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Variability of the Behavioral Laterality in Teleostei (Pisces)

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Abstract—Factors causing variability of behavioral laterality in Teleostei are reviewed. The laterality has been revealed in many fish species belonging to various families. The best ever demonstrated example of the laterality is the different use of the right and left eyes when a fish responds to different visual objects. Magnitude and sign of the laterality differ in fishes of different species, gender, and age. Also, an observed laterality depends on how familiar a stimulus is to fishes and what it means to them, as well as their motivational level and various behavioral traits. Therefore, comparisons of the laterality among different fish species should be based on experimental methods that also take into account those behavioral differences among them that are not directly linked to the laterality.

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INTRODUCTION

Functional laterality (bilateral asymmetry) of the vertebrate nervous system relates to the development of their adaptive behavior and cognitive functions (Bianki, 1985; Bianki and Filippova, 1987). That is why the study of evolution and primary displays of functional laterality become an important problem of evolutionary biology (Vallortigara et al., 1999) at the early stages of the lower vertebrates' evolution, particularly in fish. Numerous investigations of behavioral responses' laterality in teleosts were carried out to date (Bisazza et al., 1998b). The aim of these investigations is to clarify the origin and paths of the evolution of behavioral laterality, its dependence on the asymmetry of brain functions and morphological traits, its adaptive value and the inter-relations of laterality of different behavioral responses. At the same time, despite the presence of extensive experimental data, the attainment of this aim is obstructed by variability of behavioral laterality caused by their dependence on many factors influencing fish behavior. Our review is an attempt to systematize the present data on fish behavioral responses in which laterality is manifested, its dependence on the sing of these responses, on the motivational state of the fishes themselves and on external factors. At the same time, we do not attempt to give the full bibliography on this research area but concentrated our attention on those publications that, in our opinion, most completely demonstrated the variability of laterality and the problems related to its experimental studies.

1. Group and Individual Laterality

Usually for qualitative assessment of behavioral laterality a so-called coefficient of laterality is used: CL = [R – L]/[R + L], where R and L denote the parameters of reactions associated with the choice of either right or left direction, respectively. For example, while studying the laterality of fish motion in a round aquarium, the R symbol denotes the distance with which fish went for a certain time clockwise (“to the right”) and L symbol—the distance counterclockwise (“to the left”) (Nepomnyashchikh and Gremyatchikh, 1993). To compute CL values, the time spent by fish moving clockwise or in the opposite direction may be used instead of distance (Bisazza et al., 1997b). While studying the responses to different objects, R and L denote, respectively, the number of right and left turns of fish relative to an object (Bisazza et al., 2000).

If the mean CL value in a group of specimens differs statistically significantly from zero, then it is common to say that the laterality is of group type (Bianki, 1985). If in the repeating experiments the same individual prefers some definite direction, it is commonly treated as an indication of an individual laterality in animals (Bianki, 1985; Bianki and Filippova, 1987). As we will see later, both types of laterality may be present in the same sample of fish where individual laterality of some specimens does not necessarily coincide with group laterality.

2. Laterality of Fish Responses to Various Objects

Group laterality. Probably, group laterality is most evidently manifested in the fish when they respond to objects that they see in the aquarium. Response to their own reflection in the mirror was studied in eight species belonging to five teleost orders. Fish preferred to move along the mirror in a way that allowed them to observe the reflection with their left eye (Sovrano et al., 1999, 2001). However, in general, such group laterality may have a different sign in different species (see below).

Moreover, different populations of the same species may differ in this respect. For example, during experiments *Brachyraphis episcope* (Poeciliidae) and *Rivulus brunneus* (Cyprinodontidae) caught in water bodies with high abundance of predators used the right eye to track the predator. At the same time the specimens from water bodies with low predator pressure exhibited no preference of either eye. This shows that manifestation of behavioral laterality may depend on ecological factors in fishes' natural habitats (Brown et al., 2004). It should be noted, however, that it is uncertain if the observed differences in laterality were caused by inherited factors or a fish's individual experience.

