

Population lateralisation and social behaviour: A study with 16 species of fish

Angelo Bisazza

Università di Padova, Italy

Claudio Cantalupo

University of Memphis, USA

Maurizio Capocchiano

Università di Padova, Italy

Giorgio Vallortigara

Università di Trieste, Italy

We investigated turning responses in 16 species of fish faced with a vertical-bar barrier through which a learned dummy predator was visible. Ten of these species showed a consistent lateral bias to turn preferentially to the right or to the left. Species belonging to the same family showed similar directions of lateral biases. We performed an independent test of shoaling tendency and found that all gregarious species showed population lateralisation, whereas only 40% of the non-gregarious species did so. The results provide some support to the Rogers (1989) hypothesis that population lateralisation might have been developed in relation to the need to maintain coordination among individuals in behaviours associated with social life.

INTRODUCTION

Evidence of behavioural lateralisation in low vertebrate species has recently been reported from several laboratories (fish: Bisazza, Rogers, & Vallortigara, 1998a; Cantalupo, Bisazza, & Vallortigara, 1995; Fine et al., 1996; Miklosi, Andrew, & Savage, 1998; amphibians: Bauer, 1993; Bisazza et al., 1996; Green, 1997; Robins et al., 1998; Vallortigara et al., 1998; reptiles: Deckel, 1995,

Correspondence should be sent to Angelo Bisazza, Dipartimento di Psicologia Generale, Università di Padova, Via Venezia 8, 35131, Padova, Italy. Email: bisazza@psico.unipd.it

We wish to thank A. Miklosi, L. Regolin, and J. Ward, for reading and commenting on the manuscript, and A.W. Deckel and L.J. Rogers for thoughtful reviews. This project was supported by a grant from MURST.

1997). Given the now extensive evidence for the presence of lateralisation among birds and mammals (reviewed in Bradshaw & Rogers, 1993), investigations in lower vertebrates appear to be crucial for understanding the evolutionary origins of cerebral lateralisation.

We recently devised a simple behavioural test in fish to reveal lateral asymmetries reflecting preferential eye use during scrutiny of biologically relevant visual stimuli (Bisazza, Pignatti, & Vallortigara, 1997a). Male mosquitofish (*Gambusia holbrooki*) faced with an obstacle (a vertical-bar barrier) behind which a group of females was visible, preferentially circled around the obstacle leftwards (thus maintaining monocular fixation on the target with their right eye). The same bias was observed using a simulated predator (a fish lure used for open-sea fishing) as a target (in this species, this can induce turning around the barrier in order to perform predator-inspection responses). The lateral asymmetry was task- and stimulus-dependent. It disappeared when the task was made difficult by forcing the fish to lose visual contact with the goal (i.e. with a U-shaped barrier) or using less attractive targets (i.e. a group of males or an empty environment). Moreover, mosquitofish faced with an opaque barrier were found to turn preferentially rightward, thus providing further evidence that the leftward bias observed with the females or with the predator could not be accounted for in terms of a purely motor bias.

The test is quite easy to perform and is capable of revealing asymmetries even with very small sample sizes, which makes it a suitable method for cross-species investigation. Right-left direction of detour to approach a group of females was recently measured in males of five species of poeciliid fishes (Bisazza, Pignatti, & Vallortigara, 1997b). When motivational factors were properly assessed, all five species showed lateralisation in the same direction. These results suggested that the direction of lateral asymmetries tends to be strikingly similar in closely related species, at least in the family Poeciliidae. The aim of this paper is to extend the comparative analysis of functional lateralisation of detour behaviour to a larger number of species of fish, belonging to different families.

EXPERIMENT 1

A major problem facing comparative analysis of behaviour is related to the need to equalise the so-called "contextual variables", namely differences between species that are not directly related to the function under examination (lateralisation) but which could possibly affect the results. Use of sexual targets appears to be problematic because of differences between species in sexual motivation (see Bisazza et al., 1997b; 1998b); on the other hand, the use of a natural predator (or a naturalistic dummy predator) raises the problem that different species could be frightened by different visual stimuli and responsive to different "releasers". There is not a perfect solution to this problem. We

adopted what seemed to us a reasonable solution: the use of a "learned" dummy predator, i.e. an artificial object bearing only feeble "naturalistic" features and thus unlikely to elicit species-specific escape responses. The fish learned the aversive nature of this dummy predator through experience.

Methods

Subjects. A total of 16 species of fish, belonging to 13 different families, were used (see Figure 2 for names and phylogenetic relationships). The numbers of individuals tested for each species are reported in Table 1. (*Girardinus falcatus*, *Jenynsia multidentata*, *Xenotoca eiseni*). Three species were wild-caught near Padua (*Knipowitschia punctatissima*, *Lepomis gibbosus*, *Padogobius martensi*). The other 10 species (*Ancistrus* sp., *Barbus conchoni*, *Betta splendens*, *Brachydanio rerio*, *Channa obscura*, *Corydoras aeneus*, *Gyrinocheilus aymonieri*, *Pterophyllum scalare*, *Syngnathus pulchellus*, and *Trichogaster trichopterus*) were purchased from local pet shops. Fish of the species *Jenynsia multidentata* were all females, and those of the species *Girardinus falcatus* and *Betta splendens* were one half males and one half females. For all other species the sex could not be determined because the fish were not in reproduction.

