Neocortical Development

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AUTHORS' NOTE:

This book is out of print. Raven Press no longer exists. The copyright to this book is being transferred to us. We want to make this information available to all who are interested in neocortical development. In the files available for download, we add a few pages that review some of the relevant literature that has been published since 1991. Our observations in 1991 are relevant to the multitude of gene expression studies done since the mid-90s and up to the present day. Many of the hypotheses that we proposed in this book have been confirmed by these studies. We also re-examine cell migration in the neocortex; the labeling patterns in our autoradiograms are consistent with studies showing tangential migration of GABA-ergic cells from germinal zones in the basal ganglia into the developing neocortex. We invite your comments on our work, and would like to answer any questions that you want to ask about how your research correlates with our findings.

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Preface

The neocortex is the crown of the mammalian central nervous system both literally and figuratively. Because an animal can carry out many of its vital functions after structural or functional decortication, the neocortex is not essential for survival in the strict sense of the term. However, there is an abundance of direct and indirect evidence that suggests that the neocortex plays a crucial role in the control of higher perceptual processes, cognitive functions, and intelligent behavior. Ascending the phylogenetic scale, the six-layered neocortex steadily expands relative to the rest of the brain, a phenomenon referred to as progressive neencephalization. This expansion first becomes manifest as the smooth neocortical mantle (lissencephalic pallium) spreads over the rest of the forebrain and the midbrain. A later manifestation of progressive neencephalization, one especially pronounced in larger mammals, is the increasing convolution of the cortical surface. This brings about an increase in the ratio of nerve cell bodies and dendrites relative to the cortical afferents and efferents, reflecting gains in processing capability and computing power of the cortical gray matter. In parallel with progressive neencephalization, there is an increase in the number of different cytoarchitectonic subdivisions of the neocortex, particularly of those regions traditionally referred to as "association areas." It is widely assumed that the evolutionary growth of mental life that reaches its zenith in humans is attributable to the progressive expansion and elaboration of the neocortex.

Neuroanatomists have been studying the structural organization of the neocortex for centuries. This began with dissections aided by the naked eye and was followed by light microscopic examinations of regional differences in neocortical cytoarchitectonics. There is still an effort to unravel the gross and fine circuitry of the neocortex using chemical, biochemical, and physiological tracer techniques at light and electron microscopic levels of resolution. The investigation of the functional organization of the neocortex became possible with the introduction of electrical stimulation and recording techniques in the last century, and advances in electronics and computer techniques in this century are helping us to understand how information is conveyed to, and processed in, the neocortex. Neuropsychologists using ablation techniques, as well as electrical stimulation and recording procedures with implanted electrodes in conscious animals, have contributed their share to our current understanding of how the neocortex controls behavior. However, the investigation of the morphogenetic development of the neocortex was lagging behind the anatomical, physiological, and psychological studies of its structure and function. Gross descriptions of the developing neocortex in animals and humans were beginning to become available at the turn of the century. But the initial efforts of neuroembryologists to analyze the cytological processes underlying neural development tended to focus on the relatively simple caudal portion of the neural tube that gives rise to the spinal cord. This state of affairs began to change in the second half of this century. A steadily growing number of articles are now being published in various journals that deal with the development of the neocortex in a great variety of species and at different stages through the embryonic, fetal, and early postnatal periods. A few edited volumes have also appeared that contain valuable contributions by experts who deal with some selected aspect of neocortical development in one or another species. However, to our knowledge there is not a book currently available, written by a single team of investigators, that specifically deals with the development of the mammalian neocortex as a whole.

