Consistency among different tasks of left–right asymmetries in lines of fish originally selected for opposite direction of lateralization in a detour task

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Received 6 March 2000; received in revised form 4 January 2001; accepted 12 February 2001

Abstract

Lines of fish, Girardinus falcatus preferentially turning rightward (RD) or leftward (LD) when facing a dummy predator visible behind a barrier have been obtained through selective breeding. To check whether lateralization was maintained in other behavioral responses, five different tests were carried out. They comprised measures of (1) turning direction in a T-maze; (2) proportion of clockwise and anticlockwise direction of rotation in a circular arena; (3) preferential eye use by females during shoaling behavior (i.e. while looking at their own mirror image reflection); (4) preferential eye use by males during sexual behavior (i.e. while turning around a barrier to join a group of females); and (5) preferential eye use by males during agonistic behavior (i.e. while attacking a rival visible in a mirror). In all five tests the two selected lines showed opposite direction of lateralization. Results thus indicate that behavioral asymmetries in the detour test are predictive of lateralization in other types of behavioral tests. Moreover, results show that RD and LD fish have a similar but left–right reversed pattern of subdivision of cognitive/behavioral functions, which is suggestive of a similarly left–right reversed (mirror image) brain organization. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Genetic of lateralization; Fish; Behavioural asymmetry; Asymmetric eye use; Laterality; Evolution of lateralization

1. Introduction

For a long time brain lateralization has been considered a characteristic unique to the human species, associated with language and handedness. In the last 20 years, however, evidence showing that functional and structural lateralization of the brain is widespread among vertebrates [14] including fish, reptiles and amphibians [11,38,39] has accumulated rapidly. The genetic bases of cerebral lateralization are, however, poorly understood. Studies with animals have been mostly confined to the mouse model of pawedness. It has been claimed that within an inbred strain, approximately half the mice are left pawed and half are right pawed; among different strains, the left–right direction of paw preference seems not to be genetically determined [17,18]. In contrast, the degree of lateralization of paw preference appears to be genetically determined, as demonstrated by the fact that both strains highly and weakly lateralized can be selected starting from a heterogeneous stock [18,19]. In apparent distinction to mice studies, human handedness has generally shown significant, though low, parent–offspring correlations for direction of handedness [17], whereas it is uncertain whether there is heritability for degree of handedness [3,17,24,26].

More recent research on animal lateralization suggests, however, that the difference between human and non-human lateralization is not clear-cut. The claim that pawedness in mice exists only at the individual, but not population, level has been questioned. Waters and Denenberg [40] found that when large samples of in-
bred mice were used, a significant right pawedness on a lateral paw preference test and a left pawedness on another reaching test were observed. Moreover, it has been claimed that in some strains of mice the direction of paw usage may also be genetically determined [4,5]. Research in other species is scanty. Heritability of hand preference has been observed in chimpanzees [22], but interspecies cross-fostering experiments suggest that it is not due to genetic mechanisms [23]. Westergaard and Suomi [41] investigated lateral biases for looking, reaching and turning in capuchin monkeys. They found evidence for maternal and paternal contributions to the direction of looking bias, but no evidence for contribution of either parent to the direction of reaching bias. These authors also found evidence of differential maternal and paternal contributions to the direction of offspring turning bias. No evidence of parental contribution to the strength of lateral bias for any of such measures was observed. This strongly suggests the opportunity to move from handedness to other, different measures of behavioral laterality in non-human species.

Handedness in humans is likely to be multi-determined, but it is not the only possible behavioral manifestation of cerebral lateralization. Actually, because of obvious differences in external morphology, in most non-human species we are bound to employ behavioral measures of laterality which are different from the traditional preferences in limb usage. In fish, for instance, behavioral lateralization at the population level has recently been reported from several laboratories (reviewed in [11]). The poeciliid *Girardinus falcatus* has been studied quite extensively (reviewed in [39]). This fish show consistent population biases to detour a vertical-bar barrier through which a target-stimulus is visible. The direction taken depends on the nature of the stimulus used and it is determined by eye preference during visual scrutiny of the stimulus [21]. Using a dummy predator, *G. Falcatus* turn preferentially leftward (at the population level, leftward turning occurs with a frequency of approx. 65%); similarly, they use the right eye preferentially during free fixation of the same, potentially dangerous, object [21,12].