Species of the families Cyprinidae (*Barbus conchoni* and *Brachydanio rerio* in this study) and Poeciliidae (*Girardinus falcatus*) have been the subject of several social studies and are with few exceptions shoaling fishes (Pitcher & Parrish, 1993). Angelfish (*Pterophyllum scalare*) are also known to shoal outside the reproductive phase (Bergmann, 1968). Catfish (Siluriformes) are bottom-dwelling fishes and can be either social or solitary. *Corydoras* are usually gregarious fishes whereas species of genus *Ancistrus* are described as solitary and aggressive to each other. The latter often live in waters where dissolved oxygen sometimes falls very low and they are therefore forced to air-breathe to survive. To reduce predation large groups go up for air at the same time, a behaviour that may be considered analogous to shoaling in other fishes (Kramer & Graham, 1976).

Jenynsia multidentata (formerly *J. lineata*: see Ghedotti & Weitzman, 1996) is a small livebearing fish native to South America. Males are aggressive to each other and both sexes tend to be solitary (Bisazza, Pilastro, & Manfredi, in press). *Knipowitschia punctatissima* and *Padogobius martensi* are freshwater Gobiidae, endemic in Italy. As in most species of this family, males are aggressive and do not tolerate each other (see for example Torricelli et al., 1988 for *P. martensi*). Neither sex shows a tendency to shoal although larvae may sometimes be observed in aggregates (Bisazza, personal observation). In the fighting fish, *Betta splendens*, both sexes are very aggressive. Males cannot share the same tank but females can be kept in groups although it is not known if they form shoals in nature (Simpson, 1968).

No study has specifically investigated the shoaling behaviour in the remaining species. Sunfishes (*Lepomis gibbosus* in this study) live in colonies during the breeding season but each male defends a small territory around the nest. As regards *Xenotoca eiseni* only sexual behaviour is known in detail (Bisazza, 1997). Observations of fish living in aquaria and in artificial ponds suggest that both adults and young have little tendency to form shoals (Bisazza, personal observations). Pipefish (*Syngnathus pulchellus*, in this study) show generally little shoaling (Vincent, Ahnesjö, & Berglund, 1994).

Four species were previously used in laterality studies. Two, *B. rerio* and *G. falcatus*, showed laterality at the population level, the two other, *B. splendens* and *J. multidentata*, showed laterality only at the individual level (Bisazza, Cantalupo, & Vallortigara, 1997c; Cantalupo et al., 1995, 1996; Miklosi et al., 1998).

Each species of fish was kept in glass aquaria, 60 × 60 × 35cm, in groups of no more than 15 subjects per aquarium. The aquaria contained plants (*Ceratophyllum* sp.) and were lit with neon lamps (18W) under a photoperiod of 15 hours. Water was filtered and maintained at a constant temperature of 25°C. Food was provided and calibrated for the different species. All subjects not belonging to the laboratory stock were maintained in the laboratory aquaria for at least seven days before starting the experiment.

There were two exceptions to the general maintenance rules just described: male *Betta splendens*, because of their aggressiveness, were housed individually; *Knipowitschia punctatissima* and *Padogobius martensi* were maintained in plexiglass aquaria in a relatively colder room (15°C) because these species commonly live in cold water.

Apparatus. The apparatus has been described in detail elsewhere (Bisazza et al., 1997a). It consisted of a large tank (60 × 94cm and 36cm in height) with a runway in the middle (7 × 40cm) allowing the fish inside to face, at both ends of the runway, a barrier behind which was the target (see Figure 1). Each barrier (17 × 17cm) was 10cm in front of the target and consisted of a series of yellow cylindrical plastic bars (0.25cm in diameter) aligned vertically and spaced 0.25cm apart. Each target was a "learned" (see later) predator which consisted of a rectangular (10 × 7cm) white net and two yellow discs (16mm in diameter) with black "pupils" (6mm in diameter) horizontally arranged in the centre as "eyes". The net could be moved by a blue-coloured stud. Water in the tank was 11cm deep. Two fluorescent lamps (15W) were located one above each of the two stimuli. The apparatus was located in a completely darkened room.

Procedure. During pre-test, on alternate days for 10 consecutive days each fish was chased in turn with the net-predator for at least 10 seconds within its aquarium; then the fish was caught and transferred to another identical aquarium located on one side of the first aquarium. The aim of the pre-test was to ensure

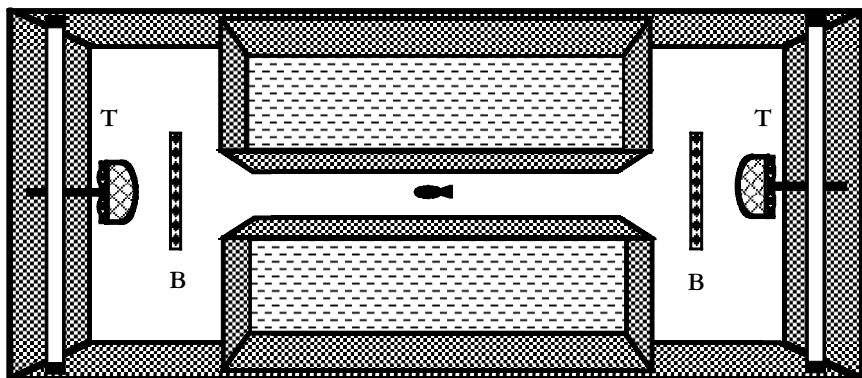


Figure 1. Schematic representation of the test apparatus used for Exp. 1. Fish had to swim along the runway (alternately in opposite directions) in order to face a target (T) behind a barrier (B). The right or left direction of turn of the fish in front of the barrier was recorded.

that fish learned about the net-predator, with the stress associated with being pursued and caught as aversive outcome. Small adaptations of the procedure were necessary for some species: *Gyrinocheilus aymonieri* and *Brachydanio rerio* are most difficult to catch, and in this case a larger ($12.5 \times 10\text{cm}$) net was used for both learning and testing; *Syngnathus pulchellus* crawl on the bottom and thus a smaller net was used ($7.5 \times 6\text{cm}$) and the “eyes” were lowered (5cm from the bottom) in the net to make them more conspicuous to the fish.