Quite often fish of the same species, for example, those from family Poeciliidae use their right and left eye for different purposes. Thus, females of *Gambusia holbrooki* track their reflection in the mirror and the free space predominantly with their left eye. However, while being close to the predator, they usually turn to it with their right eye (De Santi et al., 2001). Furthermore, different functions of the right and left eye complement one another: females get closer to the predator (observing it with their right eye) if they see their own mirror reflection from the left. Obviously, the mirror reflection is interpreted as an indication of the presence of a conspecific specimen (Bisazza et al., 1999). On the other hand, *G. holbrooki*, as well as *Xenotoca eiseni*, may display aggression towards their own mirror reflection or another fish. During aggressive displays in most cases, they turn to an opponent with the right eye (Bisazza and De Santi, 2003).

Laterality in the use of either left or right eye depends also on the object novelty. As the fish of different species get accustomed to the object, they may more often turn to observe it with another eye (CL sign changes). In other cases habituation leads a fish to observe the object using its right and left eye with equal frequencies or to turn to the object directly watching it with both eyes simultaneously (in both cases CL is close to zero). At the same time laterality of fish response to its own reflection vanishes after staying in an aquarium with a mirror for five minutes, probably as a result of habituation (Sovrano et al., 2001). It was shown also that *Brachydanio rerio* (Cyprinidae) turns to an unfamiliar object in such a way that it is being observed by the frontal sector of the right eye's field of view. On the contrary, after the same object was presented to the fish for the second time, the frontal sector of the left eye's field of view is being used predominantly (Miklòsi et al., 1997). When adult *B. rerio* are given small color balls for the first time, the fish observe them mainly with the right eye and then try to bite them. After the ball is given repeatedly, right eye preference, as well as bites, disappears and fish orientate themselves relative to the object in such a way that they observe it with both eyes simultaneously. However, if the fish are given a ball of a different color, the preference of the right eye is restored and bites restart (Miklòsi et al., 1997; Miklòsi and Andrew, 1999; Miklòsi et al., 2001). Therefore, fish predominantly use the right eye when they encounter an unfamiliar object. Further, for observation of a familiar object, they also use the left eye. Such forms of behavioral laterality can be seen even in early fry of *B. rerio* (Watkins et al., 2004; Barth et al., 2005).

Responses related to other organs of sense and not only vision may also be lateral (Andrew and Watkins, 2002). Thus, blind cave fish *Astyanax fasciatus* show a clear tendency to turn to an unknown object (protrusion on the side of the aquarium) that is sensed by the lateral line with their right side. This evidences the preference of right body side lateral line organs for the studying of new objects. However, after fish get accustomed to the experimental setup and are habituated to the object, this preference vanishes (Burt de Perera and Braithwaite, 2005).

Individual laterality. As a rule, the presence of group laterality in a given species of fish does not mean that all specimens behave themselves in a similar manner. In the aforementioned example with *G. holbrooki* (De Santi et al., 2001), the group laterality was determined by the CL sign of individual laterality in the majority of specimens while the lesser part of specimens behaved in an opposite way or did not display laterality at all. In some other cases, only individual laterality may be observed, e.g., in Siamese fighting fish (*Betta splendens*, fam. Anabantidae). In repetitive trials males turned with the same eye, both to their own mirror reflection during aggressive displays and to females during courtship. The numbers of males preferring either right or left eye was approximately equal (Cantalupo et al., 1996). However, further experiments with another sample of specimens showed that group laterality may take place also in the aggressive behavior of fighting fish: the majority of males turned to their own reflection or to their opponent with the right eye (Bisazza and De Santi, 2003). Such differences in the results of different experiments with specimens of the same species show that behavioral laterality is a variable characteristic of behavior, which probably depends on many factors including those not considered by researchers (see Section 4).

Conclusions. Lateral response to objects in the environment is a result of preferential use of one body side sensory organs (the eyes first of all) for evaluation of unfamiliar and potentially important objects. The presence of laterality and its sign depend on the fish species and its gender, object novelty, and also on the form of behavior to which the object is related (foraging, predator avoidance, courtship or aggression).

