Lateralization in a partial migrating roach population

Mattias Engman

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Abstract

Lateralization is the functional specialization to use one brain hemisphere to carry out certain cognitive tasks. Lateralization is widespread across numerous taxa and gives the organism the possibility to increase neural capacity without increasing brain size. The degree and direction of lateralization varies within populations, suggesting that there also are disadvantages to being lateralized. Here I examined correlates between behavioral lateralization and alternative migratory strategies in a partially migratory population of Roach (*Rutilus rutilus*). I assessed behavioral lateralization in migratory and resident phenotypes and also measured the repeatability of behavioral lateralization in this species. My results show no signs of lateralization in either migrant or resident fish, which suggests that there is a disadvantage, like lower ability to evaluate the environment equally with both eyes, connected to being lateralized

Introduction

Functional lateralization of the brain was first discovered among animals in the 1970s and has now been found in a range of taxa including birds, fish, amphibians, reptiles, mammals and even insects (Rogers & Anson, 1979; Nottebohm, 1971; Bisazza et al., 2000; Robins et al., 1998; Robins et al., 2005; Denenberg et al., 1978; Pascual et al. 2004). Lateralization is often studied through vision where the right eye (and left side of the brain) has mostly been associated with responses which require analytical processing and the left eye (and right hemisphere) with actions demanding fast responses and of emotional character (Rogers & Andrew, 2002).

The traditional theoretical explanation for having a lateralized brain is that it increases the neural capacity as functions can be divided between the two brain halves rather than simply duplicated (Levy, 1977). Rogers & Anson (1979) showed that by inhibiting the left hemisphere in chicks, the ability to distinguish grains from pebbles was deteriorated while no effect was seen by inhibiting the right hemisphere. Other studies on the ability to perform dual tasks have shown that lateralized individuals are more efficient in their foraging while being disturbed by another stimulus like a predator or harassing male (Rogers et al., 2004; Dadda & Bisazza, 2005; Dadda & Bisazza, 2006). Further evidence supporting the theory of computational advantage includes studies on fish where lateralized individuals showed increased schooling performance (Bisazza & Dadda, 2005), escape performance (Dadda et al. 2010) and higher ability to spatially reorient themselves (Sovrano, 2005), regardless of their left or right bias.

Another advantage of having a lateralized brain could be in organisms with laterally placed eyes, like in many species of fish and birds, where these could provide different inputs. By having a dominant hemisphere, the organism can maintain a proper course of action and filter contradicting inputs (Vallortigara & Rogers, 2005). By switching location of two barriers of different colors, Vallortigara (2000) showed that chickens, with one eye covered while searching for an object behind one of the barriers to larger extent choose to search behind the barrier in the right position when using their left eye and behind the barrier of right color using their right eye. When tested with both eyes, results did significantly differ from the right eye but not from the left eye, suggesting that the color analysis of the left hemisphere is suppressed.

A disadvantage of visual lateralization can obviously be the decreased responsiveness when a stimulus approaches on the “wrong” side. (Rogers, 2002). Vallortigara et al. (1998) studied two species of toads of which one would tongue-strike earlier if the prey entered the visual field from the right. Another example is lateralized individuals of the Goldbelly topminnow (*Girardinus falcatus*) – fish were presented to one high-quality shoal with more individuals or individuals of the same size as the focal individual on one side versus a low-quality shoal with less individuals or individuals of a smaller size than the focal individual on their other side (Dadda et al., 2009). Due to their eye preference, they would more often choose the low quality shoal compared with their non-lateralized conspecifics.