At test, each fish was first introduced into the apparatus without any predator and kept in there for three minutes to become accustomed to the environment. Then the predators were introduced (first the one on the opposite side to that occupied by the fish) and testing started. During each testing trial, the fish was gently pushed using a pair of green fish-nets (very different from the ones used as “predators”) to the starting point of the runway. The fish swam along the runway until it faced the barrier. The right or left direction of turn taken by the fish as it left the runway was recorded. After complete detouring of the barrier had occurred, the fish was kept in the compartment for 10 seconds before the subsequent trial began. To account for any possible asymmetry in the test apparatus, test trials were performed alternately on the two symmetrical ends of the runway; moreover, the positions of the two barriers and of the targets alternated for different animals and the fluorescent lamps (see Figure 1) were periodically rotated. Ten test trials for each individual were given.

Data analyses. Lateral asymmetries were analysed by computing for each subject a “laterality index” using the formula:

$$[(\text{Turn to the right} - \text{Turn to the left}) / (\text{Turn to the right} + \text{Turn to the left})] \times 10$$

Positive values would thus indicate a preference for turning to the right side, negative values a preference for turning to the left side. Departures from random choices (0%) were estimated by one-sample two-tailed *t*-tests performed on the mean values of the laterality indices for each species. Differences across species were estimated by the analysis of variance (ANOVA) following checking of assumptions of normality and homogeneity of variance.

Results

Results are shown in Table 1 and Figure 2. As can be seen, 10 out of 16 species showed a significant population bias in turning. The difference between species was significant [*F*(15,175)=4.987 *P*=.001]. There were no differences associated with sex in the two species in which gender effects could be evaluated (*Betta splendens*: *N*=18 *t*=1.81; *Girardinus falcatus*: *N*=14 *t*=0.95). Some of the species that proved to be lateralised here had been previously shown to be lateralised in different tests; for instance, *G. falcatus* (Cantalupo et al., 1995) and *B. rerio* (Miklosi et al., 1998).

Non-lateralised species could be formed of individuals that are on average less lateralised than individuals of lateralised species. Alternatively, non-

TABLE 1
Experiment 1

Species	<i>n</i>	Laterality Index Mean ± SD	<i>t</i>	<i>P</i>
<i>Ancistrus sp.</i>	11	3.8 ± 2.44	5.19	**
<i>Barbus conchoni</i>	15	2.1 ± 3.42	2.42	*
<i>Betta splendens</i>	18	-1.1 ± 4.91	-.96	ns
<i>Brachydanio rerio</i>	18	1.7 ± 3.49	2.16	*
<i>Channa obscura</i>	12	1.6 ± 4.41	1.31	ns
<i>Corydoras aeneus</i>	7	4.4 ± 3.86	-3.60	**
<i>Girardinus falcatus</i>	14	-4.2 ± 4.35	-3.68	**
<i>Gyrinocheilus aymonieri</i>	11	1.63 ± 4.54	1.19	ns
<i>Jenynsia multidentata</i>	9	2.2 ± 3.07	2.17	ns
<i>Knipowitschia punctatissima</i>	9	-2.6 ± 2.0	-4.00	**
<i>Lepomis gibbosus</i>	10	-2.8 ± 3.422	-2.58	*
<i>Padogobius martensi</i>	7	-1.4 ± 1.51	-2.50	*
<i>Pterophyllum scalare</i>	10	3.6 ± 4.50	2.53	*
<i>Syngnathus pulchellus</i>	9	1.3 ± 5.29	.85	ns
<i>Trichogaster trichopterus</i>	17	2.0 ± 3.46	2.38	*
<i>Xenotoca eiseni</i>	12	-1.0 ± 4.71	-.74	ns

Laterality index for the 16 species. Significance of population biases was calculated with one sample Student *t* test (**P*<.05; ***P*<.01).

