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Evolution of Neocortex

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1. Introduction

In this chapter I shall attempt to derive the outlines of a theory of neocortical evolution from a series of observations based mainly on the anatomy and physiology of cerebral cortex in living animals. Such an exercise in evolutionary inference is by its nature a speculative enterprise. Hopefully, it will serve to guide future comparative, developmental and biophysical studies that might shed some additional light on this intriguing but inaccessible topic. To illustrate organizational features of cortex, I have drawn examples mainly from visual cortex.

2. General Features of Cortical Organization

2.1. Horizontal Expansion

Compared across all mammals, the surface area of the neocortical sheet varies by nearly five orders of magnitude* while the thickness of neocortex varies by less than one order of magnitude.† Therefore, evolutionary changes in

**Sorex minutus* has a cortical surface area of approximately 30 mm² (Brauer and Schober, 1970). Elias and Schwartz (1969) provide data for brain volume and cortical surface area in six cetacean species. On the bases of these data it is possible to estimate the cortical surface area of the largest mammal, the blue whale (*Balaenoptera musculus*) for which there is only a direct measurement of brain weight (6800 g) available (Crile and Quiring, 1940). Extrapolating from the data for the smaller whales, the blue whale would be expected to have a cortical surface area of about 1,350,000 mm².

†The vertical thickness of neocortex varies from a minimum of about 0.6 mm in the long-fingered bat (*Miniopterus schreibers'i*) as measured from a published photomicrograph with brain shrinkage due to celloidin embedding taken into account (Igarashi and Kamiya, 1972) to a maximum of about 5 mm.

neocortex have occurred mainly parallel to the cortical surface (horizontally) and have been sharply constrained in the vertical dimension. The neocortical sheet stands in marked contrast to other telencephalic structures, which have a radial or nuclear organization.

2.2. Constraints on Vertical Expansion

The common feature of vertical cortical architecture is the apical dendrite of the pyramidal neuron, which receives stratified inputs from different sources. Possible active processes involving dendritic spines may enable the apical dendrite to perform a number of basic logic operations that form a crucial part of cortical circuitry (Shepherd and Brayton, 1987). The apical dendrite may be subject to biophysical constraints that limit its length, which in turn may limit the maximum vertical thickness of neocortex.

2.3. Architectural Uniformity

The cellular architecture of neocortex is remarkably uniform throughout its horizontal extent* (Creutzfeldt, 1978). This basic neocortical uniformity suggests that all of neocortex arose from a single precursor structure, most probably in the dorsolateral telencephalon of an ancestral reptile.†

2.4. Developmental Uniformity

The entire neocortical sheet appears to develop as a unit in each hemisphere in the embryo. Synaptogenesis proceeds along the same time course throughout the cortex (Rakic *et al.*, 1986). The cortex does not appear to develop on an area-by-area basis. The one apparent exception is that the myelination of primary sensory areas occurs much earlier than in higher areas (Flechsigs, 1904).

*It sometimes has been suggested that the number of neurons under a particular sized patch of cortical surface (striate cortex excepted) is constant for all mammals (Bok and Taalman Kip, 1939; Rockel *et al.*, 1980). However, Haug's (1987) measurements in 29 species indicate that the actual density of cortical neurons under a square millimeter of cortical surface varies by about a factor of 10 with the lowest being in the elephant and the highest in the woolly monkey.

†The line of ancient reptiles that were ancestral to mammals separated from basal groups of reptiles very soon after their appearance in the fossil record approximately 300 million years ago (Carroll, 1988). The dorsolateral telencephalon in these early reptiles may have resembled the comparable structure in living amphibians, which contains pyramidal cells located near the ventricle with their apical dendrites radiating out toward the external surface of the brain (Kemali and Braitenberg, 1969). This basic pattern is retained in mammalian neocortex with the proliferation of additional cellular laminae. The dorsal ventricular ridge found in living reptiles and derivative structures in birds may also have emerged from portions of the dorsolateral telencephalon in the ancestral reptiles and represent a parallel development to portions of neocortex in these animals. These structures lack pyramidal neurons with their characteristic apical dendrites and instead have their own distinctive neural architecture (Ulinski, 1983, 1986). Thus, the dorsal ventricular ridge may constitute a more derived and specialized condition than neocortex.

