Female non-aggressors were more strongly lateralized than the male

non-aggressors but male aggressors were more strongly lateralized than the female aggressors.

Discussion

Convict cichlids navigating in a novel environment preferentially use either their left or right eye, and therefore either their left or right cerebral hemisphere. Which hemisphere is used depends on both their sex and their propensity to aggression. Contrary to work in other animals (e.g. rats, cats, humans; Bianki & Filippova 2001), we did not find an overall trend for males to be more lateralized than females. Our results suggest that the sexes in fact have different patterns of lateralization depending on underlying individual differences. These results are novel because they suggest a link between a personality characteristic, aggressiveness, and strength of cerebral lateralization at an individual level. The causal relationships between these factors remain to be determined.

Personality characteristics have been described in the convict cichlid and appear to have important consequences for parental behaviour (Budaev et al 1999). Females and males usually assume different roles in the parental care process but these roles are somewhat variable (Itzkowitz et al 2005) and some animals adhere to their sex role more tightly than others. Parental care is cognitively demanding, and sex roles in parental care may have selected for different patterns of cerebral lateralization in each sex of the convict cichlid.

These results emphasize a point made by Bianki and Filippova (2001), that sex should always be considered when studying cerebral lateralization, because males and females differ in the way their brains are organized. Our results demonstrate that sex differences in brain organization interact with individual differences in behaviour, and these factors must be studied simultaneously.

Some authors (*e.g.* Vallortigara & Rogers 2005) have suggested that variation in the strength of lateralization can be explained by the fact that lateralized animals may have lateral biases in behaviour or perception when biologically relevant stimuli are equally likely to appear on either side. The suggestion is that these biases could counteract the cognitive processing advantages of cerebral lateralization. Our results suggest that variation in cerebral lateralization may be adaptive, because animals with different personalities have different patterns of lateralization which may allow them to process information in different ways. If variability in personality is maintained by frequency dependent selection acting on different life-history strategies (Wolf et al 2007), then variation in cerebral lateralization may also be selected for.

In conclusion, our results suggest an association between personality, sex and cerebral lateralization in a cichlid fish. We believe that further study will reveal greater generality of this phenomenon.

All protocols were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee.

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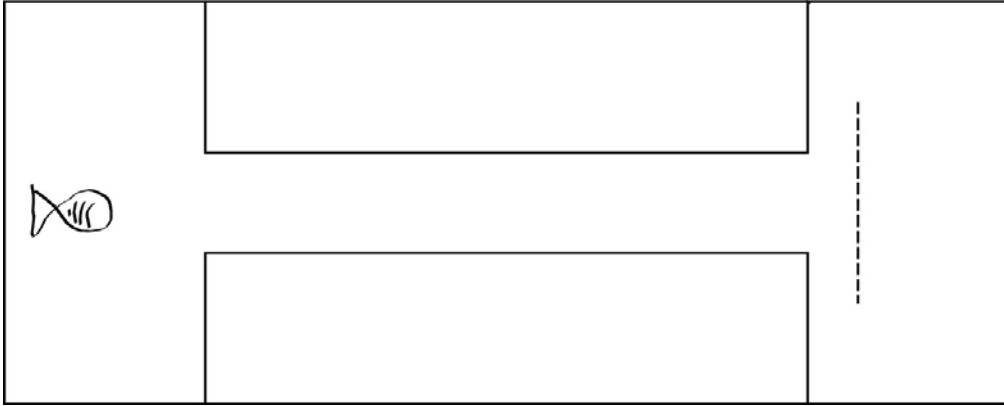


Figure 1. A schematic representation of the detour testing apparatus (*based on:* Bisazza et al 1997). Fish had to swim down the central channel and detour around the barrier (dotted line) to explore the chamber behind. Direction of detour was recorded for each of 10 trials. Successive trials were run in opposite directions.

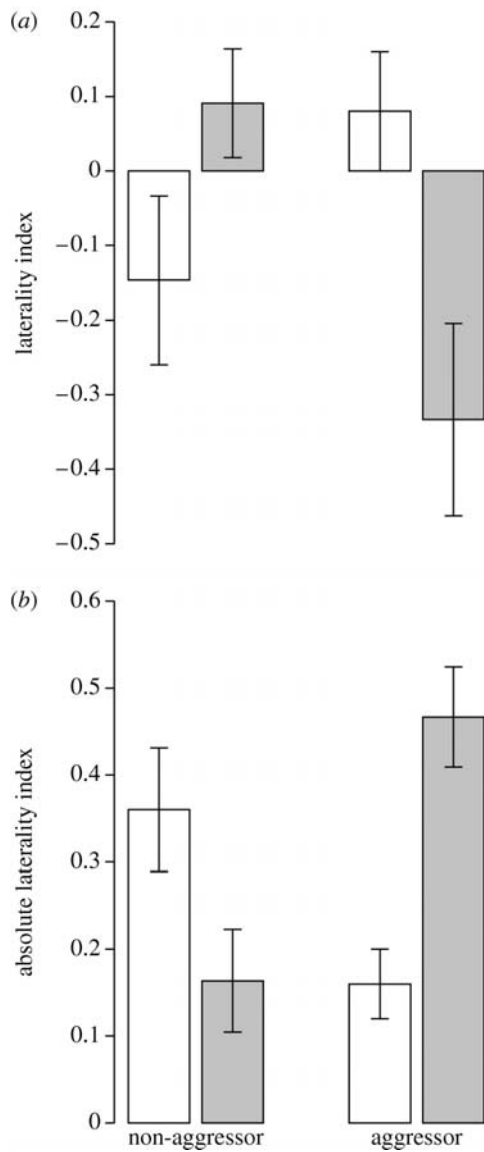


Figure 2. (a) Average laterality index scores (\pm s.e.m.) for females (white bars) and males (grey bars) that attacked or did not attack their mirror image within 10 min. There is a significant interaction between sex and aggressor status on LI ($p = .01$). (b) Average absolute laterality index scores (\pm s.e.m.) for females (white bars) and males (grey bars) that attacked or did not attack their mirror image within 10 min. There is a significant interaction between sex and aggressor status on absolute LI ($p = .002$).

**Paper II: Individual differences in cerebral lateralization are
associated with shy-bold variation in the convict cichlid**

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2009

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Introduction

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

Fish have proven to be a useful system in the study of cerebral lateralization from an evolutionary perspective. Fish have no overlap in their visual fields and each eye projects almost entirely to the contralateral hemisphere. Cerebral lateralization can be tested in fish by assessing asymmetries in eye use (Facchin et al 1999). Early patterns of vertebrate lateralization may have remained relatively unchanged in fish due to the comparative stability of the pressures of life in the water (Vallortigara & Bisazza 2002).