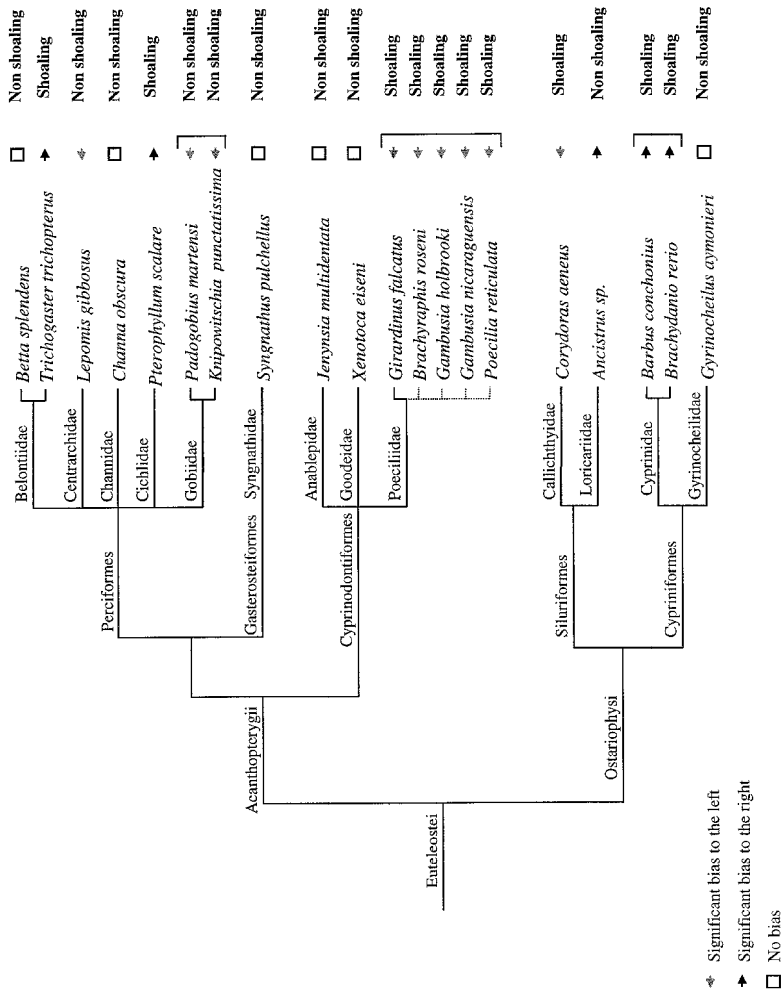


Figure 2. Phylogenetic relationships of the species used in the experiment (based on Nelson, 1994). Dotted lines indicate species that have been studied previously (Bisazza et al., 1997b, 1998) in the same detour test. Arrows indicate the direction of lateralisation; squares indicate the absence of any population bias.

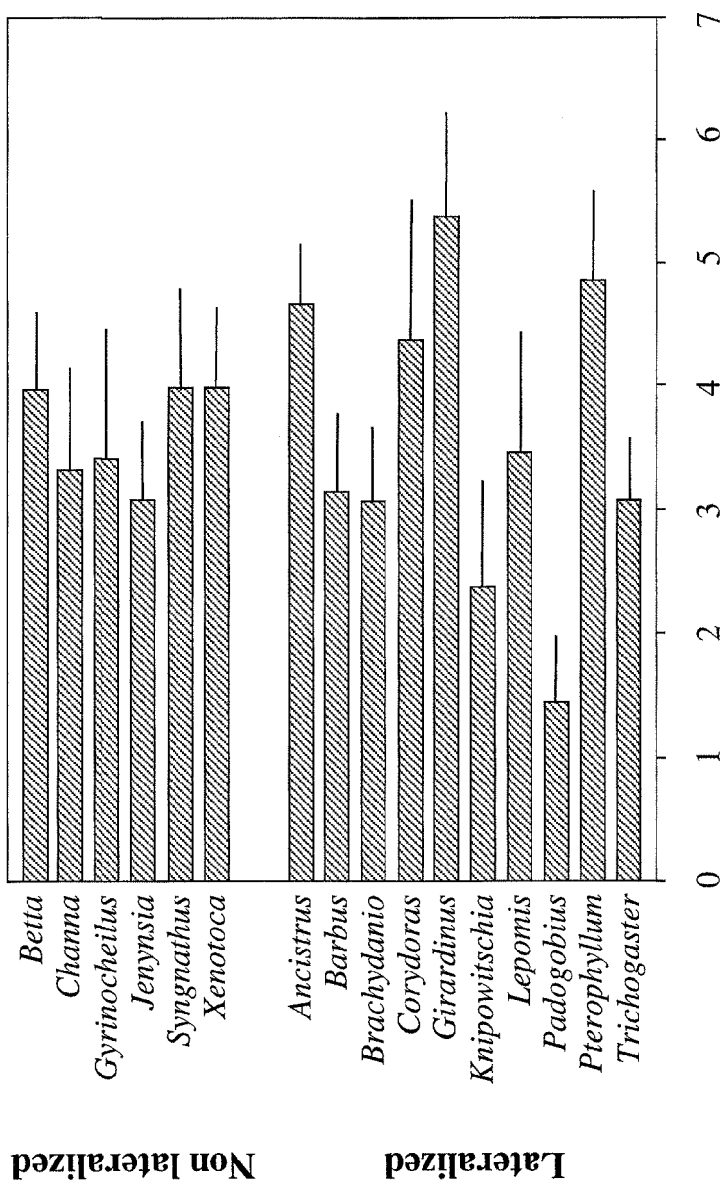
lateralised species could be formed of individuals that are lateralised to the same degree as those of lateralised species, but with a nearly identical number of individuals with right and left directions of asymmetry in the population. Figure 3 shows the absolute values of the laterality index, that is, the degree of deviation from identical rightward or leftward turning irrespective of the direction of deviation. There were no significant differences between species [$F(15,175)=1.264$ n.s.], nor any significant differences between lateralised and non-lateralised species (contrast analysis: $t=0.187$ df=175 n.s.). This suggests that non-lateralised species were characterised by individuals having the same degree of asymmetry as the lateralised species, but with a more equiprobable distribution of right-and left-biased individuals within the population sample.