2.5. Functional Diversity

In contrast to the horizontal uniformity of the neocortex in architecture and development, some of the functions of different cortical areas are remarkably diverse. Much of the neocortical surface is devoted to topographically organized representations of the sensory domains of vision, touch, and hearing and to the muscles, although other portions appear to be nontopographic. The functional differences probably are largely the result of differences in connections with other brain structures.

2.6. Expansion of White Matter

One consequence of the horizontal extension of cortex in evolution is that a large portion of the telencephalon must be devoted to fiber pathways in the white matter that connect different parts of the neocortical sheet.* This is strikingly evident when one compares the brain of a bird such as an owl with a mammal with a similarly sized brain (see Fig. 1). The Wulst, the structure in the owl with analogous connections and neural response properties to visual cortex, is a massive cellular aggregation that *lacks* pyramidal cells with apical dendrites characteristic of neocortex (Pettigrew, 1979). The avian Wulst contains a single map of the visual field unlike the multiple areas present in mammalian visual cortex (Pettigrew, 1979).

3. Comparisons with Reptiles

In searching for the origin of neocortex it is useful to compare cortical organization in reptiles and mammals, although no living reptile is truly representative of the reptilian ancestors of mammals.

3.1. Laminar Connections

Reptilian cortex receives its input in layer 1, where incoming fibers terminate at different levels on apical dendrites. For example, in reptilian visual cortex, the lateral geniculate nucleus input terminates on the distal third of apical dendrites while intercortical connections terminate on the proximal two-thirds

*When the volumes of different components of the brains of insectivores and primates are plotted relative to body size, the white matter associated with neocortex has the steepest slope of all the components (Frahm *et al.*, 1982). For this group of mammals, neocortical volume expands with an exponent of 0.67 relative to body size while the neocortical white matter has an exponent of 0.86, which indicates that proportionally more white matter is required to serve an increasingly large cortex. For example, when the neocortex and associated white matter are summed together, the white matter constitutes 6.7% of the total in *Sorex minutus* and 41.9% in *Homo sapiens*. About one-third of the entire human brain is devoted to white matter associated with neocortex.

of the apical dendrites (Ulinski, 1988). Similar connections are present in layer 1 in mammalian primary visual neocortex, but the main ascending input terminates in layer 4 (Tigges *et al.*, 1977; Diamond *et al.*, 1985). Reptilian visual cortex (area D2) contains two cellular layers both of which contain cells that project back to the lateral geniculate nucleus (Heller and Ulinski, 1987). Apparently intermixed with these cells are neurons that project to other cortical regions and to other subcortical structures (Desan, 1984). Mammalian neocortex contains many cellular layers with specialized inputs and outputs for each layer. Neurons in layers 2 and 3 of primary visual neocortex project to higher cortical areas while neurons in layer 6 project back to the lateral geniculate nucleus (Lund *et al.*, 1975). This laminar pattern of ascending and descending connections is characteristic of many cortical areas (Rockland and Pandya, 1979; Maunsell and Van Essen, 1983; Van Essen, 1985; Pandya *et al.*, 1988). Neurons with ascending outputs and feedback neurons are present in both reptiles and mammals, but in mammals they are organized in distinct laminae.

