Taking turns: some aspects of behavioural lateralization in schooling fish

Julie Lucas[1], Paulo Branco[2], Kaj Hulthén[3]

Fish swimming 2011

[1]Littoral, Environment and Societies (LIENSs) Laboratory, UMR 6250 – CNRS, University of La Rochelle, 17000 La Rochelle, France

[2]Forest Research Centre, Technical University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal

[3]Department of Biology, Lund University, Ecology Building, 223 62 Lund, SE

Keywords – Lateralization, detour test, Teleost fish, *Aulorhynchus flavidus*, *Ammodytes hexapterus*, *Gasterosteus aculeatus*

Contact :
Julie Lucas
UMR6250LIENSs CNRS-ULR
2, rue Olympe de GOUGES
17000 LA ROCHELLE

Abstract

Lateralization of cognitive functions seems to be exceptionally widespread in nature and have been demonstrated to occur in multiple taxa. Previous studies using fish as models have suggested that social behaviours such as schooling may covary with behavioural lateralization at the population-level. Here, we assess the strength, degree and repeatability of behavioural lateralization in schooling fish. Two of the species studied (*Aulorhynchus flavidus* and *Gasterosteus aculeatus*) were found to express population-level symmetry in the direction of lateralization whereas one species (*Ammodytes hexapterus*) showed no indication of population-level lateralization. We also provide evidence that behavioral lateralization is repeatable over time. From our cross-species comparisons we conclude that population-level lateralization is not necessarily related to a gregarious life-style. Further studies should test repeatability over longer periods of time and the role of lateralization in schooling behavior.

Introduction

Important advance within the burgeoning field of behavioural ecology have revealed that fundamental traits previously regarded exclusively human are widespread in nature. A key human trait now considered to be ubiquitous among species as diverse as mammals, birds, fish, amphibians and reptiles is the division of cognitive function in either brain hemisphere, (for thorough reviews see e.g. Bradshaw 1988, Drea 1996, Bisazza et al. 1998b, Vallortigara et al. 1999). Laterality may be broadly defined as when responses derived from cerebral lateralization are manifested in behavioural side bias. Individuals in a population may exhibit the same pattern of lateralization and express symmetry in the direction of bias. Conversely, profound variation in laterality may be expressed between individuals within a single population, with each individual expressing a tendency for either a left- or right- bias even though no symmetry in lateralization at the population level occurs (Rogers and Andrew 2002). Over the past two decades, teleost fish has emerged as important model organisms for studying many aspects of cerebral lateralization (Bisazza and Brown 2011). In fish, the phenomenon of laterality has been shown to have far-reaching implications for a diverse range of behaviours with ecological significance. For example, important studies have documented a positive relationship between the degree of lateralization and performance in schooling behavior (Bisazza and Dadda 2005), spatial orientation (Sovrano et al. 2005) and even escape performances (Dadda et al. 2010)..

Belonging to a social group of animals may infer advantages in terms of food acquisition and predator avoidance (Pitcher et al. 1982, Magurran 1990). Needless to say, the cohesion of such units is dependent on synchronous maneuvers by the individual members. Accordingly, is has been suggested that bias for turning preference at the population level will occur to a higher degree in social species since it promotes the coordination among individuals (Rogers and Andrew 2002). Empirical evidence in support of this hypothesis comes from a cross-species comparison involving 16 species of fish from 13 different families. All species with a social behavior also expressed laterality at the population level whereas more solitary species tended to express laterality at the individual level (Bisazza et al. 2000).

In this study, we investigate the direction and strength of behavioral lateralization in three species of schooling fish, and test the repeatability of lateralized behavior in detour tests.

