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Review

Why the embryo still matters: CSF and the neuroepithelium as interdependent regulators of embryonic brain growth, morphogenesis and histiogenesis

Angel Gato [a], Mary E. Desmond [b,*]

[a] Departamento de Anatomía y Radiologia, Facultad de Medicina, Universidad de Valladolid, Avda Ramón y Cajal 7, 47005 Valladolid, España
[b] Department of Biology, Mendel Science Center, Villanova University, Villanova, PA 19085, USA

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ABSTRACT

The key focus of this review is that both the neuroepithelium and embryonic cerebrospinal fluid (CSF) work in an integrated way to promote embryonic brain growth, morphogenesis and histiogenesis. The CSF generates pressure and also contains many biologically powerful trophic factors; both play key roles in early brain development. Accumulation of fluid via an osmotic gradient creates pressure that promotes rapid expansion of the early brain in a developmental regulated way, since the rates of growth differ between the vesicles and for different species. The neuroepithelium and ventricles both contribute to this growth but by different and coordinated mechanisms. The neuroepithelium grows primarily by cell proliferation and at the same time the ventricle expands via hydrostatic pressure generated by active transport of Na^+ and transport or secretion of proteins and proteoglycans that create an osmotic gradient which contribute to the accumulation of fluid inside the sealed brain cavity. Recent evidence shows that the CSF regulates relevant aspects of neuroepithelial behavior such as cell survival, replication and neurogenesis by means of growth factors and morphogens. Here we try to highlight that early brain development requires the coordinated interplay of the CSF contained in the brain cavity with the surrounding neuroepithelium. The information presented is essential in order to understand the earliest phases of brain development and also how neuronal precursor behavior is regulated.

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Introduction

Initially, the embryonic brain is a hollow fluid-filled tube. The development of the neural tube involves three distinct phases: formation of the tube (neurulation), polarization of the tube into an anterior expanded brain and posterior spinal cord and histiogenesis of the neuroepithelium throughout. Much attention has been given to the analysis of the mechanisms that form the tube via neurulation as well as the later period of embryonic brain development involving cell differentiation of the neuroepithelium. However, little attention has been given to the phase of early brain development in between these two periods during which time the anterior part of the neural tube, the future brain enlarges many fold. In fact, in human embryos, the brain increases 100,000 fold in volume during this period (Desmond and O'Rahilly, 1981). Not only is the growth immense but it is rapid.

Moreover, most embryological research of the brain and spinal cord comprising the central nervous system (CNS) has focused on the neuroepithelium. This emphasis on the neuroepithelium ignores the existence of the brain ventricles[1] filled with cerebrospinal fluid (CSF) and its role in early brain development. Today several research findings have generated sufficient evidence to support the hypothesis that the CSF is directly involved in early brain development. The main objective of this review is to demonstrate that the bi-dimensional impact of CSF with the neuroepithelium must be taken into account in our global understanding of brain development.

With the aim to expose in an ordered way what is known about the influence of CSF in early brain development, we develop a diagram which illustrates the line of argument in this review. As a general consideration, research, much of which has been developed by the authors and their collaborators, support the idea that CSF contributes to brain development by two general mechanisms:

1. CSF is a main force driving brain growth and morphogenesis during early brain development. Several research findings have shown that the normal growth and morphogenesis of the embryonic brain requires the pressure generated, within a closed ventricular

[1] Although correct embryological phraseology for the embryonic CNS is the neural tube comprised of a cavity or presumptive ventricles, to simplify we use ventricle throughout to describe the cavity for both the embryonic and adult brain. Likewise, we use CSF to describe the fluid for both embryonic and adult brains and use brain to refer to both the neuroepithelium and ventricular space.

* Corresponding author. Fax: +1 610 519 7863.
E-mail address: mary.desmond@villanova.edu (M.E. Desmond).

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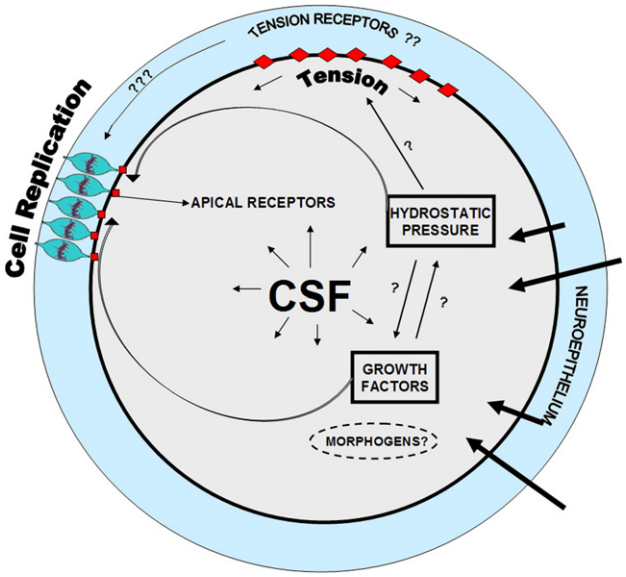