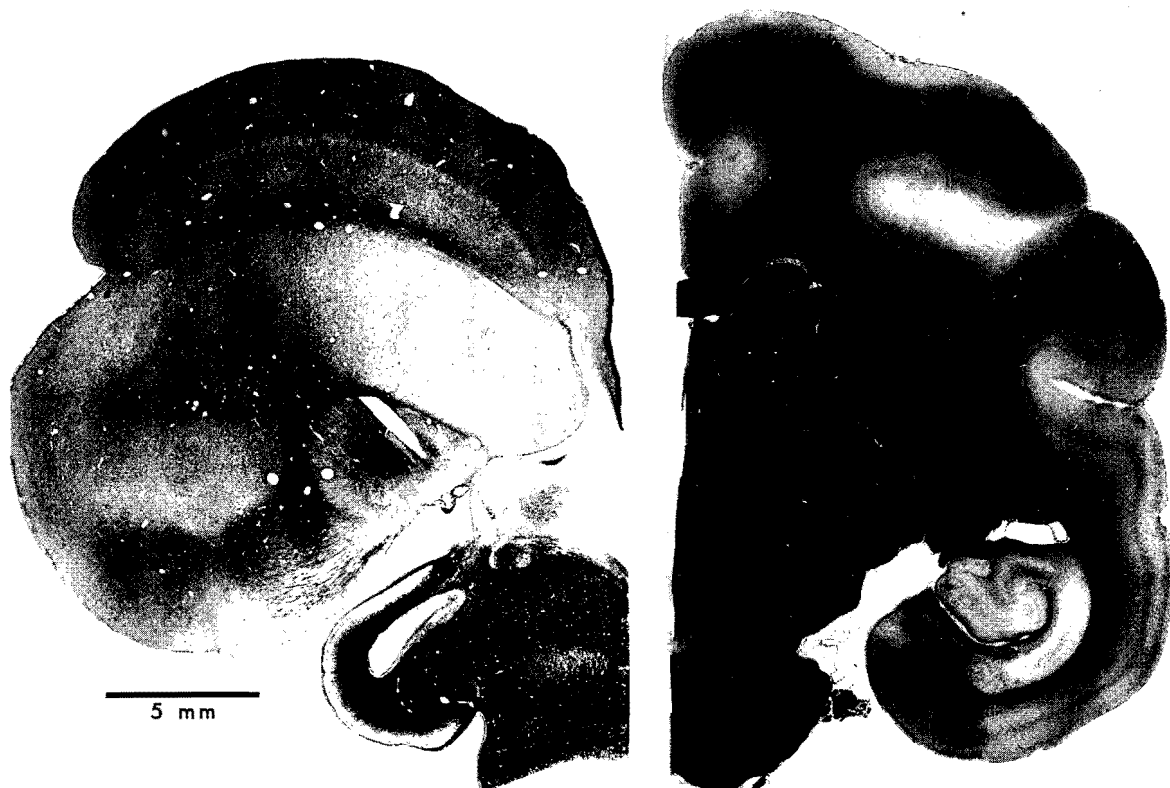


Figure 1. Fiber-stained coronal sections through the fore-brain of an owl (left) and an owl monkey (right). Note the much more extensive portion of the brain devoted to fiber pathways in the white matter in the monkey as compared to

the owl. The owl section was stained with the Gallyas silver technique; the owl monkey section was stained with the Heidenhain hematoxylin technique.

3.2. The Derivation of Neocortical Laminae from Ancestral Reptilian Cortex

The laminar organization of the mammalian cortex could have been derived from ancestral reptilian cortex by mutations that regulated neural proliferation and the migration of cells in the cortical plate during development. For example, the laminar segregation of neurons projecting back to the lateral geniculate nucleus could have been achieved by modulating cell adhesion processes during neural migration (Pinto-Lord *et al.*, 1982; Edelman, 1987; McConnell, 1988).

3.3. Organization for Identification and Storage of Environmental Constancies

In reptiles, there is a crude topographic order in the projection from the lateral geniculate nucleus to visual cortex (Ulinski, 1988), while in mammals there is a high degree of topographic order in the geniculocortical projection (Polyak, 1932). Similarly, the receptive field organization of visual cortex in turtles is crudely topographic with very large receptive fields (Mazurskaya, 1971, 1972), while the receptive field organization of primary visual cortex in mammals is highly topographic (Kaas *et al.*, 1970; Allman and Kaas, 1971b; Sousa *et al.*, 1978; Van Essen, 1979). The original cortical organization probably was either crudely topographic or nontopographic with global receptive fields. Cortex was probably devoted to the identification and storage of behaviorally relevant environmental constancies. For example, in the olfactory domain, individual conspecifics might be identified on the basis of different volatile organic compounds emitted by each animal. Since these volatile compounds tend to occur in mixtures that are characteristic of that individual and since they are received over a broad range of concentrations and in a complex chemical environment, the crucial task of the olfactory system is to identify the *pattern* characteristic on an individual independent of concentration and against the confusing background of other odors. Thus, the basic functions of olfactory cortex are to identify constancies within the environment and to store these constancies for future behavioral contingencies (Haberly, 1985).