Materials and methods

(a) Fish species

The species included in the study were Tubesnout (*Aulorhynchus flavidus*), Sandlance, (*Ammodytes hexapterus*) and three-spined stickleback (*Gasterosteus aculeatus),* all known to show marked schooling behaviour (Limbaugh 1962, Hart 1973, Ward et al. 2002). Beach seining around San Juan Islands, Washington USA was the primary method of collection, although an anadroumos population of sticklebacks was sampled by dip-netting in a nearby estuary. The fish were transported to Friday Harbor Laboratories and housed in seawater flow-through tanks at a temperature of 11.12±0.91°C and under natural light conditions. Tubesnouts (N=73), sandlances, (N=51) and sticklebacks, (N=36 + 48) were all acclimatized for at least three days before behavioural assays.

(b) Lateralization

We used a standard detour test to assess individual behavioural lateralization (Bisazza et al. 1998a). Fish were transferred into a double T-maze runway with a narrow channel with barriers at both ends (fig. 1). Prior to behavioural assays, we blocked one end of the runway were the fish were acclimatised during two minutes preceding the behavioural assay. When this time had elapsed, the fish were given access to the runway and coaxed with a dip-net until the subject were halfway into the runway. At this point, it was left to swim freely and without influence of the operator until it faced the opaque barrier where it made the decision to turn right or left. The detour behaviour to the left or the right when the fish faced the barrier was observed and resisted by a direct observer as well as by a video camera placed above the maze and facing down. Videos were recorded on “mov – mpeg4 format” using H264 Webcam deluxe ver3.68. The test apparatus were scaled to compensate for size-differences between species (sandlance and tubesnout, 263cm length x54cm width x15cm width channel with the barriers placed 15 cm away from runway ends, sticklebacks 122cm length x 40cm width x7cm width channel with the barriers placed 7 cm away from runway ends). Water depth in the maze was 10 cm for sandlances and tubesnouts, and 4 cm for sticklebacks. All trials were conducted within the natural light regime in order to match the circadian rhythm of the study species. For each individual, we conducted ten consecutive trials allowing for a relative lateralization index to be calculated. The index is ranging from -100 to 100, where the extreme values correspond to total left and right bias, respectively.

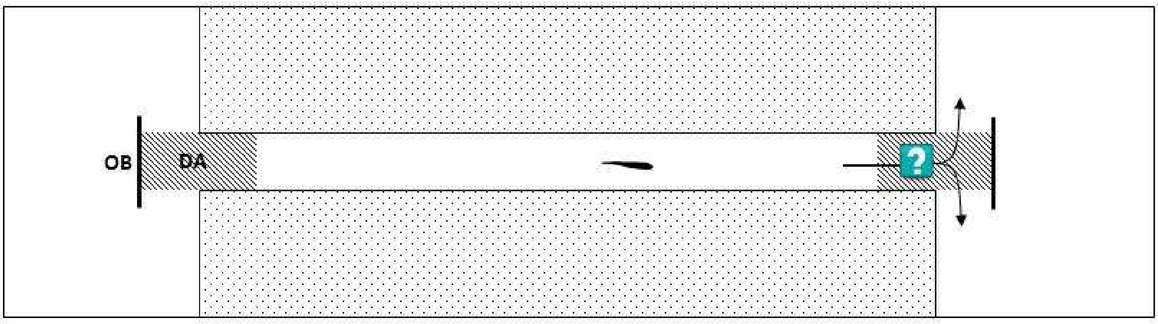

Figure 1. Schematic representation of the double T-maze apparatus. Fish could swim along the runway (alternately in opposite directions); left/right turning directions were recorded. OB: opaque barrier, DA: Decision area

(c) Repeatability of Lateralization

To determine whether lateralization is repeatable over time we tested 50 tubesnouts for lateralization following the procedures described in b). After the detour test each fish was tagged with a code of 3 colors visual implant elastomer (Northewest Marine Technology, Inc.) (VIE hereafter). In the following day the lateralization tests were repeated for the tagged fish.

