Developmental Biology xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Developmental Biology

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

Gliogenesis in lampreys shares gene regulatory interactions with oligodendrocyte development in jawed vertebrates

Tian Yuan, Joshua R. York, David W. McCauley*

Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019, USA

ARTICLE INFO

Keywords:
Gliogenesis
Oligodendrocytes
Lamprey
Evolution

ABSTRACT

Glial cells in the nervous system regulate and support many functions related to neuronal activity. Understanding how the vertebrate nervous system has evolved demands a greater understanding of the mechanisms controlling evolution and development of glial cells in basal vertebrates. Among vertebrate glia, oligodendrocytes form an insulating myelin layer surrounding axons of the central nervous system (CNS) in jawed vertebrates. Jawless vertebrates lack myelinated axons but it is unclear when oligodendrocytes or the regulatory mechanisms controlling their development evolved. To begin to investigate the evolution of mechanisms controlling glial development, we identified key genes required for the differentiation of oligodendrocytes in gnathostomes, including *Nkx2.2, SoxE* genes, and *PDGFR*, analyzed their expression, and used CRISPR/Cas9 genome editing to perturb their functions in a primitively jawless vertebrate, the sea lamprey. We show in lamprey that orthologs required for oligodendrocyte development in jawed vertebrates are expressed in the lamprey ventral neural tube, in similar locations where gnathostome oligodendrocyte precursor cells (OPC) originate. In addition, they appear to be under the control of conserved mechanisms that regulate OPC development in jawed vertebrates and may also function in gliogenesis. Our results suggest that although oligodendrocytes first emerged in jawed vertebrates, regulatory mechanisms required for their development predate the divergence of jawless and jawed vertebrates.

1. Introduction

Animal nervous systems are composed of neurons and glia. Neurons transmit electrical impulses that coordinate sensory and motor responses by the animal to its environment. Glia provide structural, nutritive, and maintenance support for neurons (Jakel and Dimou, 2017). Recently, there has been increasing interest in glial cells as it has become clear that they participate in many important aspects of activity within the nervous system (Banerjee and Bhat, 2007; Barres, 2008; Min and Nevian, 2012; Nave and Trapp, 2008; Sakry et al., 2015). Glial cells make up only 10% of the *Drosophila* nervous system, whereas they may contribute nearly 50% of cells present in the human brain (Azevedo et al., 2009; Herculano-Houzel, 2014; Ito et al., 1995). However, the importance of such trends in glia/neuron ratios is not clear, and it remains controversial whether there is a common phylogenetic origin of glia (Losada-Perez, 2018). Moreover, the differences in glia/neuron ratios across vertebrates have been explained as a function of increasing brain size, as well as being related to differences in the size of neurons (Herculano-Houzel, 2014). Therefore, understanding mechanisms regulating development and evolution of glial cells will be instructive for explaining the evolution of animal nervous systems.

A key evolutionary innovation of the vertebrate nervous system is the formation of myelinating glia that surround and insulate axons to increase the speed of electrical conductivity, facilitating rapid responses by animals. All jawed vertebrates (gnathostomes) possess myelinated axons in both the central and peripheral nervous systems, but myelin is absent in living basal jawless (agnathan) vertebrates (Bullock et al., 1984). In gnathostomes, the myelin sheath is formed by two different glial cell types. Oligodendrocytes originating in the ventral neuroepithelium of the neural tube myelinate axons within the central nervous system (CNS) (Compston et al., 1997; Nave, 2010; Sherman and Brophy, 2005), while neural crest-derived Schwann cells ensheath axons of peripheral neurons (Kettenmann and Ransom, 1995).

Oligodendrocytes are considered to be unique to jawed vertebrates and are derived from precursor cells in the ventral neural tube. Oligodendrocyte precursor cells (OPCs) arise primarily from the pMN and p3 ventral neuroepithelial domains along the neural tube (Fu et al., 2002; Kessaris et al., 2008) from which motor neurons and V3 interneurons respectively are also derived (Fig. 1) (Briscoe and

* Corresponding author.
E-mail address: dwmccauley@ou.edu (D.W. McCauley).

https://doi.org/10.1016/j.ydbio.2018.07.002
Received 21 March 2018; Received in revised form 2 July 2018; Accepted 2 July 2018
0012-1606/ © 2018 Elsevier Inc. All rights reserved.