Recent research effort has focused on understanding the costs and benefits of cerebral lateralization from a functional perspective (Rogers 2000; Vallortigara & Rogers 2005; Vallortigara 2006). It has been suggested that cerebral lateralization has been selected for because it provides a cognitive processing advantage (Rogers 2000). Empirical research using both embryological manipulations (Rogers et al 2004) and artificial selection (Dadda & Bisazza 2006) on the strength of lateralization has supported this hypothesis. Animals with stronger lateralization appear to have an increased ability to attend to multiple

stimuli simultaneously compared to those with a weaker hemispheric specialization.

Despite the described advantages of possessing a lateralized brain, most species studied so far exhibit substantial variation at the individual level in both the strength and direction of lateralization (Vallortigara & Bisazza 2002). The theoretical model of Ghirlanda and Vallortigara (2004) appears to provide a reasonable explanation for the maintenance of variation in the direction of lateralization. The observed individual variation in the strength of lateralization however, remains difficult to explain.

Evidence suggests that cerebral lateralization is related to individual differences in behaviour. Nervousness and boldness are associated with handedness in chimpanzees (Hopkins & Bennett 1994) and macaques (Westergaard et al 2003). Lateralization is related to emotionality in horses (Larose et al. 2006). Extroversion and emotionality are associated with greater cerebral asymmetry in humans (Howard et al 1994; Hagemann et al 1999). Non-lateralized chicks give more distress calls and take longer to resume foraging after exposure to a simulated predator than lateralized chicks (Dharmaretnam & Rogers 2005). Brown et al. have found that different populations of the same fish species differ in both boldness (2005) and cerebral lateralization (2004; 2007a). Reddon and Hurd (2008) found that strength of cerebral lateralization in convict cichlids was related to individual differences in aggressiveness. The relationship between individual differences in behaviour and cerebral lateralization may be an important factor in understanding the maintenance of their variability.

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

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

Methods

Subjects consisted of 100 adult convict cichlids, 56 females and 44 males that had never been tested for lateralization or boldness. Two males failed to complete all phases of testing and were excluded from the analysis. Prior to experimentation, animals were housed in 95l (75 x 31 x 41 cm) mixed sex communal aquaria at densities of approximately 15 fish per aquarium. Aquaria were maintained on a 12:12h light:dark cycle and water temperature was held

constant at $25 \pm 1^\circ\text{C}$. Fish were fed daily on a variety of frozen or dried prepared fish foods. All protocols were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee.

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

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

discarded. Each fish received ten trials run towards alternating ends of the tank. After each trial, the fish was allowed to rest for two minutes while the barrier was repositioned at the opposite end of the tank.

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

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

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

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

After laterality testing, each fish was tested for placement on the boldness-shyness continuum. Boldness was scored based on the time to emerge from a shelter into a novel environment (Brown & Braithwaite 2004; Brown et al 2005; Brown et al 2007b). The boldness testing apparatus (Brown et al 2007b) consisted of a 38l aquarium (50 x 27 x 30cm) filled with water to a depth of 11cm. At one

end of the aquarium there was an opaque Plexiglas box (15 x 15 x 20cm) with no ceiling and a removable door at one end. Subjects were placed inside the box and allowed to acclimate for 5 minutes. After the acclimation period, the door was raised and the fish was free to swim out of the box to explore the unfamiliar environment. Each trial was filmed from behind an opaque curtain. Fish were scored for their delay to emerge from the start box, which was counted when the fish stuck its head out of the box past the opercula. Eleven females and five males failed to emerge within five minutes and were excluded from further analysis; additionally two males emerged from the shelter in less than 10 seconds and were excluded as outliers. The delay to emerge scores were log-transformed for normality.

Results

Right and left eye use was equally common in both the novel (one-sample $t = -1.79$; $df = 79$; $p = .08$; Fig. 1) and familiar (one-sample $t = -0.42$, $df = 79$, $p = .68$; Fig. 1) contexts in this population. Eye use was not random at the individual level, each fish tended to favor either the right or left eye in both the novel (one-sample $t = 10.74$, $df = 79$, $p < .001$; Fig. 2) and familiar environments (one-sample $t = 12.27$, $df = 79$, $p < .001$; Fig. 2). LI in the novel and familiar contexts was not significantly correlated ($R^2 = .013$, $F_{1,78} = 1.02$, $p = .32$)

There was no significant difference between males and females in lateralization in the novel ($t = 0.09$, $df = 78$, $p = .93$; Fig. 1) or familiar ($t = 0.61$, $df = 78$, $p = .55$; Fig. 1) contexts. The absolute value of LI also did not differ

between the sexes in either the novel ($t = -1.04$, $df = 78$, $p = .30$; Fig. 2) or familiar ($t = -.60$, $df = 78$, $p = .55$; Fig. 2) environments. Similarly, there was no difference between males and females in their boldness scores ($t = 0.55$, $df = 78$, $p = .58$).

Analysis of covariance demonstrated a significant correlation between absolute strength of laterality scores in the familiar environment and the latency to emerge from shelter in the boldness task ($R^2 = .131$, $F_{1,78} = 11.76$, $p = .001$; Fig. 3a), and no effect of the sex of the animal ($R^2 = .004$, $F_{1,78} = 0.31$, $p = .58$). No such relationship existed between boldness and laterality in the novel environment ($R^2 = .001$, $F_{1,78} = 0.05$, $p = .82$; Fig. 3b).

Discussion

On average, convict cichlids appeared to be lateralized at the individual, but not the population level when exploring both novel and familiar environments. We demonstrated that variation in the strength of cerebral lateralization when exploring a familiar space is related to variation in a personality-like characteristic; boldness. Animals that had stronger hemispheric bias when exploring a familiar environment behaved more boldly in a novel one.

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

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

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

There is good reason to believe that cerebral lateralization may be linked to personality through underlying neural mechanisms (Andrew 2006). Barth et al (2005) have demonstrated that at least two neural mechanisms underlie lateralized behaviour, and that those mechanisms may assort independently of one another. *Frequent-situs-inversus* (*fsi*) are a strain of zebrafish that show a complete reversal of viscera and neuroanatomy. *fsi* animals show a concordant reversal of some but not all lateralized behaviours (Barth et al 2005). Furthermore *fsi* zebrafish tend to be more bold in novel environments than wild type animals. Presumably this is because behaviours that are often lateralized to opposite hemispheres tend to co-occur in the same hemisphere more often in *fsi* fish (Barth

et al. 2005). It is known that different lateralized abilities can assort independently within individuals (Rogers 2002; Andrew et al. 2004; McGreevy & Rogers 2005).

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

Evidence is accumulating suggesting that variation in boldness reflects variation in life history strategies (Wolf et al 2007; Smith & Blumstein 2008). Bolder animals grow faster but also suffer higher mortality (Stamps 2007). Different patterns of cerebral lateralization may be connected to this trade off. Strongly lateralized animals may have a cognitive advantage that allows them to more effectively process information about their environment, but puts them at a greater risk of predation or other dangers. This hypothesis would predict that strongly lateralized individuals may as a result favor current reproduction over future reproduction and behave in a bolder manner consistent with this life-history strategy. The relationship we have observed between the strength of the cerebral

lateralization and placement on the shy-bold continuum may reflect different solutions to the tradeoff between the benefits of symmetry and asymmetry.