3. Laterality of Obstacle Detouring

Group laterality. When fish meet an obstacle, they make a detour of it either from right or left and, in the choice of detouring direction, the group laterality is manifested. This laterality was studied in 16 fish species belonging to 13 families (Bisazza et al., 2000). The obstacle represented a barrier made of vertical bars. The fish were able to see through the barrier a model of a predator against which the defense response was developed beforehand. After the learning period, the fish avoided the barrier in order to inspect the predator. Each fish was placed in front of the barrier ten times and the direction preference was determined as the difference between numbers of right and left turns. The representatives of 10 out of 16 species exhibited consistent group tendency to turn to a definite direction. It was also revealed that, in species of the same family, the signs of group laterality coincide more often than in the species belonging to different families.

It was also shown that the direction of obstacle detouring depends on the nature of the objects that fish see through the barrier. For instance, males of *G. holbrooki* exhibited a constant tendency to left turns if either females or a predator model were beyond the barrier but no preference was observed if other males or open space were there. The trend to a left turn had also vanished in the case if the barrier was U-shaped and males, when avoiding it, were compelled to swim in the opposite direction from the target. Finally, if the barrier was not transparent, males preferred to turn right. These results assume that the laterality of turns when fish make a detour of an obstacle reflects the asymmetry in eye functions. The objects that cause an interest are tracked by the right eye (resulting in left turns in front of the barrier), while, in the case of a nontransparent barrier, the same eye is used for tracking the open space not protected by the barrier (Bisazza et al., 1997c).

The data obtained as a result of similar trials with poecilid fishes (*Gambusia nicaraguensis*, *Poecilia reticulata*, *Brachyraphis roseni* (Bisazza et al., 1997c), and *Girardinus falcatus* confirm that the laterality of obstacle detouring is related to different eye functions (Bisazza et al., 1998a). At the same time preferable direction of the obstacle detouring differs in different species even if the object beyond the barrier has similar importance (e.g., females). In other words, the sign of laterality is species-dependent.

Preferable direction of obstacle detouring may change and even any preference may vanish along with habituation of fish to experimental conditions, including the objects placed beyond the barrier (Bisazza et al., 1997c). Besides, the direction of detouring depends on the level of fish motivation. For example, females of *G. holbrooki* and *G. falcatus* that saw males beyond the barrier did not exhibit a preference towards any direction if they were kept together with males before the experiment. However, after a two month-long keeping apart from males, they had shown a tendency to turn left which can be explained by a higher level of sexual motivation in females (Bisazza et al., 1998a).

Choice of motion direction in the T-maze may also be lateral in fish which is, perhaps, caused by the same factors as in the case of the obstacle detouring. During repeated trials in the maze, some young specimens of Nile tilapia (*Oreochromis niloticus*; Cichlidae) show consistent preference to right turns, while others do not exhibit any preference (Gonçalves and Hoshino, 1990a, 1990b).

Individual laterality. If in case of obstacle detouring the fish of any species exhibit the group laterality, it does not mean that all specimens prefer the same direction of detouring. The results of the experiments given above (Bisazza et al., 2000) have shown that, in any of the species studied, there are specimens showing stabile preference to either right or left turns. In other words, in all these species, the individual laterality of obstacle detouring is presented. The group laterality appears due to an uneven ratio of “right” vs. “left” specimens. The group laterality is more pronounced in social fish species which, according to Bisazza et al. (2000), is due to the necessity to coordinate motions of individual fish in school, while in the solitary living species, only individual laterality presents.

Conclusions. Most likely, the choice of a turn direction during the detour is not an independent manifestation of behavioral laterality. It relates to the asymmetry of right and left eye functions during the study in the environment of the objects differing in their novelties and importance. Even if there are no specific objects within the fish visual field (as in case of the detouring of a nontransparent barrier), a determined eye is used to check the unknown and potentially dangerous space.

4. Rotational Laterality

Group laterality. One of the most common methods to reveal behavioral laterality consists of the registration of motion direction of an animal along the perimeter of the circle enclosure or in a ring corridor (rotational laterality). Numerous reports on group rotational laterality in fish exist. Lapkin and coworkers (1989) placed in a round aquarium a number of juvenile roach (*Rutilus rutilus*) and bream (*Abramis brama*) caught in the wild. Most often, this fish moved counterclockwise. This phenomenon lasted about 25 days. Before the known direction of motion was finally established, changes of clockwise and counterclockwise coordinated fish motions were observed. This coincided in time with the period of increased locomotory activity during the spring and fall migrations of juveniles of these species and was absent in other times of the year. Authors assumed that within the limited aquarium space and at high fish density the need to increase locomotory activity is realized in a form of a coordinated one-way motion.