Though the direction of lateral bias appears to be consistent in different experiments [9,10,12] and even among closely related species [10,13], large individual variability in the natural populations is obviously present. Bisazza et al. [8] have shown the existence of a strong correlation between parents and offspring in the direction of lateral bias with an estimate heritability exceeding 0.5. We thus started a selective-breeding program to produce lines of fish showing opposite directions of turning in the detour test (the dummy predator was used as the target-stimulus in the behavioral test). Data relative to the initial generations indicate a significant response to selection in all lines and a similar response in the two directions ([38], Bisazza et al., in prep.). These findings suggest a major role of genetic factors in the determination of the direction of the lateral bias in these fish, a phenomenon that, up to now, has been claimed to occur only in human species [2,3,20] and maybe in one species of non-human primates [41].

An open issue, however, is whether individuals of different selected lines differ in the direction of lateralization for a single specific function (the one involved in the particular test used) or selection has occurred for the overall left–right organization of the brain, thus producing consistently different patterns of laterality in a variety of different behavioral tests. The issue is crucial even with respect to human lateralization. It has been claimed that in normal subjects there seems to be no correlation between the strength of different forms of lateralization in the individuals [16]. Different functions may well be lateralized in the two hemispheres by relatively independent mechanisms and apparent complementarity of functions may be a statistical phenomenon, only occurring because a majority of the population is left-hemisphere dominant for verbal tasks and right-hemisphere dominant for visuo-spatial tasks [15,27]. However, the issue remains controversial because some recent studies reported correlations (though quite low) between the strength of different forms of lateralization (e.g. [32]) and in animals it has been found that arousal can mediate the relations between different forms of lateralization [34]. Moreover, it should be noted that in humans there are no equivalents of artificially selected lines for direction of lateralization.

Here we tried to address these issues using the animal model provided by our fish. *G. falcatus* selected for opposite direction of laterality in the detour test underwent five different behavioral tests (three measuring visual lateralization, two motoric lateralization), in order to check for generality and consistency of their left–right asymmetries.

2. Methods

Fish used in this study were males and females of *Girardinus falcatus*. In all five tests we compared two groups of fishes with opposite laterality in the detour test. Left detour (LD) fish turned 80% or more leftward in the detour test; right detour (RD) fish turned 80% or more rightward in the detour test. Individuals were maintained in small heterosexual groups (10–15 fish) of the same laterality, kept in 70-l glass aquaria with abundant vegetation (*Ceratophillum* sp.).

The procedure of the detour test has been described in detail elsewhere [9,10,12]. Briefly, the apparatus consisted of a large tank with a swimway in the middle
allowing the fish inside to face, at both ends of the swimway, a vertical-bar barrier behind which the visual stimulus was located. The visual stimulus consisted in a dummy-predator: a fish lure used for open sea fishing. Fish were scored in the detour test as part of a selection program to obtain lines with different laterality ([38], Bisazza et al., in prep.). We used fish of second, third and fourth generation from four lines (two RD and two LD) after they produced their second litter (approx. 5–6 months old).

Interrater reliability for three tests (Turning direction in T-maze, Rotational preference and Eye use by shoaling females) was determined from videotapes in a reduced sample of the subjects. Scoring was done by two independent raters. Pearson’s correlation coefficients were respectively $r = 0.97 (n = 12)$, $r = 0.99 (n = 12)$ and $r = 0.98 (n = 12)$; $P < 0.01$ for all measurements. The two other experiments (Males’ eye preferences in scrutinizing females and Males’ eye preferences during intrasexual attacks) were scored by two independent raters. Interrater reliability was respectively $r = 0.94 (n = 20)$ and $r = 0.99 (n = 20)$; $P < 0.01$ for all measurements. Since there was good interrater agreement only the results for Rater I are given.

