

“Handedness” in fishes

Stéphan G. Reebs
Université de Moncton, Canada
2008

Handedness – or lateralization, to use jargon – is defined as the tendency by an individual to favour one side of the body over the other. It reflects the fact that the right and left hemisphere of the brain can become specialized for certain tasks. It used to be thought that only humans were lateralized (we are right or left-handed), but more and more studies are revealing that other vertebrates, and even invertebrates, exhibit at least some degree of “handedness” – the quotation marks denoting the fact that the body parts involved may have nothing to do with hands, and may in fact be eyes, or legs, or even a single organ that can bend to one side, like the mouth.¹ Some of these studies involve fishes.

Sound production in channel catfish

The channel catfish, *Ictalurus punctatus*, makes a sound when it is distressed, such as when it faces a dominant individual, or more prosaically when it is held snugly by an experimenter’s hand. The sound comes from the rubbing of a bony process at the base of the first spine of the pectoral fin against a groove in the pectoral girdle. Thus the sound can be produced by either the right or the left pectoral fin. In a study of 20 catfish raised in an aquaculture pond, Michael Fine and his collaborators found that 9 of these fish showed a significant preference for one fin over the other. Of these 9 fish, 8 favoured the right fin. The percentage of times the right pectoral was used in these 8 fish was, respectively, 83, 71, 91, 92, 100, 89, 100, and 71. The only southpaw (southfin?), for its part, used its left pectoral 84% of the time.

The fish could also produce a series of sounds by alternating the right and left fin. The 8 fish that favoured their right fin during single sound production almost always started their sound series with the right fin, while the only single-sound lefty almost always started its series with the left fin.²

The human-like preponderance of right-“handedness” in these fish is striking, but remember that more than half of the 20 fish in fact showed no sign of lateralization.

I am not aware of any follow-up to this intriguing 1996 study.

Ventral fin use in gouramis

The three-spot (= blue) gourami, *Trichogaster trichopterus*, is blessed with greatly elongated ventral fins. There are taste buds and free nerve endings on those fins, and

the fish uses them to investigate new objects. In a study published by Angelo Bisazza and colleagues in 2001, 12 individual gouramis were presented with 27 novel plastic objects, and the first ventral fin used by each fish to touch any of the objects was noted. The published paper does not give details of the percentage of time each gourami used each fin, but seven individuals were said to show a significant or nearly significant preference for the left fin, four did not prefer one fin over the other, and only one showed a nearly significant preference for the right fin.³

Gonopodium use in poeciliids

In guppies, mollies and swordtails, fertilization is internal. Males inseminate females by using a modified anal fin, called a gonopodium, to transfer sperm to the female. The gonopodium is bent to one side or the other during copulation attempts. A 1952 study found that some males favoured the right side while others favoured the left. However, the preference was not absolute: within each individual, a side was seldom used more than 66% of the time.⁴

Eye use

The body of many fishes is compressed laterally, which means that each eye tends to face sideways. Therefore it is not always easy for a fish to inspect an object with both eyes. A fish may instead turn its side towards the object and inspect it with one eye only. Is there a preference for one side over the other?

The most commonly adopted approach to answer this question is the detour test, in which a fish must swim down a corridor and then detour to the left or to the right as they come upon a transparent barrier behind which lies a novel object or another fish. The detour forces the fish to use one eye only to view the scene. Many experiments of this kind have been done by Angelo Bisazza at the University of Padua, in concert with Giorgio Vallortigara at the University of Trieste, both in Italy.

These experiments were done at first with the eastern mosquitofish *Gambusia holbrooki* and also with another poeciliid, the goldbelly topminnow *Girardinus falcatus*. The experiments revealed a significant tendency to view a predator or a potential mate with the right eye. The fish used their right eye about twice as often as their left eye.⁵ But further work has showed that even though some individuals in these two species are fairly consistently right-eyed (and by fairly consistently, I mean that the right eye was used twice as often, or more, than the left eye), and that such fish are the majority in the population as a whole, there are also some fairly consistent left-eyed individuals in the bunch, as well as some individuals that show no preference.⁶

Other species have been tested with a predator behind the transparent barrier. Six species have showed no eye preference at the population level (*Betta splendens*, *Channa obscura*, *Gyrinocheilus aymonieri*, *Jenynsia multidentata*, *Syngnathus*

pulchellus, and *Xenotoca eiseni*). Four showed the same right eye bias as the mosquitofish and topminnow (*Corydoras aeneus*, *Knipowitschia punctatissima*, *Lepomis gibbosus*, *Padogobius martensi*), and five had a left eye bias at the population level (*Ancistrus* sp., *Barbus conchoni*, *Danio rerio*, *Pterophyllum scalare*, *Trichogaster trichopterus* – in this latter case, note the similarity with the left ventral fin bias towards new objects mentioned above). The lateralized species tended to be the more gregarious ones.⁷