4. Neocortex Retains Ancient Features of Global Organization

The ancient nontopographic organization has been retained in neocortex in spite of the high degree of topographic order present in many neocortical areas. Even in primary visual cortex, the true receptive field for many neurons is very much larger than the receptive field mapped in conventional studies (Allman *et al.*; in press). The extensive nonclassical surround is revealed by presenting stimuli simultaneously within and outside the classical receptive field and determining the influence of the outside stimuli. The stimuli presented beyond the classical receptive field often have profound and highly selective effects on

the responses within the classical receptive field (Allman *et al.*, 1985, in press). The large nonclassical receptive fields probably subserve integrative functions such as perceptual constancies and the separation of figure from background. For example, neurons in the fourth visual area (V4) appear to extract color constancy using their nonclassical receptive fields (Zeki, 1983; Desimone *et al.*, 1985) in a manner similar to Land's (1986) retinex theory.* Thus, just as olfactory cortex would extract constancies concerning the edibility of a particular fruit on the basis of a pattern of volatile compounds emitted at a certain stage of ripeness over a broad range of chemical concentrations, similarly V4 would extract parallel constancies concerning edibility of a particular fruit on the basis for the spectral pattern of reflectances at a particular stage of ripeness over a broad range of lighting conditions. In each case the cortex would determine that the sweet-smelling red fruit is good to eat in the wet early morning as well as in the dry afternoon. The development of the capacity of cerebral cortex to extract behaviorally significant constancies over a very broad range of physical conditions fits into the general context of vertebrate evolution. Kluver (1942) proposed that just as mechanisms have evolved to maintain a constant internal physiological environment in higher organisms, which create for them an independence from external environmental conditions, similarly the perceptual constancy functions of visual cortex "guarantee varying degrees of freedom from the visual milieu." These metabolic and perceptual constancy mechanisms are of enormous adaptive value but are energetically and computationally very expensive and highly interdependent (see Section 8).

5. Evolution of New Areas

It has sometimes been suggested that the ancient neocortex was nontopographic and that the topographically organized areas developed more recently and the primary sensory areas the most recently (Sanides, 1970; Morgane *et al.*, 1986; Pandya *et al.*, 1988). According to the evidence presented previously, it is likely that in the reptilian precursors of mammals the cortex was nontopographic or only crudely topographic and that aspects of this ancient organization are preserved in neocortex. However, the presence of highly organized sensory maps in neocortex of monotremes (Bohringer and Rowe, 1977), marsupials (Sousa *et al.*, 1978), and primitive eutherian mammals (Kaas *et al.*, 1970) suggests that neocortical maps are old features going back to the common origin of mammals early in the Mesozoic era more than 200 million years ago. Similarly, in the hedgehog, a mammal that has retained many primitive features of early eutherian mammals, most of the neocortex is devoted to a small number of topographically organized areas (Kaas *et al.*, 1970). These data suggest that the neocortex present in Mesozoic mammals contained a small number of areas, some of which contained well-defined topographic maps while others may have lacked topography. In these early mammals, the topographic organization was superimposed on an ancient pattern of global cortical organization.

The comparative data suggest that many new areas have developed in the

*The achievement of color constancy does not require a cerebral cortex; it is present in goldfish (Ingle, 1985).

course of neocortical evolution in different lines of descent. These areas have been more easily delineated within highly organized sensory representations, but they may also exist in the less topographically organized neocortex. About 50 million years ago, in the early stages of primate evolution, there was a great expansion in the size of the occipital and temporal lobes indicative of an expansion of visual cortex (Radinsky, 1967; Allman, 1977). The skulls of these early primates possessed a number of other features characteristic of modern primates such as the presence of orbits indicative of large, frontally directed eyes (Allman, 1977). The visual cortical expansion in the early primates may have been due both to an enlargement of existing areas and to the development of new areas (Allman and McGuinness, 1988). The enlargement of existing areas was probably linked to the expansion of the representation of the central retina associated with frontally directed eyes and higher acuity in the central visual field. In addition some of the array of higher cortical visual areas present in both prosimian and simian primates may have emerged at this early stage in primate evolution (Allman and McGuinness, 1988; Sereno and Allman, 1990). The great similarity in the number and organization of the cortical visual areas in old and new world monkeys suggests that the basic pattern for simian visual cortex was established before the divergence of these lines about 40 million years ago (Sereno and Allman, 1990).

While primary visual area can be easily homologized in different orders of mammals and thus appears to be relatively ancient (Kaas *et al.*, 1970), it is much more difficult to establish interorder homologies for higher cortical areas (Baker *et al.*, 1981; Tusa *et al.*, 1981). The greater variability in the patterns of organization in the higher cortical visual areas in different mammalian orders suggests that these areas are more recent phylogenetic developments that arose independently in different mammalian orders (Sereno and Allman, 1990).