2.1. Turning direction in a T-maze

Thirty RD (12 males and 18 females) and 30 LD (14 males and 16 females) fish were used for this experiment.

The apparatus consisted of a large tank ($60 \times 94 \times 36$) with a swimway in the middle. At the each end of the swimway a bifurcation with an opaque barrier forced the fish to turn either right or left to enter the large end compartment (see Fig. 1). The fish was initially introduced in one of the end compartments (randomly chosen) for 3 min in order to become accustomed to the environment; then the fish was gently pushed using a pair of fish-nets at the starting point of the swimway. The fish thus moved along the swimway and, when reaching the end, it made a turning choice. The left or right direction of turn taken by the fish when leaving the swimway was recorded. The procedure was repeated in the opposite direction until 10 consecutive trials were completed. Lateral asymmetries were analyzed by computing for each subject the percentage of clockwise rotation.

2.2. Rotational preference

Ten RD (5 males and 5 females) and 10 LD (5 males and 5 females) fish were used for this experiment.

Rotational preferences have been used to measure behavioral laterality in several species of mammals (reviewed in [14]) and more recently in teleost fishes [7]. The procedure used in this study is the same employed for testing another species of fish, Gambusia holbrooki (see [6,7] for details). The experiment was carried out in a completely darkened room. The apparatus consisted in a circular arena of a white plastic material (50 cm in diameter and 75 cm high) filled with 15 cm of water and lit from above with a single lightbulb (100 W) located in the center. Each fish was dip-netted in its aquarium and transported in a small container into an adjacent room where it was introduced into the experimental tank and kept in there in darkness for 30 s in order to become accustomed to the novel environment. Then the lightbulb was switched on and the behavior of the fish was video recorded for 10 min. Lateral asymmetries were analyzed from videorecording by computing for each subject the percentage of clockwise rotation.

2.3. Eye use by shoaling females

The subjects used for this experiment were 19 adult females (9 RD and 10 LD).

The eye preferentially used to look at a companion fish was measured using the mirror test [36]. In the test, the companion-image is actually provided by the mirror image of the subject itself. Only females were used in this test, because males show little affiliative tendencies in this species (see below for a different use of mirror stimulation in males).

Testing was performed within a tank ($44 \times 22$ cm) with mirrors as the two longer walls and opaque screens as the shorter walls. The tank was lit from above by a fluorescent lamp (18 W); water was 25 cm deep. Above the testing apparatus a video camera was
mounted in order to videotape the fish behavior. Each fish was tested singly, by placing it into the test apparatus and video recording its behavior for 10 min. Fish positions were scored from videotapes every 2 s; two measures were taken: (1) the eye used to look at the mirror while the fish swam parallel to its own image; and (2) the eye used to look at the mirror, with an angle included between 0 and 90°, when the fish was in a stationary position or during attempts to approach and touch the mirror image. Previous evidence has shown that the two body postures which are most usual in fish during fixation of a target are the one in which the fish is ‘oblique’ to the target (approx. 0–20°) [30] and the one in which it is ‘parallel’ to the target (e.g. during swimming in school).

2.4. Males’ eye preferences in scrutinizing females

Subjects used for this experiment were 20 adult males (10 RD and 10 LD).