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

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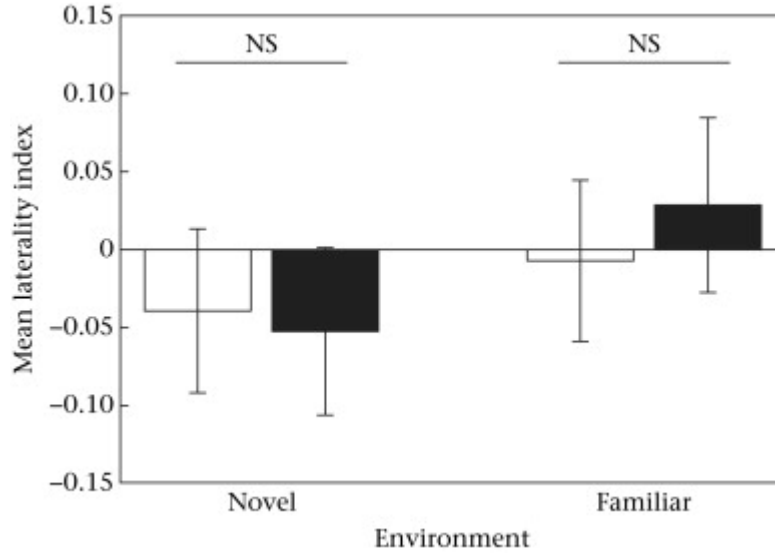


Figure 1. Average LI scores for the novel and familiar contexts. Positive scores are right hemisphere biased, negative scores are left hemisphere biased. LI does not differ from zero in the novel ($p = .077$) or familiar environments ($p = .68$). There is no difference between females (open bars) and males (shaded bars) in either the novel ($p = .93$) or familiar ($p = .55$) context.

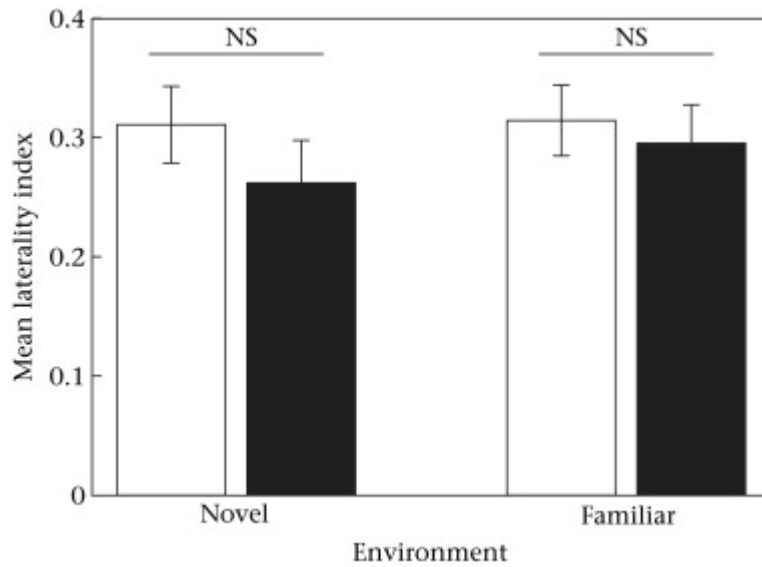


Figure 2. Average absolute LI scores for the novel and familiar contexts.

Absolute LI is significantly different from zero in both the novel ($p < .001$) and familiar environments ($p < .001$). There is no difference between females (open bars) and males (shaded bars) in either the novel ($p = .30$) or familiar contexts ($p = .55$).

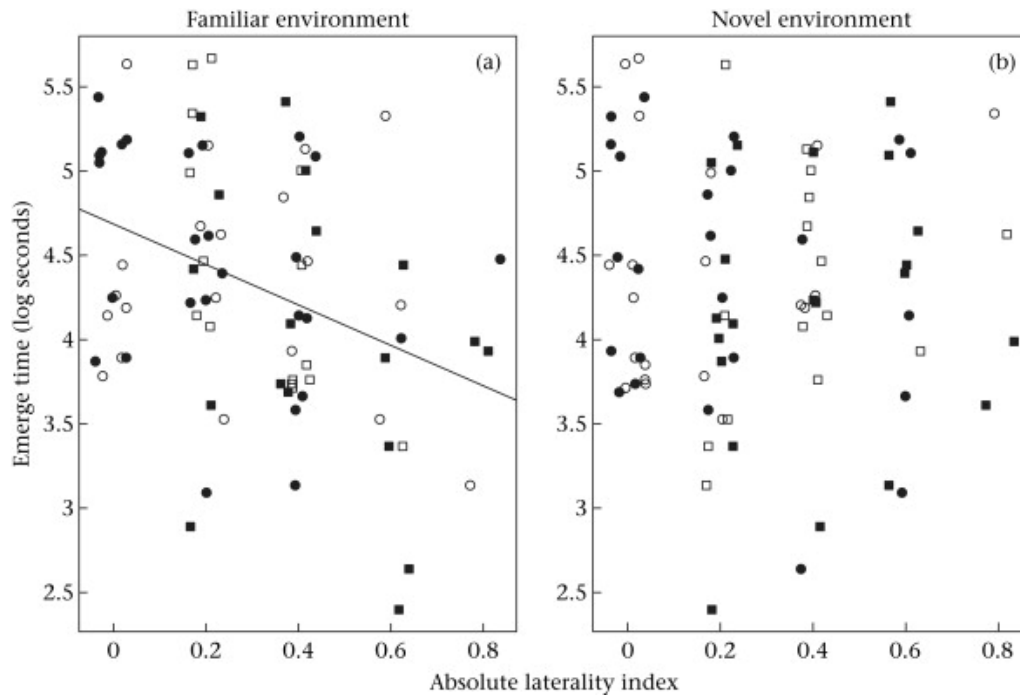


Figure 3. The linear relationship between latency to emerge from a shelter and absolute laterality scores is significant in a) the familiar environment ($p = .001$) but not in b) the novel environment ($p = .82$). Open points denote males, filled points denote females; squares denote negative (left hemisphere biased) LI scores while circles denote positive (right hemisphere biased) or neutral (unbiased) LI scores.