6. Mechanisms for the Emergence of New Areas

A common mode of evolution appears to have been the duplication of existing structures and the subsequent divergence of the duplicates (Gregory, 1935; Allman and Kaas, 1971a; Allman, 1987). Presumably, an initial mutation produced the duplication and mutations in subsequent generations differentially influenced the development of the duplicates so that they diverged in structure and function. Duplication also appears to be the principal means whereby new genes have emerged in evolution (Lewis, 1951; Ohno, 1970; Li, 1983).

A possible model for the differentiation of existing cortical areas and the acquisition of new areas is provided by the mechanisms for segmental differentiation in *Drosophila* embryogenesis. Early in the development of *Drosophila*, the actions of genes establish a polar gradient and a set of distinct stripes corresponding to half segments, which in turn are differentiated from a common replicated pattern by the action of the homeotic genes (see Fig. 2). Scott and Carroll (1987) have proposed an evolutionary scenario for insect development. "The development of the largely identical segments of an annelid-like ancestor may have depended on the function of a gene similar to *ftz* that was expressed in stripes and directed the formation of repeating pattern elements. The homeotic genes could have arisen by duplication and divergence of the *ftz*-like gene—an

extension of the proposal by E. Lewis (1951) that homeotic genes arose by duplication and divergence" (Scott and Carroll, 1987, p. 695). Sets of homeotic genes controlling the development of the head and body are located in the *Antennapedia* and *Bithorax* chromosomal complexes, respectively. The order of the homeotic genes in the *Bithorax* complex corresponds approximately to the anatomical arrangement of the segments controlled by these genes (Lewis, 1978). The regulatory actions of the homeotic genes bring about the differentiation of the initially identical segments (Lewis, 1978).

Each of the homeotic genes contains a 180-bp sequence of DNA, called the "homeobox," which shows a high degree of correspondence. Multiple homeobox-containing genes are also found in vertebrates, including frogs, mice, and humans (McGinnis *et al.*, 1984; Gehring, 1985; McGinnis, 1985). In mice, where they have

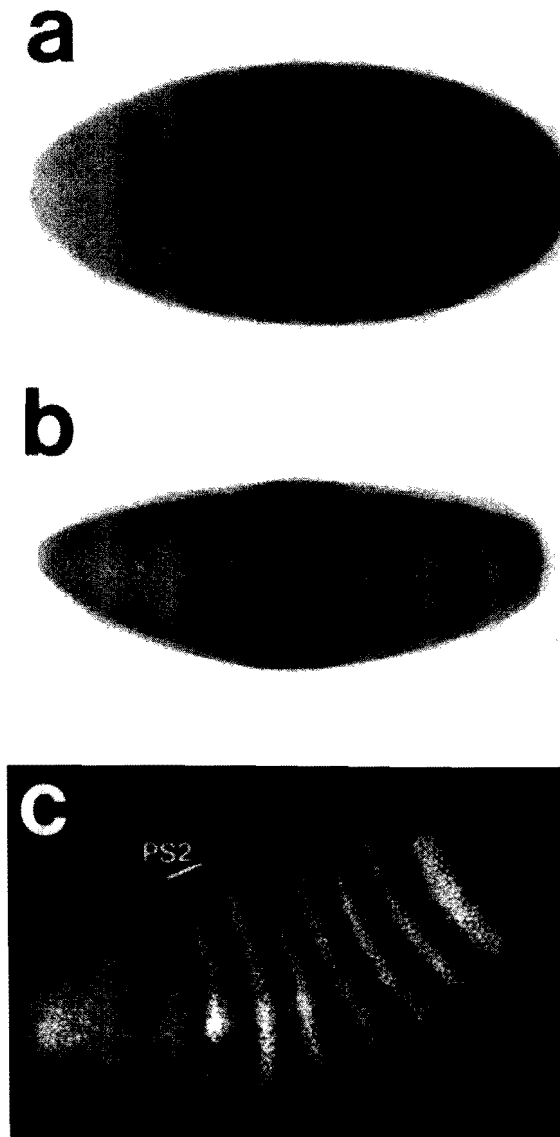


Figure 2. Expression patterns of gene products in *Drosophila* development from Scott and Carroll (1987). Whole mount embryos were permeabilized and stained with antibodies against gene products. Anterior is to the left and ventral is down in each panel. The embryos are about 0.5 mm long. The embryos are at the blastoderm stage (2.5–3.5 hr of development) when the approximately 6000 cells form a monolayer covering the yoke. (a) Expression of the *caudal* gene product (MacDonald and Struhl, 1986), a nuclear protein that is distributed in a gradient in the early blastoderm embryo. Staining is with peroxidase, so the protein signal appears black. (b) Expression of the *Kruppel* gap gene nuclear protein (Gaul *et al.*, 1987) detected with peroxidase stain. The broad band corresponds approximately to parasegments 4–6. (c) Expression of the *fushi tarazu* (*ftz*) pair-rule gene product detected by immunofluorescence so the nuclear protein signal appears white. The anterior edges of the stripes mark the anterior edges of the parasegments; the extent of parasegment 2 is indicated.