Eye preferences of males when they turned around a barrier to join a group of females were measured. Males of *G. falcatus* usually stop their sexual activity when placed in a novel environment [12]. In order to circumvent this problem, fish were tested in their home tank. The apparatus consisted in a glass tank (68 × 68 × cm). A double-funnel-shaped central compartment (see Fig. 2a) was obtained with glass panels. A vertical-bar barrier (17 × 17 cm, ‘B’ in Fig. 2a) was located at the end of the small (10 cm in length and 6.5 cm in size) central corridor of the double-funnel-shaped area. The bars (2.5 mm in diameter, spaced 2.5 mm apart) were made of yellow cylindrical plastic material. In front of the apparatus was located a small tank (20 × 20 × 20 cm) that contained two females, forced to remain in a central position by means of two glass panels (see Fig. 2a). Green opaque plastic screens covered all the walls of both tanks to prevent the animals from looking outside; the apparatus was located in a darkened room and two one-way mirrors were placed over both tanks allowing the experimenter to monitor the behavior of fish without being seen.

The day before the experiment one male (the experimental animal) and one female were inserted in the central compartment of the larger tank. Observations were made ten minutes every hour to ascertain whether the male have started normal sexual activity. Males that did not show sexual behavior within 6 h were not considered for the experiment and substituted with another animal that underwent the same procedure. Then the female was removed from the larger tank leaving the male alone. The smaller tank, without any fish, was made visible by removing an opaque panel that occluded it. This was done to habituate the test animal to the sight of the novel environment. The following day the opaque panel was briefly (10 min) reinserted to allow the experimenter to locate two (novel) females in the small tank. The panel was then removed while the experimental subject was in the back portion (close to the filter) of the larger tank. At this point the male could notice the females and, moving along the small corridor, turn around the barrier to join them. The eye used by the male to fixate the females when it came out from the corridor was recorded during 20 consecutive trials (inter-trial interval approx. 10 min). The panel was then lowered again and, after an inter-trial interval of 10 min, the entire procedure was repeated.

2.5. Males’ eye preferences during intrasexual attack

Subjects used for this experiment were 20 adult males (10 RD and 10 LD).

Males were tested for eye preference while attacking a rival. Eye preference was measured by recording the direction taken by a fish while approaching a mirror placed in its home tank. The apparatus consisted in a glass tank (68 × 68 × 35 cm), located in a...
darkened room, comprising a large area (top in Fig. 2b) and a small area that were connected by a corridor (see Fig. 2b). Green opaque plastic screens covered the walls of the tank. A one-way mirror (OM in Fig. 2b), placed in the frontal portion of the apparatus, provided the stimulus image for the testing fish and was used by the experimenter, from the outside, for observation. Thick vegetation, placed in the large area, provided females with refuge. Three females were kept in the tank at least 48 h before the test. Females were fed only in the back portion of the apparatus, so that the area with the thick vegetation was rarely left by them. A single male was inserted in the apparatus and left in there overnight in order to become accustomed to the environment. The following day, after a check of sexual activity by the male, eye preferences while attacking the ‘rival’ image in the mirror was measured. This was done by observing body turning (allowing use of the monocular field of the left or right eye) when the fish went out from the small corridor (which forced the fish to maintain a perpendicular orientation which was immediately lost at the exit) and approached the mirror to attack its own image. After the fish come in contact with the mirror an opaque screen was interposed between the mirror and the tank until the male abandoned the area and moved to the rear of the apparatus. Then the screen was removed to allow the next observation. Seventy successive observations were performed. Only aggressive approaches were taken into consideration, i.e. those preceded by aggressive display (lowering of the gonopodium and spreading of the fins). To check whether the one-way mirror actually provided the proper stimulation, at the end of the experiment 20 additional observations were carried out using as a stimulus a real male conspecific. The one-way mirror was removed and substituted with a glass through which the testing fish could fixate the conspecific. The conspecific was confined in the center of a small glass thank; to avoid any bias produced on the test fish by the posture adopted by the conspecific itself, the latter was maintained in a perpendicular position by use of transparent flanking plastic walls.

2.6. Data analyses

In the first two tests, turning direction and rotational preferences, percentages of rightward and leftward turning and of clockwise and anticlockwise direction of rotation were measured. In the other three tests, percentages of left and right eye use were measured. For all these measures, departures from chance level (50%) were estimated by one-sample two-tailed t-tests. Differences between the two lines of fish and between sexes were estimated by analysis of variance or by t-tests.