**Paper III: Sex differences in the cerebral lateralization of a cichlid
fish when detouring to view emotionally conditioned stimuli**

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Introduction

Cerebral lateralization, the selective processing of information in one hemisphere of the brain, is widely distributed throughout the vertebrates (Bisazza et al 1999; Vallortigara et al 1999; Rogers 2000; Rogers 2002; Vallortigara & Rogers 2005; Vallortigara 2006a) and may be a universal feature of the vertebrate nervous system (Vallortigara 2006b). Cerebral lateralization has also been demonstrated in several invertebrate taxa (Letzkus et al 2006; Rogers & Vallortigara 2008; Letzkus et al 2008; Kight et al 2008) and has probably evolved independently multiple times (Davison et al 2008). The taxonomic ubiquity of lateralization, combined with demonstrations of cognitive advantages to those who possess it, suggests that lateralization may be favored by natural selection (Rogers et al 2004; Sovrano et al 2005; Bisazza & Dadda 2005; Vallortigara & Rogers 2005; Dadda & Bisazza 2006a,b).

The lateralization of emotion has been demonstrated in a variety of animals, and the production or inhibition of certain emotional states may represent a key function of lateralization (Andrew & Rogers 2002). There is an extensive literature on the lateralization of emotions in humans, and in general, the results have indicated that positive or approach related emotions tend to be processed in the left hemisphere (LH) while negative or withdrawal emotions are processed in the right hemisphere (RH; Andrew & Rogers 2002; Davidson 1995). These results have received some limited support in animals, with findings indicating that the RH controls attack and fear responses while the LH controls approach, inhibition of aggression, manipulation of objects and foraging responses (Andrew & Rogers

2002; Vallortigara & Rogers 2005). A noteworthy example conducted by Quaranta et al (2007) found that domestic dogs tend to wag their tails to the right, indicating left hemisphere activation, when viewing their owners (positive emotional valence), and to the left, indicating right hemisphere activation when viewing an unfamiliar dominant conspecific (negatively valent). There are however, reports that some species of fish tend to show the opposite pattern, using their right eye (LH) to view predators (Bisazza et al 1998; Facchin et al 1999; Brown et al 2004) or attack conspecifics (Bisazza & de Santi 2003). Furthermore, some species of fish show only individual and not population level biases to view predators (Bisazza et al 2000) or attack conspecifics (Cantalupo et al 1996).

Most of the above animal examples use stimuli that naturally elicit an emotional reaction (e.g. a live or naturalistic model, predator). Far fewer studies have tested lateralization in response to conditioned emotional stimuli. Conditioned emotional reactions are a key component of emotional behaviour, and involve different neural mechanisms than intrinsically emotionally relevant stimuli (LeDoux 1996). There are two studies that we know of that have investigated lateralized response to conditioned emotional stimuli. De Boyer De Roches et al (2008) found that horses responded to an object with a conditioned association to veterinary care (negative emotional valence) with their left eye (RH) but had no population level response to an object associated with feeding (positive valence). Bisazza et al (2000) used a conditioned dummy predator (an elaborated dip-net) which had been used to chase the fish in their home tanks prior to testing. Bisazza et al found that some species of fish have a population

level tendency to use their left eye (RH) to view the conditioned predator while others use their right eye (LH) and still more have individual but not population level preferences.

Sex differences can have important effects on the pattern of lateralization observed within a species (Bianki & Fillippova 2000; Reddon & Hurd 2008) and have been extensively investigated in the domestic chick (Vallortigara & Andrew 1991; Vallortigara & Andrew 1994; Vallortigara et al 1994; Regolin & Vallortigara 1996). In general, males tend to be more strongly lateralized than females (Bianki & Fillippova 2000) however the effects of sex may be more subtle and interact with other intrinsic characteristics of the individual, such as aggressiveness (Reddon & Hurd 2008). Among the studies that investigated lateralized responses to emotionally conditioned stimuli, there has been no attempt to look at sex differences. De Boyer De Roches et al (2008) used all female animals and Bisazza et al (2000) could not sex the animals in their study save for one species in which they used all females.

Chemical alarm signals are released by many species of fish when they are attacked and damaged by a predator (Chivers & Smith 1998). These substances appear to have evolved for non-communicative functions such as defense against pathogens, parasites and UVB radiation (Chivers et al 2007). These substances have subsequently taken on an alarm function, and signal that a conspecific has been damaged nearby and that a predator may be in the vicinity (Chivers et al 2007). When detected, these damage-induced alarm signals elicit both short term and long term anti-predator responses in conspecifics (Chivers & Smith 1998;

Brown 2003; Brown & Chivers 2006). When exposed to the skin extract of conspecifics, convict cichlids exhibit anti-predator behaviours characterized by reduced movement, area avoidance, and decreases in foraging rate and aggression (Wisenden & Sargent 1997; Alemadi & Wisenden 2002; Brown et al 2004; Foam et al 2005; Pollock et al 2005).

Associative conditioning allows fish to learn about novel predators through pairing with conspecific chemical alarm signals (Brown 2003; Kelly & Magurran 2003; Brown & Chivers 2006; Ferrari et al 2007). Fish can also learn conditioned fear responses to arbitrary, non-biological stimuli if they are paired with conspecific alarm signals (Yunker et al 1999; Wisenden & Harter 2001; Brown 2003; Brown & Chivers 2006). Associations with chemical alarm signals are formed quickly, often in only one trial (Brown & Chivers 2006).

The current study examines the lateralization in responding of both male and female convict cichlids (*Archocentrus nigrofasciatus*) to emotionally conditioned, visual stimuli. One stimulus was given an appetitive (positive valence) association through pairing with food after a period of food deprivation. The other stimulus was given an aversive (negative valence) association through pairing with conspecific damage induced alarm signal.

Methods

Subjects consisted of 40 adult convict cichlids (*Archocentrus nigrofasciatus*), 20 of each sex, acquired from local suppliers. Prior to experimentation, animals were housed in 95l (71 x 31 x 41 cm) mixed-sex

communal aquaria at densities of approximately 15 fish per aquarium. Aquaria were maintained on a 12:12 h light cycle, and temperature was held constant at $25 \pm 1^\circ\text{C}$. Animals were fed twice daily on a mixture of dried, prepared fish foods. All experimental animals had previously served as subjects in other behavioural experiments, but no fish had undergone any testing for at least 30 days prior to the onset of this study.

Damage induced chemical alarm signal was collected following Pollock et al (2005). Seven adult convict cichlids (five males and two females; mean standard length = $55.09 \pm 7.98\text{mm}$) were used as donors. All fish were sacrificed by decapitation, and skin fillets were extracted from both flanks of each fish. Fillets were chopped finely and immediately placed into 100ml of chilled, distilled water. After thoroughly stirring, the mixture was filtered through polyester floss to remove any particulate matter. 200ml of distilled water was added to dilute the solution to 300ml total. The solution was frozen at -20°C in 15ml aliquots for future use.