Lateralization at the population level occurs when most of the individuals in a population are biased to the same direction (Rogers 2002). Commonly, 65-90% of the individuals in a population have a left eye which is better at vigilance against a predator than their right eye (Vallortigara & Rogers, 2005). However, there is little evidence of what factors determine these proportions in a population. Lateralization has shown some plasticity to environmental conditions. Light and predator cues in the prenatal period has been shown to increase lateralization for chickens and fish (Rogers, 1990; Dadda & Bisazza, 2012; Jozet-Alves & Hebert, 2012). Rats handled in their infancy showed signs of lateralization in contrast to the ones not handled (Denenberg et al., 1978). Recently Domenici et al. (2011) showed that CO_2 can disrupt lateralization in fish larvae and Gehring (et al. 2012) reported that the European robin’s lateralization of its magnetic compass could be reversed within hours by obstructing eye input during its first year of age. Brown et al. (2007) found that lateralization also can be an inherited trait in the poeciliid *Brachyraphis episcopi*, which increases in populations from habitats with higher predation pressure. Others have argued that the variation in a population is created by frequency-dependent selection where there is an equilibrium between the social gain of behaving similar to conspecifics but a cost in being predictable to predators (Ghirlanda & Vallortigara, 2004; Vallortigara & Rogers, 2005).

Wilzeck et al. (2010) studied lateralization of the magnetic compass in pigeons by temporarily covering one eye in an orientating task. The pigeons were successful in orienting themselves using either eye but the left eye tended to confuse the learned direction with the opposite. Lateralization of the magnetic compass seems to be even stronger in European robins, which seem unable to orient themselves when using only their left eye (Wiltschko et al. 2002; Gehring et al., 2012). In a population of silver eels, migration performance was reduced by blocking both or only the right nostril whereas when blocking the left nostril, the eels performed similar to eels with both nostrils free (Westin 1998). While lateralization has been shown to increase performance in spatial tasks (Sovrano et al., 2005) it’s also possible that it can inhibit exploratory behavior (Brown & Braithwaite, 2005). Individuals of *B. episcopi* from more lateralized populations are slower at completing a maze than individuals from less lateralized populations.

Previous studies have documented links between behavioral lateralization and exploratory behavior, e.g. navigation and orientation. However, no studies have tested whether behavioral lateralization is linked to different migratory strategies (i.e. resident and migratory phenotypes). Partially migratory populations offer a unique opportunity to answer this question since only a fraction of the population migrates whereas others remain as residents in the same environment year-round. Roach (*Rutilus rutilus*), a common freshwater fish, have been shown to be partial migrants where some individuals migrate into connected streams and wetlands during winter whereas other individuals remain as residents in the lake (Skov et al., 2008). Partial winter migration of roach have been suggested to be driven by temperature-dependent changes in the ratio between predation risk (p) and growth potential (g) (Christer Brönmark et al., 2008). Food is more rare in the streams and thus gives a reduced growth (Jakob Brodersen et al., 2008) while predation is also lower while in the lake it's the opposite conditions with higher growth potential and higher predation pressure (Skov et al., 2008). As lower predation pressure can decrease behavioral lateralization compared with populations from habitats experiencing intense predation (Brown et al., 2004), it is also possible to expect less lateralization in the migrants. In this roach population, the personality trait boldness has been shown to affect migration behavior at the individual level (Chapman et al., 2011). Other studies have documented a correlation between boldness and behavioral lateralization (Brown et al., 2004 & 2005; Reddon & Hurd, 2009). Therefore, there are reasons to expect that behavioral lateralization is a trait that differs between migrants and residents.

Increased understanding of cognitive ability in fish can help predicting effects of population collapses and how populations interact with other parts of the ecosystem (Fernö et al. 2011). Partial migration in roach has been suggested to influence the stability and transitions of alternative stable states in lakes (Jakob Brodersen et al. 2008a) thus more knowledge of the migration processes can provide better understanding of lakes' ecological state. The aim of this study was to test if migrant and resident roach in an established partially migrating population show different degrees and directions of behavioral lateralization. I predicted that the migrating roaches are more lateralized as they are bolder and have a higher need for orientation.