(d) Data and statistical analysis

To make a comparison between fish and illustrate their lateralization, a relative lateralization index (Lr hereafter) (Bisazza et al. 1998) (formula1) was calculated:

[(Turn to the right - Turn to the left) / (Turn to the right + Turn to the left)]*100

Formula 1

In Lr index, fish were attributed a value that ranged between -100 (10 turns to the left) and 100 (10 turns to the right).To ascertain laterality, a one-sampled t-test was performed on the mean value of the distribution of Lr by testing it against a theoretical mean (0) expected for random decisions. If this discrepancy was found to be significant, the population was defined as lateralized.

To determine whether lateralization is repeatable over time we preformed a Wilcoxon matched pair test to compared the values of the two lateralization tests and ascertained if an individual had maintained the same lateralization trend, or if it had changed its preference.

Results

1. Lateralization

Definition of lateralization in different coastal species:

Tubesnouts

73 tubesnouts were tested for lateralization with a detour test, and a bias towards right turns was discovered to exist at the population level (*t test* = 3.262, *p* = 0.0017; *n* = 73; mean = 12.88). Figure 2 shows that this population is moderately lateralized to the right, the mean is displaced to the right of 0, which would be the expected mean value of a random distribution.

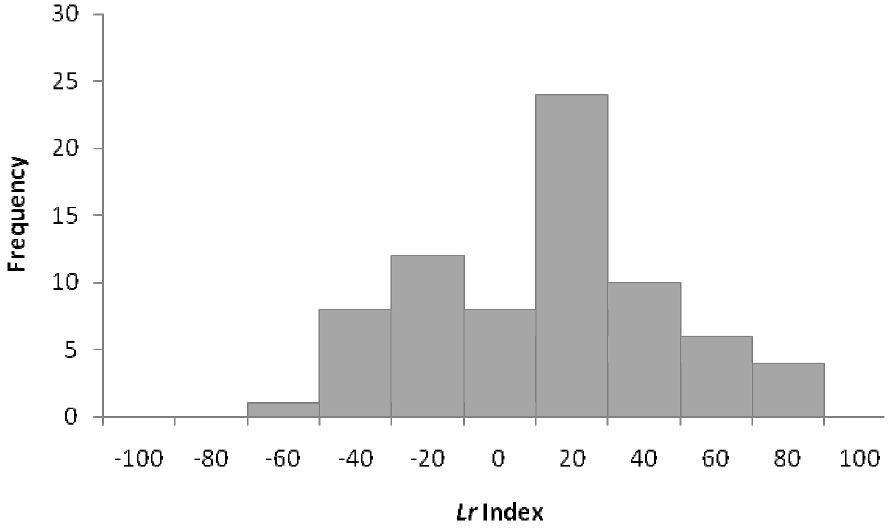

Figure 2 – Frequency distribution of the relative lateralization index (*Lr*) for tubesnouts. A value of -100 represents a fish with 10 left turns in 10 trials; 0 value corresponds to a fish with 5 turns to the left and 5 turns to the right; 100 value corresponds to a fish with 10 turns to the right in 10 trials.

Sand lances

51 sand lances were tested for lateralization with a detour test, and no statistical bias for asymmetrical left or right turns was discovered at the population level (*t test* = 1.139, *p* = 0.260; *n* = 51; mean = -5.49). In figure 3 is visible the non

laterality of this population, the distribution is similar to a normal distribution of random choice events.