This book is the outcome of our own current investigations on neocortical development in which we relied on a limited number of techniques and concentrated on a single species, the rat. The lissencephalic cortex of the rat is far less complex structurally than the convoluted cortex of a carnivore or primate. This represents an advantage from the experimental point of view because a study of the entire cortical mantle is possible. The major techniques and materials that we have used are limited to the following: (a) We have prepared a large collection (several hundred specimens) of high quality, methacrylate-embedded Nissl-stained sections that cut through the neocortex in the three cardinal planes. This material was used, first, to describe daily changes in the growth of the neocortex at the histological and cytological levels, and second, as normative material for comparisons with observations made in experimentally manipulated embryos; (b) A large collection (several hundred specimens) of embryos that received injections of $[^3H]$thymidine to label multiplying precursors of neurons and glia were prepared for autoradiography. Three variants of this technique were used. First, long-survival autoradiography after multiple injections was used to determine the time of origin of different classes of neurons in different regions of the developing cortex on successive embryonic days in neonates and adults. Second, short-survival autoradiography (2 hours) after single injections was used to locate the sites of cell proliferation and their magnitude as a function of embryonic age. Third, sequential-survival autoradiography (consecutive 24 hour intervals) after single injections was used to follow the dynamics of cell proliferation in the cortical germinal matrices; to trace the migration and temporary pause of cells through the subventricular and intermediate zones of the cortex; and to determine the time of arrival, final distribution, and settling of young neurons in the cortical gray matter. Finally, we used low-level x-irradiation as an ancillary technique to study changes in the cellular dynamics of the germinal matrices giving rise to neurons and glia, and to investigate certain aspects of neuronal differentiation. Because our techniques are best suited to study developmental change during the embryonic period at the histological level, developmental changes during the postnatal period at the cellular and subcellular levels, i.e., dendritic differentiation and synaptogenesis, have not been investigated.

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Abbreviations

a, A	anterior
abt	anterior basal telencephalic neuroepithelium
ABT	anterior basal telencephalon (differentiating)
AC	anterior commissure
AD	anterodorsal thalamic nucleus
AI	agranular insular cortex
AID	agranular insular cortex, dorsal part
AIP	agranular insular cortex, posterior part
AIV	agranular insular cortex, ventral part
AL	anterolateral
AM	anteromedial thalamic nucleus
ap	alar plate of neuroepithelium
APO	anterior primary olfactory cortex
AV	anteroventral thalamic nucleus
bg	basal ganglia neuroepithelium
BG	basal ganglia (differentiating)
bp	basal plate of neuroepithelium
bt	basal telencephalic neuroepithelium
BT	basal telencephalon (differentiating)
caz	callosal zone
cc	cerebral cortical neuroepithelium
CC	corpus callosum
ce	cerebellar neuroepithelium
CG	cingulate cortex
CG1	cingulate cortex, area 1
CG2	cingulate cortex, area 2
CG3	cingulate cortex, area 3
ch1, Ch1	channel 1 of developing cortex
ch2, Ch2	channel 2 of developing cortex
chp	choroid plexus rudiment
CL	claustrum
col	collapsed neuroepithelium
CP	cortical plate
CPa	cortical plate, anterior
CPp	cortical plate, posterior
d, D	dorsal
DC	diencephalon
DL	dorsolateral
DM	dorsomedial
DP	dorsal peduncular cortex
E	embryonic day
ECL	lateral entorhinal cortex
ECM	medial entorhinal cortex
ez	ependymal zone
FI	fimbria
FL	forelimb area
FM	foramen of Monro
FR	motor area
FR1	frontal cortex, area 1
FR2	frontal cortex, area 2
FR3	frontal cortex, area 3
fu	site of fusion of prosencephalon
GCC	genu of corpus callosum
GU	gustatory cortex
h	head of lateral cortical stream
HC	hippocampal commissure
hi	hippocampal neuroepithelium
HI, HP	hippocampus (differentiating)
HL	hindlimb motor area
hy	hypothalamic neuroepithelium
HY	hypothalamus (differentiating)
ib1	first inferior band
ib2	second inferior band
ibt	intermediate basal telencephalic neuroepithelium
IBT	intermediate basal telencephalon (differentiating)
ic	inferior collicular neuroepithelium
IC	internal capsule
ICP	insular cortical plate
IL	infralimbic area
inr	infundibular recess
iz, IZ	intermediate zone
izl	lower intermediate zone
izm	middle intermediate zone
izu, IZu	upper intermediate zone
l, L	lateral
lcs, LCS	lateral cortical stream
LL	lateral limbic cortex
lo, h	low, heavy (labeling pattern in late cortical neuroepithelium)
lo, l	low, light (labeling pattern in early cortical neuroepithelium)
LT	lower tier of the cortical plate (layers VI–V)
lv, LV	lateral ventricle
m, M	medial
mc	mitotic cells
MC	mesencephalon
ML	medial limbic cortex
mn	zone of migrating neurons
MOC	motor cortex
mr	mammillary recess
MS	mesencephalon
mSP	migrating subplate neurons
mz, MZ	mitotic zone of neuroepithelium
NC	neocortex
ne, NE	neuroepithelium (ventricular zone)
OB	olfactory bulb