Among the lateralised species, five turned leftwards (*C. aeneus*, *G. falcatus*, *L. gibbosus*, *K. punctatissima*, *P. martensi*) and five turned rightwards (*Ancistrus sp.*, *B. conchoni*, *T. trichopterus*, *B. rerio*, *P. scalare*). Within the same family, however, the direction of lateralisation tended to be the same (*Gobiidae*, *Cyprinidae*, and see also *Poeciliidae* in previously published work, Bisazza et al., 1997b).

EXPERIMENT 2

Why are some species of fish lateralised and others not? Clearly, no straightforward conclusion could be drawn on the basis of a single behavioural task. In other classes of vertebrates it has been shown that lack of lateralisation in a particular task does not imply that the species should not be lateralised in other tasks. For instance, the parrots *Amazona amazonica* do not appear to show any siringal asymmetry in the control of vocalisation, but they appear to have footedness (see Bradshaw & Rogers, 1993). Also, the common marmosets (*Callithrix jacchus*) have individual hand preferences but no population bias of handedness; they do, by contrast, have a strong population bias for eye preference and facial expression (Hook-Costigan & Rogers, 1995).

On the other hand, our data suggest that the species showing no lateralisation at the population level do show lateralisation at the individual level. The main issue would thus be better characterised as follows: Why are some species of fish lateralised at the *population* level and others not? Rogers (1989) has stressed that if possessing an asymmetric brain confers some biological advantage to the individual, there is in principle no reason why the direction of asymmetries should be the same in all (or most) individuals of a population. Perhaps the original early condition could have been that of brain asymmetry at individual level. However, if lateralisation manifests its effects on the everyday behaviour of organisms, for instance producing preferential eye use in animals with laterally placed eyes (Dharamaretnam & Andrew, 1994) and thus determining conspicuous lateral biases in motor behaviour (Vallortigara et al., in press), then the direction of the asymmetries would be of extreme importance in all the



Absolute value of laterality index

Figure 3. Absolute values of the laterality index (and S.E.M.) for lateralised and non-lateralised species.

conditions in which animals must coordinate their behaviour in relation to that of their conspecifics. Consider a school of fish, i.e. a synchronised and polarised swimming group. To a fish in the school, the best direction of predator-escape response depends on the direction taken by the majority of individuals within the school. Also, having one eye (and one side of the brain) that, for instance, recognises a stimulus as a dangerous predator while the other eye treats the same stimulus as innocuous would disrupt cohesion of a school if lateralisation were at the individual level. This leads to the intriguing possibility that population asymmetries (as opposed to individual asymmetries) would be more typically encountered among social rather than solitary species. Gregarious behaviour such as shoaling is in some sense a matter of degree rather than an all-or-none characteristic of a species. Nonetheless, ethologists are accustomed to categorise a species as more or less social than another on the basis of naturalistic observations. Unfortunately, shoaling tendency has been experimentally addressed in a limited number of fishes. Fish belonging to families Poeciliidae and Cyprinidae are known for the most part to live in aggregates; conversely, siamese fighting fish and freshwater gobiids tend to be solitary and often intolerant of each other (see introduction). Little established information exists for most of the other species used in this study. In order to provide a first empirical test of the hypothesis even for the less known species, we decided to measure directly the tendency to shoal in the 16 species of fish studied.

Method

Subjects. A total of 16 naive fish for each one of the same 16 species used in Exp. 1 were tested. Individuals of the species *Betta splendens* were females. For the other species sex could not be determined. Fish were reared in the same conditions as in Exp. 1.

Apparatus and procedure. The experimental apparatus consisted of an aquarium, $66 \times 66 \times 34$ cm (level of the water 24 cm), with a series of lines on the floor and one line in the middle to subdivide it into a series of 9 identical squares, and 18 identical sectors ($22 \times 22 \times 17$ cm; see Figure 4). Four animals were placed into the aquarium; they were kept in there for 30 seconds to become accustomed to the new environment; then the position occupied by each fish in each sector was recorded every 20 seconds. The test was repeated four times for each species, using four different animals every time.

Data analyses. A "shoaling index" was computed on the basis of the average number of fish occupying a sector (see Figure 4). The index scored 4 when all fish were located on the same sector, 2 when two fish were located in one sector and two fish in another sector, 1.3 when two fish were located in the same sector and the other two fish were in two different sectors, and 1 when

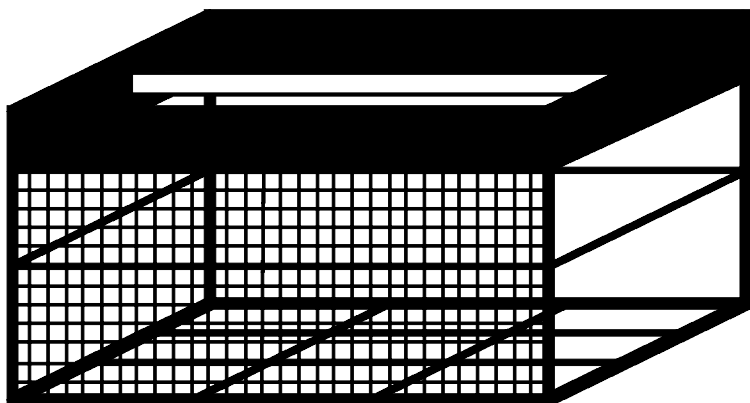


Figure 4. Schematic representation of the apparatus used for Exp. 2. The position occupied by fish within the sectors identified by the lines traced on the floor and walls of the aquarium was recorded as a measure of their tendency to shoal.

