

Proliferation zones in the salmon telencephalon and evidence for environmental influence on proliferation rate

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Received 8 February 2005; received in revised form 7 June 2005; accepted 7 June 2005

Available online 5 July 2005

Abstract

Cell proliferation occurs in the brain of fish throughout life. This mitotic activity contributes new neurons to some brain subdivisions, suggesting potential for plasticity in neural development. Recently we found that the telencephalon in salmonids (salmon, trout) is significantly reduced in fish reared in hatcheries compared to wild fish, and that these differences resulted in part from rearing conditions. Here, we describe localized areas of cell proliferation in the telencephalon of juvenile coho salmon (*Oncorhynchus kisutch*) and begin to explore whether mitotic activity in these areas is sensitive to environmental conditions. Using the 5-bromo-2'-deoxyuridine (BrdU) cell birth-dating technique, we localized proliferating cells in the telencephalon to three distinct zones (proliferation zones 1a, 1b, and 2). We measured the volumes of these zones and showed that they grew at different rates relative to body size. We also found that variation in environmental rearing conditions altered the density of BrdU-labeled cells in proliferation zone 2, but not in zones 1a or 1b. However, this change in mitotic activity did not generate a difference in telencephalon size. These results suggest that environmental conditions, and associated changes in swimming activity or social structure, may influence rates of cell proliferation in the fish forebrain.

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Keywords: Forebrain; Neurogenesis; Brain size; Brain morphology; Plasticity; Fish; Enrichment; Hatchery

1. Introduction

Brain structure and function can be dramatically affected by the environmental conditions that an animal experiences during development (for reviews, see [Mohammed et al., 2002](#); [van Praag et al., 2000](#)). For instance, in rats, differences in the laboratory housing environment can induce significant changes in the dimensions of the cerebrum ([Walsh et al., 1971, 1973](#)), as well as changes in brain weight ([Bennett et al., 1969](#); [Rosenzweig and Bennett, 1969](#)). More recently, enrichment of the rearing environment has also been linked to changes in the rate of cell proliferation and neuron survival in

the brain of adult mice rodents ([Kempermann et al., 1997](#); [van Praag et al., 1999, 2000](#)).

While most work has focused on laboratory rodents, the generation of new cells in the fish brain far exceeds that of the mammalian systems that have been studied ([Zupanc, 2001a](#)). For example, in adult weakly electric fish *Apteronotus leptorhynchus*, it has been estimated that, on average, 0.2% of the cells in the brain are in S-phase during any 2 h period ([Zupanc, 2001b](#)). Areas of cell proliferation have also been identified in several brain regions in adult stickleback (*Gasterosteus aculeatus*; [Ekström et al., 2001](#)) and sea bream (*Sparus aurata*; [Zikopoulos et al., 2000](#)). Some of these newly divided cells have been shown to differentiate into neurons in the olfactory bulb and cerebellum ([Byrd and Brunjes, 2001](#); [Zupanc, 2001b](#)), and new neurons recruited from these proliferation zones may contribute to the regenerative ability documented in the central nervous system of fishes ([Stuermer et al., 1992](#);

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Sullivan et al., 1997). Such elevated levels of proliferative activity may thus mediate life-long brain growth in fish (e.g., Birse et al., 1980; Mueller and Wullmann, 2002), as well as provide for plasticity in how fish brains develop and respond to environmental variability.

Recent evidence from captively propagated salmonids (trout, salmon) suggests that environmental influences may alter brain phenotype in fish reared in hatcheries (Marchetti and Nevitt, 2003; Kihlslinger et al., 2003). Initial studies in rainbow trout (*Oncorhynchus mykiss*) showed that the telencephalon and other brain regions are significantly reduced in fish reared in hatcheries compared to those reared in the wild (Marchetti and Nevitt, 2003). It is not known, however, whether such differences in gross brain morphology result from artificial selection in hatcheries or can develop in an individual's lifetime. In subsequent studies with genetically similar strains of Chinook salmon (*Oncorhynchus tshawytscha*) reared both in hatcheries and in the wild, we have shown that differences in the volume of the olfactory bulb and telencephalon can develop within one year (Kihlslinger et al., 2003). These findings suggest that the conditions that salmonids experience during development can have profound effects on neural phenotype.

