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EDITORIAL

Cortical Evolution Conference, 2018

This special volume on Cortical Evolution includes articles based on presentations given by the authors at the *Cortical Evolution 2018* Conference that took place in Las Palmas, Spain. The goal of the Cortical Evolution Conferences is to promote the dissemination of the latest concepts on factors that drive evolution of the mammalian cerebral cortex. This issue features original research and review articles focusing on the development of the cerebral cortex in different species and on the adult anatomy of the cerebral cortex, and their implication in evolution.

One of the topics covered was prenatal development of the cortex in different mammalian species. The Dehay group reported that stage-specific changes in internuclear kinetic migration are constrained by the cell cycle in mice. They showed that while in early stages of cortical development the apical nuclear movement corresponded to G phase, at mid-corticogenesis the apical nuclear movement was initiated during S phase, suggesting that internuclear kinetic migration of progenitor cells with a short cell-cycle differs from that of progenitor cells with longer cell-cycle duration, independent of the species. The Borrell group used two-photon microscopy to analyze the morphology of the leading process in radially migrating neurons and found that neurons with branched processes were more frequent in ferret than in mouse, and proposed that branching of the leading process of excitatory neurons may represent an evolutionary mechanism that induces lateral migration and promotes cortical folding. Nakajima et al. used electronic microscopy to describe the presence of transitory clusters of excitatory and inhibitory immature neurons in the outer most region of the developing cortex that they term the "primitive cortical zone" during late stages of development. Clusters were observed in mouse, and similar clusters with expanded radial dimension were also present in monkey and human. Nakajima and colleagues propose that maturation of neurons in the clusters contributes to functional integration between cortical neurons, and that this process may contribute to evolution of the primate cortex. The Noctor group reported on a unique subtype of microglial cell that is located near the lateral ventricle in the prenatal cerebral cortex of rat and rhesus monkey and that they named periventricular microglia. They showed that periventricular microglia make extensive contact with the soma and pial process of mitotic neural precursor cells dividing at the surface of the lateral ventricle, and exhibit notable morphological and connectional differences across species, including terminal bouton-like structures that contact neural precursor cells in monkey but not in rat. These findings suggest differential function among species and are consistent with a role for microglia in the regulation or progenitor cell function during cortical development and evolution. The groups of Molnár and Hoerder-Suabedissen used transgenic mouse lines to study the postnatal subplate zone and found that it is very sparsely populated with GABAergic neurons. They also confirmed that a small proportion of subplate GABAergic neurons forms long-range projections to contra- and ipsilateral cortex and also to subcortical targets.

Research presentations on the adult cortex included those of Huttner's laboratory who discussed a study of 13 species of primates, including human, and showed large variations in the patterns of folding of the dorsal cortex among primates (evolved cortex), while other cortices that displayed more conserved patterns (conserved cortex). Huttner and colleagues posit that the conserved and evolved cortices constitute two distinct sequential events in the mammalian evolution. The Manger laboratory analyzed the nature of white matter interstitial cells in a lesser ape, the lar gibbon. They found that these cells are very abundant in the white matter, are positioned close to cortical layer VI, and express nitric oxide synthase (nNOS), calretinin, and some parvalbumin, but not calbindin. These data provide a key to understanding the phylogeny of the cerebral cortex and the pathology of many neurodevelopmental diseases. The Martínez-Cerdeño laboratory examined interlaminar astrocytes (ILA) in the cerebral cortex of 46 mammalian species, including 22 primates, encompassing most orders of therian mammals. They found that there are two types of ILA, which they termed pial and subpial ILA. Pial and subpial ILA express GFAP and other astrocyte makers, have a soma positioned in layer I, and interlaminar processes that run perpendicular to the pia. However, these cells differed in their somatic morphology, position within layer I, and presence across species. They also described the presence of rudimentary ILA in some species, such in rodents. Martínez-Cerdeño and colleagues reported that pial ILA were present in all mammalian species analyzed, subpial ILA were absent in marsupalia, and typical subpial ILA were only found in primates. While the density of ILA somata only varied slightly, the complexity of ILA processes greatly varied across species, with great apes, including human, exhibiting ILA with the highest morphological complexity. They also showed that ILA contact neurons, elements in the pial meninges, and capillaries. These data suggest a role in blood–brain barrier function, and in facilitating communication between neurons, astrocytes, capillaries, meninges, and cerebrospinal fluid. Dooley and Krubitzer used the paradigm of bilateral enucleation in very early development of the opossum to demonstrate that S1 receives dense inputs from novel cortical fields and that the density of cortical and thalamocortical connections was altered. These findings demonstrated that sensory

systems develop in tandem and that an alteration of sensory input in one system can affect the connections and organization of other systems. Heculano-Houzel used a data set of 700 species to show that maximal longevity, age at sexual maturity, and longevity in birds and mammal species correlated with the number of cortical neurons. In addition, in this volume Casanova and Casanova reviewed the minicolumnar organization and function of the human cerebral cortex, its evolution across primates, and role in human pathology. The Puelles group looked into the classic theory of concentric mammalian allo-, meso-, and neo-cortical domains. This theory postulates that a central neocortical island of six-layered tissue is separated by a surrounding mesocortical ring of four- and five-layered tissue from a peripheral allocortical ring comprising three-layered cortical tissue. They recapitulated the concentric ring concept in mammals using mouse as a model and considered a potential causal patterning scenario using topologic models. They also explored how this theory may apply to pallium models that have recently been proposed for sauropsids.

The species-specific response of the cerebral cortex to insult or disease was also discussed. The Juliano group reported on work using the gyrencephalic ferret as an animal model to investigate Zika virus infection. While rodents develop signs of infection, they usually do not show the severe disease found in human; however, Juliano and colleagues presented evidence showing that ferrets display a series of features that are compatible with Zika infection in human. They used imaging and histological analysis to show that, as in human, Zika virus did not have an equivalent effect on each fetus. Their data showing that a reduced brain size and skull malformations occurred in infected ferrets suggest that the ferret may be a valuable model to study the effects of Zika virus infection on brain development.

In addition to evo-devo studies of cortical evolution, several primatologists and paleobiologists participated in the Cortical Evolution meeting. In this volume, Brunner described paleoneurological analysis of the endocranial cavity in extinct species to make inferences on brain evolution, and work to distinguish endocranial variations due to changes in brain structure versus cranial constraints. Brunner and colleagues also reviewed the importance of the fossil record for understanding evolution of the cerebral cortex across extinct *Homo* species.

Martínez-Cerdeño and Noctor close this volume with commentary on the round table discussion that took place at the Cortical Evolution 2018 Conference. Participants discussed key differences and advantages of different animal models for study of cortical evolution and disease, and enumerated criteria for choosing appropriate animal models for specific scientific questions. Participants provided thoughtful dialog and careful consideration of the advantages of different species and stressed the importance of broadening the scope of studies by including more species when possible to further advance research in all fields of study.

ORCID

Verónica Martínez-Cerdeño https://orcid.org/0000-0002-9613-3603

Stephen C. Noctor https://orcid.org/0000-0001-5236-4525

Verónica Martínez-Cerdeño[1]

Stephen C. Noctor[2]

[1]*Pathology and Laboratory Medicine, UC Davis, Davis, California*

[2]*Psychiatry and Behavioral Sciences, UC Davis, Davis, California*

Correspondence

Verónica Martínez-Cerdeño, Pathology and Laboratory Medicine, UC Davis, Davis, California.

Email: vmartinezcerdeno@ucdavis.edu