every fish was located on a different sector. Some species prefer to remain on the surface or on the bottom, whereas others move in all positions when located within an aquarium. The latter have therefore a lower probability of being located by chance in the same sector of the aquarium. Thus, on the basis of the frequency with which every species occupied the lower or the upper parts of the aquarium, we ran a computer simulation of the movements of four individuals on the hypothesis that they were not interacting with each other. The program was written in Delphy, Version 3, and simulated random, independent movements of four fish among the 18 sectors (9 lower and 9 upper) of the tank. Transition between the nine sectors of the same level had the same probability of occurrence, while share of time spent in the lower and upper levels could be set differently for each species. Mean and SD of 10,000 replications were computed for each species. The empirical indices could thus be compared with those computed on the basis of the computer simulation, which was assumed to represent the null hypothesis of the absence of any gregarious tendencies. Comparisons between empirical and simulated gregariousness indices were carried out by Student *t*-tests (two-tailed). We estimate as “more social” the species for which a significant difference between empirical and simulated shoaling indices appeared.

Results

Results are shown in Table 2. As expected, the different species showed differential preferences for the upper and lower parts of the aquarium. There were significant differences between empirical and simulated shoaling indices in seven species; however, in one of these species, *Padogobius martensi*, the

TABLE 2
Experiment 2

Species	Observed Shoaling Index	% of Time in the Lower Half	Simulated Shoaling Index	Comparison observed-simulated
<i>Ancistrus sp.</i>	1.42 \pm .36	75.2	1.14 .23	t = 1.52 NS
<i>Barbus conchoniuis</i>	2.41 \pm .42	41.6	1.11 .20	t = 6.075 **
<i>Betta splendens</i>	1.24 \pm .13	42.7	1.11 .20	t = 1.811 NS
<i>Brachydanio rerio</i>	2.90 \pm .34	56.6	1.11 .20	t = 10.41 **
<i>Channa obscura</i>	1.27 \pm .17	80.0	1.15 .23	t = 1.33 NS
<i>Corydoras aeneus</i>	1.79 \pm .32	96.5	1.21 .39	t = 3.55 *
<i>Girardinus falcatus</i>	2.75 \pm .75	34.0	1.13 .21	t = 4.285 *
<i>Gyrinocheilus aymonieri</i>	1.22 \pm .12	99.0	1.23 .29	t = -0.091 NS
<i>Jenynsia multidentata</i>	1.33 \pm .08	100	1.23 .29	t = 2.267 NS
<i>Knipowitschia punctatissima</i>	1.09 \pm .09	99.5	1.23 .29	t = -2.85 NS
<i>Lepomis gibbosus</i>	1.36 \pm .16	62.0	1.12 .21	t = 2.92 NS
<i>Padogobius martensi</i>	1.15 \pm .02	98.3	1.22 .27	t = -4.88 *
<i>Pterophyllum scalare</i>	2.64 \pm .57	66.8	1.13 .21	t = 5.281 *
<i>Syngnathus pulchellus</i>	1.17 \pm .10	100	1.12 .28	t = -1.16 NS
<i>Trichogaster trichopterus</i>	1.87 \pm .09	55.6	1.11 .19	t = 15.95 **
<i>Xenotoca eiseni</i>	1.41 \pm .01	29.8	1.14 .22	t = 3.11 NS

Observed shoaling index was compared with the value obtained from computer simulation on the null hypothesis that individuals were not interacting with each other. Such value varied from species to species depending on the proportion of the aquarium in use. Significance of the difference was assessed by means of Student *t* test.

empirical index was significantly lower than expected on chance, indicating that individuals of this species avoided each other. Thus, there remained six species in which the shoaling index significantly exceeded that computed on the basis of the null hypothesis, and these species could therefore be considered as the most shoaling, or "social". All these six species were lateralised in the previous

experiment. In contrast, among the 10 "less social" species 4 were lateralised and 6 were not. The difference between "social" and "less social" species was significant at Fisher exact test ($P = .026$ one-tailed). Fish belonging to the same families are strictly related, therefore, it might be questionable to consider these species as "independent events"; we thus reduced the sample to only 14 species (considering only one species for the families Gobiidae and Cyprinidae instead of two species): however, the outcome of the statistical test remained unchanged (Fisher exact test: $P = .027$ one-tailed).

GENERAL DISCUSSION

The most important result of this study seems to be that behavioural lateralisation is quite widespread among fish. Ten out of sixteen species of fish studied showed lateralisation at the population level. In the remaining six species, individuals appeared to be lateralised to the same degree but the proportion of right- and left-biased individuals was balanced within the population sample. Together with evidence from other laboratories studying fish (Fine et al., 1996; Miklosi et al., 1998) and the results obtained with amphibians, both anurans (Bisazza et al., 1996; Vallortigara et al., 1998) and urodels (Green, 1997), and with reptiles (Deckel, 1995), these results suggest that there was an ancient origin of cerebral lateralisation. The large number of species that appear to be lateralised among lower vertebrates suggests either that having asymmetrical brains is such an important feature of the nervous system that natural selection has "invented" it several times, or, perhaps more reasonably, that birds and mammals actually inherited it from their chordate ancestors.