3. Results

3.1. Overall comparison of the two lines in the five tests

Overall differences between lines in the direction of laterality (Fig. 3) were analyzed by two factors ANOVA (selected line × type of experiment). No statistically significant main effect was found (selected line, $F_{1,129} = 3.06$; type of experiment, $F_{4,129} = 1.03$) but there was a highly significant interaction (lines × experiment, $F_{4,129} = 18.6$; $P < 0.001$) because the direction of the difference changes in each test.

We also examined the degree of lateralization exhibited by the two lines in different tests to check whether
differences in the strength of lateralization could be observed. We used a factorial design with selected lines and type of experiment as factors and found that there were no statistically significant effects (selected lines: \( F_{1,129} = 0.71 \); type of experiment: \( F_{4,129} = 0.19 \); lines \& experiment: \( F_{4,129} = 0.74 \)).

3.2. Turning direction in T-maze

In the T-maze (Fig. 3 top), RD fish tended to turn right (mean \( \pm \) S.D.: 58.7 \( \pm \) 23.3\%; \( t_{20} = 2.06; P = 0.048 \)) and LD fish to turn left (mean \( \pm \) S.D.: 31.3 \( \pm \) 21.1\%; \( t_{29} = -4.83; P < 0.001 \); Fig. 3a). A two-way analysis of variance revealed a highly significant difference between RD and LD fish (\( F_{1,56} = 21.88; P < 0.001 \)) but no gender difference (\( F_{1,56} = 0.14 \); ns) nor interaction (\( F_{1,56} = 0.08 \); ns).

3.3. Rotational preference

LD and RD fish lines differed in the preferred direction of rotation. LD fish rotated more often clockwise (mean \( \pm \) S.D.: 59.3 \( \pm \) 20.8\%; \( t_{9} = 1.41; P = 0.19 \); Fig. 3 top) while RD fish showed the opposite tendency (mean \( \pm \) S.D.: 37.1 \( \pm \) 16.3\%; \( t_{9} = -2.5; P = 0.034 \)). A two-way analysis of variance showed that there was a significant difference between RD and LD fish (\( F_{1,16} = 6.29; P = 0.023 \)) but no gender differences (\( F_{1,16} = 0.09 \); ns) or interaction (\( F_{1,16} = 0.01 \); ns).

3.4. Eye use by shoaling females

On average we measured 34.3 \( \pm \) 14.1 observations with parallel position and 218 \( \pm \) 41.8 observations with angular position. While swimming along the mirror in a parallel position, RD fish tended to keep their mirror image on the left side while LD fish did the reverse (Fig. 3 middle). Right eye use (RE) amounted to 38.9 \( \pm \) 16.6\% (\( t_{8} = -2.01; P = 0.079 \)) in RD fish and to 66.9 \( \pm \) 13.4\% (\( t_{3} = 3.98; P = 0.003 \)) in LD fish (Fig. 3 middle). The difference between RD and LD fish was highly significant (\( t_{17} = 4.07; P < 0.001 \)). When considering the time spent by fish turned toward the mirror in an angular position, there was still a statistical difference in eye preference (\( t_{17} = 2.33; P = 0.032 \)), but this time in the opposite direction (RD fish: 54.5 \( \pm \) 5.1\%; \( t_{8} = 2.62; P = 0.031 \); LD fish: 43.8 \( \pm \) 12.8\%; \( t_{9} = -1.53; P = 0.161 \)).

It could be that the opposite lateralities observed during parallel and oblique body positions reflect differently lateralized mechanisms associated with stimulation of different areas of the retinae; temporal and nasal areas of high cone density are present in the retina of several species of fish [30]. However, whatever the mechanisms producing these different lateralization patterns, the important thing in this context is that the two selected lines of fish showed opposite (mirror-image) direction of lateralization with both body positions.

