



# Pattern formation during development of the embryonic cerebellum

F. V. Dastjerdi<sup>1</sup>, G. G. Consalez<sup>2</sup> and R. Hawkes<sup>1\*</sup>

<sup>1</sup> Faculty of Medicine, Department of Cell Biology and Anatomy, Genes and Development Research Group, Hotchkiss Brain Institute, University of Calgary, Calgary AB, Canada

<sup>2</sup> Division of Neuroscience, San Raffaele Scientific Institute, Milan, Italy

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## \*Correspondence:

R. Hawkes, Faculty of Medicine, Department of Cell Biology and Anatomy, University of Calgary, 3330 Hospital Drive N.W., Calgary, AB T2N 4N1, Canada.  
e-mail: rhawkes@ucalgary.ca

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—Marchan 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—Marchan et al., 2010) and mammals (reviewed in Sillitoe et al., 2005; Marchan 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; Marchan 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; Haller et al., 1999; Apps and Garwicz, 2005; Wädiche and Jahr, 2005).

# Pattern Formation During Development

**E Durkheim**



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*Pattern Formation During Development* ,1997      **Pattern Formation** George M. Malacinski, 1984      **Pattern formation** ,1984      **Growth and Development in Plants (Textbook Series: 21st Century Biology and Agriculture)** K.V. Krishnamurthy, 2015-06-01 The topic of the book is covered at the cellular tissue organ and organism levels and inputs from all these hierarchical levels of plant organization have been carefully integrated to get a holistic picture of growth and development in plants The book will be useful to undergraduate post graduate and research students and teachers of botany plant sciences plant biotechnology agriculture and forestry      Growth Patterns in Physical Sciences and Biology Jaun-Manuel Garcia-Ruiz, Enrique Louis, P. Meakin, Leonard M. Sander, 2012-12-06 During the past decade interest in the formation of complex disorderly patterns far from equilibrium has grown rapidly This interest has been stimulated by the development of new approaches based primarily on fractal geometry to the quantitative description of complex structures increased understanding of non linear phenomena and the introduction of a variety of models such as the diffusion limited aggregation model that provide paradigms for non equilibrium growth phenomena Advances in computer technology have played a crucial role in both the experimental and theoretical aspects of this enterprise Substantial progress has been made towards the development of comprehensive understanding of non equilibrium growth phenomena but most of our current understanding is based on simple computer models Pattern formation processes are important in almost all areas of science and technology and clearly pattern growth pervades biology Very often remarkably similar patterns are found in quite diverse systems In some case dielectric breakdown electrodeposition fluid fluid displacement in porous media dissolution patterns and random dendritic growth for example the underlying causes of this similarity is quite well understood In other cases vascular trees nerve cells and river networks for example we do not yet know if a fundamental relationship exists between the mechanisms leading the formation of these structures      **Somites in Developing Embryos** Ruth Bellairs, 2013-11-11 Somite development is a unique and important topic unique because somitic mesoderm is the first tissue to become segmented important because the somites once established exert a profound influence on other segmental structures which form later Somite development is of interest at a number of levels In one aspect demarcation of a specific number of somites and size regulation it is a particularly intriguing example of embryonic pattern formation especially in view of its possible relation to homoeobox controlled segmentation in insects At another level somite development has long been

studied by comparative anatomists but only recently has new light been thrown on such subjects as segmentation of the head proposed in the 18th century by Goethe and now a live issue for developmental biologists. Somites are simple when they first appear but very complex structures arise from them. These include the vertebrae and the axial and other muscles and consequently there is a wealth of morphogenetic problems to be explored. Sometimes their morphogenesis is disturbed by genetic or environmental factors and there are many clinical conditions which arise as a result.

**Genetics of Pattern Formation and Growth Control** Society for Developmental Biology. Symposium, 1990-10. Topics covered in this volume intended for geneticists and developmental biologists include the origin of polarity, establishment of cell fate, the role of growth factors in development, genetic control of pattern formation and use of transgenic organisms in the study of development.

