Neuroscience 331 (2016) 134–147

PATTERNS OF OLFACTORY BULB NEUROGENESIS IN THE ADULT ZEBRAFISH ARE ALTERED FOLLOWING REVERSIBLE DEAFFERENTATION

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Abstract—Adult brain plasticity can be investigated using reversible methods that remove afferent innervation but allow return of sensory input. Repeated intranasal irrigation with Triton X-100 in adult zebrafish diminishes innervation to the olfactory bulb, resulting in a number of alterations in bulb structure and function, and cessation of the treatment allows for reinnervation and recovery. Using bromodeoxyuridine, Hu, and caspase-3 immunoreactivity we examined cell proliferation, differentiation, migration, and survival under conditions of acute and chronic deafferentation and reafferentation. Cell proliferation within the olfactory bulb was not influenced by acute or chronic deafferentation or reafferentation, but cell fate (including differentiation, migration, and/or survival of newly formed cells) was affected. We found that chronic deafferentation caused a bilateral increase in the number of newly formed cells that migrated into the bulb, although the amount of cell death of these new cells was significantly increased compared to untreated fish. Reafferentation also increased the number of newly formed cells migrating into both bulbs, suggesting that the deafferentation effect on cell fate was maintained. Reafferentation resulted in a decrease in newly formed cells that became neurons and, although death of newly formed cells was not altered from control levels, survival was reduced in relation to that seen in chronically deafferented fish. The potential effect of age on cell genesis was also examined. While the amount of cell migration into the olfactory bulbs was not affected by fish age, more of the newly formed cells became neurons in older fish. Younger fish displayed more cell death under conditions of chronic deafferentation. In sum, our results show that reversible deafferentation affects several aspects of cell fate, including cell differentiation, migration, and survival, and age of the fish influences the response to deafferentation. **© 2016 IBRO. Published by Elsevier Ltd. All rights reserved.**

Key words: teleost, bromodeoxyuridine, neurogenesis, olfactory bulb, deafferentation, reafferentation.

INTRODUCTION

Adult neurogenesis in the vertebrate brain has become widely recognized in the past two decades, with the olfactory system emerging as an excellent model system for studies investigating adult brain plasticity. The olfactory system is easily accessible, has well-documented morphology and circuitry, and has an innate, persistent adult neurogenic capacity in the peripheral olfactory epithelium (Moulton et al., 1970; Graziadei and Graziadei, 1979) and the central olfactory bulb (Altman, 1969; Kaplan and Hinds, 1977; Bayer, 1983; Corotto et al., 1993; Adolf et al., 2006; Grandel et al., 2006).

In the adult mammalian brain, the subgranular zone of the dentate gyrus (Zupanc et al., 2005; Adolf et al., 2006; Grandel et al., 2006) in the hippocampus (Altman and Das, 1965; Kaplan and Hinds, 1977) and the subventricular zone of the lateral wall of the lateral ventricles (Altman, 1969; Kaplan and Hinds, 1977) are the two regions of constitutive neurogenesis. Stem cells in the subgranular zone generate neuroblasts that mature into granule cells of the hippocampus (Altman and Das, 1965; Kaplan and Hinds, 1977; Altman and Bayer, 1990). In the subventricular zone, neural stem cells generate neural precursor cells (Lois and Alvarez-Buylla, 1993; Luskin, 1993) that migrate through the rostral migratory stream into the olfactory bulb (Luskin, 1993; Lois and Alvarez-Buylla, 1994; Rousselot et al., 1995; Doetsch and Alvarez-Buylla, 1996; Jankovski and Sotelo, 1996). Once the neural precursor cells reach the olfactory bulb, most mature into granule and periglomerular interneurons (Luskin, 1993; Lois and Alvarez-Buylla, 1994; Betarbet et al., 1996; Winner et al., 2002).

The adult zebrafish brain displays more abundant adult neurogenesis, with 16 distinct neurogenic niches that are distributed along the entire rostro-caudal brain axis (Zupanc et al., 2005; Adolf et al., 2006; Grandel et al., 2006). Two of these are equivalent to the mammalian subventricular zone and subgranular zone: the telencephalic ventricular zone and dorsolateral domain, respectively (Zupanc et al., 2005; Adolf et al., 2006; Grandel et al., 2006). The zebrafish telencephalic ventricular zone maintains a population of neural stem cells that generate neural precursor cells characteristically similar to those generated in the mammalian subventricular zone (Zupanc et al., 2005; Lam et al., 2009; März et al., 2010; Kishimoto et al., 2011). These cells migrate through a

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Abbreviations: BrdU, 5-bromo-2′-deoxyuridine; GL, glomerular layer; ICL, internal cellular layer; KLH, keyhole limpet hemocyanin; ONL, olfactory nerve layer; PBS, phosphate-buffered saline.

http://dx.doi.org/10.1016/j.neuroscience.2016.06.026
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rostral migratory stream to the olfactory bulb and differentiate into mature interneurons (Zupanc et al., 2005; Adolf et al., 2006; Grandel et al., 2006; Kishimoto et al., 2011).