Here we begin to explore the mechanisms by which environmental conditions alter brain size by localizing zones of cell proliferation in the salmon telencephalon. Our aim was to identify areas of proliferation that may be responsive to environmental conditions. Given that differences in telencephalon size were noted in previous studies comparing hatchery and wild-reared fish (Marchetti and Nevitt, 2003; Kihlslinger et al., 2003), the telencephalon seemed an obvious place to look for areas of proliferation that might be sensitive to environment. This approach is similar to that applied in mammalian systems, where numerous studies have explored how environmental enrichment affects the rate of neurogenesis in the dentate gyrus of the hippocampus (i.e., Kempermann et al., 1997; van Praag et al., 2000). In this preliminary study, we used the established 5-bromo-2'-deoxyuridine (BrdU) immunocytochemical cell birth-dating technique to localize zones of mitotic activity in the salmon telencephalon. We then asked how the size of these proliferation zones changes with growth of the fish. Lastly, we measured the density of BrdU-labeled cells in these zones and quantified the volume of the telencephalon to ask whether differences in rearing environment may be linked to differences in rates of proliferation or to changes in telencephalon size.

2. Materials and methods

2.1. Animals

Fertilized coho salmon (*Oncorhynchus kisutch*) eggs were obtained from the Iron Gate Fish Hatchery located on the Klamath River, California, USA. Eggs hatched in

standard flow-through rearing trays in January 2000, and juvenile salmon parr were reared at the Center for Aquaculture and Aquatic Biology facility of the University of California, Davis. Once the yolk sac was absorbed, fry were moved to circular rearing tanks (1.2 m diameter, 380 L capacity). On March 20th, 2000, fish were transferred to rearing treatment tanks and maintained there until sacrifice on July 25th, 2000. Fish were exposed to ambient photoperiod both prior and during the experiment. All procedures were approved by the Animal Care and Use Committee (Protocol # 8482) of the University of California, Davis.

2.2. Rearing treatment tanks

Salmon parr were reared in two treatments that differed in habitat structure. The 'simple' (control) treatment lacked physical structure but had greater spatial variation in water flow velocity, while the 'structurally complex' (experimental) treatment was augmented with physical structures (i.e., cinder blocks, gravel), but had a more uniform hydrodynamic environment. For both treatments, salmon parr (40 fish per tank) were reared in 1.2 m diameter, circular flow-through tanks. Water was provided from an on-site aquifer, chilled to 11 ± 1 °C, and entered the tanks at 15 ± 1 L/min. Fish in both treatments were fed ad libitum.

For the 'simple' treatment, water entered through a spray bar (21.6 cm long, 1.27 cm diameter), circled the tank, and exited through a central drain. Spatial variation in the hydrodynamic environment was quantified by measuring water velocity with a flow meter (Flo-Mate™ Model 2000, Marsh-McBirney Inc., Frederick, MD) at 2/3 water depth (~10 cm from the bottom) in the center of fourteen 30 cm squares that comprised a grid over the bottom of the tank. Mean water velocity for the simple treatment tanks was 0.08 m/s with a variance of 0.002 (m/s)². The average water depth was 30 cm.

For the structurally complex treatment, the bottom of each tank was covered with gravel, and concrete cinder blocks (1 small, $19.1 \times 19.1 \times 19.1$ cm cinder block, and 5 large, $39.4 \times 19.1 \times 19.1$ cm cinder blocks in each tank in the same positions) were added for structure. Water entered the tanks through an elongated spray bar (41.9 cm long $\times$ 1.27 cm diameter) directed toward the center of each tank. Water thus flowed across the tank, eventually exiting through a large drainpipe (71.1 cm long $\times$ 5.08 cm diameter) parallel but on the opposite side of the tank as the spray bar. Mean water velocity for the structurally complex tanks was only 0.01 m/s with a variance of 0.0001 (m/s)². Average water depth was ~58 cm due to the added structure.

2.3. BrdU immunocytochemistry

Salmon parr (approximately 6 months after hatching) were anesthetized (MS-222 immersion, 1:1000, Crescent Research Chemicals), weighed and measured, and given a single intraperitoneal injection of BrdU (40 µL/g body wt of

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