OC	orbital cortex
OC1B	occipital cortex, area 1 binocular part
OC1M	occipital cortex, area 1 monocular part
OC2L	occipital cortex, area 2 lateral part
OC2M	occipital cortex, area 2 medial part
OCL	lateral occipital cortex
OCM	medial occipital cortex
ole	olfactory epithelium
olp	olfactory placode
olv	olfactory ventricle
op	olfactory pit
or	optic recess
ov	optic vesicle
p, P	posterior
PAR	parietal cortex
PAR1	parietal cortex, area 1 (Somatosensory)
PAR1l	parietal cortex, area 1 lateral part (Somatosensory)
PAR1m	parietal cortex, area 1 medial part (Somatosensory)
PAR2	parietal cortex, area 2 (Somatosensory)
pbt	posterior basal telencephalic neuroepithelium
PBT	posterior basal telencephalon (differentiating)
PCP	primordial cortical plate
PI	pineal gland
PICP	piriform cortical plate
pl, PL	primordial plexiform layer
PM	posteromedial
PO	preoptic area
POST	posterior
PPL	primordial plexiform layer
PPO	posterior primary olfactory cortex
PR	perirhinal
prc	prosencephalic central canal
prv	prosencephalic neuroepithelium
pt	pretectal neuroepithelium
PT	pretectum
r	reservoir of lateral cortical stream
RC	rhombencephalon
RF	rhinal fissure
Rp	Rathke's pouch
RS	retrosplenial cortex
RSA	agranular retrosplenial cortex
RSG	granular retrosplenial cortex
sb	superior bridge
sb1	first superor band
sb2	second superior band
sb3	third superior band
sc	superior collicular neuroepithelium
SSC	splenium of corpus callosum
se	septal neuroepithelium
SE	septum (differentiating)
SL	lateral somatosensory area
SM	medial somatosensory area
SP	subplate (layer VII)
SSC	somatosensory cortex
sSP	temporary positions of subplate neurons
sv, SV	subventricular zone
svl	lower subventricular zone
svu	upper subventricular zone
sz, SZ	synthetic zone of neuroepithelium
sIV	sojourn zone of layer IV neurons
sV	sojourn zone of layer V neurons
sVI	sojourn zone of layer VI neurons
TC	telencephalon
te	tegmental neuroepithelium
TE	temporal cortex (Auditory)
TE1	temporal cortex, area 1 (Auditory)
TE2	temporal cortex, area 2 (Auditory)
TE3	temporal cortex, area 3 (Auditory)
tf, TF	transitional field of neocortex
th	thalamic neuroepithelium
TH	thalamus (differentiating)
tlv	telecephalic vesicles
TT	tenia tecta
up, h	up, heavy (labeling pattern in late cortical neuroepithelium)
up, l	up, light (labeling pattern in early cortical neuroepithelium)
UT	upper tier of the cortical plate (layers IV–II)
v, V	ventral
VB	ventrobasal thalamic nucleus
VBL	ventrobasal thalamic nucleus, lateral
VBM	ventrobasal thalamic nucleus, medial
VC	visual cortex
VL	ventrolateral
VM	ventromedial
VM	ventromedial thalamic nucleus (Fig. 16–3)
VPm	ventroposteromedial thalamic nucleus (also called VM)
vz, VZ	ventricular zone (neuroepithelium)
VZa	anterior ventricular zone
VZp	posterior ventricular zone
v3	third ventricle
v3d	third ventricle, dorsal
v3v	third ventricle, ventral
WH, WM	white matter
I	layer I of neocortex
II	layer II of neocortex
III	layer III of neocortex
IV	layer IV of neocortex
V	layer V of neocortex
VI	layer VI of neocortex