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Review article

Development and evolution of cortical fields

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ABSTRACT

The neocortex is the brain structure that has been subjected to a major size expansion, in its relative size, during mammalian evolution. It arises from the cortical primordium through coordinated growth of neural progenitor cells along both the tangential and radial axes and their patterning providing spatial coordinates. Functional neocortical areas are ultimately consolidated by environmental influences such as peripheral sensory inputs. Throughout neocortical evolution, cortical areas have become more sophisticated and numerous. This increase in number is possibly involved in the complexification of neocortical function in primates. Whereas extensive divergence of functional cortical fields is observed during evolution, the fundamental mechanisms supporting the allocation of cortical areas and their wiring are conserved, suggesting the presence of core genetic mechanisms operating in different species. We will discuss some of the basic molecular mechanisms including morphogen-dependent ones involved in the precise orchestration of neurogenesis in different cortical areas, elucidated from studies in rodents. Attention will be paid to the role of Cajal–Retzius neurons, which were recently proposed to be migrating signaling units also involved in arealization, will be addressed. We will further review recent works on molecular mechanisms of cortical patterning resulting from comparative analyses between different species during evolution.

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Abbreviations: NE, neuroepithelial cells; RG, radial glial cells; V1, primary visual area; A1, primary auditory area; S1, primary somatosensory area; M1, primary motor area; AP, anteroposterior; DV, dorsoventral; VP, ventral pallium; PSB, pallial sub-pallial boundary; TCA, thalamo-cortical afferents; V^{HO}, higher-order visual area; SGL, subpial granular layer cells.

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1. Introduction

The mammalian neocortex, which is the control center of our cognitive functions, responsible for behavior and social activities, is the brain structure that shows major expansion during evolution. The neocortex arises from the dorsal telencephalon and is composed by different types of neurons that are generated after the exponential expansion of neural stem cells known as neuroepithelial cells (NE) and which later differentiate into radial glial cells (RG). Among the features, which are unique to the neocortex as opposed to other brain regions, is the radial neuronal organization in six major layers, composed of earlier and later born neurons positioned according to an inside-out sequence. Each layer contains multiple distinct neuronal populations and functionally distinct connectivity. The neocortex shows a spatial organization (in the tangential dimension) called arealization, which represents the subdivision of the neocortex into functionally distinct cortical areas. The basic plan of a mammalian neocortex is constituted by four primary areas: visual (V1), auditory (A1), somatosensory (S1) and motor (M1) cortices. Primary areas relay input information from the periphery (visual, auditory and somatosensory) and control motor output. These are functionally interconnected to "higher-order areas" that act as specialized processing or integrating centers (O'Leary and Sahara, 2008; Krubitzer and Dooley, 2013); the latter being largely added during neocortex evolution. Area identity starts to be established early during development but its ultimate determination depends also on environmental cues brought notably by peripheral axons branching in cortical areas (O'Leary, 1989; O'Leary et al., 1994). During evolution, different neocortical territories expanded unequally. Species-specific neocortical areas were formed and coincidentally region-specific expression of genes was also reported (Abrahams et al., 2007; Johnson et al., 2009; Kang et al., 2011; Chen et al., 2011), suggesting a convergent evolution between brain structure and gene regulation. Causal or as a consequence of anatomical changes, increasing neuronal complexity and plasticity is also pronounced during evolution. For instance, the morphology of human pyramidal neurons and their plasticity in response to environmental cues show extensive changes with area-specific differences (Elston et al., 2001; Van Pelt and Uylings, 2002; Elston, 2003). Thus, the area-specific degree of neuronal maturation is likely involved in functional specification of the human brain. To understand the involvement of genetic and environmental factors in controlling the size and unequal expansion of cortical areas of the mammalian neocortex, in this review, we will first discuss some fundamental mechanisms involved in the establishment of early cortical patterning during development and differences that may have arisen during the course of cortical evolution.

2. Radial organization of the cerebral cortex: neurogenesis during evolution

2.1. Changes in cortical proliferative regions

To build up cytoarchitectonically and functionally different brains as observed during evolution, various genetic and cell biological processes are involved. Changes in the number of neurons generated may rely on changes in the proliferative capacities of the progenitor zone, which can occur through changes of intrinsic cell-cycle kinetics, and/or modifying the access of progenitor cells to environmental factors. Indeed, the mammalian neocortex has complexified its proliferative domains in the course of evolution to give rise to different sets of progenitor cells, likely having increased proliferative capacities, which may have resulted in the emergence of area-specific differences in neurogenesis.

