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Research report

The relationship between growth, brain asymmetry and behavioural lateralization in a cichlid fish

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ABSTRACT

Cerebral lateralization, the partitioning of cognitive tasks to one cerebral hemisphere, is a widespread phenomenon among vertebrates. Despite this diversity, every species studied to date shows substantial individual variation in the strength of lateralization. The neural basis of this trait is unclear, although asymmetries in cerebral structures have been investigated for over a century. The habenular nuclei, for example, have been shown to present striking neuroanatomical and/or neurochemical asymmetries in species ranging from jawless fish to mammals. In teleost fish, these nuclei are relatively symmetrical in most species. Those teleosts that do have asymmetrical habenular nuclei, show varying patterns of asymmetry in different species. Here we investigate the relationship between individual variation of asymmetry in the habenula of a South American cichlid fish, *Geophagus brasiliensis*, and behaviour in a commonly used test for visual laterality in fish, the detour task. We show that the strength of asymmetry in the habenula is correlated with strength of behavioural lateralization in the detour task. Both the strength and direction of habenular asymmetry are correlated with individual differences in growth rate. We suggest that this relationship results from processes linking growth rate and sexual differentiation to frequency-dependent variation in life-history strategies. To our knowledge, this is the first study to demonstrate a relationship at the individual level between neural asymmetry and lateralized behaviour in a fish.

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1. Introduction

Asymmetries in brain function are a widespread phenomenon among vertebrates [8,44] and may be a universal feature of the vertebrate nervous system [55,56,58,59]. It has long been assumed that there is a cognitive advantage to cerebral lateralization [43] and evidence has been accumulating in support of this idea. Studies involving developmental manipulations in the chick [43,46,58] and artificial selection for the strength of lateralization in a freshwater fish [6,17,18,49] have indicated that cerebral lateralization enhances an individual's ability to simultaneously attend to multiple stimuli.

Despite the described advantages of having a functionally lateralized brain, substantial individual variation in the strength of lateralization exists in all species studied to date [16,57]. If lateralization is a beneficial trait, one would expect natural selection to drive it to fixation. The benefits of being lateralized may trade-off against the benefits of symmetrical organization in a world where things are equally likely to occur on either side [15,16,58]. Strongly lateralized animals may have motor or sensory deficits when performing tasks or detecting stimuli on their non-preferred side [58]. These deficits may be of particular importance to animals with laterally placed eyes and limited interhemispheric connectivity (e.g. birds, fish, reptiles and amphibians [6,8,43]) Frequency dependent selection operating on the trade-off between the advantages of symmetry and asymmetry may maintain both phenotypes within a population ([11,42]; also see: [29,33,54,58] for examples of frequency-dependent selection operating on the direction of lateralization).

Fish have been invaluable in furthering our understanding of cerebral lateralization. Most fish species have laterally placed eyes that project entirely to the contralateral hemisphere, allowing functional lateralization to be assessed by asymmetries in eye use [19,23,50,51].

Growth depensation, the exaggeration of size differences within a cohort when raised as a group, is a common feature of the life history of fishes [36]. Fish which behave more boldly when faced with risky situations also tend to have higher growth rates [27,38,62]. Growth rate may be a component of a general life-history strategy in which some animals in a population grow quickly, but do so at a greater risk of predation or other dangers, while others grow more

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slowly, but engage in less risky behaviour [5,52]. It is possible that cerebral lateralization may also be a component of a more general life-history strategy in which strongly lateralized individuals favor current reproduction, behave more boldly and grow faster, while more symmetrical individuals demonstrate the opposite characteristics [42]. There is some empirical support for this hypothesis. Lateralized chicks give fewer alarm calls and suffer shorter foraging interruptions in response to a simulated predator attack compared to non-lateralized animals [20]. Strongly lateralized domestic dogs demonstrate less anxiety to loud, unknown noises, than do less lateralized animals [10]. More strongly lateralized male convict cichlids behave more aggressively than less lateralized males [41]. Convict cichlids of either sex that have greater cerebral lateralization also behave more boldly in novel environments [42].

There is substantial interest in understanding the neural basis of lateralized behaviour. In humans and other primates, gross anatomical asymmetries between the cerebral hemispheres have been studied for over a century (reviewed in ref. [61]). Passerine birds have an asymmetry in the vocal control pathways [39]. Asymmetries in the visual pathways have been found in pigeons and chicks [30,45] and these anatomical asymmetries underlie some of the asymmetries in visually guided behaviour in these species.

The best known example of asymmetry in the brain is the habenular nucleus [57]. From jawless fish to mammals, this structure presents striking neuroanatomical and/or neurochemical asymmetries (reviewed in ref. [14]). In all vertebrates, the habenula is a component of a highly conserved pathway belonging to the limbic system, and connects the forebrain with the ventral midbrain [53]. Although the exact purpose of the habenula remains somewhat debatable, several functions have been proposed for it, including learning and memory, nocioception, olfactory responses, feeding and mating behaviours (reviewed in ref. [37,47]).