However, several issues remain unresolved, and the present data may provide some preliminary, tentative answers. A first problem concerns the direction of lateralisation. There is some evidence among higher vertebrates (and partly even among lower vertebrates) for similarities in the direction of the asymmetries for certain tasks (roughly, the right side of the brain seems to be mostly involved in spatial tasks, and the left side in communicative and categorisation functions, see Andrew, 1991; Bradshaw & Rogers, 1993; Bisazza et al., 1998a). However, exceptions to the rule have been described and, most importantly, there is evidence that the direction of the asymmetry could be influenced by factors such as early stimulation of the embryo and hormones (Rogers, 1995). It should be noted, however, that similarity in direction is not a necessary condition for homology. It could be that vertebrates share a genetic predisposition for developing asymmetric brains, but that different species show variations in direction of lateralisation depending on the role played by epigenetic and ecological factors. Alternatively, it is perhaps more parsimonious to assume that the properties of perceptual lateralisation are constant among vertebrates and that there are other factors which could vary between species and produce

different expression of lateralisation in our detour task. For example, motivational factors could be likely candidates: some species might be more fearful, and this could affect the importance of inhibition of Mauthner cells mediating escape during approach to inspect the predator (see also Miklosi et al., 1998). The speed of swimming fish and thus the point at which "decisions" are taken could also be important: a species that dashes round the barrier might decide at a distance, whereas a slow moving fish might decide close to the barrier and this might affect eye use. It is quite intriguing that our data suggest that closely related species tend to manifest similarities in the direction of the asymmetries. The fish families for which more than one species was available (i.e. Gobiidae, Poeciliidae, and Cyprinidae) showed an identical direction of lateralisation within the family and different directions for different families. Results obtained for three families are probably not sufficient to draw a conclusion, but they surely constitute an interesting starting point. Obviously, similarity in direction among more closely related fish is compatible with both the hypothesis of specular organisation of lateralisation in certain (less related) species, and with the hypothesis of spurious factors affecting detour performance of different species (for instance, it is likely that closely related species would be more similar in emotional/motivational responses). To clarify these issues work complementary to that described here is needed: namely, studying species in a variety of tasks to check whether reversal of the direction of lateralisation occurs invariably in different species or is merely task-dependent.

The other major issue is to understand why some species of fish tend to exhibit lateralisation at the individual but not population level (see for instance Bisazza & Vallortigara, 1996; Bisazza et al., 1997c; Cantalupo et al., 1996). In part, this could depend on the task. It could be that some species would reveal population asymmetries only in certain tasks. However, at least one of the species studied here, *B. splendens*, has consistently revealed a lack of population lateralisation in a variety of tasks (Cantalupo et al., 1996). Rogers (1989) has proposed the intriguing hypothesis that the alignment of the direction of lateralisation in the majority of individuals in a population occurs as a consequence of the need to coordinate social behaviour. Our results do provide some support to this hypothesis. Of the 16 species we studied, the most social ones all showed lateralisation at the population level; among the less gregarious species only 40% showed population lateralisation. Although results indicate an association between gregariousness and lateralisation, a proper test of the hypothesis would require that phylogeny should be taken into account (Harvey & Pagel, 1991; Ridley, 1983). Several tools have been developed recently in the field of comparative method (see Martins, 1996, for recent reviews); however, given the small number of species studied, the nature of the variable observed and the lack of an accurate phylogeny of the group, the application of such methods to the data presented in this study would be premature. Comparative

behavioural studies with large numbers of species are difficult to perform and extremely time-consuming. Nevertheless, we believe that an increased availability of this sort of comparative data would be crucial to the development of our understanding of the evolutionary origins of cerebral lateralisation.