3.5. Males’ eye preferences in scrutinizing females

While approaching females, RD males used more often the right eye (68 \( \pm \) 10.8\% of right eye use; \( t_{9} = 5.24; P < 0.001 \)), while LD males used more often the left eye (36.5 \( \pm \) 10\% of right eye use; \( t_{9} = -4.26; P < 0.002 \); Fig. 3 bottom). The difference between RD and LD males was highly significant (\( t_{18} = 6.75; P < 0.001 \)).

3.6. Males’ eye preferences during intrasexual attacks

When tested for eye preference while attacking a rival RD males used more often the left eye (37.6 \( \pm \) 13.7\% of right eye use; \( t_{9} = -2.87; P = 0.018 \)) while LD males used more often the right eye (62 \( \pm \) 10.5\% of right use; \( t_{9} = 3.6; P = 0.006 \); Fig. 3 bottom). The difference between RD and LD males was highly significant (\( t_{18} = 4.48; P < 0.001 \)). Similar results were obtained when using a natural male conspecific as the stimulus-target (RD: 38.7 \( \pm \) 17.3\%; LD: 62.4 \( \pm \) 21.1\%; \( t_{18} = 2.75; P = 0.013 \)); the correlation between the measures in the two conditions was statistically significant (\( r = 0.66; P = 0.002 \)).

4. Discussion

In all five tests RD and LD selected lines showed opposite direction of lateralization. This extends and confirms a previous study [21] showing opposite eye preferences between RD and LD individuals in a viewing test in which a dummy predator and a more neutral stimulus (a red ball) were used. Overall, the results indicate that the two different directions of lateralization exhibited by the selected lines of fish are strongly correlated with each other and that behavioral asymmetries in the detour test are predictive of laterality in other, very different, behavioral tests. Another striking feature that emerges in all five tests of laterality (as well as in the two viewing tests of Facchin et al. [21]) is that the average laterality of RD and LD fish has almost identical value, though opposite in direction. There seems to be a difference here with respect to human handedness, for right-handers seem to be more consistently lateralized on other measures of laterality than left-handers are [15,20,27]. However, the behavioral lateralizations studied here may bear a closer resemblance to other forms of cerebral lateralization in humans (e.g. perceptual and cognitive lateralization).

If one assume that the nature of the behavioral functions measured in these tests was different, then the results might suggest that RD and LD fish have an
identical, though left–right reversed (i.e. mirror image), pattern of localization of cognitive/behavioral functions in the left and right side of their brains. Alternatively, it could be claimed that the behavioral tests all measure essentially the same basic function. Three of the tests employed directly measured eye preferences, while the performance in the remaining two tests could be at least affected by eye preferences [7,9]. Thus, it could be that the genetic lines selected for turning left or right in the detour test differ for the localization of a single function which is affecting a variety of behavioral tests. The nature of this hypothetical common function would remain, however, quite obscure. It is clearly not a generic preference to use one eye, because the direction of the bias is affected by the type of stimulus scrutinized and, even when the physical stimulus is the same (e.g. mirror image reflection) it generates different lateral biases depending on the behavior elicited and on the gender of the animals. LD fishes, for instance, use the right-eye system to monitor a predator or when they attack a rival. The left-eye system is used in contrast to scrutiny a novel neutral stimulus [21] and in males to monitor females while approaching. The pattern relative to social stimuli is less clear, but still pointing to differential specializations. Shoaling females (LD lines) apparently prefer to maintain their companion visible on the right side, while, when in front of their mirror image, they show a left eye preference. RD fish do exactly the reverse. Note that the analysis of fish with intermediate scores at the detour test (i.e. fish showing no consistent left–right preferences) is not considered in this work. In the study of Facchin et al. [21] these fish exhibited a smaller degree of laterality and a stronger tendency to alternate the use of the left and right eye with all types of stimuli. Interestingly, their progeny showed a similar lack of laterality, suggesting that the genetic pattern of the overall natural population composition should be quite complicated.