In hagfish, lampreys, chondrichthyes, and non-teleost bony fishes, the habenular nuclei exhibit marked anatomical asymmetries [9,13,40,48,63] but in teleosts these nuclei are described as being mostly bilaterally symmetric, with only a few exceptions [14]. Another difference between teleosts and other vertebrates is the within group constancy in the directionality of the asymmetry. In hagfish, lampreys, and non-teleost bony fishes, the habenula is larger on the right than the left, while in chondrichthyes it is larger on the left. In those teleost species which do present asymmetries, the direction of the asymmetry varies between species [14].

Most reports of habenular asymmetries stem from qualitative observations in small number of specimens for each species [14]. Quantitative studies of individual variation in habenular asymmetry are completely lacking in teleosts. Two studies have examined individual variation in this trait within a vertebrate species. In the frog *Rana sculenta*, the volume of the left medial nuclei of the habenula increased during the reproductive season, increasing the strength of the asymmetry, [35]. In chickens, males showed a directional asymmetry, with a bigger habenula on the right side, while females presented significant individual asymmetries, but with equal probability of a bias to the right or left side [31,32].

While the neural substrates of some lateralized behaviours have been identified (e.g. [30,45]), the relationship between individual variation in lateralization of neuroanatomy and individual variation in lateralization of behaviour, remains unclear. The widely noted asymmetry of the habenula and its function in several, fitness-related behaviours that may be tied to functional lateralization [22,57], makes it a good candidate for exploring the neuroanatomical correlates of lateralized behaviour. Barth et al. [3] showed within a mutant zebrafish line in which up to 25% of individuals show situs inversus (in which asymmetries in the viscera and brain, including the habenulae, are reversed) that a subset of behaviours were reverse lateralized in those fish with situs inversus affecting the habenula. In a recent study, Facchin et al. [22] found that selection for behavioural lateralization in zebrafish affected the frequency of individuals that have the species typical leftward asymmetry of the habenula versus the less common rightward asymmetry. Selection for left eye (right hemisphere) use during mirror image inspection tended to enhance the frequency of individuals with a leftward asymmetry of the habenula. However, selection for right eye (left hemisphere) use, tended to increase the frequency of individuals with directionally reversed neural asymmetry in the strain.

Here we investigate the relationship between individual variation of asymmetry in the habenula of a South American cichlid fish, *Geophagus brasiliensis*, and behaviour in a commonly used test for visual laterality in fish, the detour task [7,8,12,23,34,41,42]. The cortical pretectal nucleus (COPn) was also measured as a control area. The COPn was chosen as a control due to the similar size with the habenula and the clear margins of the nucleus. This nucleus, part of the pretectum, lies dorsomedial to the superficial pretectal zone and it has been shown to connect the optic tectum with the nucleus glomerularis in the caudal diencephalon, suggesting some role in visual behaviours [24].

2. Methods

2.1. Subjects

Subjects consisted of 26 adult *Geophagus brasiliensis*, 15 males and 11 females. All the individuals originated from the same clutch, which was produced in the lab from parental stock obtained from a local supplier. All of the fish were housed in a 95 L (71 cm × 31 cm × 41 cm) aquarium as juveniles and transferred into a 440 L (183 cm × 48 cm × 50 cm) aquarium at adulthood where they remained together until testing. The water temperature was maintained at 25 ± 1 °C and the fish were exposed to a 12:12 h light cycle. The fish were fed daily on a mixture of frozen or dried prepared fish foods. The fish were approximately 18 months old at the time of testing. “Principles of laboratory animal care” (NIH publication No. 86-23, revised 1985) were followed, as well as all national laws. All protocols were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee (protocol #544706).

2.2. Behavioural testing

Animals were tested for lateralization using a detour task [7]. All fish were naïve to this task, so the detour apparatus represented a novel environment. The details of this procedure have been reported in greater detail elsewhere (see ref. [41]). Briefly, the detour task consisted of a large Plexiglas aquarium (195 cm × 30 cm × 29 cm), divided into two equal parts by a narrow runway (10 cm × 75 cm). At the start of testing, each fish was placed into one of the two chambers with the runway occluded by an opaque Plexiglas door. At the beginning of each trial the door was lifted and the fish was gently coaxed from towards the beginning of the runway using a dipnet. At the distal end of the runway was a partially occluding barrier which the fish had to detour around to enter the chamber on the opposite side. As the fish moved around the barrier it could view the environment with only one eye. Based on which direction the fish chose to swim around the barrier we could assess which eye, and hence which hemisphere, it preferred to use to view the environment. At the end of each trial, the fish was confined to that chamber while the vertical bar barrier was repositioned at the opposite end. Each fish received 10 trials run in opposite directions. Upon completion of 10 detour trials, a laterality index (LI) was computed for each fish using the formula:

$$\text{Laterality Index} = \frac{\text{Right Turns} - \text{Left Turns}}{\text{Right Turns} + \text{Left Turns}}.$$

We also computed the absolute value of LI for each fish, as LI may obscure individual variation in the strength of lateralization [12]. Previous research on another cichlid species [41,42] has shown that the strength and not the direction of lateralization correlates with other behaviours. After testing, we took standard length (measured from the snout to the caudal peduncle) measures for each fish as an index of size.

