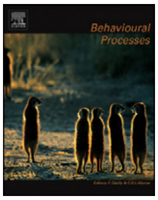
Behavioural Processes 91 (2012) 115–118

Contents lists available at SciVerse ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Prenatal light exposure affects development of behavioural lateralization in a livebearing fish

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ARTICLE INFO

Article history:
Received 4 May 2012
Received in revised form 31 May 2012
Accepted 20 June 2012

Keywords:
Fish
Lateralization
Light exposure

SUMMARY

The existence of individual differences in handedness and other lateralized functions is an unresolved problem. Genetic factors account for only a small proportion of the variance but the contribution of environmental influences is still largely unexplored. In chicks and zebrafish the amount of environmental light reaching embryos during development greatly influences the lateralization of adults. To investigate whether a similar effect is present in livebearers, we measured behavioural lateralization in ten-day-old goldbelly topminnows born from females that have been maintained at high or low light intensities during pregnancy. Fish from high-light treatment were significantly lateralized in both visual and motor tests while fish exposed to low light intensities were not. As observed in chicks and zebrafish, the main consequence of light exposure was the alignment of the laterality of different individuals in the same direction. Lateralization is known to affect a number of fitness-related traits in topminnow and we suggest that light influence may be part of an adaptive mechanism allowing to adjust the developmental trajectories of offspring to the prevailing environmental conditions.

1. Introduction

The left and the right side of the vertebrate brain are specialized for different functions but considerable variation exists both within and between populations in the strength and direction of lateralization of cognitive functions. Many authors have argued that these differences may be hereditary and that phenotypic diversity is maintained by a balance of different selective forces (Hori, 1993; McManus, 2002).

Game theoretical analysis has shown that polymorphism in lateralization can be maintained by negative frequency-dependent selection when individuals with the same lateralization as the majority of the population enjoy a better coordination during social actions while rare phenotypes have an advantage in fights or are less predictable to predators (Billiard et al., 2005; Ghirlanda and Vallortigara, 2004).

Significant heritability has been reported for handedness in human and non-human primates (Llaurens et al., 2009; Hopkins et al., 2001), for laterality of antipredator behaviour in Girardinus falcatus (Bisazza et al., 2007) and for laterality of social behaviour in zebrafish (Dadda et al., 2010). In general, genetic factors account for only a fraction of individual variation and there is increasing evidence that environmental and epigenetic factors play an important role in modulating the development and the expression of brain asymmetries (Brown et al., 2007). Identified factors include asymmetry in the physical structure of the environment (Collins, 1975), prenatal influence of stress hormones (Fride and Weinstock, 1988) or androgens (Schaafsma et al., 2009) and exposure of embryos to light (Rogers, 1990).

Some authors have suggested that these effects may represent adaptive mechanisms, allowing parents to adjust the developmental trajectories of their offspring to the prevailing environmental conditions (Vallortigara and Rogers, 2005). For example, mothers experiencing stressful situations, such as predator attacks, at the time of embryo formation might adaptively influence the laterality pattern of their offspring through the different amount of glucocorticoids deposited in the egg or crossing the placenta (Diaz, 1995; Rogers and Deng, 2005).

One of the best known effects is that induced by the light stimulation on chick embryos. The amount of light that enters through the eggshell in the last days prior to hatching influences many aspects of visual lateralization (reviewed by Vallortigara and Rogers, 2005) and has an important effect on the capacity of chicks to perform two concurrent tasks such as feeding and predator vigilance (Rogers et al., 2004). Some have argued that environmental cues, such as social density or an abundance of predators, by influencing the choice of laying site by the hen or the time she spend on the nest, may modulate development of

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http://dx.doi.org/10.1016/j.beproc.2012.06.008

lateralization in chicks and ultimately generate phenotypes with coping strategies appropriate for that environment (Andrew et al., 2009; Vallortigara and Rogers, 2005).

Light effects on lateralization are not limited to birds. In zebrafish, light vs dark incubation of developing embryos determines large differences in lateralization that, in turn, affects many aspects of behaviour including response to social stimuli, exploration of a novel area and propensity to approach potentially dangerous objects (Andrew et al., 2009).

Poeciliids are a neotropical family of live-bearing fish that have been extensively used as a model for the study of cerebral lateralization (Bisazza and Brown, 2011; Bisazza, 2011). In these species habitat characteristics often vary considerably even within the same water body and a gravid female living in the dense vegetation exposes its developing embryos to much lower light intensity than a female living in sparsely vegetated areas. Here we investigate the effects of light stimulation during early development in the goldbelly topminnow G. falcatus by measuring visual and motor lateralization in 10-day-old fish born from females that have been maintained at two different light intensities during pregnancy.