Subjects were emotionally conditioned in groups of ten with an equal number of males and females per group. Each group was placed into a 95l (71 x 31 x 41 cm) aquarium that was completely visually isolated from the rest of the room using white paper. A transparent, water filled, plastic container (18 x 9 x 15 cm) was used for stimulus presentation. The container was hung inside the aquarium from the front pane so that it was completely submerged near the surface of the water. Two different stimuli were used in this experiment, a standard green tennis ball and a small, blue rectangular pipette tray (12 x 4 x 8

cm). A 2m length of rubber hose ran into the aquarium water so that alarm substance could be remotely administered to the tank. The water was continuously filtered through two external power filters, containing activated carbon, at a combined rate of 1134 l/hr. The emotional valence (positive or negative) assigned to each object was counterbalanced across groups of ten fish. Both objects were novel to the animals at the beginning of the study.

Emotional conditioning took place over the course of nine days. On day one, the fish were placed in the conditioning tank. Fish were allowed to acclimatize to the conditioning tank for the first three days of the experiment. During this time, the fish were food deprived. Starting on day four, one of the two stimuli was presented by placing it into the submerged plastic container. Each stimulus was presented simultaneously with either a typical feeding of prepared fish flakes (appetitive stimulus) or a 15ml dose of the alarm signal solution (aversive stimulus). Convict cichlids responded to conspecific alarm signals with species typical antipredator behaviours including reduced activity (Wisenden & Sargent 1997) whereas convicts respond to food presentation with increased activity and vigorous foraging behaviours (*pers. obs.*). Presentations of each of the stimuli alternated each day for six days so that each stimulus was paired with its contingency three times for each group of ten fish. On days ten and eleven the fish were tested for lateralized responding to each of the stimuli using a detour task. Between each group of ten fish the conditioning tank sat unused for four days while being continuously filtered through activated carbon and then

underwent a 30% water change. New activated carbon media was used for each group of ten fish.

The details of the detour apparatus have been described elsewhere (Reddon & Hurd 2008, 2009). Briefly, the apparatus consisted of a large Plexiglas aquarium (195 x 30 x 29 cm) divided into two compartments by a long narrow channel (10 x 75cm). The fish was placed in one of the chambers, with an opaque Plexiglas door blocking off the entrance to the channel. At the opposite end of the channel, a vertical bar barrier (15cm across) consisting of alternating bars of black and opaque Plexiglas, was placed in front a water filled plastic container (18 x 9 x 15 cm) containing either the positively or the negatively conditioned stimulus.

Each trial began when the opaque door was removed allowing the fish access to the channel. The fish was gently coaxed towards the mouth of the channel using a black dip net. The fish would swim down the channel and detour around the vertical bar barrier in order to view the stimulus behind. As the fish moved around the barrier, it could view the stimulus with only one eye. In fish, each eye projects almost entirely to the contralateral hemisphere and cerebral lateralization can be assessed by measuring asymmetries in eye use (Facchin et al 1999; Sovrano et al 1999; De Santi et al 2001; Sovrano & Andrew 2006). Each fish received ten trials for each stimulus run in opposite directions towards alternating ends of the detour apparatus. After ten trials for the first stimulus, there was a five minute rest period before the fish was tested using the other stimulus. The stimulus that was tested first was counterbalanced across subjects.

After testing, we calculated a laterality index ($LI = [\text{right detours} - \text{left detours}] / [\text{right detours} + \text{left detours}]$) for each fish, viewing each stimulus. We also computed the absolute value of LI for each stimulus as LI may obscure individual variation in the strength of lateralization (Brown et al 2007; Clotfelter & Kuperberg 2007; Reddon & Hurd 2008, 2009; Reddon et al 2009). All statistical analysis was conducted using SPSS v. 15.0. All values are reported as mean \pm standard error. All protocols were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee (protocol # 544706).

Results

We found no overall population level directional bias in either sex towards using their right vs. left eye to view emotionally conditioned stimuli. Male convict cichlids on average, were equally likely to use their right or left eye to view the positively or negatively valent stimuli (positive: one sample $t = 1.124$, $df = 19$, $p = .28$; negative: one sample $t = 1.49$, $df = 19$, $p = .15$; Fig 1). Females were also equally likely to use either eye to view the positively (one sample $t = 0.20$, $df = 19$, $p = .84$; Fig 1) or negatively (one sample $t = .86$, $df = 19$, $p = .40$; Fig 1) valent stimuli. There was no correlation between each fish's LI when viewing the positively valent stimuli and LI when viewing the negatively valent stimuli for either sex (males: $r_{(18)} = 0.33$, $p = .16$; females: $r_{(18)} = .25$, $p = .28$).

In the case of the absolute value of LI, we found that individuals of both sexes showed significant lateralization both when viewing positively (males: one sample $t = 4.93$, $df = 19$, $p = <.001$; females: one sample $t = 8.32$, $df = 19$, $p =$

<.001; Fig 2) and negatively (males: one sample $t = 6.83$, $df = 19$, $p = <.001$; females: one sample $t = 5.34$, $df = 19$, $p = <.001$; Fig 2) emotionally valent stimuli. There was no significant correlation between the strength of lateralization for positively and negatively valent stimuli in fish of either sex (males: $r_{(18)} = .29$, $p = .21$; $r_{(18)} = .13$, $p = .58$).

We conducted a mixed effects ANOVA on LI with stimuli as a within subjects factor and sex, stimulus testing order and object used as positive or negative stimuli as between subjects factors. This test revealed no main effect of stimulus valence or any interactions (all F 's < 3.6 ; all p 's $> .05$). A mixed effects ANOVA looking at the absolute strength of lateralization (Table 1) with stimuli as a within subjects factor and sex, stimulus testing order, and object used as positively or negatively valent stimuli as between subjects factors, revealed a significant interaction between emotional valence of the stimulus and sex on the strength of lateralization ($F_{(1, 32)} = 5.36$, $p = .027$; Fig 2). There was no main effect of stimulus valence and no other interactions (all F 's < 2.8 ; all p 's $> .05$).

Discussion

Female convict cichlids have a stronger visual lateralization when viewing positively valent stimuli and males have a stronger visual lateralization when viewing negatively valent stimuli. This relationship is not affected by which object was used as an appetitive or aversive stimulus, or by which stimulus was tested first.

Convict cichlids of either sex do not have a population level lateralization for viewing either positively or negatively valent stimuli. This result is in agreement with previous work on convict cichlids (Reddon & Hurd 2008, 2009) showing that convicts are lateralized at the individual but not population level.

There is however a slight, non-significant tendency for males to view both positively and negatively valent stimuli with their left eye, and hence process the information with their right hemisphere (Fig. 1). Existing literature on many vertebrates (Andrew & Rogers 2002; Vallortigara & Rogers 2005), including some species of fish (Bisazza et al 2000), has shown that strong emotional reactions are controlled by the RH. The literature on fish seems to indicate that some species use their RH to assess predators, while others use their LH or have individual level preferences only (Bisazza et al 2000). Bisazza et al. (2000) found that in fish, only those species which have strong schooling tendencies, show population level alignment of their lateralized behaviour. Convict cichlids do not school as adults, although they do exhibit schooling-like behaviour as parentally-dependent juveniles (Espmark & Knudsen 2001; Alemadi & Wisenden 2002). Anuran tadpoles demonstrate shoaling behaviour prior to metamorphosis and show a significant tendency to view their mirror image with their left eye during this stage of life (Bisazza et al 2002). Investigating the lateralization of behaviour in parentally-dependent juvenile convict cichlids and comparing it with the patterns of lateralized behaviour seen in adults may help to clarify this issue. Adult convict cichlids appear to have a similar pattern of lateralization as the non-schooling fishes in Bisazza et al (2000) and Cantalupo et al (1996).