2.3. Neuroanatomical measurements

Immediately following behavioural testing, fish were sacrificed by placing them in a 0.2% solution of 2-phenoxiethanol (p-1126, Sigma, St. Louis, MO). They were then decapitated and the head was immersed in 4% paraformaldehyde in phosphate buffer pH 7.4 (PF). After 2–3 weeks the brain was extracted from the skull, embedded in gelatin, and placed in 30% sucrose in 0.1 M PB for cryoprotection. Using a freezing-stage microtome, 40 μm sections were collected in 0.1 M phosphate buffered saline and mounted onto gelatinized slides. After air-drying, the slides were stained with

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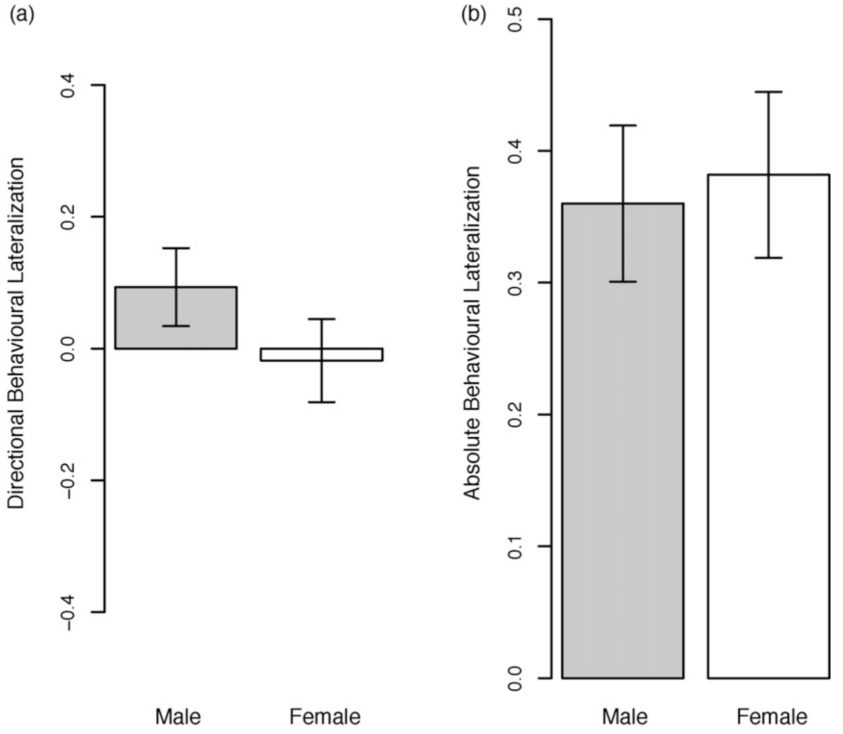

Fig. 1. (a) Mean ± SE behavioural laterality index for *G. brasilensis*. Positive scores indicate a right detour bias, negative scores indicate a left detour bias. (b) Mean ± SE absolute behavioural laterality index.

cresyl violet, dehydrated through a graded ethanol series, cleared in Hemo-D, and coverslipped with Permount.

Sections were viewed with a compound light microscope (Leica DMRE, Richmond Hill, ON). Images were acquired using a Retiga EXi *FAST* Cooled mono 12-bit camera (Qimaging, Burnaby, BC).

Microphotographs of every section were taken throughout the rostrocaudal extent of the each of the measured nuclei. Measurements of the area of each side of each nucleus were taken directly from these photos using Image J, (U.S. National Institutes of Health, Bethesda, MD, USA, http://rsb.info.nih.gov/ij/). Volumes were calculated by multiplying the area of the nuclei in each section by the thickness of the section (40 μm) and then adding them together.

Habenula measurements were taken from 12 males and 10 females. COPn measurements were taken from 13 males and 9 females. Some nuclei could not be measured on one, or both sides due to damage during preparation of the tissue, and thus not all of the 26 behaviour-tested individuals have nuclei asymmetry data.

A laterality index (LI) was calculated for each nuclei in each individual. This was done using the following formula:

$$\text{Laterality Index} = \frac{\text{Volume right} - \text{Volume left}}{\text{Volume right} + \text{Volume left}}.$$

Similar indices have been used previously for measuring asymmetries in brain structures [31,60]. Absolute values were also computed in order to access the overall strength of lateralization.

3. Results

We found no evidence of a population level bias in the direction of behavioural lateralization for *Geophagus brasilensis* of either sex (males: one sample $t = 0.88$, df = 14, $p = 0.41$; females: $t = -0.134$, df = 10, $p = 0.90$; Fig. 1a). In other words *G. brasilensis*, as a species, do not tend to be either “right brained” or “left brained” in the detour task. However, the behaviour of *G. brasilensis* is significantly lateralized at the individual level in both males (one sample $t = 6.08$, df = 14, $p = <0.001$; Fig. 1b) and females (one sample $t = 6.06$, df = 10, $p = <0.001$; Fig. 1b). In other words, each individual fish does tend to have a preference for either the right, or the left.

The habenula (Fig. 2) was found to be very similar in structure to what has been previously reported for another species of cichlid fish, *Haplocromis burtoni* [24]. Briefly, it consisted of a cup-shaped protrusion into the third ventricle at the rostral-most portion of the diencephalon, with a thick layer of small, darkly staining cells against the ventricular wall and a more lateral neuropil. As in *H. burtoni*, there was no apparent difference between the dorsal and ventral portions of the nucleus (Fig. 2).

