Seminars in Fetal & Neonatal Medicine 21 (2016) 356–364

Contents lists available at ScienceDirect

Seminars in Fetal & Neonatal Medicine

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

Review

Structure–function relationships in the developing cerebellum: Evidence from early-life cerebellar injury and neurodevelopmental disorders

Catherine J. Stoodley [a,*], Catherine Limperopoulos [b]

[a] Department of Psychology and Center for Behavioral Neuroscience, American University, Washington DC, USA
[b] Diagnostic Imaging and Radiology, Children's National Health Systems, Washington DC, USA

Keywords:
Cerebellum
Fetal
Preterm
Autism
Developmental diaschisis
Cognition

SUMMARY

The increasing appreciation of the role of the cerebellum in motor and non-motor functions is crucial to understanding the outcomes of acquired cerebellar injury and developmental lesions in high-risk fetal and neonatal populations, children with cerebellar damage (e.g. posterior fossa tumors), and neurodevelopmental disorders (e.g. autism). We review available data regarding the relationship between the topography of cerebellar injury or abnormality and functional outcomes. We report emerging structure–function relationships with specific symptoms: cerebellar regions that interconnect with sensorimotor cortices are associated with motor impairments when damaged; disruption to posterolateral cerebellar regions that form circuits with association cortices impact long-term cognitive outcomes; and midline posterior vermal damage is associated with behavioral dysregulation and an autism-like phenotype. We also explore the impact of age and the potential role for critical periods on cerebellar structure and child function. These findings suggest that the cerebellum plays a critical role in motor, cognitive, and social–behavioral development, possibly via modulatory effects on the developing cerebral cortex.
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1. Introduction

There is an increasing appreciation of the importance of the contributions of the cerebellum to the developing brain. Emerging evidence from fetal, neonatal and pediatric populations supports the existence of a regional functional topography of the cerebellum, and provides testable hypotheses for clarifying the role of the developing cerebellum in motor, cognitive, and social/behavioral development. Here, we review data from very preterm infants following early-life cerebellar injury, infants with cerebellar malformations, older children with cerebellar injury (e.g. pediatric posterior fossa tumors), and neurodevelopmental disorders to clarify the potential importance of cerebellar structure–function relationships in the developing brain.

Cerebellar development follows a highly orchestrated series of developmental processes. Between 20 and 40 weeks of gestation, the cerebellum undergoes an exuberant period of growth, during which time the rapid growth of the cerebellum is unparalleled by that of any other cerebral structure [1,2]. This developmental pattern strongly suggests the presence of a critical period for cerebellar development, which in turn is central to both the cerebellum's vulnerability and the developmental repercussions of injury, which are capable of disrupting this highly regulated, programmed developmental course.

At the systems level, disrupted or aberrant cerebellar growth could have significant effects on the developing cerebral cortex [3]. As described below, the cerebellum is richly interconnected with regions of the cerebral cortex supporting movement, cognition, and affective regulation [4]. The cerebellum is thought to modulate these cerebro-cerebellar circuits to support the optimization of behavior, with a particular role in procedural learning and skill acquisition. It is therefore possible that during early development – a period of intense skill acquisition – the cerebellum serves to optimize both structure and function in the cerebral cortex (see [5] for discussion). We argue that early disruption of the cerebellum – be it due to preterm birth, prenatal cerebellar developmental lesions (i.e. malformations), cerebellar posterior fossa tumors in early childhood, or developmental disorders – could exert significant,

* Corresponding author. Address: Department of Psychology and Center for Behavioral Neuroscience, American University, 4400 Massachusetts Ave. NW, Washington, DC 20016, USA. Tel.: +1 (202) 885 1785; fax: +1 (202) 885 1023.
E-mail address: stoodley@american.edu (C.J. Stoodley).

http://dx.doi.org/10.1016/j.siny.2016.04.010
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long-lasting, and wide-ranging changes in the structure and function of cerebro-cerebellar systems, with long-term effects on behavior.

2. Cerebellar anatomy and functional topography

The cerebellum is located in the posterior fossa and comprises ~10% of the volume of the brain. It is connected to the brainstem via the cerebellar peduncles: the superior peduncle contains fiber tracts carrying information from the cerebellum to the cerebral cortex via the thalamus; the middle peduncle consists of fiber tracts which travel from the cerebral cortex to the cerebellum via the pontine nuclei; and the inferior peduncle carries both afferent and efferent fiber tracts connecting the cerebellum with the vestibular system and spinal cord, as well as incoming projections to the cerebellum from the inferior olive. The cerebellum itself consists of two cortex-covered hemispheres connected by the midline vermis, with a core of white matter in which the deep cerebellar nuclei are embedded. The cerebellar cortex is divided into ten lobules (I–X based on nomenclature detailed in [6]; see Fig. 1): lobules I–V make up the anterior lobe of the cerebellum; lobules VI–IX the posterior lobe; and lobule X the flocculonodular

