



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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