It would be of interest to compare the fish pattern which emerges from these experiments with what is known about complementarity of lateralization of functions in humans, in particular with respect to handedness and its association with cerebral dominance [15,27]. There are two problems with such a comparison, however. First, differently from the fish data, where highly inbred strains are used, data on humans have been collected on natural populations and, according to current genetics models [3,28], little can be said with certainty about an individual's genotype on the basis of his/her handedness phenotype. Second, with the fish model it was the extent of a preference which was measured. When studying handedness in humans, on the other hand, one can distinguish between how skilled is the person's performance with a particular hand and how he/she prefers to use that particular hand for even relatively unskilled tasks [27–29].

It may appear somewhat hazardous to discuss together lateralization in species which are phylogenetically so disparate. However, it should be remembered that directional asymmetries (those showing, at the population level, a departure from the expected biological baseline of a 50:50 ratio) cannot just happen, they have to be maintained by selective mechanisms [28] and see also [1,33,37] for recent discussions of the presumed biological advantages associated with directional asymmetries. Genes producing directional asymmetries are rare in biological evolution; the genes which determine situs seem to be very similar in vertebrates [35]. One of the best known genetic model of human lateralization [25] assumes that there is an autosomal locus, at which there are two alleles, D (for dextral) and C (for chance) and that the D allele appeared quite recently in human evolution from a mutation of one of the genes which normally cause the cardiac rudiment to grow slightly more on the left side (the hypothesis being that the mutated gene would cause early neural tissue to develop differently on the left side, see [27]). It is interesting to observe that fish data indicate bidirectional genetic coding (right vs. left forms of lateralization) whereas the D and C alleles indicate unidirectional coding (dextral vs. non-dextral).

Human genetic models of handedness posit a gene for directional biases that induces population-level handedness. In our fish, in contrast, one can selectively breed for bimodal distribution of laterality. Note that this is particularly intriguing because the detour task, on the basis of which the fish lines were created, is typically directionally shifted in these fish. Thus, one would expect that selective breeding for only one direction of laterality would be possible. Whether this would imply a different mechanism of inheritance in the two species is unclear: handedness could be a special case of laterality (e.g. [31]) and genetic models for other forms of human cerebral lateralization are not available. We simply do not know whether the current (and whatever contrasting) genetic models of human lateralization based on measures of handedness are general enough to account for the genetic bases of brain lateralization as such. Moreover, it is perfectly plausible that different mechanisms of genetic transmission developed in different species on the basis of a common set of homologous genes.

Evidence for directional asymmetries in the behavior of non-human species is now striking (reviews in [37,39]). Animal lateralization clearly poses some problems for current human-centered genetic models and, to account for them, Corballis [20] recently proposed that the C allele would have been producing a 66:33 ratio rather than the 50:50 ratio expected on the basis of pure biological noise (i.e. the so-called fluctuating asymmetries). Indeed, a 66:33 ratio is found ubiquitously in evidence of lateralization of several vertebrate species.
(11,37,39) but see also [31] for similar ratios in the human species). The problem with this idea is that even a 66:33 ratio represents a truly directional asymmetry, not a fluctuating one. Thus, one would be forced to hypothesize (as Corballis apparently does) that there have been two mutations in evolutionary history, one determining the (early) appearance of a gene for animal lateralization and one for (later) human lateralization. It seems to us, however, that this is a unnecessarily complicated scenario and we would be rather inclined to the idea of a unique, ancient origin of lateralization in all vertebrates. At any event, whatever the relationship, if exist, in terms of evolutionary history between fish and human lateralization, it seems that in both cases the gene(s) involved exhibit pleiotropy, with independent effects on different cerebral lateralities.

Acknowledgements

We thank Iva Doimo and Lucilla Facchin for help with testing animals in part of the experiments. The research was supported by an Italian MURST grant.

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