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Aggression, sex and individual differences in cerebral lateralization in a cichlid fish

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Cerebral lateralization is an evolutionarily ancient adaptation, apparently ubiquitous among vertebrates. Despite demonstrated advantages of having a more lateralized brain, substantial variability in the strength of lateralization exists within most species. The underlying reasons for the maintenance of this variation are largely unknown. Here, we present evidence that the strength of lateralization is linked to a behavioural trait, aggressiveness, in the convict cichlid (*Archocentrus nigrofasciatus*), and that this relationship depends on the sex of the fish. This finding suggests that individual variation in behaviour may be linked to variation in cerebral lateralization, and must be studied with regard to the sex of the animal.

Keywords: cerebral lateralization; animal personality; aggressiveness; sex differences; convict cichlids

1. 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 fishes is of particular interest as early patterns of vertebrate lateralization may have remained relatively unaltered in this taxon (Vallortigara & Bisazza 2002). Cerebral lateralization can be measured in fishes by assessing asymmetries in eye use as fishes do not 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 the strength of lateralization suggests that individual animals with strongly lateralized brains enjoy cognitive advantages including an improved ability to multitask when compared with those with weaker hemispheric specialization. Despite these advantages, substantial variability is seen in both the direction and strength of lateralization at the individual level (Vallortigara & Bisazza 2002). Ghirlanda & 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 as to 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 animal 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 and 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 & 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 fishes, which are exposed to different predation pressures, differ in both lateralization (Brown *et al.* 2007) and personality (Brown *et al.* 2005).

Many species, across a range of taxa, show a consistent population bias towards right-hemisphere control of aggressive responses (reviewed in Rogers 2002). Evidence from fishes 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.

2. MATERIAL AND METHODS

Subjects consisted of 40 adult convict cichlids, 20 of each sex, purchased from local suppliers. The fish were housed in 95 l (75×31×41 cm) mixed-sex communal aquaria prior to and following experimentation. The aquaria were maintained at 25±1°C on a 12 L : 12 D cycle. The 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 (figure 1) consisted of a large aquarium (195×30×29 cm) filled with water to a depth of 11 cm. The aquarium had two compartments joined by a narrow runway (10×75 cm). A movable barrier (15 cm across and extending up above the surface of the water), consisting of alternating 0.75 cm 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 acclimatize for 2 min. 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

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

runway using a black dip net (13×10 cm). 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 2 min 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),

$$(\text{right} - \text{left})/(\text{right} + \text{left}) = \text{laterality index}.$$

Absolute values of LI were also computed. The 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 57 l aquarium (45×32×40 cm) 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 acclimatize for 24 hours, 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, it was scored as an 'aggressor'.

3. 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 females and 11 were males. There was no significant difference in the likelihood that males or females were aggressors (Yates $\chi_1^2=0.989$, $p=0.32$). Neither LI nor absolute LI differed significantly from normality (Kolmogorov–Smirnov tests: $Z=1.1$, $p=0.18$; $Z=1.2$, $p=0.11$, respectively).

There was a significant association between detour direction and the interaction between aggressor status and sex ($R^2=0.156$, $F_{1,38}=7.05$, $p=0.01$; figure 2*a*). Female non-aggressors and male aggressors tended to turn left (thus using their right visual field that projects to the left side of their brain), while female aggressors and male non-aggressors had a slight tendency to turn right.

The strength of lateralization was significantly influenced by an interaction between sex and aggressor status ($R^2=0.234$, $F_{1,38}=11.58$, $p=0.002$; figure 2*b*).

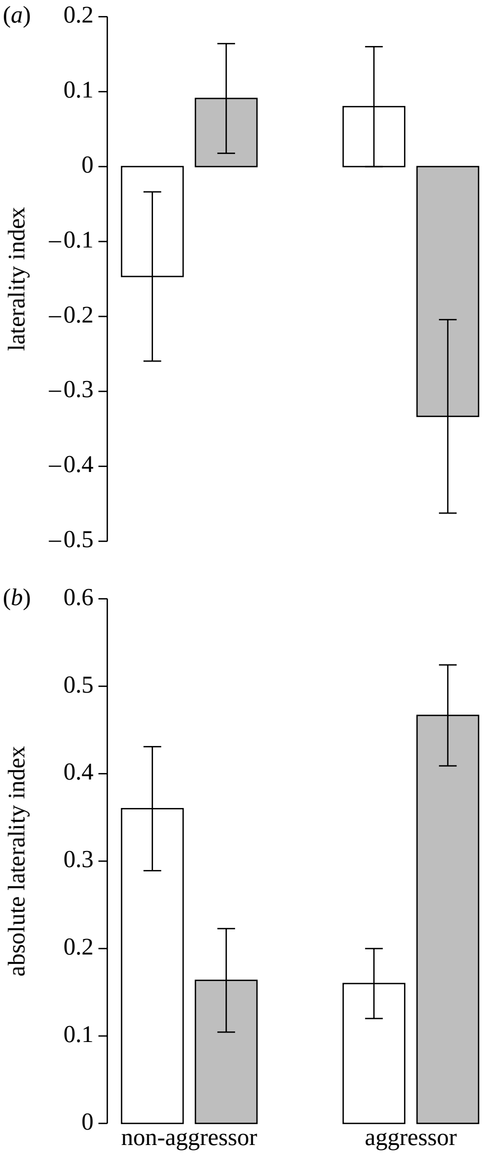

Figure 2. (*a*) Average LI scores (±s.e.m.) for females (white bars) and males (grey bars) that attacked or did not attack their mirror image within 10 min. There is a significant interaction between sex and aggressor status on LI ($p=0.01$). (*b*) Average absolute LI scores (±s.e.m.) for females (white 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 ($p=0.002$).

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

4. 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 as 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 & 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 that may allow them to process information in different ways. If variability in personality is maintained by frequency-dependent selection 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 the greater generality of this phenomenon.

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