It was similarly shown that marine fish of different species, placed in large amounts in the circle enclosure, swim along its perimeter in most cases clockwise, less often counterclockwise or change direction by an irregular manner (Suyehiro and Takizawa, 1968). It was also noted that encaged bleak (*Alburnus alburnus*; Cyprinidae) (Kuznetsov, 1975), smelt (*Osmerus eperlanus*; Osmeridae) under natural conditions (Permitin and Polovkov, 1975), and anchovy (*Engraulis encrasicholus*; Engraulididae) in open sea (Borisov, 1955) tend to concentrate around the submerged source of light, moving around it clockwise.

In all these experiments, the interrelations of fish may have influence on both extent of manifestation of rotational laterality and the fact of its appearance. However, similar group laterality can be seen in solitary specimens as well. The majority of juvenile specimens of Mozambique tilapia (*Oreochromis mossambicus*; Cichlidae), placed one at a time in a round aquarium, exhibited preference to a clockwise motion (Hepomnyaschikh and Gremyatchikh, 1993). Similar preference was revealed in mosquitofish (*G. holbrooki*) (Bisazza and Vallortigara, 1996, 1997).

In the cited works, as well as in the majority of other similar studies, functional laterality in fish was determined based on the result of a single experiment, and the duration of the majority of such experiments did not exceed 15 min. In fact, in all these experiments, a part of the specimens moved in the direction opposite to the direction of motion of the majority of fish. However, this does not mean that differences in preferable direction are caused by individual variability (e.g., genetic, age, or gender) of specimens in the studied sample. As it will be shown below, preferable direction may change in the same specimen during the experiment. Such like variability could affect CL, especially if the duration of experiment is short.

Dependence of group rotational laterality on sources of light. The majority of researchers studied rotational laterality in fish either under natural lighting conditions or using the point source of light placed above the center of the aquarium or cage. One may assume that in these cases rotational laterality represents the response to a light source: fish may interpret it as either the sun (the angle to which serves as a reference point during migrations) or as an unknown object that causes interest. These assumptions were tested by several researchers. Migrating fish *Cheirodon pulcher* prefer to move in a ring corridor clockwise in the presence of a light source above the center of the enclosure. If this source was substituted then by diffuse light, the above mentioned preference remained unchanged. However, if the fish was placed in the diffuse lit corridor just from the very beginning of the trial, they do not exhibit any directional preference (Levin and Gonzalez, 1994).

Similarly the hypothesis concerning the sun-compass navigation in females of *G. holbrooki* (Bisazza and Vallortigara, 1996) was tested. The experiments were carried out in a circle aquarium with a light source above its center. It was presumed that fish interpret the light source as the sun at the angle to which they may have to orient under natural conditions, moving off the shores when avoiding predators. To test this assumption, the females from the natural population were observed during different day times differing in the sun positions. Consequently, the direction of fish motion in relation to its position must be also be different. During the daytime, females preferred to move counterclockwise. In the morning, they moved clockwise which always corresponded with their movement off the shores (with respect to the sun position in their natural habitat). The preference in the direction was revealed in males neither in the morning nor in daytime. However, authors explain this by the fact that mosquitofish males are subject to predator attacks less often (Bisazza and Vallortigara, 1996). If the light source above the aquarium center was substituted by three sources placed on its periphery, then rotational laterality in the same females disappeared. Finally, laboratory-raised females were also lacking laterality. These facts also confirm the assumption that the group rotational laterality under new conditions in mosquitofish relates to the sun-compass orientation (Bisazza and Vallortigara, 1996). Other authors also relate the laterality in fish motion direction to migrational orientation (Gleiser, 1981).