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**Brain abnormalities due to genetic alterations or developmental exposure to environmental factors** Kazuhiko Sawada, Atsushi Yoshiki, Shigeyoshi Saito, 2022-08-31 **Physiological Systems in Insects** Marc J. Klowden, Subba Reddy Palli, 2022-09-24 Physiological Systems in Insects Fourth Edition explores why insects have become the dominant animals on the planet Sections describe the historical investigations that have led us to our current understanding of insect systems Integrated within a basic physiological framework are modern molecular approaches that provide a glimpse of the genetic and evolutionary frameworks that testify to the unity of life on earth This updated edition describes advances that have occurred in our understanding of hormone action metamorphosis and reproduction along with new sections on the role of microbiomes insecticide action and its metabolism and a chapter on genetics genomics and epigenetic systems The book represents a collaborative effort by two internationally known insect physiologists who have instructed graduate courses in insect physiology As such it is the ideal resource for entomologists and those in other fields who may require knowledge of insect systems Presents updated information on key physiological principles Covers detailed and instructive figures for visual enhancement Provides flowing text without the interruption of citations Includes evolutionary considerations throughout also providing a discussion on the implications of molecular techniques and discoveries Encourages further reading with a complete bibliography at end of each chapter *Biological Regulation and Development* Robert F. Goldberger, 2013-11-11 The motivation for us to conceive this work on regulation was mainly our belief that it would be fun and at the same time productive to approach the subject in a way that differs from that of other

treatises We thought it might be interesting and instructive for both author and reader to examine a particular area of investigation in a framework of many different problems Cutting across the traditional boundaries that have separated the subjects in past volumes on regulation is not an easy thing to do not because it is difficult to think of what interesting topics should replace the old ones but because it is difficult to find authors who are willing to write about areas outside those pursued in their own laboratories Anyone who takes on the task of reviewing a broad area of interest must weave together its various parts by picking up the threads from many different laboratories and attempt to produce a fabric with a meaningful design Finding persons who are likely to succeed in such tasks was the most difficult part of our job In the first volume of this treatise most of the chapters dealt with the mechanisms of regulation of gene expression in microorganisms This second volume involves a somewhat broader area spanning the prokaryotic eukaryotic border

*Origination of Organismal Form* Gerd B. Muller, Stuart A. Newman, 2003-01-03 A more comprehensive version of evolutionary theory that focuses as much on the origin of biological form as on its diversification The field of evolutionary biology arose from the desire to understand the origin and diversity of biological forms In recent years however evolutionary genetics with its focus on the modification and inheritance of presumed genetic programs has all but overwhelmed other aspects of evolutionary biology This has led to the neglect of the study of the generative origins of biological form Drawing on work from developmental biology paleontology developmental and population genetics cancer research physics and theoretical biology this book explores the multiple factors responsible for the origination of biological form It examines the essential problems of morphological evolution why for example the basic body plans of nearly all metazoans arose within a relatively short time span why similar morphological design motifs appear in phylogenetically independent lineages and how new structural elements are added to the body plan of a given phylogenetic lineage It also examines discordances between genetic and phenotypic change the physical determinants of morphogenesis and the role of epigenetic processes in evolution The book discusses these and other topics within the framework of evolutionary developmental biology a new research agenda that concerns the interaction of development and evolution in the generation of biological form By placing epigenetic processes rather than gene sequence and gene expression changes at the center of morphological origination this book points the way to a more comprehensive theory of evolution

*The Shaping of Life* Lionel G. Harrison, 2010-12-23 Biological development how organisms acquire their form is one of the great frontiers in science While a vast knowledge of the molecules involved in development has been gained in recent decades big questions remain on the molecular organization and physics that shape cells tissues and organisms Physical scientists and biologists traditionally have very different backgrounds and perspectives yet some of the fundamental questions in developmental biology will only be answered by combining expertise from a range of disciplines This book is a personal account by Professor Lionel Harrison of an interdisciplinary approach to studying biological pattern formation It articulates the power of studying dynamics in development that to understand how an

organism is made we must not only know the structure of its molecules we must also understand how they interact and how fast they do so     *Epigenetics* Benedikt Hallgrímsson, Brian K. Hall, 2011-04-11 If you want to understand evolution you need to understand the murky world of epigenetics A hearty congratulations should be paid to Hallgrímsson and Hall who provide reliable and steady illumination Bernard Wood Center for the Advanced Study of Hominid Paleobiology George Washington University

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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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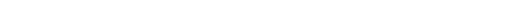
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