The Siamese fighting fish *Betta splendens* may not be lateralized at the population level, but that does not mean that individuals are not. It may be that there are as many left-eye specialists as right-eye ones, making for a balanced population. Indeed, one study has revealed that many male *Betta*, when they give an aggressive display to a mirror image of themselves, tend to do so by always presenting the same side. It can be the right or the left side, depending on the individual, but it tends to be consistent for each (here, by consistent, I mean one side being used at least 60% of the time). Moreover, courtship display to a female tends to be done with the same side as the aggressive displays to other males or to mirror images.⁸

A mirror image may be interpreted as a rival by bellicose fishes like *Betta*, but for other fishes they may simply represent a peaceful shoalmate. When presented with a mirror, seven species showed a slight preference for looking at the mirror with the left eye. These species were *Xenopoecilus sarasinorum*, *Xenotoca eiseni*, *Gambusia holbrooki*, *Danio rerio*, *Pterophyllum scalare*, *Phoxinus phoxinus*, and *Gnatonemus petersii*. On average, they used their left eye 55-65 % of the time.⁹

An emerging picture is that many species may slightly favour the right eye to view “exciting” fish, such as a predator or a potential mate, and the left eye to view “ordinary” fish, such as shoalmates or one’s own image.¹⁰ Knowing that the information sent by an eye on one side is processed by the brain hemisphere on the other side, preferential eye use can be interpreted as task specialization by each brain hemisphere. Here we could say that the left brain (right eye) of a fish is specialized for evaluating predators or potential sexual partners while the right brain (left eye) is specialized for social interactions of a non-sexual nature.

This notion can have an impact on the results of one particular experimental manipulation. Many fish species are known to cautiously approach potential predators, presumably to find out whether the predators are hungry and about to attack. This behaviour is called “predator inspection”. The inspectors prefer to approach the predator as part of a group (see page on Cooperation). One set-up for studying this phenomenon is a linear raceway with a predator at the end. A mirror can be placed alongside one of the raceway walls, and one can measure whether a lone inspector draws closer to the predator when there is a mirror (giving the illusion that the fish is part of a duo) as compared to when there is no mirror. Indeed, studies with sticklebacks and guppies had found this to be the case (again, see page on Cooperation).

The mosquitofish is one of the species that sometimes inspect predators. Its tendency for viewing predators with the right eye and conspecifics with the left eye was already well known, so the question arose whether it mattered if the mirror was installed on the left wall or the right wall in the experimental set-up for predator inspection. The answer turned out to be yes. Inspectors moved closer to the predator when the mirror was on the left side of the raceway. The interpretation of this result is that having the mirror on the left allowed the fish to use both eyes for the tasks they were good at: looking at the predator with the right eye and checking on the “companion” with the left eye. Tests with another inspector known to have lateralized eye use, the European minnow *Phoxinus phoxinus*, have yielded similar results.¹¹

Any advantage to eye use lateralization?

The above experiments suggest that one advantage of hemispherical brain specialization may be the ability to cope with two simultaneous tasks. Angelo Bisazza and his students have sought evidence for this in fish, using the goldbelly topminnow. The reason they chose that species is that, as already mentioned, some individuals can be found that consistently look at a predator with their right eye, some with their left eye, and some that show no preferential eye use. Moreover, these behavioural characteristics are inheritable, so that selective breeding can generate stocks that are reliably designated as right-lateralized, left-lateralized, or non-lateralized. These three categories can be compared in various behavioural tests.

In one experiment, topminnows could leave their home tank and enter a side compartment that gave them access to food (live brine shrimps) but that also revealed the presence of a live predator in a nearby tank (a pumpkinseed sunfish 62 cm away). The topminnow had to try to catch the live prey while monitoring the activities of the predator. Right- and left-lateralized fish did not differ in the amount of time it took them to capture their first 10 brine shrimps. Non-lateralized fish, however, took twice as long. This was not caused by a relative inability by the non-lateralized fish to catch prey, because in a control situation where the predator was removed from view, all three categories of topminnows took the same amount of time to catch their first 10 shrimps. Rather, it was the non-lateralized fish’s relative inability to do two things at once (catch prey and watch for the predator) that slowed them down. A neat ancillary observation –confirming that the topminnow stocks were well selected, and that they devoted different parts of their brain to different tasks– was that about 70% of the time, the right-lateralized fish kept their right eye on the predator and caught shrimps positioned on their left side, and vice-versa for the left-lateralized fish. Non-lateralized fish showed no such tendencies.¹²