Cortical neurons arise from NE, multipotent neural progenitor cells characterized by their (i) self-renewing capacity and (ii) their potential to give rise to three major neural cell types: neurons, astrocytes and oligodendrocytes (Bertrand et al., 2002; Jandial et al., 2008). NE are highly polarized cells arranged in a single layer that forms the ventricular zone (VZ) (Bystron et al., 2008). The VZ is colonized by blood vessels. On one side it faces the ventricles filled with lipoprotein- and membrane particle-rich cerebrospinal fluid, and on the other the basal lamina, a rich source of extracellular molecules (Vaccarino et al., 1999; Raballo et al., 2000; Götz and Huttner, 2005). This highly dynamic and rich micro-environment provides "stem cell niche–like" features to the NE during development (Lehtinen and Walsh, 2011), crucial for the regulation of neurogenesis and neuronal diversity. Following the onset of cortical neurogenesis, a "secondary" proliferative region, the subventricular zone (SVZ), is formed from NE cells. SVZ progenitor cells continue to proliferate for approximately one-two rounds of divisions in mice before undergoing self-consuming divisions that give rise to neurons (Noctor et al., 2004; Miyata et al., 2004; Haubensak et al., 2004; Shitamukai et al., 2011; Wang et al., 2011). The SVZ is further divided into an inner (ISVZ) and outer SVZ (OSVZ) in primates and carnivoras, which corresponds to an anatomical separation by the inner fiber tract (Reillo et al., 2011; Smart et al., 2002). OSVZ progenitor cells undergo multiple rounds of self-proliferative division followed by the direct generation of neurons (Hansen et al., 2010; Fietz et al., 2010; LaMonica et al., 2013; Betizeau et al., 2013). The anatomical appearance of the OSVZ is not unique to primates but is rather common across mammalian species which have a gyrencephalic neocortex (Smart et al., 2002; Hansen et al., 2010; Fietz et al., 2010; Reillo et al., 2011; Shitamukai and Matsuzaki, 2012).

During mammalian cortical evolution, the number of cortical plate neurons has massively increased, in particular the upper (supragranular) layer neurons (layers 2–3), which comprise a larger proportion of the cortex in humans compared to rodents (Hill and Walsh, 2005). Several reports have correlated this increase with the massive enhancement of specific types of progenitor cells found in the OSVZ (Smart et al., 2002; Hansen et al., 2010; Fietz et al., 2010); therefore, this acquisition and expansion of OSVZ progenitor cells is often considered as an evolutionary adaptive change. The size of the OSVZ is correlated with the increase in neocortical size. Is it a consequence of prolonged neurogenesis mediated by different environmental influences or is it caused first by intrinsic changes in cell-cycle kinetics? To answer these questions, several studies analyzed the dynamics of the cell-cycle in distinct progenitor cells in different species (Lukaszewicz et al., 2005; Arai et al., 2011; Reillo and Borrell, 2012; Betizeau et al., 2013).

2.2. Proliferative capacities and cell-cycle kinetics

In the mouse (a lissencephalic rodentia) at embryonic day (E) 14.5, progenitor cells in the VZ have a shorter total cell-cycle length compared to SVZ progenitor cells, due to a specific lengthening of the S phase and a shortening of the G1 phase (Pilaz et al., 2009; Arai et al., 2011). VZ and SVZ progenitor cells can both be further subdivided into proliferative and neurogenic populations (Iacopetti et al., 1999). In both VZ and SVZ, neurogenic progenitor cells have a shorter total cell-cycle length compared to that of proliferative progenitor cells, mainly due to a shorter S phase (Arai et al., 2011) (Table 1), indicating that neurogenic division is linked to a total cell-cycle shortening. Therefore, proliferative SVZ progenitor cells have the longest cell-cycle (Arai et al., 2011) and the duration of the total cell-cycle in VZ and SVZ progenitor cells is progressively increased during development in rodents (Caviness et al., 1995; Takahashi et al., 1995). In the ferret (a gyrencephalic carnivora) progenitor cells in the VZ showed no obvious differences in their total

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