Manuscript received 25 January 1999

Revised manuscript received 26 April 1999

REFERENCES

- Andrew, R.J. (1991). The nature of behavioural lateralization in the chick. In R.J. Andrew (Ed.), *Neural and behavioural plasticity. The use of the chick as a model* (pp. 536–554). Oxford University Press, Oxford.
- Bauer, R.H. (1993). Lateralization of neural control for vocalization by the frog (*Rana pipiens*). *Psychobiology*, 21, 243–248.
- Bergmann, H.-H. (1968). Eine deskriptive Verhaltenanalyse des Segelflossers (*Pterophyllum scalare* Cuv. & Val., Cichlidae, Pisces). *Zeitschrift für Tierpsychologie*, 25, 559–587.
- Bisazza, A. (1997). Sexual selection constrained by internal fertilization in the livebearing fish *Xenotoca eiseni*. *Animal Behaviour*, 54, 1347–1355.
- Bisazza, A., Cantalupo, C., Robins, A., Rogers, L., & Vallortigara, G. (1996). Right-pawedness in toads. *Nature*, 379, 408.
- Bisazza, A., Cantalupo, C., & Vallortigara, G. (1997c). Lateral asymmetries during escape behaviour in a species of teleost fish (*Jenynsia lineata*). *Physiology and Behavior*, 61, 31–35.
- Bisazza, A., Facchin, L., Pignatti, R., & Vallortigara, G. (1998b). Lateralization of detour behaviour in poeciliid fish: The effect of species, gender and sexual motivation. *Behavioural Brain Research*, 91, 157–164.
- Bisazza, A., Pignatti, R., & Vallortigara, G. (1997a). Detour tests reveal task- and stimulus-specific neural lateralization in mosquitofish (*Gambusia holbrooki*). *Behavioural Brain Research*, 89, 237–242.
- Bisazza, A., Pignatti, R., & Vallortigara, G. (1997b). Laterality in detour behaviour: Interspecific variation in poeciliid fish. *Animal Behaviour*, 54, 1273–1281.
- Bisazza, A., Pilastro, A., & Manfredi, S. (in press). Sexual competition, coercive copulation and mate assessment in the one-sided livebearer (*Jenynsia multidentata*; Pisces: Anablepidae). *Ethology*.
- Bisazza, A., Rogers, L.J., & Vallortigara, G. (1998a). The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, amphibians, and reptiles. *Neuroscience and Biobehavioural Review*, 22, 411–426.
- Bisazza, A., & Vallortigara, G. (1996). Rotational bias in mosquitofish (*Gambusia holbrooki*): The role of lateralization and sun-compass navigation. *Laterality*, 1, 161–175.
- Bradshaw, J.L., & Rogers, L.J. (1993). *The evolution of lateral asymmetries, language, tool use, and intellect*. New York: Academic Press.
- Cantalupo, C., Bisazza, A., & Vallortigara, G. (1995). Lateralization of predator-evasion response in a teleost fish (*Girardinus falcatus*). *Neuropsychologia*, 33, 1637–1646.
- Cantalupo, C., Bisazza, A., & Vallortigara, G. (1996). Lateralization of displays during aggressive and courtship behaviour in the siamese-fighting fish (*Betta splendens*). *Physiology and Behavior*, 60, 249–252.
- Deckel, A.W. (1995). Laterality of aggressive responses in *Anolis*. *Journal of Experimental Zoology*, 272, 194–200.
- Deckel, A.W. (1997). Effects of alcohol consumption on lateralized aggression in *Anolis carolinensis*. *Brain Research*, 756, 96–105.

- Dharmaretnam, M., & Andrew, R.J. (1994). Age- and stimulus-specific use of right and left eyes by the domestic chick. *Animal Behaviour*, *48*, 1395–1406.
- Fine, M.L., McElroy, D., Rafi, J., King, C.B., Loesser, K.E., & Newton, S. (1996). Lateralization of pectoral stridulation sound production in the channel catfish. *Physiology and Behavior*, *60*, 753–757.
- Ghedotti, M.J., & Weitzman, S.H. (1996). A new species of *Jenynsia* (Cyprinodontiformes: Anablepidae) from Brazil with comments on the composition and taxonomy of the genus. *Occasional Papers of the Natural History Museum of The University of Kansas Pap. No. 179*, 1–25.
- Green, A.J. (1997). Asymmetrical turning during sex in the smooth newt, *Triturus vulgaris*. *Animal Behaviour*, *54*, 343–348.
- Harvey, P.H., & Pagel, M.D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hook-Costigan, M.A., & Rogers, L.J. (1995). Hand, mouth and eye preferences in the common marmoset (*Callithrix jacchus*). *Folia Primatologica*, *64*, 180–191.
- Kramer, D.L., & Graham, G.B. (1976). Synchronous air breathing, a social component of respiration in fishes. *Copeia*, 689–697.
- Martins, E.P. (1996). *Phylogenies and the comparative method in animal behavior*. Oxford: Oxford University Press.
- Miklosi, A., Andrew, R.J., & Savage, H. (1998). Behavioural lateralisation of the tetrapod type in the zebrafish (*Brachydanio rerio*). *Physiology and Behavior*, *63*, 127–135.
- Nelson, J.S. (1994). *Fishes of the World* (3rd Edn.). New York: John Wiley & Sons.
- Pitcher, T.J., & Parrish, J.K. (1993). Functions of shoaling behaviour in teleosts. in T.J. Pitcher (Ed.), *Behaviour of teleost fishes* (2nd Ed.). London: Chapman & Hall.
- Ridley, M. (1983). *The explanation of organic diversity. The comparative method and adaptations for mating*. Oxford: Clarendon Press.
- Robins, A., Lippolis, G., Bisazza, A., Vallortigara, G., & Rogers, L.J. (1998). Lateralized aggressive responses and hind-limb use in toads. *Animal Behaviour*, *56*, 875–881.
- Rogers, L.J. (1989). Laterality in animals. *International Journal of Comparative Psychology*, *3*, 5–25.
- Rogers, L.J. (1995). *The development of brain and behaviour in the chicken*. Wallingford: CAB International.
- Simpson, M.J.A. (1968). The display of the siamese fighting fish, *Betta splendens*. *Animal Behaviour Monographs*, *1*, 1–73.
- Torricelli, P., Parmigiani, S., Lugli, M., & Gandolfi, G. (1988). Intermale aggression in *Padogobius martensi* (Günter) (Pisces, Gobiidae): Effect of size and prior residence. *Monitore Zoologico Italiano*, *22*, 121–131.
- Vallortigara, G., Regolin, L., & Pagni, P. (in press). Detour behaviour, imprinting and visual lateralization in chicks. *Cognitive Brain Research*.
- Vallortigara, G., Rogers, L.J., Bisazza, A., Lippolis, G., & Robins, A. (1998). Complementary specializations of the right and left hemifield for predatory and agonistic behaviour in toads. *NeuroReport*, *9*, 3341–3344.
- Vincent, A., Ahnesjö, I., & Berglund, A. (1994). Operational sex ratios and behavioural sex differences in a pipefish population. *Behavioral Ecology and Sociobiology*, *34*, 435–442.