2. Materials and methods

Eight groups of 5 females each, 4 for the high light intensity treatment (HL) and 4 for the low light intensity treatment (LL), were maintained each in a glass tank (80 cm × 40 cm × 36 cm). In HL treatment the tank was surrounded with green plastic material (Poliplak) and top-covered with white plastic. The tank was lit by means of 4 neon lamp (18 W). Two lamps were attached to the top cover. In natural water bodies considerable amount of light reaches the horizontal surfaces, especially near the surface (Bauer et al., 2003; Brakel, 1979). By converse in a small aquarium most light reaches horizontal surfaces. To compensate for this factor the remaining two neon lamps were placed outside the tank adjacent to the glass, just below water level. In the LL treatment the glass tank was surrounded and covered with black plastic material. The entire tank was lit by means of a single 8 W neon lamp attached on the top cover.

Two replicas of the tanks for the HL and LL treatments were made so that 4 groups of 5 females (2 HL groups and 2 LL groups) underwent the two treatments at the same time.

Illuminance was measured by a United Detector Technology (UDT 350). The values measured at the water surface were 8550 lux in the HL and 392 lux in the LL treatment. They are within the range of light intensities observed in natural environment for Poecilia reticulata, the closest relative of G. falcatus for which data are available (Reznick et al., 2001). An estimate measure of the light reaching experimental fish laterally (average of six underwater measurement per condition) was 2633 lux in the HL treatment and 9 lux in the LL treatment.

Aquaria were maintained at a constant temperature (27 ± 1 °C) and photoperiod (08.00–20.00 h). In order to keep water characteristics as similar as possible between the two experimental conditions, the experimental tanks exchanged water with an adjacent compartment containing an air pump, a water filter and aquatic plants. Fish were fed twice a day with commercial food flakes and live Artemia *nauplii*.

Females were inserted in the treatment tank when they were close to parturition. The first batch of fry was not included in the analyses and females lasted in the treatment tank until the next birth. Tanks were checked daily and as soon as fry were found they were immediately transferred in smaller glass tanks (19 cm × 30 cm × 50 cm) provided with live plants, gravel on the floor, air-filter and maintained at a constant temperature (27 ± 1 °C) and photoperiod (08.00–20.00 h).

We tested 84 10-day-old topminnows, 47 born from females maintained during pregnancy at the HL treatment and 37 from females maintained at the LL treatment. Fry were collected at birth and housed in standard laboratory conditions until the experiment began.

Mirror test. Twenty-nine HL and 21 LL fish were observed in this test. We employed a modification of the apparatus used by Dadda et al. (2010). Briefly the apparatus consisted of a small plastic aquarium (20 cm × 20 cm × 25 cm) with eight mirrors (5.5 cm × 8 cm; length/height) placed around the aquarium's walls to create an octagonal shape. The bottom of the aquarium was white. A hollow transparent cylinder was placed at the centre of the apparatus that could be lifted via a nylon thread connected on a pulley system allowing the fish to explore the new environment. The apparatus was filled with 4 cm of water and lit by four neon lights (8 W) placed along the aquarium's walls. A video camera was positioned above the apparatus at a distance of 1 m.

Each subject was dip-netted from his home tank and transported to the apparatus where he was gently released into the cylinder. After a 2-min period the cylinder was lifted and the subject's swimming behaviour was immediately recorded for a period of 10 min. At the end of the experiment the subject was captured and released back to his home tank. Each subject was observed once.

Video recordings were analyzed using a computer program (Ciclic Timer Version 1.3). For computing the laterality index we considered the observations in which the fish was swimming along a mirror within a maximum distance of 3.5 cm. Observations made while the fish was perpendicular to the mirror were not considered.

Rotational preference in a familiar environment. Eighteen HL and 16 LL fish were observed in this test. We employed a modification of the apparatus used by Bisazza et al. (2005) and consisted in a ring-shaped swimway (inner radius 5 cm, outer radius 10 cm, height 4 cm) made of green plastic material filled with 3 cm of water. Each subject was housed singly in a swimway. A video camera was mounted approximately 1 m above the apparatus. The camera recorded four adjacent swimways. Each subject was placed into the apparatus at 12:00 a.m. and left undisturbed until 10:00 a.m. of next day. The subject's behaviour was then recorded for 1 h. The entire apparatus was lit by four neon lights (8 W) connected on a timer (8:00 a.m. to 20:00 p.m. L–D cycle). Lateral asymmetries were analyzed from video recordings by computing for each subject the proportion of counter-clockwise rotations.

3. Results

3.1. Mirror test

Subjects from HL and LL treatments did not differ significantly in the time spent shoaling (mean ± SD HL: 511.79 ± 58.47; LL: 530.52 ± 64.05, $t(48) = 1.074$, $p = 0.288$). HL Subjects showed a significant left-eye preference ($t(28) = 3.43$, $p = 0.002$, Fig. 1(a) whereas LL subjects did not show asymmetries in eye preference ($t(20) = 0.03$, $p = 0.975$). The difference between the two groups was significant ($t(48) = 2.36$, $p = 0.022$).

The low laterality index in LL fish, may derive either from the subject being on average poorly lateralized or from the group being composed of an equal proportion of left and right lateralized individuals. When we used the absolute index of laterality (0,5 – |laterality index|), which provides a measure of the degree of lateralization independently from its direction. HL and LL fish did not differ (HL: 0.11 ± 0.021; LL 0.09 ± 0.015; $t(48) = 0.55$, $p = 0.58$).