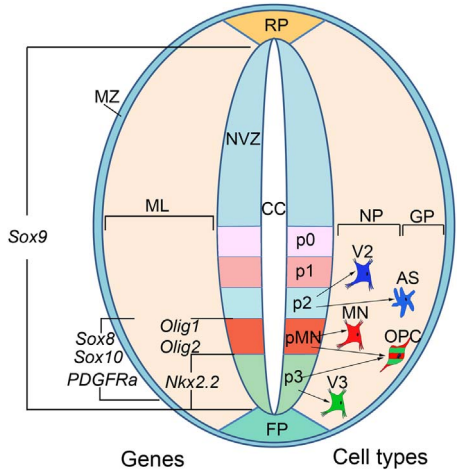

Fig. 1. Developmental origins of neural progenitor cell types and differential gene genes expression in ventral domains of the developing vertebrate neural tube. Glial cells and neurons in vertebrates share progenitor regions. p0 to p3 domains produce different glial and neuronal populations. The two ventral most domains, pMN and p3, where *Olig1*/2, *Nkx2.2*, *Sox8*, *Sox10*, and *PDGFR*a are expressed give rise to oligodendrocyte precursors (OPCs), as well as motor neurons and V3 interneurons (V3). AS, astrocytes; CC, central canal; FP, floor plate; GP, glial precursors; ML, mantle layer; MZ, marginal zone; NP, neuronal precursors; NVZ, neuroepithelial ventricular zone; RP, roof plate; V2, V2 interneurons.

Ericson, 2001; Zhuang and Sockanathan, 2006). Research in chick and mouse models has also revealed that there is a small population of OPCs that originate in the dorsal neural tube (Cai et al., 2005; Cameron-Curry and Le Douarin, 1995; Vallstedt et al., 2005; Zhu et al., 2011). However, whether this dorsal OPC population exists in all vertebrates is still unknown. Newly formed OPCs migrate from the pMN and p3 domains toward the marginal zone, where cells from both domains express key regulatory factors including the SoxE genes (*Sox8*, *Sox9*, and *Sox10*), *Olig1*, *Olig2* and *Nkx2.2* (Fu et al., 2002). *Olig1* and *Olig2* also regulate differentiation of motor neurons while *Nkx2.2* regulates the differentiation of V3 interneurons and perineurial glia (Holz et al., 2010; Zhou and Anderson, 2002). On the other hand, functions of SoxE genes in the CNS, particularly *Sox8* and *Sox10*, are restricted to OPCs (Pozniak et al., 2010; Stolt et al., 2004, 2005). *Sox9* expression in presumptive neural stem cells throughout the neuroepithelial ventricular zone specifies glial fate and blocks neurogenesis in the CNS (Stolt et al., 2003). *Sox9* deletion in the mouse model reduces numbers of OPCs, while mice lacking *Sox10* have normal numbers of OPCs that fail to mature, indicating a terminal differentiation role for *Sox10* in oligodendrocyte development (Stolt et al., 2002). Finally, platelet derived growth factor receptors (*PDGFR*) respond to PDGF signals to promote OPC survival; in mice, the survival and migration of OPCs largely depends on PDGF-AA in the CNS (Baroti et al., 2016; Stolt et al., 2006). These findings identify a core conserved set of transcription factors and an intercellular signaling system that together coordinate the development of OPCs in jawed vertebrates (Fig. 1).