Dependence on other factors. Rotational laterality depends not only on the sun-compass orientation. In a work by Bisazza and Vallortigara (1997), the motion of mosquitofish (*G. holbrooki*) males was studied in a circle aquaria in the presence of females (or predators). The females and/or predators were placed under the transparent cap in the center of the aquarium. In one variant, the cap was empty. In the presence of the predators, the males were moving predominantly clockwise. In the presence of the females, the trend was the same, although weaker. In the empty aquarium, fish demonstrated a weak preference of counterclockwise direction. In this experiment, the aquaria were also lit from the top by a point source of light. However, dependence of motion direction on the presence of other fish indicates that the obtained results cannot be explained only by the response to a light source. It is likely that, to track the objects in water, mosquitofish males use mainly the right eye which results in their clockwise motion in the presence of other fish.

As was already noted in Section 2, females of mosquitofish and of some other poecilid and cyprinid fishes use predominantly the left eye to track their own mirror reflection (before they get used to it). As a result, in the aquarium with mirror wall, they move clockwise. However, this rotational laterality vanishes fast along with habituation (Sovrano et al., 2001).

Visual reference marks placed along the periphery of a circle aquarium may suppress the rotational laterality if these marks stimulate exploratory behavior. If black vertical stripes are painted on the aquarium wall, juvenile Mozambique tilapias (*O. mossambicus*) actively explore them, turning towards a stripe and swimming to it from different sides, constantly changing direction. As a result, laterality peculiar to tilapia vanishes due to constant changes in direction (Nepomnyashchikh and Gremyatchikh, 1993).

Perhaps all these results may be due to group laterality in the use of the right and left eye in different situations. As was already noted, mosquitofish (*G. holbrooki*) make a detour of a nontransparent obstacle by the way that the free, not protected by an obstacle spaces are controlled by a determined eye (Bisazza et al., 1997b). In a circle aquarium, Mozambique tilapia (*O. mossambicus*) move mainly along the wall before they get used to conditions (Nepomnyashchikh and Gremyatchikh, 1992). It may be assumed that the trend to move clockwise in tilapia relates to that they check the internal space of the aquarium mainly by their right eye. However, this assumption has to be tested.

Individual laterality. We discussed, above, the manifestations of rotational laterality under new conditions for fish. In order to reveal individual rotational laterality, it is necessary to repeat observations of the same specimen. If CL sign in repeated experiments will be the same, then the individual laterality exists. Relevant observations were carried out on mosquitofish (*G. hollbrooki*) (Bisazza and Vallortigara, 1996). The fish caught in the wild were observed in a ring corridor over five days, 15 min every day. At the first day of observation, no preferable direction was noted in males while females exhibited group laterality of motion (clockwise). Later on, group preference of this direction vanished. Besides, in the majority of both male and female specimens, preference for individual direction (clockwise or counterclockwise) was found, as evidenced by the correlations of their individual CL values in repeated trials. The CL correlation between the last days of observation was higher than between the second and third days. At the same time, there was no correlation between the first and latter days. The authors explain such changes in the mosquitofish behavior by the presence of two types of rotational laterality in these fish. One of them, the group laterality, is displayed on the first day and probably relates to the response to unknown conditions. The second one, the individual laterality, is masked at the beginning but then is displayed and gets stronger along fish habituation to the experimental conditions.

Similar behavior was observed in goldfish (*Carassius auratus*; Cyprinidae) juveniles under similar experimental conditions. At the first day of the experiment, the group trend to counterclockwise motion was observed (Nepomnyashchikh, 2005). However, in later days, this trend had vanished and had been changed by the individual laterality. As in mosquitofish, the vanishing of group laterality in gold fish is probably due to habituation to conditions of the experimental aquarium.

Laterality and fish exploratory behavior. Fish explore unknown space and this exploratory behavior may potentially influence the extent of observed laterality. First, the motion of fish along the perimeter of the circle aquarium is interrupted by exploring some of its parts which is accompanied by frequent changes of motion direction. These explorations are spontaneous since they can be observed also in case any of the potential reference marks are absent in the uniformly lit aquarium. Such change in motion direction takes place less frequently in Mozambique tilapia (*O. mossambicus*) (Nepomnyashchikh and Gremyatchikh, 1992) and more often in goldfish (Nepomnyashchikh, 1998). At the same time, absolute CL values are higher in tilapia (Nepomnyashchikh and Gremyatchikh, 1993) than in goldfish (Nepomnyashchikh, 2005) or, in other words, laterality in tilapia is more pronounced. It is clear that frequent change in motion direction may lead to decrease in laterality. That is why observed differences between tilapia and goldfish are not necessarily due to real peculiarities of the CNS asymmetry in these species. Rather they may result from different intensities of exploratory behaviors masking the rotational laterality.