We found a significant correlation between directional asymmetry of the habenula and standard length ($R^2 = 0.50$, $F_{(3,18)} = 6.0$, $p < 0.01$; Fig. 3). Smaller fish tended to have larger left habenulae while larger fish tended to have larger right habenulae. Analyses of

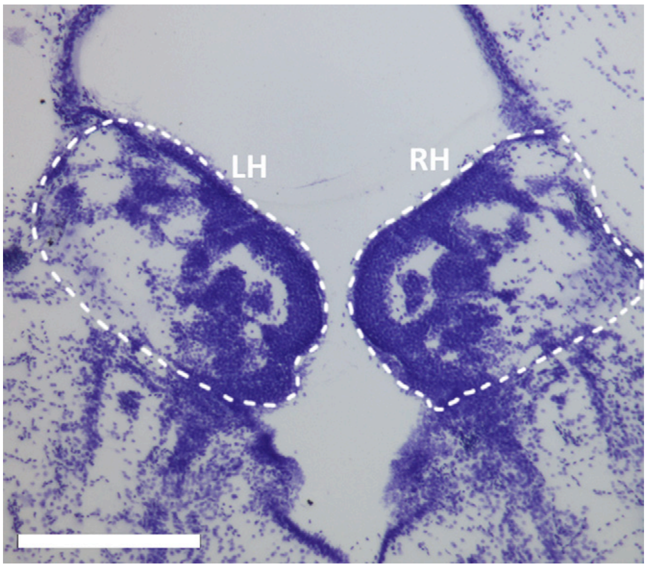

Fig. 2. Brightfield microphotograph of a coronal section through the habenula of a *G. brasilensis*. Scale bar = 200 μm.

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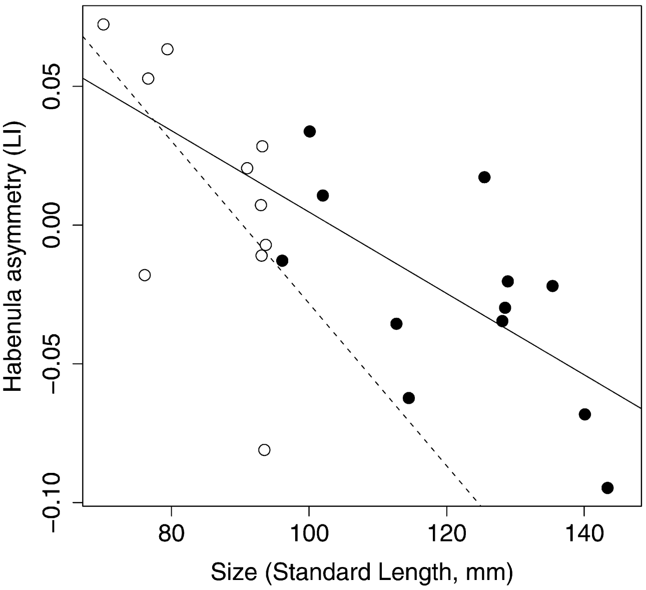

Fig. 3. The linear relationship standard length and habenular laterality index ($p < 0.01$). Males: closed circles and solid line; females: open circles and dashed line.

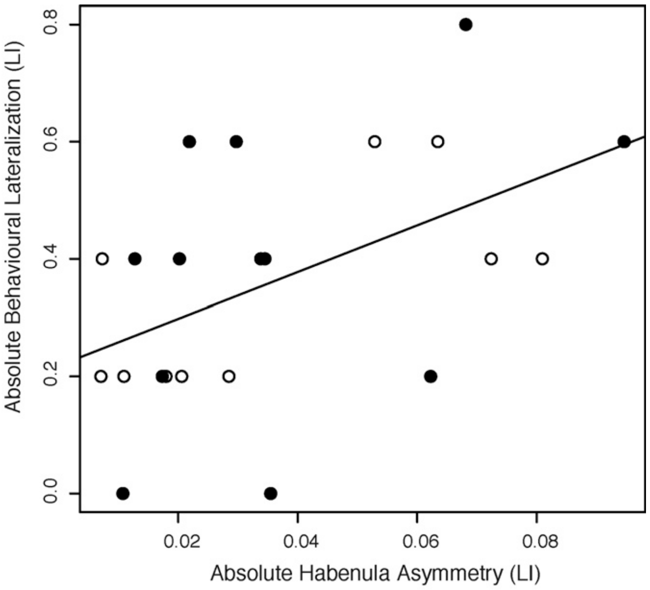

Fig. 5. The linear relationship between absolute habenular laterality index and absolute behavioural laterality index in all fish ($p = 0.018$).

covariance (ANCOVA) showed no effect of sex ($p = 0.41$) or interaction between sex and size ($p = 0.31$). We found no correlation between directional behavioural lateralization and size ($R^2 = 0.002$, $F_{(1,24)} = 0.05$, $p = 0.83$; Fig. 4a). We did however, find a positive correlation between size and the strength of behavioural lateralization for males but not females (males: $R^2 = 0.406$, $F_{(1,13)} = 8.88$, $p = 0.011$; females: $R^2 = 0.039$, $F_{(1,9)} = 0.890$, $p = 0.37$; Fig. 4b). We also found a positive correlation between the strength of habenular asymmetry and the strength of behavioural asymmetry ($R^2 = 0.496$, $F_{(1,20)} = 6.529$, $p = 0.019$; Fig. 5). An analysis of covariance revealed no sex difference ($F_{(1,18)} = 0.046$, $p = 0.83$) or interaction between sex and absolute habenular asymmetry effect ($F_{(1,18)} = 0.0067$, $p = 0.94$) on behavioural asymmetry.