Fig. 1. A schematic diagram based on a transverse section through the midbrain region that explains the interdependence of the interactions of hydrostatic pressure created by the CSF and growth factors within the CSF upon the behavior of the neuroepithelium. Fluid crosses the neuroepithelium via an osmotic gradient (large arrows on right). The CSF generates expansion of the luminal surface indicated by arrows emanating from the word CSF. Growth factors most likely stimulate mitosis of the neuroepithelial cells via apical receptors symbolized by the red boxes on the ventricular surface by the mitotic cells. There may also be a bidirectional influence of growth factors on hydrostatic pressure and vice versa. Hydrostatic pressure may stretch the inner surface of the neuroepithelium and may stimulate mitotic activity via tension receptors such as focal adhesion kinases (FAKs) on the surface or within the neuroepithelial cells.

system, via accumulation of CSF within them, and that this accumulation of CSF within the embryonic brain ventricles occurs via an osmotic gradient. The CSF pressure promotes the expansion of the brain creating a tension state in the neuroepithelium which stimulates cell proliferation and suggests the presence of tension receptors.

2. Recently it has been demonstrated that, at early stages of development, CSF exerts an intense trophic influence on the behavior of neuroepithelial cells, regulating neuroepithelial cell survival, proliferation and differentiation. The interaction of CSF which has a complex composition, including growth factors and morphogens, with the apical surface of neuroepithelial cells has elicited marked influences upon mitosis, apoptosis and differentiation.

We propose as a major thesis of this review that these two components, CSF and neuroepithelium, are totally interdependent working as a functional entity regulating brain growth, morphogenesis and neuroepithelial cellular behavior in early brain development (Fig. 1).

Formation of the CNS

We begin by summarizing briefly the main morphological steps during early formation of the central nervous system (CNS).

There are three embryological tissues, ectoderm, mesoderm and endoderm that form the major tissues and organs of the vertebrate body. Ectoderm, the outer layer of early embryo differentiates into neural ectoderm, neural crest and skin ectoderm.

Once the cells of the neuroectoderm organize into a flat plate along the dorsal surface, they bend into a tube and at the same time become committed primitive neurons. The formation of the tubular CNS from the neural plate (neurulation) has been reviewed extensively (Jacobson, 1981; Jacobson and Gordon, 1976; Smith and

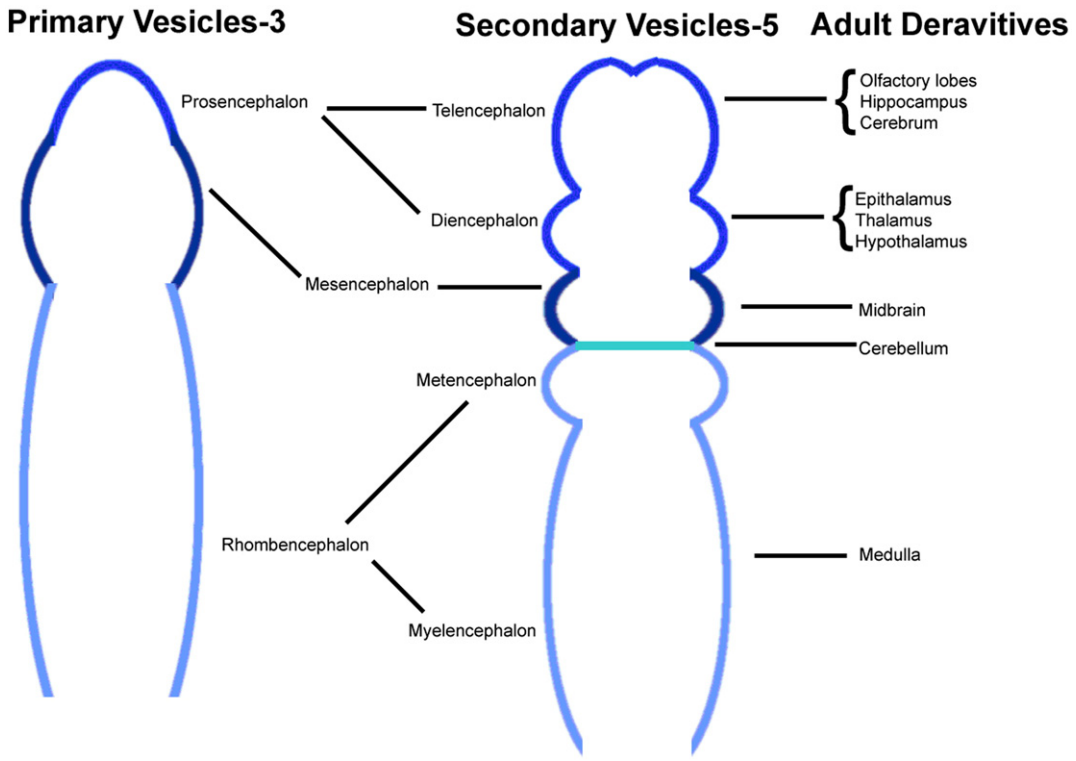

Fig. 2. A schematic diagram of the dorsal view of embryonic brain vesicles. Initially the CNS has three vesicles that then form five vesicles from which all of the adult derivatives develop. Only a few of the adult derivatives are shown in the last column. The three vesicles have been colored different shades of blue to illustrate the specific derivatives of the prosencephalon and rhombencephalon. Note that the cerebellum forms from the posterior part of the mesencephalon and anterior part of the metencephalon. (Modified from Bally-Cuif et al., 1995).

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