One of the additional proliferating domains identified in adult zebrafish is the olfactory bulb (Zupanc et al., 2005; Grandel et al., 2006). Proliferating cells are found scattered throughout the three diffuse concentric layers of the adult zebrafish olfactory bulb (Byrd and Brunjes, 2001; Zupanc et al., 2005; Adolf et al., 2006; Grandel et al., 2006): the outermost olfactory nerve (ONL), the middle glomerular (GL), and the inner internal cellular (ICL) layers. Approximately half of the newly generated cells in the bulb express a neuronal identity (Zupanc et al., 2005; Adolf et al., 2006). Nevertheless, the number of proliferating cells is so meager that it is not considered a major source of newly generated cells (Zupanc et al., 2005; Grandel et al., 2006). Thus, similar to mammals, the addition of newly generated cells to the adult zebrafish olfactory bulb consists primarily of the migration of cells into the bulb from the telencephalic ventricular zone and not intrinsic bulbar cell genesis.

The effect of afferent input on the adult olfactory bulb, while not fully elucidated, has been shown to be crucial for homeostatic maintenance of this brain region, and sensory deprivation has been shown to be deleterious. Sensory deprivation has been achieved through various deafferentation methods, including reversible, unilateral naris occlusion. In juvenile rats, the reduction in bulb volume and tyrosine hydroxylase expression seen with naris occlusion is reversed with the restoration of sensory input (Cummings et al., 1997). An alternative model of reversible deafferentation involves chemical ablation of the olfactory epithelium with a single application of Triton X-100, $ZnSO_4$, or methyl bromide. These lesions also result in a reduction in olfactory bulb weight and volume (Margolis et al., 1974; Harding et al., 1978; Schwob et al., 1999) and a decrease in tyrosine hydroxylase expression (Nadi et al., 1981; Baker et al., 1983). Recovery of the mammalian olfactory epithelium is substantial but incomplete at 30 days post lesion, with mature neurons reaching near control numbers at 4–6 weeks (Schwob et al., 1995; Herzog and Otto, 1999; Cummings et al., 2000). Thus, deafferentation through these methods allows investigation into short- and long-term effects on the olfactory bulb and its recovery.

In the adult zebrafish, reducing afferent input has similar effects on the olfactory bulb. Previous study in our lab has demonstrated that intranasal irrigation with Triton X-100 detergent produces an immediate degenerative effect on the olfactory epithelium followed by rapid regeneration of olfactory sensory neurons within five days (Iqbal and Byrd-Jacobs, 2010). A permanent, complete deafferentation method had shown previously that significant deafferentation-induced morphological alteration of the olfactory bulb occurred only following several weeks of deafferentation (Byrd, 2000). Thus, our lab developed a novel method for investigating the effects of long-term deafferentation and reafferentation of the olfactory bulb using repeated intranasal irrigation of detergent. This procedure results in reduction of olfactory bulb volume and tyrosine hydroxylase expression, while cessation of intranasal irrigation results in restoration of the olfactory epithelium, reinnervation of the olfactory bulb, and recovery of bulb volume and tyrosine hydroxylase expression (Paskin et al., 2011). Part of this loss of olfactory bulb volume is likely due to increased cell death since complete ablation of the olfactory organ by cautery results in a rapid, substantial increase in cell death (Vankirk and Byrd, 2003). Further, with this same manipulation, a gradual reduction in total cell number in the bulb occurs over several weeks (Byrd, 2000). Cell genesis does not appear to play a major role in this volume reduction following cautery since cell proliferation increased after this manipulation, although fate was affected (Villanueva and Byrd-Jacobs, 2009).

In the present study we used reversible deafferentation. Further, we investigate the possibility that cell genesis accounts, at least in part, for the deafferentation-induced reduction of olfactory bulb volume and reafferentation-induced recovery of bulb volume. We hypothesized that the diminished olfactory bulb volume seen following reduced afferent input is due to decreased cell genesis or reduced migration of newly formed cells into the olfactory bulb and that cessation of intranasal irrigation will result in the reversal of olfactory bulb volume reduction through increased cell genesis or enhanced migration of cells into the olfactory bulb.

EXPERIMENTAL PROCEDURES

A commercial vendor was used to obtain adult male and female zebrafish, *Danio rerio*, all of which were aged 5–9 months and approximately 3–4 cm in length. Additional adult male and female zebrafish, age 12–15 months, were a gift from Dr. Don Kane's lab. Fish were maintained in 28.5 °C, aerated, conditioned freshwater tanks with a 14-h light:10-h dark cycle and fed flake food twice daily at 7–9 am and 3–5 pm. Intranasal infusions and intraperitoneal injections were performed between 7 am and 10 am. Western Michigan University's Animal Care and Use Committee approved all experimental procedures. Precautions were taken to minimize the number and suffering of fish.

Chemical lesioning of the olfactory epithelium

Chemical lesioning was achieved by employing the protocol described previously (Iqbal and Byrd-Jacobs, 2010; Paskin et al., 2011). Briefly, zebrafish were anesthetized with MS222 (0.03%; Sigma, St. Louis, MO, USA) until they no longer responded to tail pinch and approximately 1 μL of a 0.7% Triton X-100 and 0.005% Methylene Blue solution prepared in 0.1 M phosphate-buffered saline (PBS) was applied to the right nasal cavity. The untreated left side was used as an internal control. Following the 10 s it takes for intranasal infusion of the detergent, the fish were maintained on ice for 2 min out of water to prevent dilution of the detergent solution and ensure sufficient exposure as well as to maintain an appropriate level of anesthetization. The fish were then returned to their aquarium. In 3-week treated fish (chronic deafferentation group) this treatment was repeated every

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