We measured the COPn as a control nucleus and found no relationship between standard length and directional COPn asymmetry ($R^2 < 0.001$, $F_{(1,20)} < 0.001$, $p = 0.98$) or absolute COPn asymmetry ($R^2 = 0.01$, $F_{(1,20)} = 0.207$, $p = 0.65$). There was also no relationship between the directional asymmetry of the COPn and the directional asymmetry of the habenula ($R^2 = 0.08$, $F_{(1,16)} = 1.30$, $p = 0.27$), or between the magnitude of the COPn asymmetry and the magnitude of the habenular asymmetry ($R^2 = 0.07$, $F_{(1,16)} = 1.23$, $p = 0.29$). The COPn was not related to the directional ($R^2 = 0.01$, $F_{(1,20)} = 0.22$, $p = 0.64$) or the absolute strength ($R^2 = 0.001$, $F_{(1,20)} = 0.02$, $p = 0.90$) of the asymmetry in behavioural lateralization. In short, none of the effects seen in the habenula asymmetry were seen in the COPn asymmetry. There was a non-significant trend towards larger asymmetries in the habenula than the in COPn (mean absolute habenular LI = 0.04 ± 0.006, mean absolute COPn LI = 0.024 ± 0.003; paired $t = 1.93$, df = 17, $p = 0.071$).

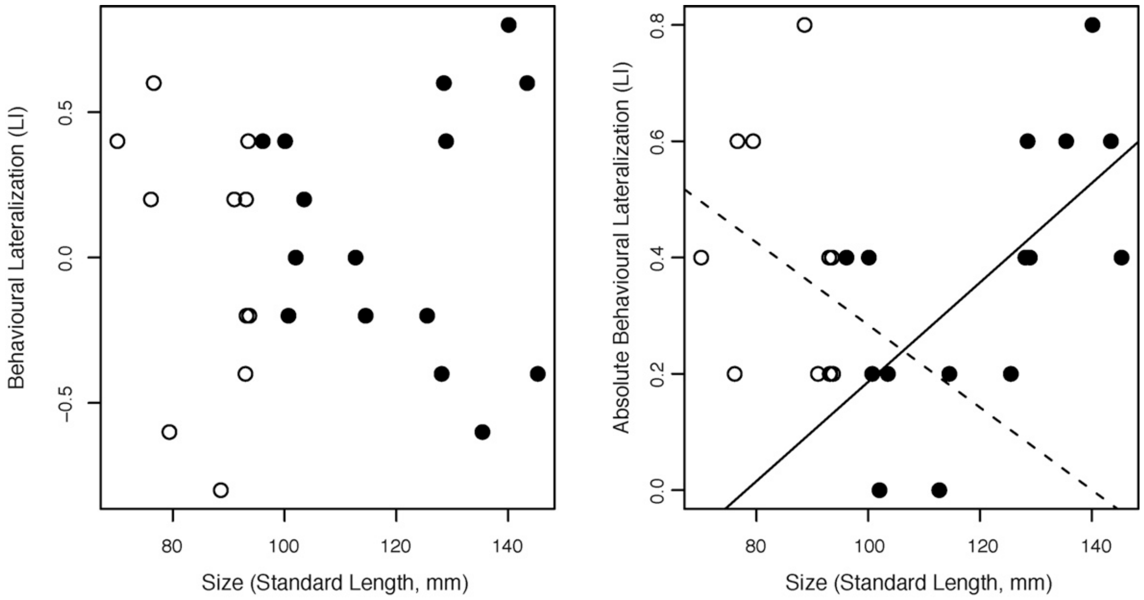

Fig. 4. The relationship between standard length and (a) behavioural laterality index, (b) absolute laterality index for behaviour (males: $p = 0.01$; females: $p = 0.37$). Males: closed circles and solid line; females: open circles and dashed line.

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4. Discussion

G. brasilensis showed variation in habenular asymmetry which correlated with body size. We suggest that the identical ages and growth environments of these fish mean that individual variation in size results from differences in growth rate and other growth depensation effects. The slowest growing animals within a cohort therefore have left-ward biased habenula while the fastest growing animals have a larger right habenula. Animals with a stronger habenular asymmetry also showed stronger behavioural asymmetry in the detour task. Neither of these effects is true of the other brain nucleus we measured. Males, but not females, that grew faster, demonstrated stronger behavioural lateralization than slower growing males. Females appeared to show a similar effect, slower growing females tended to show stronger behavioural lateralization, but this effect was not statistically significant. The smallest females and the largest males appear to have the strongest behavioural lateralization (Fig. 4), but the direction of the effect seems random at the individual level. Previous work on fish and other species has indicated that the strength, not the direction, of lateralization is correlated with other behavioural traits (e.g. [6,10,16,17,18,41,42,49]). The relationship between the direction of habenular asymmetry and the direction of behavioural asymmetry appears to be random at the individual level. In zebra fish, projections to the interpeduncular nucleus (IPN), the main target of the habenula in the midbrain, are bilateral [1]. This may help to explain why there is no correlation between the direction of habenular asymmetry and behavioural asymmetry, but data on the symmetry of these projections is lacking in all other teleost species.