Our results reinforce the point made by Bianki and Fillipova (2000) that sex differences may have important effects on the pattern of cerebral lateralization observed within a species. However, contrary to the findings of Bianki and Fillipova, we did not reveal a general tendency for males to be more strongly lateralized than females. In contrast we found that both sexes are equally lateralized on average, but one sex may appear more strongly lateralized than the other, depending on the emotional valence of the stimuli that are used. Reddon and Hurd (2008) found an interaction between sex and a personality-like characteristic, aggressiveness, on the pattern of lateralization in the convict cichlid. The relationship between sex and lateralization in convicts is complex and appears to depend on both intrinsic and extrinsic factors.

Convict cichlids are a monogamous and biparental species that demonstrate elaborate parental behaviours and a long period of parental care (Wisenden 1995). While both parents contribute to the care of the offspring, the mother and father tend to have sex typical roles in the parental care process (Budaev et al 1999). Males tend to actively defend against predators and other dangers while the female engages in more of the direct care of the offspring including fanning the eggs and larvae and feeding the free-swimming juveniles (Budaev et al 1999). It is possible that these differences in parental care behaviour may have selected for different patterns of lateralization in each sex of the convict cichlid. If sex differences in parental behaviour underlie the sex differences in behavioural lateralization in the convict cichlid these differences may be exaggerated or muted at different times in the reproductive process. It would be

fruitful to test convict cichlids for lateralization at different stages of the reproductive process.

In conclusion we found that male convict cichlids are more strongly lateralized in response to positively valent emotional stimuli while females are more strongly lateralized to negatively valent stimuli. Our study is one of only a few that looks at the lateralized responses to conditioned emotional stimuli, and the first to examine sex differences in this trait. Our study is also, to our knowledge, the first to test for lateralization in response to a stimulus that has been associated with a damage induced, chemical alarm signal. Using damage induced alarm signals may be a useful technique for future studies investing lateralized responses to emotionally valent stimuli.

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Source of variation	df	F	p
emotional valence	1,32	0.09	.76
sex	1,32	0.38	.54
object	1,32	2.34	.14
first tested	1,32	0.04	.83
sex x object	1,32	0.61	.44
sex x first tested	1,32	0.61	.44
object x first tested	1,32	0.08	.78
valence x object	1,32	2.47	.13
valence x first tested	1,32	2.71	.11
valence x sex	1,32	5.36	.027
sex x object x first tested	1,32	2.23	.15
valence x object x first tested	1,32	0.44	.51
valence x object x sex	1,32	0.08	.79
valence x first tested x sex	1,32	0.98	.33
valence x object x first tested x sex	1,32	0.79	.38

Table 1. Results of a mixed effects ANOVA for absolute lateralization with emotional valence (positive/negative) as a within subjects factor and object used (tennis ball/pipette tray), first stimulus tested (positive/negative), and sex as between subjects factors.

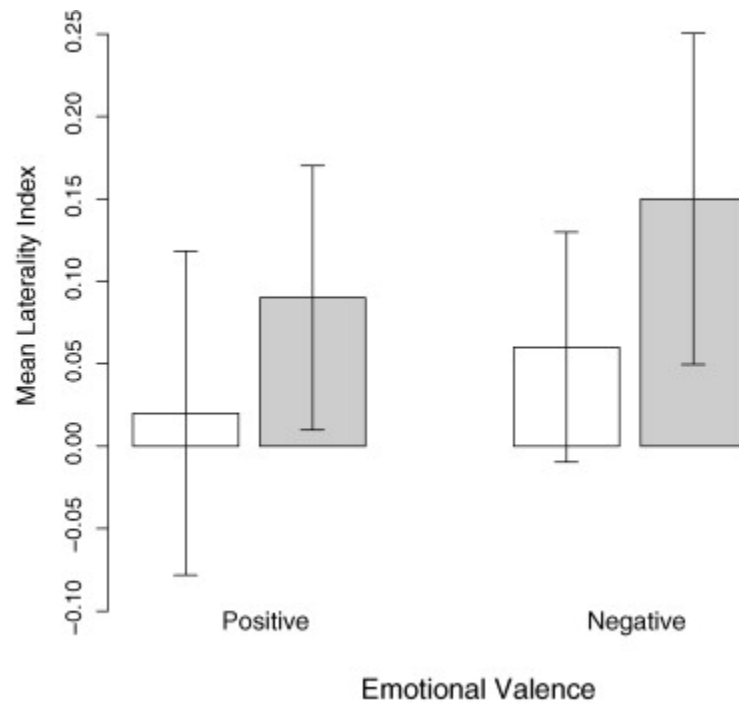


Figure 1. Mean \pm SE laterality index scores for convict cichlids viewing positively or negatively conditioned stimuli. Laterality index scores greater than zero are right-hemisphere biased and less than zero are left-hemisphere biased. Open bars = females, filled bars = males.

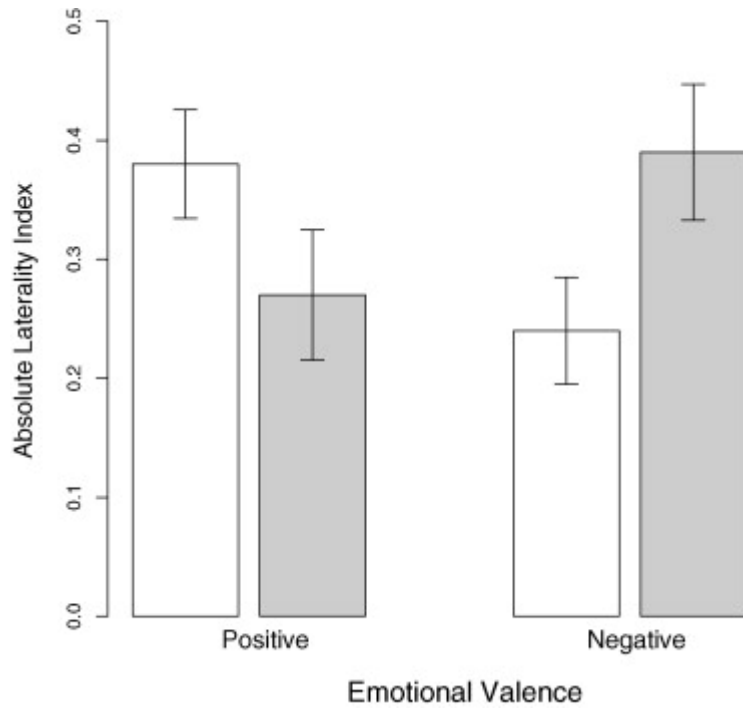


Figure 2. Mean \pm SE absolute laterality index scores for convict cichlids viewing positively or negatively conditioned stimuli. There is a significant interaction between sex and stimulus type on absolute laterality index ($p = .027$). Open bars = females, filled bars = males.