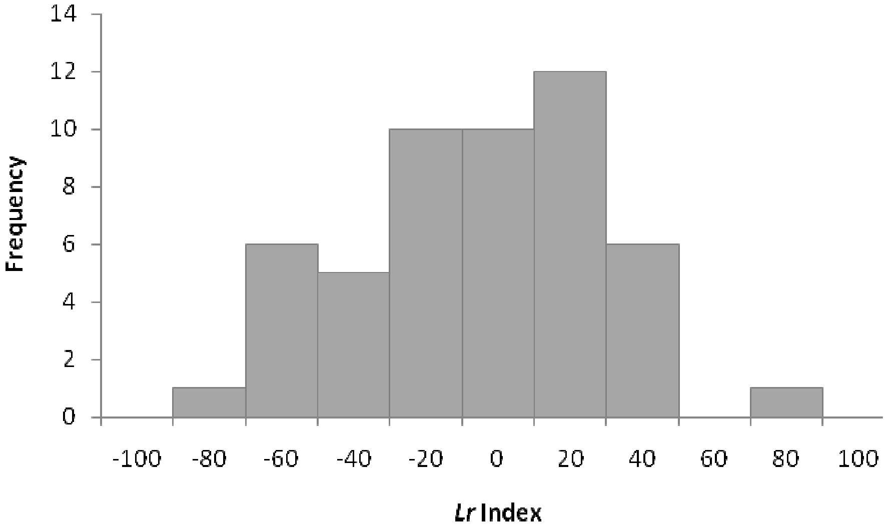

Figure 3 – Frequency distribution of the relative lateralization index (*Lr*) for sandlances. A value of -100 represents a fish with 10 left turns in 10 trials; 0 value corresponds to a fish with 5 turns to the left and 5 turns to the right; 100 value corresponds to a fish with 10 turns to the right in 10 trials.

Sticklebacks

Two populations of sticklebacks were tested lateralization with a detour test; a marine population (n=36) and a anadromous population (n=48). The marine population shows a bias to left turns, at the population level (*t test* = 7.14, *p* = <0.0001; *n* = 36; mean = -32.78). The figure 4 shows that the distribution of the *Lr* is skewed to the left. The mean shows a high displacement to the left of 0, meaning that this is a highly lateralized population, different from a population ruled by random choice. The same general results were found for the anadromous population of sticklebacks. A bias towards left turns was discovered at the population level (*t test* = 7.32, p = <0.0001; n = 48; mean = -30.83). The figure 5 shows the same trend as Figure 4 distribution of the *Lr* is skewed to the left, showing a mean highly displaced from 0, meaning that this is a highly lateralized population, different from a population ruled by random choice.

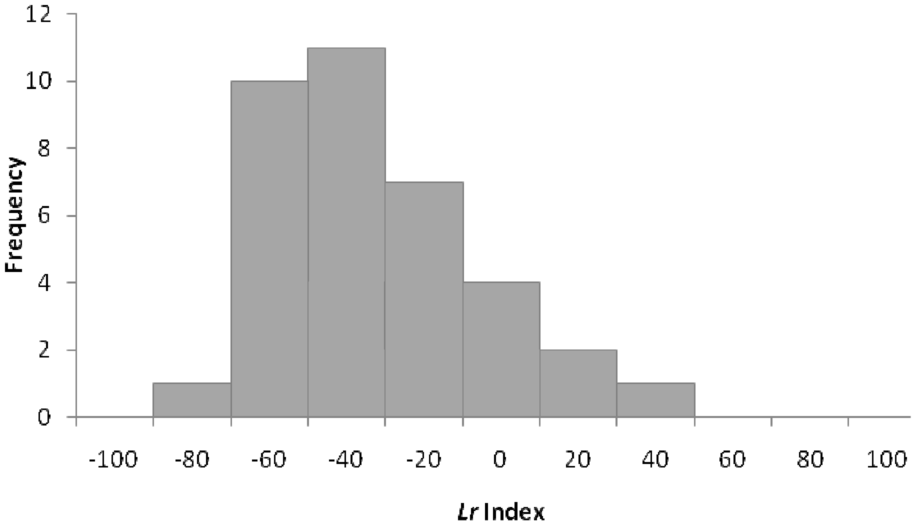

Figure 4 – Frequency distribution of the relative lateralization index (*Lr*) for the stickleback's marine population. A value of -100 represents a fish with 10 left turns in 10 trials; 0 value corresponds to a fish with 5 turns to the left and 5 turns to the right; 100 value corresponds to a fish with 10 turns to the right in 10 trials.