Recently Andrew et al. [2] showed that light exposure during development affects the lateralization of behaviour in zebra fish and argue this was due to a direct effect of the parapineal organ on the habenula. In teleosts, the parapineal organ is an unpaired dorsal invagination from the diencephalon that expresses functional photoreceptors [4,28] and projects exclusively to the left habenula [64]. All individuals in this study were raised under identical light conditions, thus the individual differences we observed in behavioural, and habenular asymmetries are most likely do to other factors.

While the behavioural asymmetry appears to vary randomly in direction, the habenular asymmetry does not. The effect of body size on directional asymmetry, combined with the sexual size dimorphism means that it is primarily the females that are left biased, and males that are right biased (Fig. 3). There are at least two potential explanations for this effect, each is associated with a different sequence of sexual differentiation. First, it is possible that the fish begin with left biased asymmetries, and become more right biased as they grow. If males grow faster than females, then the effect is entirely due to growth rate and the males in this sample fell further along in the relationship between growth and habenular asymmetry. This assumes that sex is determined first, and implies that the apparent size transition between sexes coinciding with habenular symmetry is merely coincidental. Also coincidental in this explanation is the fact that the size variation effect shows no discontinuity at the sex transition.

An alternative explanation is that the variation in size, reflecting sex independent growth rate variation, determines both habenular asymmetry and sex. In the midas cichlid, another neotropical cichlid fish, primary sexual differentiation appears to be influenced, not by endogenous factors intrinsic to each sex, but by each individual's place in the size hierarchy of its cohort early in life [26]. Thus, sex does not determine growth rate, growth rate determines sex. In this scenario, the largest males would be the most ‘male-like’ of their cohort and the smallest females the most ‘female-like’, and the habenula would be the most symmetrical in the least strongly differentiated animals. These symmetrical animals may be seen as those that are close to the sex determining cutoff. As with the vast majority of cichlid species, it is completely unknown how sexual determination and primary sexual differentiation occurs in *G. brasilensis*.

Sexual differentiation is known to have important effects on both lateralized behaviour [44], and habenular asymmetries [14]. In chickens the medial habenula demonstrates a sex-dependent asymmetry, where males always have a larger right side while females may be larger on either right or left side [31]. Treatment with testosterone during development has no effect in males, but induces male-typical rightward asymmetries in females [32]. In frogs, the asymmetry of the habenula increases during the reproductive season, especially in females [35]. Sexual hormones have been shown to affect the development of other brain asymmetries [21,25].

Animals that are more strongly sexually differentiated may represent individuals playing a more risk-prone life-history strategy focused on proximate reproductive gains. For males this may mean growing quickly by taking additional risks in order to successfully compete with other males [5,52]. Bolder fish within a population are known to have higher growth rates than individuals that are more risk averse [27,38,62]. *G. brasilensis* individuals with the strongest habenular lateralization (the smallest females and the largest males) also had the strongest behavioural lateralization (Fig. 5). Behavioural lateralization may be a reflective of a life-history strategy focused on current reproductive gains [42]. The fastest growing males also had the strongest behavioural lateralization (Fig. 4b), indicating that there may be a relationship between growth rates and laterality that is mediated by life-history strategy.

Teleosts are unique among the so-called “lower” vertebrates in that many species have relatively symmetrical habenulas, and those species that are asymmetrical may be left or right biased [14]. The fish in this cohort appear to show all three of these possible conditions. Selection favoring higher growth rates in this population could result in populations with bigger right habenulas, while selection for reduced growth rates could produce populations with larger left habenula. Such an effect may account for some of the variation in the direction of the habenular asymmetry between closely related species of teleosts. For example, the coho salmon (*Oncorhynchus kisutch*) has bigger left habenula [14] while rainbow trout (*Oncorhynchus mykiss*) have bigger right habenulae [14,64]. A phylogenetic analysis of habenular asymmetry in the salmonids may reveal life-history traits accounting for this variation.

In conclusion, we show that asymmetry in the habenula is correlated with relative growth rate and the strength of behavioural lateralization in the detour task. We suggest that this relationship results from processes linking growth rate and sexual differentiation to frequency dependent variation in life-history strategies.

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References

[1] Aizawa H, Bianco IH, Hamaoka T, Miyashita T, Uemura O, Concha ML, et al. Laterotopic representation of left-right Information onto the dorso-ventral axis of a zebrafish midbrain target nucleus. Curr Biol 2005;15: 238–43.