Method

Study system

Krankesjön is a shallow eutrophic lake in southern Sweden (55° 41′ 50″ N, 13° 28′ 40″ E). A portion of the roach population (30-70% between-year variation) migrates into the adjacent streams, one outlet and two inlets, each winter (Skov et al., 2008; Brodersen et al., 2008b). The two dominant piscivors predating on roach are northern pike (*Esox lucius*) and perch (*Perca fluviatilis*) which migrates to much less extent (2.1% and <1%) (Skov et al., 2008).

Experiment

Resident specimens of roach were collected in the northern shore of Krankesjön and migrating specimens in the connected stream Silvåkrabäcken (55° 41′ 12,35″ N 13° 29′ 55,01″ E). Electrofishing was used at both locations and was performed at two occasions in the same week during a period when there was little exchange of individuals between the two habitats (documented using passive telemetry). In order to be able to distinguish resident and migratory fish, each individual was marked with a visible elastomer implant tag (Northwest Marine Technology Inc.) After tagging, the fish were kept in a tank with a flow-through system with aerated water for at least 50 hours prior the experiment. Fish were fed daily with 100 g of frozen Daphnia.

To obtain an index of individual behavioral lateralization, we used a standard detour test (Bisazza et al., 1997). Individuals were tested in an arena made of acrylic plastic covered in grey plastic and shaped as a corridor with T-intersections at both ends (Fig. 1). Fish were allowed to acclimate in the arena for two minutes, then approached by an observer and gently coaxed with a dip-net from one end, thus making the fish swim towards the other end. This was then repeated in the opposite direction and a total of ten turns was recorded. To avoid buildup of chemical cues, approximately 8 L of water were replaced between trials. A total of 66 residents and 67 migrants were tested. After the detour test, the length (mm) and weight (g) for each individual were measured.

A lateralization index was derived from the detour test using the formula:

Relative lateralization (L_r) : (Left turns - right turns) / 10

$$Relative\ lateralization\ (L_r) = \frac{\#\ left\ turns\ -\#\ right\ turns}{Total\ \#\ turns}$$

To assess the lateralization strength without regarding direction, an absolute lateralization index was calculated using the formula:

$$Absolute\ lateralization\ (L_a) = L_r\ with\ all\ negative\ values\ muliplied\ with - 1$$

In addition, for comparison with actual results, a random binomial simulation of 66 individuals was generated.

To assess the repeatability of lateralization on the individual level, 59 residents were caught and kept in the same conditions as above. The specimens were individually tagged with PIT-tags allowing the possibility to follow each individual. Lateralization was tested two times per individual with 5-8 days between trials. Length and weight of each individual were recorded.

Analysis

Statistical analyses were completed with IBM SPSS (v. 20.0.0) except for the G-test which was done in Microsoft Excel (v.15.0.4454.1503) according to the method in Dytham (2011). The random binominal distribution was created using R (v. 3.0.0)

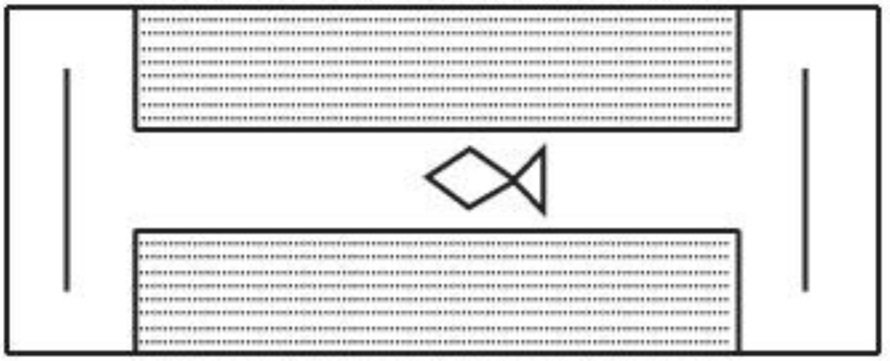

Figure 1. Shape of arena used in the detour test, as seen from above.