2. Repeatability

The Wilcoxon Matched Pairs test shows that there are no statistical significant differences (n = 50, Z = 1.094, p = 0.274) between the score attained by each fish in the two trials.

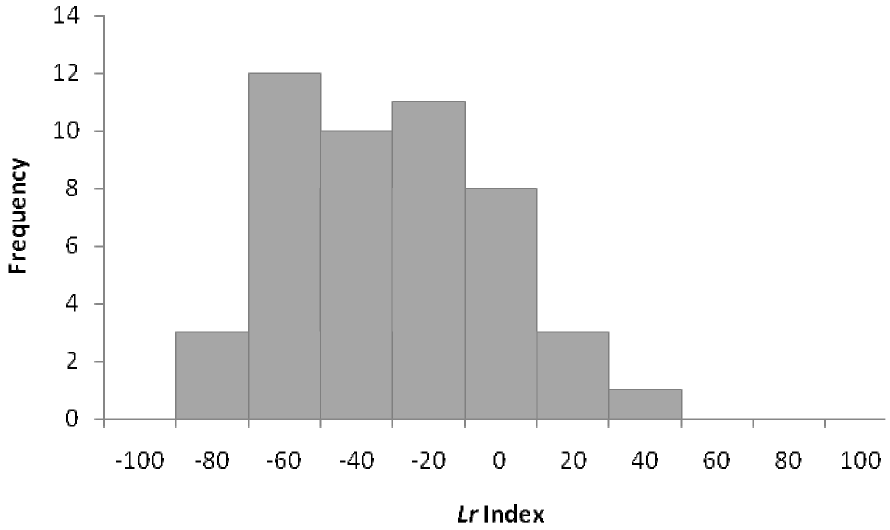

Figure 5 - Frequency distribution of the relative lateralization index (*Lr*) for the stickleback's anadromous population. A value of -100 represents a fish with 10 left turns in 10 trials; 0 value corresponds to a fish with 5 turns to the left and 5 turns to the right; 100 value corresponds to a fish with 10 turns to the right in 10 trials.

Discussion

Between-species comparisons have shown that behavioral lateralization at the population-level seems to covariate with social behaviors, such as schooling (Rogers and Andrew 2002). Given that that behavioral lateralization in the same direction infers advantages in terms of school cohesion and alignment, we predicted population-level lateralization for the social and schooling species included in this study. First, tubesnouts tended to express a small bias towards left turns in our detour trials. Secondly, strong biases for left turns were found in both the marine and anadroumous population of sticklebacks. It is interesting to note that bias seems to be shared by sticklebacks living in very different environments, (i.e. saline and brackish water). In addition, Aulorhynchidae (tubesnouts) and Gasterosteidae (sticklebacks) are two closely related species (Nelson 1971). Hence, we conclude that the results for these two species are in line with previous observations of turning bias in the same direction for congeners of social species. (Bisazza et al. 2000). However, sandlances, another species known to aggregate into schools showed no indication of population level lateralization. Consequently, this result appear to be in contrast to earlier findings (Bisazza et al. 2000). However, although schooling behavior may serve as an effective defense against predation in a number of fish species (Neill and Cullen 1974), prey also parade alternative defense tactics. A key-strategy in the sand lance to reduce the risk of predation is to bury in the sediment when not foraging and during overwintering (Reay 1970, Pinto et al. 1984) We thus speculate that this complementary and more sedentary defense strategy may decrease the need for lateralization in the same directions as conspecifics. Lateralization of the brain is something that appears to be ubiquitous among animal groups (Vallortigara et al. 1999), but as this work shows, lateralization responses may or may not tend to be homogeneous in a population. When they are we have a lateralized population, when they are not we have lateralized individuals in an overall non lateralized population.

This work also proved that behavioral lateral bias when present is something repeatable over time. It is not something of random chance; it is part of the animal's personality and as such the animal is coherent when choosing sides.

