



Pattern formation during development of the embryonic cerebellum

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The patterning of the embryonic cerebellum is vital to establish the elaborate zone and stripe architecture of the adult. This review considers early stages in cerebellar Purkinje cell patterning, from the organization of the ventricular zone to the development of Purkinje cell clusters—the precursors of the adult stripes.

Keywords: Purkinje cell, ventricular zone, zebrin, EBF2, neurogenin, stripe

INTRODUCTION—PATTERNING OF THE ADULT CEREBELLUM

The adult mouse cerebellum houses a complex topographical map (e.g., **Figure 1**). The map probably involves all cell types in the cerebellar cortex (e.g., Purkinje cells—Hawkes et al., 1985; granule cells—Hawkes and Turner, 1994; Hawkes et al., 1998; Golgi cells—Sillitoe et al., 2008; basket cells—Dermilly et al., 2011; glia—Scott, 1963); this review is focused on the Purkinje cells. The mapping of Purkinje cell antigens (e.g., zebrin II/aldolase C—Brochu et al., 1990; phospholipase (PL)CB4—Sarna et al., 2006; heat shock protein (HSP)25—Armstrong et al., 2000; CART—Reeber and Sillitoe, 2011 etc.), gene transcripts (reviewed in Sillitoe and Joyner, 2007) and transgenes (e.g., L7/pcp2-lacZ—Vandaele et al., 1991; Oberdick et al., 1993; OMP-lacZ—Nunzi et al., 1999; IP3R1-nb-lacZ—Furutani et al., 2010 etc.), has revealed multiple Purkinje cell subtypes. Each subtype has a characteristic distribution, but it seems plausible that these are all reflections of a common underlying architecture (Apps and Hawkes, 2009). First, the cerebellar cortex is divided from anterior to posterior into transverse zones: the anterior zone (AZ; ~lobules I–V), the central zone (CZ; ~lobules VI–VII; possibly further subdivided—Marzban et al., 2008), the posterior zone (PZ; ~lobules VIII–dorsal IX) and the nodular zone (NZ; ~lobules IX ventral and X; Osoi et al., 1999; Sillitoe and Hawkes, 2002). Next, each transverse zone is divided mediolaterally into parasagittal stripes. The most broadly studied marker of adult stripes is the Purkinje cell antigen zebrin II/aldolase C (e.g., Brochu et al., 1990; Ahn et al., 1994). The opposite pattern is revealed by other markers, for example PLCB4 (Sarna et al., 2006) and EBF2 (Croci et al., 2006; Chung et al., 2008). The zone-and-stripe pattern is highly reproducible between individuals and conserved across mammals and birds: zebrin II is expressed by many vertebrates (e.g., fish—Lannoo et al., 1991a,b;

Meek et al., 1992), as is EBF2 (Malgaretti et al., 1997; Bally-Cuif et al., 1998; Dubois and Vincent, 2001), but arrays of stripes are only seen in birds (e.g., pigeon—Pakan et al., 2007; chicken—Marzban et al., 2010) and mammals (reviewed in Sillitoe et al., 2005; Marzban and Hawkes, 2011). Many molecular markers are co-localized with either the zebrin II+ or zebrin II– Purkinje cells (e.g., PLCB3—Sarna et al., 2006; sphingosine kinase 1a—Terada et al., 2004 etc.). However, this is not the extent of the stripe compartmentation—other markers reveal subdivisions within stripes, subsets of stripes within the zebrin II+/– sets, and stripes in the CZ and NZ (e.g., P-path—Leclerc et al., 1992; heat shock protein (HSP)25—Armstrong et al., 2000; human natural killer cell antigen 1 (HNK1)—Eisenman and Hawkes, 1993; Marzban et al., 2004). In sum, the adult cerebellar cortex is highly reproducibly subdivided into several hundred distinct modules with >10 distinct Purkinje cell phenotypes (e.g., reviewed in Hawkes and Gravel, 1991; Hawkes, 1997; Apps and Hawkes, 2009). In the mouse, a typical stripe/module comprises fewer than a thousand Purkinje cells.

Zones and stripes are important because cerebellar patterning influences all aspects of cerebellar organization and function. Here is not the place to expound this at length, but simply to note that the Purkinje cell map serves as a scaffold around which many other cerebellar structures are organized:

1. *Afferent projections* use Purkinje cells to target their terminal fields.
2. *Interneurons* are restricted at stripe boundaries and are thought to use Purkinje cell cues to establish their own topography.
3. *Functional boundaries* align with stripe boundaries (e.g., Chockkan and Hawkes, 1994; Chen et al., 1996; Hallgren et al., 1999; Apps and Garwicz, 2005; Wädiche and Jahr, 2005).

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Yijin Wang



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Table of Contents Pattern Formation During Development

1. Understanding the eBook Pattern Formation During Development
 - The Rise of Digital Reading Pattern Formation During Development
 - Advantages of eBooks Over Traditional Books
2. Identifying Pattern Formation During Development
 - Exploring Different Genres
 - Considering Fiction vs. Non-Fiction
 - Determining Your Reading Goals
3. Choosing the Right eBook Platform
 - Popular eBook Platforms
 - Features to Look for in an Pattern Formation During Development
 - User-Friendly Interface
4. Exploring eBook Recommendations from Pattern Formation During Development
 - Personalized Recommendations
 - Pattern Formation During Development User Reviews and Ratings
 - Pattern Formation During Development and Bestseller Lists

5. Accessing Pattern Formation During Development Free and Paid eBooks
 - Pattern Formation During Development Public Domain eBooks
 - Pattern Formation During Development eBook Subscription Services
 - Pattern Formation During Development Budget-Friendly Options
6. Navigating Pattern Formation During Development eBook Formats
 - ePub, PDF, MOBI, and More
 - Pattern Formation During Development Compatibility with Devices
 - Pattern Formation During Development Enhanced eBook Features
7. Enhancing Your Reading Experience
 - Adjustable Fonts and Text Sizes of Pattern Formation During Development
 - Highlighting and Note-Taking Pattern Formation During Development
 - Interactive Elements Pattern Formation During Development
8. Staying Engaged with Pattern Formation During Development
 - Joining Online Reading Communities
 - Participating in Virtual Book Clubs
 - Following Authors and Publishers Pattern Formation During Development
9. Balancing eBooks and Physical Books Pattern Formation During Development
 - Benefits of a Digital Library
 - Creating a Diverse Reading Collection Pattern Formation During Development
10. Overcoming Reading Challenges
 - Dealing with Digital Eye Strain
 - Minimizing Distractions
 - Managing Screen Time
11. Cultivating a Reading Routine Pattern Formation During Development
 - Setting Reading Goals Pattern Formation During Development
 - Carving Out Dedicated Reading Time
12. Sourcing Reliable Information of Pattern Formation During Development
 - Fact-Checking eBook Content of Pattern Formation During Development
 - Distinguishing Credible Sources
13. Promoting Lifelong Learning

- Utilizing eBooks for Skill Development
- Exploring Educational eBooks

14. Embracing eBook Trends

- Integration of Multimedia Elements
- Interactive and Gamified eBooks

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