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[2] Andrew RJ, Dharmaretnam M, Győri B, Miklósi A, Watkins JAS, Sovrano VA. Precise endogenous control of involvement of right and left visual structures in assessment by zebrafish. Behav Brain Res 2008;196:99–105.
[3] Barth KA, Miklosi A, Watkins J, Bianco IH, Wilson SW, Andrew RJ. fsi zebrafish show concordant reversal of laterality of viscera, neuroanatomy, and a subset of behavioral responses. Curr Biol 2005;15:844–50.
[4] Bertolucci C, Foà A. Extraocular photoreception and circadian entrainment in non-mammalian vertebrates. Chronobiol Int 2004;21:501–51.
[5] Biro PA, Stamps JA. Are animal personality traits linked to life-history productivity? Trends Ecol Evol 2008;23:361–8.
[6] Bisazza A, Dadda M. Enhanced schooling performance in lateralized fishes. Proc R Soc B 2005;272:1677–81.
[7] Bisazza A, Pignatti R, Vallortigara G. Laterality in detour behaviour: interspecific variation in poeciliid fish. Anim Behav 1997;54:1273–81.
[8] Bisazza A, Rogers LJ, Vallortigara G. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. Neurosci Biobehav Rev 1998;22:411–26.
[9] Bradford MRJ, Northcutt RG. Organization of the diencephalon and pretectum of ray-finned fishes. In: Higher brain areas and functions. In: Davis RE, Northcutt RG, editors. Fish neurobiology, vol. 2. Ann Arbor, USA: University of Michigan Press; 1983. p. 117–63.
[10] Branson NJ, Rogers LJ. Relationship between paw preference strength and noise phobia in *Canis familiaris*. J Comp Psych 2006;120:176–83.
[11] Brown C. Cerebral lateralization and "social constraints" and coordinated antipredator responses. Behav Brain Sci 2005;28:591–2.
[12] Brown C, Western J, Braithwaite VA. The influence of early experience on, and inheritance of cerebral lateralization. Anim Behav 2007;74:231–8.
[13] Cole WC, Youson JH. Morphology of the pineal complex of the anadromous sea lamprey, *Petromyzon marinus* L. Am J Anat 1982;165:131–63.
[14] Concha ML, Wilson SW. Asymmetry in the epithalamus of vertebrates. J Anat 2001;199:63–84.
[15] Corballis MC. Cerebral asymmetry: a question of balance. Cortex 2006;42: 117–8.
[16] Corballis MC. Of mice and men—and lopsided birds. Cortex 2008;44:3–7.
[17] Dadda M, Bisazza A. Does brain asymmetry allow efficient performance of simultaneous tasks? Anim Behav 2006;72:523–9.
[18] Dadda M, Bisazza A. Lateralized female topminnows can forage and attend to a harassing male simultaneously. Behav Ecol 2006;17:358–63.
[19] De Santi A, Sovrano VA, Bisazza A, Vallortigara G. Mosquitofish display differential left- and right-eye use during mirror image scrutiny and predator inspection processes. Anim Behav 2001;61:305–10.
[20] Dharmaretnam M, Rogers LJ. Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. Behav Brain Res 2005;162:62–70.
[21] Diamond MC, Johnson RE, Ingham CA. Morphological changes in the young, adult and aging rat cerebral cortex, hippocampus, and diencephalon. Behav Biol 1975;14:163–74.
[22] Facchin L, Argenton F, Bisazza A. Lines of *Danio rerio* selected for opposite behavioural lateralization show differences in anatomical left-right asymmetries. Behav Brain Res 2009;197:157–65.
[23] Facchin L, Bisazza A, Vallortigara G. What causes lateralization in detour behaviour in fish? Evidence for asymmetries in eye use. Behav Brain Res 1999;103:229–34.
[24] Fernald RD, Shelton LC. The organization of the diencephalon and the pretectum in the cichlid fish, *Haplochromis burtoni*. J Comp Neurol 1985;238:202–17.
[25] Fleming D, Anderson RH, Rhees R, Kinghorn E, Bakaitis J. Effects of prenatal stress on sexually dimorphic asymmetries in the cerebral cortex of the male rat. Brain Res Bull 1986;16:395–8.
[26] Francis RC, Barlow GW. Social-control of primary sex-differentiation in the Midas cichlid. PNAS 1993;90:10673–5.
[27] Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalaski GT. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. Am Nat 2001;158:124–35.
[28] Garcia-Fernandez JM, Jimenez AJ, Gonzalez B, Pombal MA, Foster RG. An immunocytochemical study of encephalic photoreceptors in three species of lamprey. Cell Tissue Res 1997;288:267–78.
[29] Ghirlanda S, Vallortigara G. The evolution of brain lateralization: a game-theoretical analysis of population structure. Proc R Soc B 2004;271:853–7.
[30] Güntürkün O. Morphological asymmetries of the tectum opticum, in the pigeon. Exp Brain Res 1997;116:561–6.
[31] Gurusinghe CJ, Zappia JV, Ehrlich D. The influence of testosterone on the sex-dependent structural asymmetry of the medial habenular nucleus of the chicken. J Comp Neurol 1986;253:153–62.
[32] Gurusinghe CJ, Ehrlich D. Sex-dependent structural asymmetry of the medial habenular nucleus of the chicken brain. Cell Tissue Res 1985;240:149–52.