Results

Residents vs. Migrants

Lr for migrants, residents and the random simulation were all normally distributed (Kolmogorov-Smirnov test, $p > 0.5$ in all cases). A Kruskal-Wallis test showed no significant difference in L_r ($p = 0.269$) nor L_a ($p = 0.469$) among migrants, residents and the random simulation. In comparison with the random binominal simulation, there was a significant difference between residents' L_r (G-test; $G = 11.4$; $p = 0.045$) but not for migrants (G-test; $G = 10.4$; $p = 0.065$; Fig. 2). L_a for migrants (G-test; $G = 1.9$; $p = 0.59$) and residents (G-test; $G = 5.42$; $p = 0.14$) showed no difference in comparison with the random simulation. Within groups, no preference in direction were found based on a one sample t-test (Migrants: $t = 1.77$, $p = 0.082$; Residents: $t = 1.30$; Random: $t = -0.14$; $p = 0.88$)

Repeatability

In the repeatability assessment, L_r was only normally distributed in the second trial (Kolmogorov-Smirnov test; 1st: $p = 0.025$; 2nd: $p = 0.252$). As a consequence, differences were tested using Wilcoxon signed-ranks. No significant difference was found for L_r ($Z = -1.52$; $p = 0.127$), while there were a difference between the first and second trial's L_a ($Z = -2.013$; $p = 0.044$).

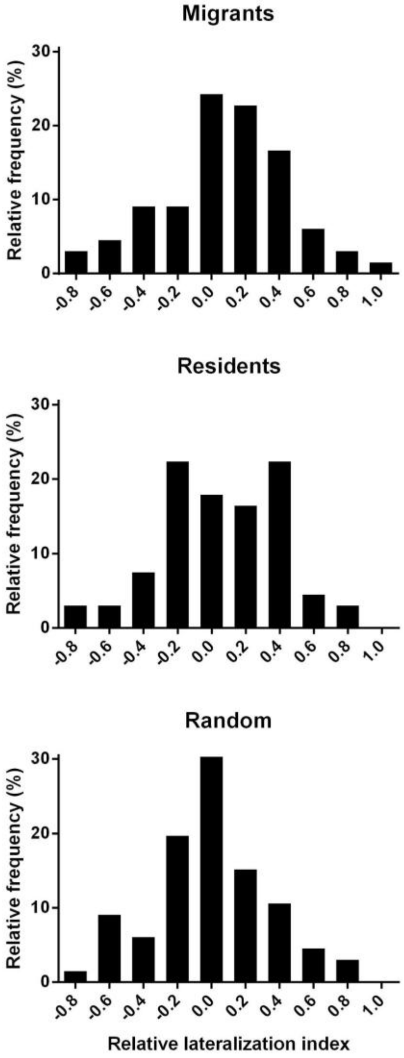

Figure 2. Relative lateralization distribution for migrants, residents and a random binominal simulation. A negative value indicates more right turns and a positive value more left turns.

Discussion

My results show no difference in the degree of lateralization between migrating and resident roach. This could imply that the conditions for the two phenotypes don't differ enough to impact lateralization or that there are opposing factors contributing to the two phenotypes' degree of lateralization. For example of the latter, one would expect the migrating population to have a higher degree of lateralization as it has to navigate to and in the stream (although the opposite is possible as well; see Brown & Braithwaite, 2005). Often the migrating roach choose the same stream every year (Brodersen et al. 2012) thus suggesting a long time memory which can be improved by hemispheric asymmetries (Pascual et al., 2004). The resident population on the other hand would benefit from lateralization due to the higher predation pressure in the lake (Brönmark et al. 2008; Dadda et al. 2010). In total there is no significant difference in absolute lateralization between either of the two roach phenotypes and the random simulation, which implies that there is no lateralization in either of the two phenotypes and that the results are a consequence of random turning behavior. This is also supported by the differences in the repeatability experiment, where the individual level of lateralization was not repeatable between two temporally separated measurements. This result would be in line with a previous study by Bisazza et al. (1997) where mosquitofish (Gambusia holbrooki) showed no sign of lateralization in an empty environment. As lateralization is not expressed in all behaviors (Bisazza & Brown, 2011), it is possible that the roach are lateralized but that an empty environment is not enough stimulus to trigger such behavior. For example, no differences where found in foraging between non-lateralized and lateralized individuals of *Girardinus falcatus* obtained by selective breeding but when adding a predator to the test, the non-lateralized individuals foraged less efficiently than their lateralized conspecifics (Dadda & Bisazza, 2006). Consideration should also be taken to habituation the test environment which has shown to have an effect in two visual tests using mirrors where five fish species showed left eye preference within the first five minutes while after the following 5 minutes there were no significant preference of eye use (Sovrano et al., 2001).