Very similar results were obtained in a test where female topminnows had to grab food flakes at the surface while fending off the mating attempts of harassing males. Lateralized females did better than the non-lateralized ones.¹³

Lateralized fish may also perform better in spatial orientation tasks. In one study single topminnows were placed in the center of a square arena. In each corner there

was an exit that allowed the fish to rejoin the shoal it came from. Only one exit was functional however, the other three being blocked. The exits could be distinguished from one another because they were marked by panels with different symbols. As compared to non-lateralized fish, lateralized individuals (it did not matter whether they were right-turners or left-turners) took fewer trials before they learned which exit was functional. Similar results were obtained when the arena was rectangular with one of the long walls being of a different colour, so that the fish had to learn that the exit was at the right end of the long wall that was not blue.¹⁴

And finally, lateralized fish may also display more cohesive shoaling. When two lateralized topminnows (it did not matter whether they were both lateralized the same way or not) were placed together in a tank, they stayed closer together and kept their bodies more parallel to each other than non-lateralized pair members did.¹⁵

Lateral line use

The lateral line is a row of pores visible on both flanks of a fish. Similar but shorter rows can also be seen on the side of the head. Irrespective of their location, each row of pores connects the outside to a canal that is recessed within the skin, or sometimes within the underlying bone. Because of this connection to the outside, each canal is filled with water, which can slush this way and that way depending on the pattern of water flow outside the body. Water flow inside the canal bends thin hairs that project from sensory cells within the canal walls. Hair-bending in turn causes the sensory cells to send a message to the brain. Some hairs can bend only along one axis, other hairs along another, and therefore the brain can deduce the direction of water movement from the identity of the sensory cells that happen to be firing signals at any one time.

Much less conspicuous than the lateral line or the head rows are a number of free-standing pores, scattered all over the body of fishes, sometimes in loose rows, sometimes in pairs, sometimes by themselves. These pores represent the openings of subcutaneous pits which also contain sensory cells and hair-like projections. These pores are considered to be part of the same system – called the lateral line system – as the head rows and the lateral line itself. However, the precise function of the pits is not quite the same as that of the canals. It is generally recognized that the pits are mostly responsive to the *directionality* of water displacement, while the canals are sensitive to *accelerations* in water displacement.

When swimming, a fish pushes water in front and to the side of itself. At a constant speed in an open area, the resistance offered by water is constant, and water flow around the fish is stable. But if the fish approaches a stationary obstacle, that object adds to the resistance of water and disrupts water flow around the body of the fish. The fish can detect this disruption and use it not only to avoid the obstacle, but also to obtain an accurate “picture” of its conformation. The lateral line can effectively replace the eyes as a means of object inspection. This is particularly useful for blind fish such as the banded astyanax (= Mexican cave fish) *Astyanax fasciatus*.

Research by Theresa Burt de Perera and Victoria Braithwaite has shown that the Mexican blind cave fish favours its right lateral line during novel object inspection.¹⁶

The two scientists introduced single cave fish into a square arena that contained a plastic object along one wall, and they recorded the number of times each fish passed the object using its left or right flank during the first 30 minutes of exposure. The 20 experimental fish used their right flank about 60% of the time on average. By the next day, when the new object had become familiar, the right flank was used about 50% of the time, as you would expect from random choice. The initial 60% value was significantly different from 50%. Similar results were obtained with ring-shaped aquaria that had novel objects placed along both the inner and outer walls (to eliminate the possibility that the right flank preference was simply a consequence of counter-clockwise swimming). So it looks like the right side of the body is slightly favoured during the exploration of a new object.