To conclude, our results suggest that behavioral lateralization is repeatable over time and might be, at the population level, a feature shared by closely related species. Lateralization appears not to be necessarily related to schooling behavior. Further work should focus on testing repeatability over longer periods of time, and on testing the direct influence of lateralization in school formation and behavior.

References:

Bisazza, A., C. Cantalupo, M. Capocchiano, and G. Vallortigara. 2000. Population lateralisation and social behaviour: A study with 16 species of fish. Laterality **5**:269-284.

Bisazza, A. and M. Dadda. 2005. Enhanced schooling performance in lateralized fishes. Proceedings of the Royal Society B-Biological Sciences **272**:1677-1681.

Bisazza, A., L. Facchin, R. Pignatti, and G. Vallortigara. 1998a. Lateralization of detour behaviour in poeciliid fish: The effect of species, gender and sexual motivation. Behavioural Brain Research **91**:157-164.

Bisazza, A., L. J. Rogers, and G. Vallortigara. 1998b. The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. Neuroscience and Biobehavioral Reviews **22**:411-426.

Bradshaw, J. L. 1988. THE EVOLUTION OF HUMAN LATERAL ASYMMETRIES - NEW EVIDENCE AND 2ND THOUGHTS. Journal of Human Evolution **17**:615-637.

Dadda, M., W. H. Koolhaas, and P. Domenici. 2010. Behavioural asymmetry affects escape performance in a teleost fish. Biology Letters **6**:414-417.

Drea, C. M. 1996. Primate laterality: Current behavioral evidence of primate asymmetries - Ward,JP, Hopkins,WD. Contemporary Psychology **41**:681-682.

Hart, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can **180**:l-740.

Limbaugh, C. 1962. Life history and ecological notes on the tubenose, Aulorhynchus flavidus, a hemibranch fish of western North America. Copeia **1962**:549-555.

Magurran, A. E. 1990. THE ADAPTIVE SIGNIFICANCE OF SCHOOLING AS AN ANTIPREDATOR DEFENSE IN FISH. Annales Zoologici Fennici **27**:51-66.

Neill, S. R. J. and J. M. Cullen. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. Journal of Zoology **172**:549-569.

Nelson, J. S. 1971. Comparison of the Pectoral and Pelvic Skeletons and of some other Bones and their Phylogenetic Implications in the Aulorhynchidae and Gasterosteidae (Pisces). Journal of the Fisheries Research Board of Canada **28**:427-442.

Pinto, J. M., W. H. Pearson, and J. W. Anderson. 1984. Sediment preferences and oil contamination in the Pacific sand lance <i>Ammodytes hexapterus</i>. Marine Biology **83**:193-204.

Pitcher, T. J., A. E. Magurran, and I. J. Winfield. 1982. FISH IN LARGER SHOALS FIND FOOD FASTER. Behavioral Ecology and Sociobiology **10**:149-151.

Reay, R. J. 1970. Synopsis of biological data on North Atlantic sand eels of the genus Ammodytes, A. tobianus, A. dubius, A. americanus, and A. marinus. FAO Fish. Synop. **82**.

Rogers, L. J. and R. J. Andrew. 2002. Comparative vertebrate lateralization. Cambridge University Press, The Pitt Building, Trumpington Street, Cambridge, CB2 1RP, UK 40 West 20th Street, New York, NY, 10011-4211, USA.

Sovrano, V. A., M. Dadda, and A. Bisazza. 2005. Lateralized fish perform better than nonlateralized fish in spatial reorientation tasks. Behavioural Brain Research **163**:122-127.

Vallortigara, G., L. J. Rogers, and A. Bisazza. 1999. Possible evolutionary origins of cognitive brain lateralization. Brain Research Reviews **30**:164-175.

Ward, A. J. W., M. S. Botham, D. J. Hoare, R. James, M. Broom, J. G. J. Godin, and J. Krause. 2002. Association patterns and shoal fidelity in the three-spined stickleback.

Proceedings of the Royal Society of London Series B-Biological Sciences **269**:2451-2455.