been most extensively studied, there are two families of homeobox-containing genes, each containing six members, located on chromosomes 6 and 11 (Martin *et al.*, 1987). There are also isolated homeobox-containing genes on other chromosomes. The homeobox encodes for a 60-amino-acid-long "homeo domain" that is rich in the basic amino acids lysine and arginine, which would enable the homeo domain to bind to DNA (Laughton and Scott, 1984). The homeo domain apparently has been strongly conserved in evolution, possibly to perform the function of binding the regulatory gene product to regulation sites in the DNA. The *in situ* hybridization of the cloned DNA of the homeotic genes is located primarily in the developing nervous system in *Drosophila*, where the genes may regulate the differentiation of neural circuitry for each segment (Scott, 1984). Homeobox-containing genes also are expressed in mammals in specific regions of the CNS (Awgulewitsch *et al.*, 1986; Davis *et al.*, 1988). Recently, they have been found in sets of segmentlike structures (rhombomeres) that innervate particular brachial arches in the developing hindbrain of the mouse (Lewis, 1989; Wilkinson *et al.*, 1989). The protein encoded by the homeobox-containing gene, *Hox 1.3*, is present in neocortical pyramidal neurons (Odenwald *et al.*, 1987).

An analogous, or even possibly homologous, hierarchical set of genes could regulate the development of cortical areas in mammals by establishing rostral-caudal and dorsal-ventral polarity in the cortex, by segmenting the cortical sheet into areas, and by differentiating the areas according to their connections. Gene duplications and subsequent divergence within the set of controlling genes could produce new areas, new connectivities, and new functions.

Turing (1952) suggested that the spatial patterns in embryogenesis could be established if two substances (morphogens) with different diffusion rates reacted with each other. The morphogens might be functionally related to the proteins encoded by the homeobox-containing genes, and interactions like those postulated by Turing may be responsible for pattern formation in *Drosophila* (Meinhardt, 1982; Akam, 1987). Major changes in the pattern, such as changes in the number of segments, could be produced by mutations altering the diffusion rates of morphogens or their interactions. Similar mechanisms might be responsible for the specification of the number of cortical areas in mammalian development.* Thus, mutations altering the physical or chemical properties of morphogens might have produced the major expansion in the number of cortical visual areas that occurred early in primate evolution.

7. The Role of Experience in Cortical Organization

The experiments of Merzenich *et al.*, (1988) in somatosensory cortex indicate that *use* influences topographic mapping in cortex, which presumably reflects the capacity to perform neural computations within different parts of the map. Thus, cortical organization is linked to behavior and has some capacity to change throughout the life span of a mammal. The neocortex may participate in epigenetic evolution. Changes in behavior that resulted in changes in cortical

*In *Drosophila* these patterns are established during a period in which the embryo is a syncytium (Akam, 1987; Ingham, 1988), which is not the case in the developing cortex (Rakic, 1988). However, it is possible that morphogens communicate among cells at this stage in cortical development.

organization could be transmitted by observational learning from one generation to the next. For example, a foraging technique might require a particular type of difficult discrimination which would result in use-dependent changes in cortical organization. This behavior and its attendant cortical manifestations could be propagated through the generations through observational learning.

8. Mammalian Energetics and Neocortex as Linked Homeostatic Mechanisms

A mammal requires 5 to 10 times more energy expenditure than does an equivalent-sized reptile (Bennett and Ruben, 1979). Most of this increased energy expenditure is devoted to homeostatic mechanisms of thermoregulation (Muller, 1985). Thus, mammals must eat a great deal more than reptiles and do so on a regular basis to avoid starvation.* My hypothesis is that neocortex evolved in tandem with the higher energy metabolism characteristic of mammals so as to assure a continuous localization of food resources. Neocortex is a topographically organized network that stores representations of the animal's interactions with its environment. The neocortical network requires an initial period of training, which I believe is manifested by infant play behavior. During this period of network training the developing infant's energy requirements are provided by its mother's milk. Thus, in this formulation, mammalian lactation and play behavior are necessary adaptations to support the linked homeostatic mechanisms of mammalian energetics and neocortex.†

9. The Expansion of Neocortex and Longevity

The relative amount of neocortex to body size tends to be greatest in mammals with the longest life span.‡ This probably relates to the high energy re-

*There are mammals such as the fat-tailed dwarf lemur (*Cheirogaleus medius*) that can go for a very long time without eating during which period their body temperature drops substantially. However it is likely that these mammals have very specialized biochemical regulatory mechanisms that enable their enzyme systems to operate over a broad range of body temperatures.