Clockwise or counter-clockwise swimming in salmon pens

Farmed salmon usually swim round and round inside their ocean pens. In the 1970s a questionnaire was distributed to nearly 50 marine farmers along the west coast of Norway, asking them among other things to note the clockwise or counter-clockwise swimming orientation of their Atlantic salmon, *Salmo salar*. What transpired is that once a pen shows a given orientation, it always keeps that orientation, throughout the tide cycles and throughout the seasons. But some pens are clockwise merry-go-rounds, whereas others are counter-clockwise. What determines the original orientation remains a mystery. It's probably not chance because neighbouring pens tend to show the same orientation, suggesting a common cause.¹⁷

Morphological lateralization

In Lake Tanganyika, cichlids of the genus *Perissodus* are specialized scale-eaters. They sneak up on other fishes from behind and snatch several scales from their flanks. Probably as an adaptation to their peculiar angle of approach and attack, the mouth of these scale-eaters does not face exactly forward. Instead it tends to open slightly to one side. Observations on *P. microlepis* have revealed that, unsurprisingly, fish whose mouth open to the right always attack the left flank of their prey, and those whose mouth open to the left always attack the right flank. In the population as a whole, about half of the fish are right-handed (right-mouthed?) and half are left-handed.¹⁸ Some degree of behavioural laterality, associated with slightly asymmetric mouths, has also been reported for another Lake Tanganyika cichlid, *Neolamprologus fasciatus*, that catches shrimps from the side.¹⁹

One population of zebrafish has been found to have more white muscles on the right-hand side of the anal region, and more red muscles on the left. Correspondingly, as the first step of their startle response –an explosive bout of intensive swimming used

to escape danger– these fish bend their body in a C towards the right side three times as often as towards the left.²⁰

In another study, out of 1689 male corkwing wrasse *Symphodus melops* caught in Ireland, 55.6 % were infected on the lefthand side by the copepod parasite *Leposiphilus labrei*, while the rest (44.4%) were infected on the righthand side. This is not a very big difference, but because of the large sample size it is statistically significant. The cause of this slight asymmetry is unknown.²¹

¹ See references given in the introduction of the following paper: Dadda, M., and Bisazza, A., 2006, Does brain asymmetry allow efficient performance of simultaneous tasks? *Animal Behaviour* 72, 523-529.

² Fine, M.L., McElroy, D., Rafi, J., King, C.B., Loesser, K.E., and Newton, S., 1996, Lateralization of pectoral stridulation sound production in the channel catfish, *Physiology and Behavior* 60, 753-757.

³ Bisazza, A., Lippolis, G., and Vallortigara, G., 2001, Lateralization of ventral fin use during object exploration in the blue gourami (*Trichogaster trichopterus*), *Physiology and Behavior* 72, 575-578.

⁴ Aronson, L.R., and Clark, E., 1952, Evidences of ambidexterity and laterality in the sexual behavior of certain poeciliid fishes, *American Naturalist* 86, 161-171.

⁵ Bisazza, A., Pignatti, R., and Vallortigara, G., 1997, Detour tests reveal task- and stimulus-specific behavioural lateralization in mosquitofish (*Gambusia holbrooki*), *Behavioural Brain Research* 89, 237-242; Bisazza, A., Pignatti, R., and Vallortigara, G., 1997, Laterality in detour behaviour: interspecific variation in poeciliid fish, *Animal Behaviour* 54, 1273-1281; Bisazza, A., Facchin, L., Pignatti, R., and Vallortigara, G., 1998, Lateralization of detour behaviour in poeciliid fish: The effect of species, gender and sexual motivation, *Behavioural Brain Research* 91, 157-164. Work by another lab with another poeciliid, *Brachyrhaphis episcopi*, has upheld the tendency for predator inspection with the right eye, but only in populations that came from high predation regions: Brown, C., Gardner, C., and Braithwaite, V.A., 2004, Population variation in lateralized eye use in the poeciliid *Brachyrhaphis episcopi*, *Proceedings of the Royal Society of London B (Suppl.)* 271, S455-S457; Brown, C., Western, J., and Braithwaite, V.A., 2007, The influence of early experience on, and inheritance of, cerebral lateralization, *Animal Behaviour* 74, 231-238.

⁶ Facchin, L., Bisazza, A., and Vallortigara, G., 1999, What causes lateralization of detour behavior in fish? Evidence for asymmetries in eye use, *Behavioural Brain Research* 103, 229-234; Bisazza, A., Facchin, L., and Vallortigara, G., 2000, Heritability of lateralization in fish: Concordance of right-left asymmetry between parents and offspring, *Neuropsychologia* 38, 907-912.

⁷ Bisazza, A., Cantalupo, C., Capocchiano, M., and Vallortigara, G., 2000, Population lateralisation and social behaviour: A study with 16 species of fish, *Laterality* 5, 269-284.

⁸ Cantalupo, C., Bisazza, A., and Vallortigara, G., 1996, Lateralization of displays during aggressive and courtship behaviour in the Siamese fighting fish (*Betta splendens*), *Physiology and Behavior* 60, 249-252.