General Discussion

Cerebral lateralization in the convict cichlid

The papers that comprise this thesis represent the first description of cerebral lateralization in the convict cichlid, an important model species in the behavioural sciences. In Paper I, I show that the pattern of lateralization depends on both the sex of the animal and each individual's intrinsic propensity for aggression. Paper II shows that convict cichlids that have a greater strength of lateralization, also behave more boldly in novel environments. The results of Paper III illustrate that male convict cichlids tend to be more lateralized to aversive stimuli while female convict cichlids are more lateralized to appetitive stimuli. Papers I and II suggest that the pattern of lateralization observed in an individual convict cichlid is related to the personality-like characteristics of the animal. Papers I and III underscore the importance of sex in determining the pattern of lateralization we observe in each individual.

Taken together, these results demonstrate that convict cichlids are lateralized at the individual level but not at the population level. In other words, each individual animal has, on average, a preferred hemisphere to perform a given task, but the population distribution of the preferred direction does not differ from 50:50, and there is no directional lateralization for the population as a whole (Vallortigara & Rogers 2005). This result is similar to what has been reported for other non-schooling fishes (e.g. Cantalupo et al 1996; Bisazza et al 2000; Clotfelter & Kuperberg 2007).

Sex differences in lateralization

Fitting with the main argument of Bianki and Filippova (2001), convict cichlids appear to have important differences between the sexes in their pattern of lateralization. Papers I and III each report important sex differences in the lateralization of behaviour in the convict. However, unlike the findings on rats, cats, humans and a handful of other model species reported in Bianki and Filippova's book, there does not seem to be a general tendency for males to be more lateralized than females. In convicts, each sex is equally lateralized on average, and the sex differences are revealed only when the interaction between sex and other factors is considered.

In the research on sex differences in the domestic chick, it has been argued that females are not in fact less lateralized than males, but that the lateralization of their behaviour appears muted in certain testing situations (Vallortigara & Andrew 1991; Vallortigara & Andrew 1994). Prior research on fish indicates that motivation may be an important factor in dictating the pattern of lateralization that is observed in each sex. Bisazza et al (1998) found that in two species of poeciliid fish, males and females demonstrated similar patterns of lateralization when detouring to view non-social stimuli, turning to the left (and hence using their right eye and left hemisphere) to view a simulated predator and to their right (using their left eye and right hemisphere) to move around an opaque barrier. However, when social stimuli were used, sex differences became apparent (Bisazza et al 1998). Females showed a consistent bias to detour to the right (and hence use their left eye and right hemisphere) to view a same sex conspecifics, while males showed no such directional tendency. Males of each species showed

a consistent bias to detour to view female conspecifics, but each species preferred a different direction. Females also showed a consistent bias to view opposite sex conspecifics, with both species detouring to the left to view males, but only after a period of sexual deprivation. Females that had not been male deprived or had been male deprived for a shorter period of time, showed no consistent bias. Bisazza et al (1998) attribute these sex differences to differences in social and sexual motivations. Females have stronger affiliative tendencies than males do, which may account for their directional bias to view same sex conspecifics. Males on the other hand, while being less interested in same sex conspecifics, and apparently not being lateralized at the group level to view them, are always interested in females, and are consistently motivated to seek copulations. As a result, males do demonstrate a population level bias to view females, although the direction of this bias is idiosyncratic for each species. Females however, are interested in males only after some period of deprivation, presumably because unlike males, they cannot increase their reproductive success simply by mating constantly. Collectively these results and the author's interpretations suggest that males and females are not fundamentally different in the laterality of their brains, and that the apparent differences in some testing situations are secondary to other differences in the biology and behaviour of the animals. Unfortunately, Bisazza et al (1998) do not report any analysis of differences in strength of lateralization between the species, sexes or testing conditions. Individuals with strong, but opposing lateralizations will cancel each other out when analyzed in terms of group means. This may obscure important individual differences with regard to

the strength, rather than direction of lateralization (Brown et al 2007).

Kaarthigeyan and Dharmaretnam (2005) reported that females have a stronger lateralization when detouring to view preferred orange colored males compared to less preferred dully colored males, suggesting that motivation may have important effects on the pattern of lateralization. In humans, it has been argued with some vigor that the observed sex differences are the result of differential activation of lateralized systems in the brain by different stimuli in each sex and not by a fundamental difference in the lateralized organization of these systems (Kinsbourne 1980). Although the existence of sex differences in lateralization remains a topic of debate, it is worth noting that sex differences in a great many aspects of brain organization, cognition, and behaviour have been reported in humans and other animals, and are generally well accepted (Becker et al 2008).

The results I have presented here cannot explicitly determine whether the sex differences that I have observed in the convict cichlid are a result of different motivation or a difference in brain organization. The results of Paper III seem to favour an interpretation based on motivation. Previous work on fish suggests that more lateralized responding is found when the animals are interested in the stimuli being viewed (Bisazza et al 1998; Kaarthigeyan & Dharmaretnam 2005). It is possible that males are more sensitive or interested in stimuli that have an aversive association while females are on average more motivated by stimuli of an appetitive nature. The biological reasons for such a difference can only be speculated upon, but may, as was noted in Paper III, owe to the different roles each sex typically fills during the extensive parental care period. Because

lateralization was measured directly to the stimuli of interest in Paper III, it is possible that differences in motivation could account for the patterns of responding that I observed. Male and female convicts in Paper III were equally lateralized on average when the interaction with the emotional association of the stimuli was not considered. The results of Paper I may be suggestive of a more fundamental difference between the sexes in terms of the lateralized organization of the brain, although again, this sex difference is only apparent when considered in its interaction with the aggressiveness of the animal. Unlike Paper III, in Paper I, lateralization was not measured in response to the stimulus of interest.

Differences in lateralization between the sexes cannot be attributed exclusively to differences in motivation to aggress, because lateralization was measured in an exploratory and not an aggressive context. The cause of sex differences in lateralization remains an open issue, and fertile ground for future investigation. Future work should aim to disentangle the importance of motivation and differences in brain organization. In the convict system, I believe that sex differences in the parental care process may underlie some of the sex differences in lateralization that I have observed, and measuring laterality in this context ought to be fruitful.

Lateralization, personality and life history strategy

Papers I and II report a relationship between cerebral lateralization and personality-like characteristics in the convict cichlid. These join a relatively small number of studies that have found such an association in animals (Carlson & Glick 1989; Branson & Rogers 2006; Rogers 2007, 2009), although there are a

few others that can be reasonably interpreted in this way, even if the authors did not originally do so (*see Dharmaretnam & Rogers 2005 for an example*).