Another possibility is that there is little gain from behavioral lateralization in this system. Even though lateralization is thought to be more common in shoaling species (Bisazza et al., 2000; Brown, 2005) like roach (Eklöv & Persson, 1995; Krause et al. 1992), it is also possible that the cost for developing lateralization is higher than the benefit. In laboratory experiments, lateralized organisms have been shown to make suboptimal choices (Dadda et al., 2009), and as most fishes have a visual field covering almost 360° and the frontal overlap is only about 10°, it seems reasonable that stimuli quite often appear in only one of the two visual hemifields (Bisazza & Brown, 2011).

Relative lateralization in the resident phenotype was significantly different from the random simulation in one statistical test (G-test). By analyzing the results graphically it is possible to see that the index is skewed to a positive number (Fig. 2). However, consideration should be taken in that the other statistical test showed no difference (Kruskal-Wallis, p-value > 0.25) and it makes little sense to see it as any other than a random result, which would disappear with higher N, as there is no significant difference in the absolute lateralization index. While there are plenty of reports on the benefits of lateralization, less is known about why directional asymmetries in populations arise (Vallortigara & Rogers, 2005). One suggestion is that a population’s directional bias is the result of the trade-off of having to coordinate actions with other asymmetrical individuals while being predictable to predators. Higher predation pressure like in lake Krankesjön (Brönmark et al., 2008) has shown to create denser and faster swimming schools (Eklöv & Persson, 1995), which could be the reason for the small directional bias in the resident population. However, some empirical evidence supports that population asymmetry is more common in shoaling species (Bisazza et al., 2000), while Bisazza & Dadda (2005) found no difference in schooling performance between schools where individuals shared the same lateral direction a schools consisting of individuals of mixed lateral direction.

Lateralization has been shown to be positively correlated to boldness in two fish species, the convict ciclid (*Archocentrus nigrofasciatus)* and the poecicliid *Brachyraphis episcopi* (Reddon & Hurd, 2009; Brown et al. 2004, 2005). Brown et al. (2004, 2007) have shown that lateralization is increased under predation pressure which partly is in contrast to Chapman et al. (2011), who found that bolder individuals of roach were more likely to migrate to a habitat with less predation than shy individuals. Together with contrasting reports of increasing and decreasing navigational performance (Sovrano et al., 2005; Brown & Braithwhite, 2005) the link between migration and navigation still remains indistinct.

In conclusion, I have found no relation between lateralization and partial migration in roach. I suggest the linkage between migration and lateralization is complex rather than a simple relationship. It may be possible that lateralized behavior is present in this roach population and could be detected using additional stimuli, such as in a dual task test. If there is no differences in lateralization between phenotypes it would imply that biomanipulation as suggested in Christer Brönmark et al. (2010) where the migrating population is removed during migration would not affect the distribution of lateralization in the population which else could have effects on survival of roach through losing the advantages of lateralization.

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Miljövetenskaplig utbildning
Centrum för klimat- och
miljöforskning
Ekologihuset
22362 Lund