†I believe that somewhat analogous developments occurred in the line leading to birds in the Mesozoic. These developments probably included the elaboration of the Wulst and dorsal ventricular ridge, thermoregulation at higher body temperature, and parenting behavior.

‡The tendency for neocortical enlargement to be correlated with longevity is evident when the neocortical progression indices of Stephan and Andy (1970) are compared with maximum life spans for insectivores and primates. The neocortical progression index is intended to show how much neocortex a mammal has relative to a comparably sized "basal insectivore" thought to represent the primitive mammalian condition. Basal insectivores have an average neocortical progression index of 1 and a relatively short life span. For example, the basal insectivores *Hemicentetes* and *Tenrec* have maximum life spans of about 2 years (Eisenberg, 1981). *Cebus* and *Pan* have a neocortical index of 59. The longevity record for *Cebus* is 54 years and there exist several very elderly chimpanzees still alive in their late 50s (M. Groves, personal communication). For humans the neocortical index is 156 and the maximum documented life span is about 115 years (C. Finch, personal communication). It is difficult to establish the maximum life span for long-lived nonhuman primates since it has only been in the past few decades that they have been kept in captivity under relatively optimal conditions of nutrition and housing.

quirements of mammals and to different strategies for coping with occasional food shortages. Short-lived mammals tend to have a high reproductive potential and relatively less neocortex. In these mammals, food shortages will produce catastrophic population declines that quickly recover with improved conditions which has been termed r-selection (MacArthur and Wilson, 1967; Wilson, 1975). Long-lived mammals have smaller litters with much greater parental investment in individual offspring (K-selection). The expanded neocortex enables metabolically active, nonhibernating, mammals to store the necessary experiences, foraging strategies, and cognitive processes to cope with periods of severe food shortage that will inevitably happen during a long life span. Viewed in this way the expansion of neocortex can be regarded as the ultimate K-selection strategy enabling organisms to survive the vicissitudes of the environment encountered during a long life span.

10. Summary

Neocortex probably arose as a specialization of the dorsolateral telencephalon in mammal-like reptiles early in the Mesozoic. My hypothesis is that the neocortex evolved in tandem with the higher energy metabolism characteristic of mammals as linked homeostatic mechanisms. These mechanisms, while computationally and energetically expensive, provided a powerful selective advantage for the early mammals. The comparative data from living primitive mammals suggest that the early neocortex contained a relatively small number of areas, most of which were topographically organized representations of the sensory modalities of vision, touch, and hearing. The topographic organization was superimposed on a preexisting global organization. Thus, neocortex possesses the capacity for very specific local representations combined with more global representations that subservise perceptual and temporal constancies. The phylogenetic expansion of the cortical sheet has been mainly horizontal with the vertical thickness limited by the information processing capabilities of the apical dendrites of pyramidal neurons. The organization of cortex is governed by a set of genes that control cell proliferation and migration. By analogy with the homeotic genes that control the differentiation of parasegments in *Drosophila* embryogenesis, the genes controlling the parcellation and expansion of cortical areas may be a family of replicated genes derived from a common primitive gene. It has been conventional to assert that different cortical areas within a modality such as vision have different functions; however, these areas share common circuitry and may to a significant degree share the capacity to perform common functions. Cortical organization is the product of the interaction and genetic and epigenetic factors. Behavioral specializations in use influence cortical organization and these behaviors and perhaps some aspects of cortical organization are transmitted from generation to generation through observational learning. Neocortex is most expanded relative to body size in species with the greatest life span. The expanded neocortex enables metabolically active mammals to store the necessary experiences, foraging strategies, and cognitive processes to cope with periods of food shortage that will inevitably occur during a long life span. Viewed in this manner, the expansion of neocortex can be regarded as the ultimate K-selection strategy.

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