I am of the opinion that individual variation in personality is maintained within populations by frequency- and/or habitat-dependent selection on life history strategy. Consistent with this idea, are the models of Wolf et al (2007, 2008), Stamps (2007) and Biro and Stamps (2008). While the details vary to some degree, all of these models focus on the basic premise that individual personalities may coexist within populations if each of these personalities is tied to a different life history strategy. For example, there may be a stable proportion of individuals that focus on current reproductive prospects, and take risks to achieve reproductive success, thereby reducing the likelihood they will be successful in the future, whereas a second group may be focused on future reproductive successes and avoid risks (Wolf et al 2007). It is possible that lateralization is an additional component of this general life history strategy. The results presented here (Papers I & II) in conjunction with previous reports, suggest that strongly lateralized individuals may be playing the risky strategy while weakly lateralized individuals represent the more cautious members of the population. In a recent study, Reddon et al (2009) reported that in the Neotropical cichlid *Geophagus brasiliensis*, males that grow faster and females that grow slower have more strongly lateralized brains both in terms of neuroanatomy and behaviour. For males, growing quickly may represent a risky life history strategy because they must brave additional perils in order to secure the required resources to sustain a higher growth rate. For females, slower growth may represent the riskier strategy

if resources are diverted away from somatic growth in favor of reproductive investment, leaving the individual more susceptible to gape-limited predation.

Frequency-dependent selection operates whenever the success of one strategy depends on how rare that strategy is within a population (Maynard-Smith 1982). Two or more strategies may coexist within a given population when the benefits of being rare are equal to the benefits of playing the most successful strategy in isolation. This balance point represents an evolutionarily stable strategy (ESS; Maynard-Smith 1982; *see* Fig. 1). Habitat-dependent selection, by contrast, operates whenever a given phenotype is more fit in a certain habitat but less fit in another. If the habitats vary on sufficiently small spatial or temporal scales, both phenotypes may be maintained in a population.

Frequency- and habitat-dependent selection, are typically considered in isolation, but may interact to produce the observed proportions of each phenotype. For example (Fig. 1) if phenotype y has greater average fitness than phenotype x in habitat A provided that less than 70% of all individuals in habitat A are of phenotype y there will be an ESS proportion of $y:x$ that is equal to 70:30 in habitat A. Habitat A, on average, is favorable to phenotype y (habitat-dependent selection) but there will still be a substantial portion of individuals of phenotype x because phenotype x is more fit when rare (frequency-dependent selection). However, in habitat B, the opposite is true and phenotype x is favored on average, but there will still be a significant proportion of phenotype y because of the advantage of being rare. If habitats A and B vary within the range of the population on a small enough temporal or spatial scale, then both phenotypes will

be maintained within the population by an interaction between frequency- and habitat-dependent selection mechanisms.

For a more concrete example that describes Figure 1, imagine that phenotype y are the strongly lateralized individuals, and phenotype x are the weakly lateralized individuals. If habitat A is relatively free of predators then it may favor strongly lateralized animals that behave more boldly and do not waste energy on summoning unnecessary fear responses. A certain proportion of weakly lateralized individuals may be maintained in habitat A because as the density of strongly lateralized individuals increases, their average fitness may decrease because of frequent and costly aggressive interactions, until it falls below the fitness of weakly lateralized individuals in this habitat. In habitat B there may be many dangerous predators which impose high fitness costs on strongly lateralized individuals, especially when they are common enough for predators to develop a successful search image. Weakly lateralized individuals may do better in habitat B because they are more wary of predators, and predators limit the strength of competition with strongly lateralized animals. Strongly lateralized individuals may be more vulnerable to predation because of sensory or motor biases that make them more predictable to predators and hence strengthening this effect (Vallortigara & Rogers 2005). Of course, strongly lateralized individuals may also have an advantage under predation because of their increased ability to multitask, allowing them to forage, copulate, etc. while remaining vigilant for predators (Vallortigara & Rogers 2005). Empirical data, particularly in natural systems, is required to clarify these issues, and this represents an important direction for

future research. The only studies, of which I am aware, that provide any elucidation on this point are those of Brown et al (2004, 2007) who have suggested that strongly lateralized fish are more common under stronger predation pressure. The generality of these results needs to be confirmed in other systems and testing conditions. An eye towards measuring individual variation in populations under strong or weak predation pressure would be a major asset in furthering our understanding of the selective forces that may maintain variation in cerebral lateralization. The convict cichlid may be an ideal model for further exploring these issues. The initial descriptions of lateralized behaviour in the convict and its relationship with personality-like characteristics that I present here will serve as essential ground work when further pursuing these questions.

Conclusions

The papers presented in this thesis explore the relationship between individual and sexual differences in the lateralization and individual differences in behaviour in the convict cichlid. My results add to a small but growing body of research that finds such relationships, and I discuss the possibility that the relationship between lateralization and personality may help to explain the maintenance of variation in the former. Future research should aim to expand and generalize these results, and in particular should attempt to place them within an ecological and evolutionary context.

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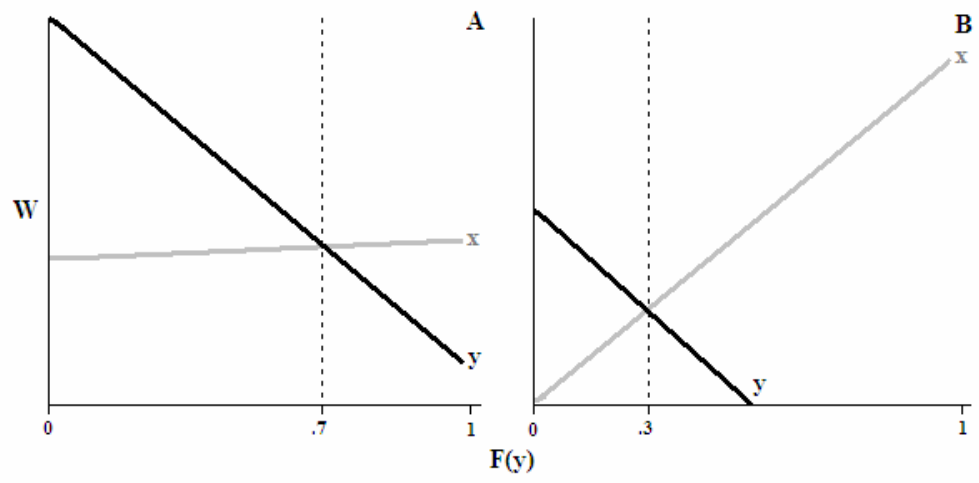


Figure 1. Average fitness (W) of an animal with phenotype x (shaded lines) or y (black lines) as a function of the frequency of phenotype y in each of two habitats, A and B. The ESS for each habitat is represented by the vertical-dashed line. See text for details.