⁹ Sovrano, V.A., Rainoldi, C., Bisazza, A., and Vallortigara, G., 1999, Roots of brain specializations: Preferential left-eye use during mirror-image inspection in six species of teleost fish, *Behavioural Brain Research* 106, 175-180; Sovrano, V.A., Bisazza, A., and Vallortigara, G., 2001, Lateralization of response to social stimuli in fishes: A comparison between different methods and species, *Physiology and Behavior* 74, 237-244. See also: Miklosi, A., Andrew, R.J., and Savage, H., 1998, *Behavioural*

lateralisation of the tetrapod type in the zebrafish (*Brachydanio rerio*), *Physiology and Behavior* 63, 127-135; Stennett, C.R., and Strauss, R.E., 2010, Behavioural lateralization in zebrafish and four related species of minnows (Osteichthyes; Cyprinidae), *Animal Behaviour* 79, 1339-1342.

¹⁰ De Santi, A., Sovrano, V.A., Bisazza, A., and Vallortigara, G., 2001, Mosquitofish display differential left- and right-eye use during mirror image scrutiny and predator inspection responses, *Animal Behaviour* 61, 305-310.

¹¹ Bisazza, A., De Santi, A., and Vallortigara, G., 1999, Laterality and cooperation : mosquitofish move closer to a predator when the companion is on their left side, *Animal Behaviour* 57, 1145-1149; De Santi, A., Bisazza, A., and Vallortigara, G., 2002, Complementary left and right eye use during predator inspection and shoal-mate scrutiny in minnows, *Journal of Fish Biology* 60, 1116-1125.

¹² Dadda, M., and Bisazza, A., 2006, Does brain asymmetry allow efficient performance of simultaneous tasks? *Animal Behaviour* 72, 523-529.

¹³ Dadda, M., and Bisazza, A., 2006, Lateralized female topminnows can forage and attend to a harassing male simultaneously, *Behavioral Ecology* 17, 358-363.

¹⁴ Sovrano, V.A., Dadda, M., and Bisazza, A., 2005, Lateralized fish perform better than nonlateralized fish in spatial reorientation tasks, *Behavioural Brain Research* 163, 122-127.

¹⁵ Bisazza, A., and Dadda, M., 2005, Enhanced schooling performance in lateralized fishes, *Proceedings of the Royal Society of London B* 272, 1677-1681.

¹⁶ Burt de Perera, T., and Braithwaite, V.A., 2005, Laterality in a non-visual sensory modality – the lateral line of fish, *Current Biology* 15, 241-242.

¹⁷ Sutterlin, A.M., Jokola, K.J., and Holte, B., 1979, Swimming behavior of salmonid fish in ocean pens, *Journal of the Fisheries Research Board of Canada* 36, 948-954. See also: Donnelly, R. E., and Reynolds, J.D., 1994, Occurrence and distribution of the parasitic copepod *Leposiphilus labrei* on corkwing wrasse (*Crenilabrus melops*) from Mulroy Bay, Ireland, *Journal of Parasitology* 80, 331-332; Juell, J.-E., 1995, The behaviour of Atlantic salmon in relation to efficient cage-rearing, *Reviews in Fish Biology and Fisheries* 5, 320-335.

¹⁸ Hori, M., 1993, Frequency-dependent natural selection in the handedness of scale-eating cichlid fish, *Science* 260, 216-219. See also: Reist, J.D., Bodaly, R.A., Fudge, R.J.P., Cash, K.J., and Stevens, T.V., 1987, External scarring of whitefish, *Coregonus nasus* and *C. clupeaformis* complex, from the western Northwest Territories, Canada, *Canadian Journal of Zoology* 65, 1230-1239.

¹⁹ Takeuchi, Y., and Hori, M., 2008, Behavioural laterality in the shrimp-eating cichlid fish *Neolamprologus fasciatus* in Lake Tanganyika, *Animal Behaviour* 75, 1359-1366.

²⁰ Heuts, B.A., 1999, Lateralization of trunk muscle volume and lateralization of swimming turns of fish responding to external stimuli, *Behavioural Processes* 47, 113-124. See also: Cantalupo, C., Bisazza, A., and Vallortigara, G., 1995, Lateralization of predator-evasion response in a teleost fish (*Girardinus falcatus*), *Neuropsychologia* 33, 1637-1646.

²¹ Donnelly, R.E., and Reynolds, J.D., 1994, Occurrence and distribution of the parasitic copepod *Leposiphilus labrei* on corkwing wrasse (*Crenilabrus melops*) from Mulroy Bay, Ireland, *Journal of Parasitology* 80, 331-332.