Although oligodendrocytes play important functional roles in jawed vertebrate nervous systems, we know surprisingly little about their evolutionary origins. Richardson and colleagues proposed a hypothesis that oligodendrocytes may have evolved to ensheath motor axons and facilitate the escape response (Richardson et al., 1997, 2000). This hypothesis is based on the observation that primary oligodendrocyte precursors arise from the same Olig1/Olig2-positive progenitors as motor neurons in the ventral neural tube. All extant vertebrates have either largely myelinated axons in the CNS and PNS (jawed vertebrates) or, have no myelin (jawless vertebrates), and thus it would be instructive to investigate how myelin first evolved. While it is not possible to determine myelinating mechanisms that arose in now-extinct jawed vertebrate ancestors, by comparing gliogenic mechanisms in jawless and jawed vertebrates, it may be possible to determine whether the regulatory network required for development of oligodendrocyte precursor cells existed in the common vertebrate ancestor, and whether this network functioned in the formation of glia associated with motor axons, or alternatively, in glia associated with axons throughout the CNS.

Our understanding of both central and peripheral gliogenesis in lampreys is rudimentary. Peripheral glial cells have been described in lampreys and were found to surround the lateral line system, yet these cells do not form myelin sheaths (Gelman et al., 2009). In the lamprey CNS, radial glial cells express keratin-like proteins that have been observed in both larval and adult lampreys (Merrick et al., 1995). Other studies have suggested that myelinating glial cells, such as oligodendrocytes, are not present in lamprey (Bullock et al., 1984). Although the origin of myelinating glia represents a key step in early vertebrate evolution, how these cells evolved is unknown. Mechanisms regulating the development and differentiation of glia in lamprey have not been explored and therefore may provide key insights into how vertebrates acquired myelinating glia.

As a starting point, we chose to investigate whether mechanisms controlling the development of oligodendrocytes are spatiotemporally conserved in lamprey. To understand if the evolutionary origin of oligodendrocytes predated agnathan-gnathostome divergence, we asked if genes controlling OPC development in gnathostomes are expressed in similar locations of the developing CNS in lamprey. Alternatively, the regulatory circuitry controlling CNS glial cell fates may have arisen independently in these groups.

To test our hypothesis, we examined the developmental expression and function of homologs to genes in lamprey that are known to regulate oligodendrocyte development in jawed vertebrates. While we have been unable to identify *Olig1* or *Olig2* homologs in lamprey, our results show that lamprey SoxE genes and *Nkx2.2* are expressed in the ventral neural tube, similar to gnathostome homologs expressed in pMN and p3 domains where OPCs originate. Later in development, *PDGFRab* and *SoxE1* are detected in putative glial cells lateral to the neural tube and notochord. Functional perturbations using CRISPR/Cas9 genome editing suggest genetic interactions similar to what have been observed in jawed vertebrates may control development along the lamprey ventral neural tube, and are suggestive of gliogenic function. We discuss our findings in the context of developmental mechanisms controlling the evolution of glial differentiation in early vertebrates.

2. Materials and methods

2.1. Embryo collection and fixation

Spawning adult sea lamprey, *Petromyzon marinus*, were collected from streams near Hammond Bay Biological Station, Millersburg, MI, and shipped to the University of Oklahoma. Animals were held in a recirculating water system maintained at 14 °C. Eggs were manually stripped from individual females and fertilized in vitro with sperm obtained from mature males. Embryos were held in 0.05× Marc's Modified Ringer solution (MMR) at 18 °C under constant flow (Lakiza et al., 2011). Embryos at selected stages (T22–26) (Tahara, 1988), were fixed in a 4% MEMFA solution (0.1 M MOPS pH7.4, 2 mM EGTA, 1 mM MgSO4 and 4% Paraformaldehyde) overnight at 4 °C, dehydrated into methanol, and stored at − 20 °C for later use (McCauley and Bronner-Fraser, 2002). All experiments were conducted according to the University of Oklahoma, Institutional Animal Care and Use Committee, protocol R15–027.

2.2. Isolation of gene sequences and phylogenetic analysis

Searches of the *Petromyzon marinus* genome on the UCSC Genome Browser, Sep 2010 WUGSC 7.0/petMar2 assembly (Smith et al., 2013) were cross referenced with *Nkx2.2* sequence (AB583552) from the Arctic lamprey *Lethenteron camtschaticum* (formerly *Lethenteron*

Download English Version:

https://daneshyari.com/en/article/8467150

Download Persian Version:

https://daneshyari.com/article/8467150

Daneshyari.com