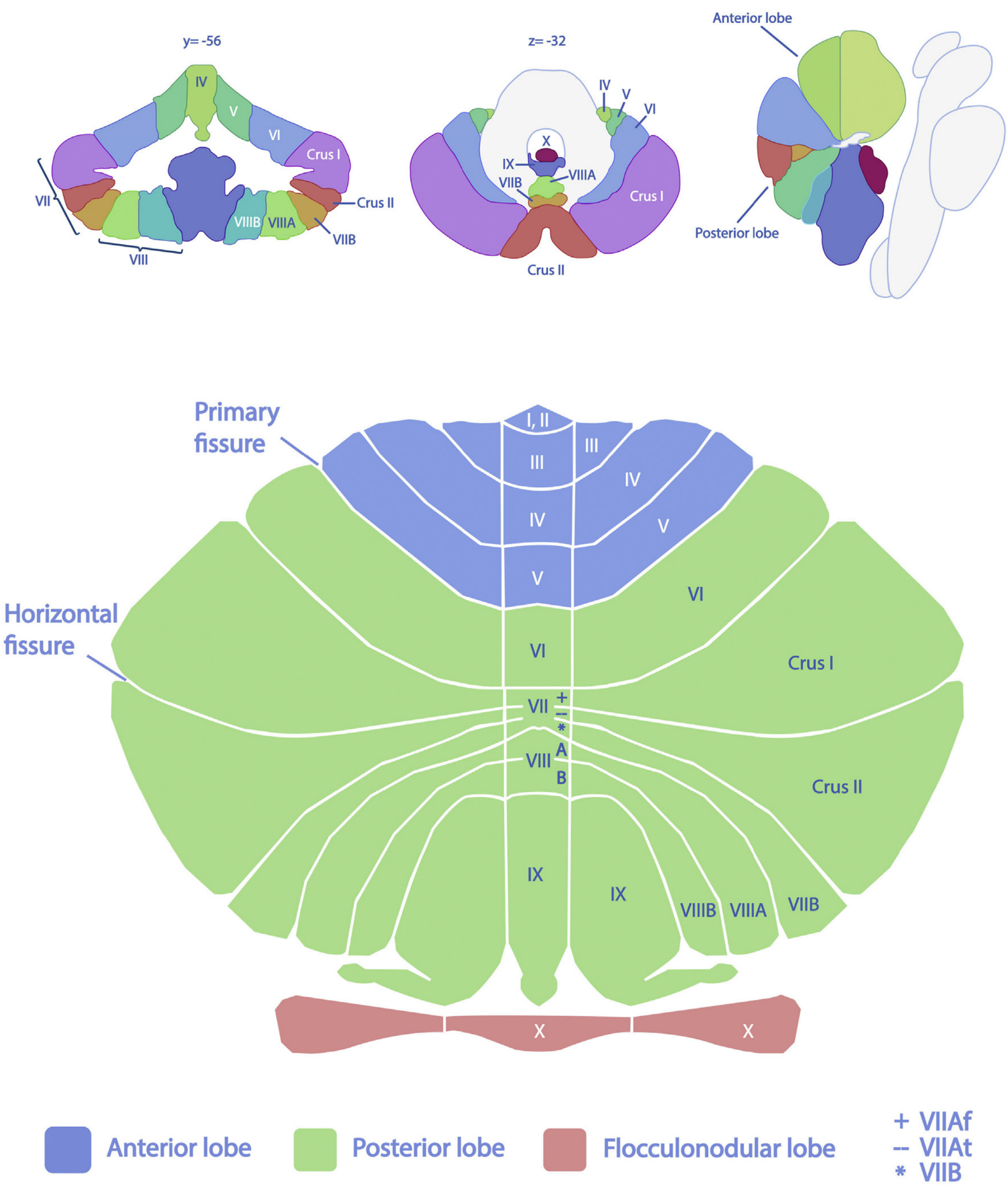

Fig. 1. Cerebellar anatomy. (Upper) Cerebellar lobules shown in coronal, axial and sagittal slices from the Spatially Unbiased Infra-tentorial Template (SUIT) cerebellar atlas; individual lobules are labeled and color-coded. (Lower) Flattened cerebellum showing lobules I–X, including the subdivisions of lobule VII (Crus I, Crus II, VIIB) and lobule VIII (VIIIA and VIIIB); the anterior (lobules I–V; blue), posterior (lobules VI–IX; green), and flocculonodular (lobule X, red) lobes of the cerebellum are shown.

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