[33] Hori M. Frequency-dependent natural selection in handedness of scale-eating cichlid fish. Science 1993;260:216–9.
[34] Kaarthigeyan J, Dharmaretnam M. Relative levels of motivation and asymmetries of viewing and detour task in guppies (*Poecillia reticulata*). Behav Brain Res 2005;159:37–41.
[35] Kemali M, Guglielmotti V, Fiorino L. The asymmetry of the habenular nuclei of female and male frogs in spring and in winter. Brain Res 1990;517:251–5.
[36] Keenleyside MHA. Parental care. In: Keenleyside MHA, editor. Cichlid fishes: behaviour, ecology and evolution. Cambridge, United Kingdom: Chapman & Hall; 1991. p. 191–208.
[37] Klemm WR. Habenular and interpeduncularis nuclei: shared components in multiple-function networks. Med Sci Monit 2004;10:261–73.
[38] Magnhagen C, Staffan F. Social learning in young-of-the-year perch encountering a novel food type. J Fish Biol 2003;63:824–9.
[39] Nottebohm F. Asymmetries in neural control of vocalization in the canary. In: Harnad S, Doty RW, Goldstein L, Jaynes J, Krauthamer G, editors. Lateralization in the nervous system. New York, USA: Academic Press; 1997. p. 23–44.
[40] Nieuwenhuys R. Chondrostean fishes. In: Nieuwenhuys R, ten Donkelaar HJ, Nicholson C, editors. The central nervous system of vertebrates, vol. 1. Berlin, Germany: Springer; 1998. p. 701–58.
[41] Reddon AR, Hurd PL. Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. Biol Lett 2008;4:338–40.
[42] Reddon AR, Hurd PL. Individual differences in cerebral lateralization are associated with shy-bold variation in the convict cichlid. Anim Behav 2009;77:189–93.
[43] Rogers LJ. Evolution of hemispheric specialization: advantages and disadvantages. Brain Lang 2000;73:236–53.
[44] Rogers LJ, Andrew RJ, editors. Comparative vertebrate lateralization. Cambridge, United Kingdom: Cambridge University Press; 2002.
[45] Rogers LJ, Deng C. Light experience and lateralization of the two visual pathways in the chick. Behav Brain Res 1999;98:277–87.
[46] Rogers LJ, Zucca P, Vallortigara G. Advantages of having a lateralized brain. Proc R Soc B 2004;271(Suppl.):S420–2.
[47] Sandyk R. Relevance of the habenular complex to neuropsychiatry: a review and hypothesis. Int J Neurosci 1991;61:189–219.
[48] Smeets WJAJ, Nieuwenhuys R, Roberts BL. The central nervous system of cartilaginous fishes. Structure and functional correlations. Berlin, Germany: Springer; 1983.
[49] Sovrano VA, Dadda M, Bisazza A. Lateralized fish perform better than nonlateralized fish in spatial reorientation tasks. Behav Brain Res 2005;163:122–7.
[50] Sovrano VA, Andrew RJ. Eye use during viewing a reflection: behavioural lateralisation in zebrafish larvae. Behav Brain Res 2006;167:226–31.
[51] Sovrano VA, Rainoldi C, Bisazza A, Vallortigara G. Roots of brain specializations: preferential left-eye use during mirror-image inspection in six species of teleost fish. Behav Brain Res 1999;106:175–80.
[52] Stamps JA. Growth-mortality tradeoffs and 'personality traits' in animals. Ecol Lett 2007;10:355–63.
[53] Sutherland RJ. The dorsal diencephalic conduction system: a review of the anatomy and functions of the habenular complex. Neurosci Biobehav Rev 1982;6:1–13.
[54] Takeuchi Y, Hori M. Behavioural laterality in the shrimp eating cichlid fish *Neolamprologus faciatus* in Lake Tanganyika. Anim Behav 2008;75:1359–66.
[55] Vallortigara G. Cerebral lateralization: a common theme in the organization of the vertebrate brain. Cortex 2006;42:5–7.
[56] Vallortigara G. The evolutionary psychology of left and right: costs and benefits of lateralization. Devel Psychobiol 2006;48:418–27.
[57] Vallortigara G, Bisazza A. How ancient is brain lateralization? In: Rogers LJ, Andrew RJ, editors. Comparative vertebrate lateralization. Cambridge, United Kingdom: Cambridge University Press; 2002. p. 9–69.
[58] Vallortigara G, Rogers LJ. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. Behav Brain Sci 2005;28:575–633.
[59] Vallortigara G, Rogers LJ, Bisazza A. Possible evolutionary origins of cognitive brain lateralization. Brain Res Rev 1999;30:164–75.
[60] Van Eden CG, Uylings HBM, Van Pelt J. Sex differences and left-right asymmetries in the prefrontal cortex during postnatal development in the rat. Dev Brain Res 1984;12:146–53.
[61] Walker SF. Lateralization of functions in the vertebrate brain. Br J Psychol 1980;71:329–67.
[62] Ward AJW, Thomas P, Hart PJB, Krause J. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). Beahv Ecol Sociobiol 2004;55:561–8.
[63] Wicht H, Northcutt RG. The forebrain of the Paciphic hagfish: a cladistic reconstruction of the ancestral craniate forebrain. Brain Behav Evol 1992;40:25–64.
[64] Yanez J, Meissl H, Anadon R. Central projections of the parapineal organ of the adult rainbow trout (*Oncorhynchus mykiss*). Cell Tissue Res 1996;285:69–74.