Second, both tilapia (Nepomnyashchikh and Gremyatchikh, 1992) and goldfish (Nepomnyashchikh and Gremyatchikh, 1997) are characterized by a known stability of motion: the longer the fish moves in a selected direction (clockwise or counterclockwise) the less is the probability of its change. This stability is obvious both while the fish moves in the direction that coincides with the sign of the group or individual laterality and the opposite. Mathematic modeling has shown that the stability of motion results in considerable CL variability in the "fish" in a model regardless of the fact that the model stipulates absolutely equal preference of direction for each specimen. As a result of such variability, statistically significant differences in CL values (up to change of the CL sign) may be revealed between the uniform model "fish" samples if these samples are small (not more than 20) and the duration of the observations is short (not more than 15 min). In the experiment with real goldfish, the same differences of CL values was observed (Nepomnyashchikh, 2005). This means that differences in values and sign of group laterality revealed in the experiments with small groups of fish belonging to different species or populations do not necessarily witness real differences in their CNS asymmetries. Similarly, an observed difference in the individual CL does not necessarily mean that specimens in a sample are really different. During the repeating observations, the CL of these specimens may change considerably.

Conclusions. The information given in the present section allows for the conclusion that the rotational laterality as well as detouring laterality is not an independent manifestation of behavioral laterality. It originates as a result of the interaction of specific experimental conditions (round aquarium) with responses to various factors. In particular, the responses to these factors are determined by the asymmetry in the right and left eye functions when fish analyze new objects. Hence, group rotational laterality may vanish after habituation to the experimental conditions and may be changed by the individual laterality that has been suppressed under unknown conditions. As for the individual rotational laterality, it may result from the asymmetry of eye or other sense organ functions but in the familiar conditions as it happens when other experimental methods are used (see sections 2 and 3). Besides vision, the rotational laterality may relate to a variety of other functions of sensory organs on the right and left body sides, e.g., the lateral line organs. This assumption may be tested by registering the direction of fish moving in the dark. However, such experiments had not been carried out yet.

The rotational laterality may be masked by responses to visual reference marks, exploration activity in fish, and by the stability of motion direction even if this direction does not coincide with the preferable one. Moreover, the influence of these peculiarities of fish behavior may lead to the change of sign of the laterality observed if a relatively small sample of fish was observed for a short time. Finally, the observed laterality in some cases may be the result of sun orientation which has no direct relation to the asymmetry of CNS or other systems of the organism.

5. Laterality of the Avoidance Response

Group laterality. An approaching predator or a sudden strong stimulation cause in fish an avoidance response: C-bend of the body in the horizontal plane and lunge leading off the danger. In cyprinids *C. auratus* and *B. rerio*, the group trend to bend right after the sharp vibration stimulus sensed by the lateral line organs was revealed. The same trend was revealed in *B. rerio* males and in females when they were chased by males. In guppy *Poecilia reticulata* (Poeciliidae) and in four cichlid species, no avoidance response laterality was observed (Heuts, 1999). During free swimming in the aquarium when the fish changes direction spontaneously but not in response to danger, the direction of turns may differ from that one at the C-bend. For instance, free swimming *B. rerio* females turn right more often (as well as when escaping males) but males turn left more frequently (Heuts, 1999).

In the immature *G. falcatus*, sudden appearance of a predator model just in front of the fish leads to a predominantly right turn. If the experiment is repeated with the interval of seven days, this laterality gradually changes by the opposite—the fish turn predominantly left. In a similar experiment, adult specimens at first exhibit only a weak trend to turn right which changes in the repeated experiments to a strong trend to left turns (Cantalupo et al., 1995).

Individual laterality. Under similar experimental conditions, other fish (*Jenynsia lineata*; Anablepidae) do not manifest the avoidance response laterality at a group level. However, half of the specimens show pronounced individual laterality as evidenced by a considerable correlation of individual CL values in repeated trials (Bisazza et al., 1997a).

