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 cortical lateralization 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
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),

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

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 aggression during this 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 \(\chi^2=0.989, p=0.32\)). 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 \((R^2=0.156, F_{1,38}=7.05, p=0.01; \text{figure 2a})\). 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 \((R^2=0.234, F_{1,38}=11.58, p=0.002; \text{figure 2b})\).

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 & Filipova 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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