Conclusions. Similar to other types of behavioral laterality, the avoidance response laterality depends on the novelty of a stimulus, as well as on the fish species and sex. At the same time as the opposite to other types of laterality, it is hard to relate the laterality in response to vibration stimulus to qualitative differences in the functions of symmetric sensory organs and analyzers in CNS. In *C. auratus*, the avoidance response laterality is manifested much stronger in the case when the fish is oriented by its head towards the vibration stimulus compared with the opposite orientation but the laterality sign does not depend on small (within 20°) deviations of the direction of stimulus action in relation to the body axis (Heuts, 1999). Besides, the avoidance response laterality was found in other fish, *G. falcatus* (Bisazza et al., 2005), upon which the vibration stimulus was directed from below the body. In this case the direction of C-bend right or left in the horizontal plane cannot be related to the orientation towards a stimulus.

6. Laterality of Fin Use

In terrestrial vertebrates starting from amphibians, the laterality in use of extremities is well known (Vallortigara et al., 1999). Similar laterality in the use of fins was revealed in some fish. For instance, channel catfish (*Ictalurus punctatus*; Ictaluridae) use pectoral fins for stridulation. Some specimens often use fins on both body sides, while others on one side predominantly, thus, showing the individual laterality. In the same fish, the group laterality takes place: most of the specimens use right-side fins more often (Fine et al., 1996).

Blue gourami (*Trichogaster trichopterus*; Anabantidae) feel different objects by modified abdominal fins. During such feeling, gourami use mainly the left fin to touch plastic or mineral objects while for live objects symmetrical fins are used with similar frequencies. Perhaps, in this case, predominant use of the left fin is a result of eye function asymmetry since gourami prefers to see an object by the left eye before probing it with a fin (Bisazza et al., 2001).

CONCLUSIONS

The experimental data show that the laterality in behavioral responses found in fish relates in most cases to the functional CNS asymmetry which is also true for higher vertebrates. This relation is demonstrated in more detail for responses to visual stimuli. Novelty of a stimulus to fish, its relation to motivation, and the extent of the motivation itself, as well as fish sex and species, determine which one of the symmetrical visual brain centers will dominate the response control. As a contradiction, the relation of avoidance response to the CNS functional asymmetry remains uncertain. Perhaps this relation is due to the asymmetry of the motor system. Besides, in some fish species, the fin use laterality is found but it is yet unclear how this relates to the CNS asymmetry.

As in higher vertebrates in fish of some taxonomic groups, the laterality at species or population level (group laterality) was revealed while in others only individual laterality presents. In some fish species no laterality was revealed at all. It would be interesting to attempt to relate these differences to fish phylogeny and ecology which may allow for understanding of the origin and adaptive importance of the vertebrate CNS functional asymmetry. However, in our opinion, not enough reliable experimental data have been accumulated yet for such attempts. This is because the variability of the behavioral laterality due to its dependence on many factors hampers its study.

In particular, the group laterality is best manifested in the response to unknown stimulus. Habituation is accompanied not only by change of sign but in some cases it leads to the full vanishing of the group laterality. It can be assumed, for example, that observed differences in the laterality of responses to visual stimulus in the fish of different species, age, and sex may be determined by the rate of their habituation to a stimulus. Under the same conditions and equal duration of the observation, it is more difficult to reveal the laterality in those fish that habituate to the experimental conditions faster. In Section 4 it was shown how the dependence of rotational laterality on the peculiarities of exploration behavior may result in contradictory conclusions about its size and sign, if theses conclusions are drawn based upon short experiments with a small number of specimens. The absence of laterality in such experiments does not necessarily indicate its real absence in fish. The same dependence of external manifestations of the laterality on the peculiarities of fish behavior may also take place in the case of responses to visual, vibration, and acoustic stimuli, avoidance response or fin usage. However, such dependence has not been studied yet. We believe it is important to emphasize that, to obtain reliable results, the experimental methods for studying the behavioral laterality must be developed with consideration of the species-specific peculiarities of fish behavior.

In conclusion, we would like to note once again that the present review does not cover the whole material accumulated by research of the fish behavioral laterality. To understand its origin and adaptive importance, it is necessary to reveal the relations between different types of behavioral laterality as well as the relation of the latter to the asymmetry of specific CNS sections and of other systems of an organism. This vast field of research needs to be reviewed separately.

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