Evolution and Development of the Cerebral Cortex
SPECIAL ISSUE
The organization of neocortex in mammals: are species differences really so different?

Leah Krubitzer

By examining a variety of mammals, it is possible to determine common features of cortical organization, and from these infer homologies across species. Such analysis also enables differences in the organization of the neocortex to be identified. Species differ in the amount of cortex that is devoted to a particular sensory system, in the size and configuration of a cortical field, in the number of cortical fields, and in the pattern of connections of homologous fields. It is suggested that the plan of organization that is retained is the result of homologous developmental events, and that modifications to this plan are generated by a limited set of mechanisms. These types of changes to the common network might account for the sensory and behavioural diversity that is observed in extant mammals.

*Trends Neurosci.* (1993) 18, 408–417

THROUGHOUT THE 20TH CENTURY, remarkable advances in techniques for studying the brain have revealed that the neocortex comprises a number of functional parts that interconnect uniquely to form processing networks. While understanding of the functional subdivisions that compose these networks has increased dramatically, studies have focused on a few species, such as some primates, cats and rats. To some extent, comparative neurobiology has remained in the background of this enormous research front. Yet comparative analyses, from molecular to behavioural levels of organization, create the foundation upon which all studies of living organisms are based. Examination of a variety of species enables us to deduce which features of these neocortical networks were established early in mammalian evolution, and are homologous in all species (Box 1), and to recognize modifications or differences in the neocortex that evolved in different lineages. Such analyses also enable us to appreciate general organizing principles of the neocortex, and potential mechanisms of modification, as well as constraints that limit neocortical evolution and, in turn, function. Thus, comparative neurobiology is an integral part of attempts to understand the functional organization of neocortex and, ultimately, the evolution of more complex functions that are generated by the neocortex, such as perception, cognition and consciousness.

Retained plan of cortical organization

Before differences across species can be understood, it is necessary to determine similarities in the organization of the neocortex in the various lineages. Primary somatosensory, visual and auditory areas (SI, VI and AI, respectively) have been identified in a number of distantly related species (Fig. 1) that represent the three major branches of mammalian evolution, that is, prosimians, metatherians and eutherians (1,2) (Box 1). Similarities in topographic organization, relative location, architectonic appearance in both tangential and standard planes of section, patterns of connections with the thalamus and cortex, and stimulus preferences for neurons in these areas, suggest that they are homologous; that is, inherited from a common ancestor (3) (Box 1). Until recently, it was thought that only these primary areas were common to all mammals, and that additional cortical fields were added independently in different lineages. However, recent work in prototherian mammals, such as the platypus (*Ornithorhynchus anatinus*) and the echidna (*Tachyglossus aculeatus*), as well as studies of several species of metatherian mammals, has led to a re-evaluation of this hypothesis. Additional areas that have been described in representatives of both lineages include the second somatosensory area (SII) or the parietal ventral area (PV), or both, a rostral deep field (R, DS or 3a), a manipulation or motor field (M or MI) (3,4), a second auditory field (at least one field in addition to AI has been identified in most mammals), and a second visual field, VIIIC/D (5) (L. Krubitzer, unpublished observations). Because these fields have similar patterns of topographic organization, interconnections and consistent architectonic features in all or most mammals investigated, it is most likely that they are homologous, rather than having arisen independently in each lineage. Thus, the plan of organization that is retained from the common ancestor (Fig. 1) appears to have been more complex than was thought previously. However, the individual cortical fields that compose this basic plan or network have clearly undergone their own independent evolution in the various lineages.

These findings of a retained plan are significant, since they indicate that some features of neocortical organization are conserved in all mammals. An appropriate analogy would be the evolution of the body plan in vertebrates. Although it has been possible to modify an existing portion of this plan by reducing or enlarging appendages or changing a forelimb into a wing, or a hindlimb into a flipper, a completely new body plan has not developed. Thus, the body plan, selected very early in vertebrate evolution (6), greatly restricts the avenues along which subsequent change can occur.

References


While the retained plan of cortical organization may be modified by changes in size, shape or organization of cortical fields, or the added fields (Figs 1 and 2), it does not appear to eliminate some elements of this plan completely to develop an entirely new plan. For example, the cortex and the retinocortical pathways in mammals are primates such as the platypus (10) and the insectivorous, star-nosed mole (Condylura cristata), whose use of vision is minimal, and a terrestrial blind mole rat (Spalax ehrenbergi), the vision is almost non-existent (11). It is possible that this genetic pleiotropy, the multiple effects of a gene on a number of functions or traits, prevents complete elimination of a particular sensory or developmental events that generate this work, because these events are tied to...
Homology

The term homology refers to characteristics that are inherited from a common ancestor (red lines in Fig. 1). When examining the neocortex, homology can only be deduced, rather than demonstrated directly. Homologies can be ascertained with varying degrees of confidence, related to the number of species examined, and the number of criteria that is used to define the structure in question. For example, the distinct laminar appearance and position of the hippocampus allows us to identify it readily in all mammals investigated. The hippocampus is proposed to be homologous, rather than having arisen independently in each lineage. Likewise, based on examination of cortical architecture, patterns of connections, position, neural-response properties, and internal organization of a particular cortical field in a variety of mammals, we suggest that the field in question is homologous. The term homology does not imply similar function (analogy). Indeed, it is highly unlikely that field VI in the prefrontal and in the macaque monkey has similar functions, since the laminae that gave rise to extent prefrontal and motor cortices and primates have evolved independently for over 150 million years.

Homology

Structures that look the same but have arisen independently in different lineages are considered homoplasy. For example, ocular dominance columns (ODCs) in cats and monkeys are homoplasy features of field VI, and are likely to have arisen through convergent evolution, since these are very distinctly related species, and other intervening lineages to which the common ancestor gave rise do not possess this feature. Thus ODCs in cats and primates are homoplasy, are not homologous, and might be analogous.

Analogy

Analogy refers simply to the same function. A classic example is the wing of the bat and the wing of a fly.

References


While the retained plan of cortical organization has been modified by changes in size, shape, and internal organization of cortical fields, or the addition of new fields (Figs 1 and 2), it does not appear possible to eliminate some elements of this plan completely, nor to develop an entirely new plan. For example, visual cortex and the retinogeniculate pathway have been retained in mammals such as the platypus and the insectivorous, star-nosed mole (Condylura cristata: Fig. 2), whose use of vision is minimal, and also in the subterranean blind mole rat (Spalax ehrenbergi), whose vision is almost non-existent. It is possible that genetic pleiotropy, the multiple effects of a single gene on a number of functions or traits, prevents the complete elimination of a particular sensory system or the developmental events that generate that sensory network, because these events are tied genetically to other crucial developmental processes. Cooper and colleagues hypothesized that a 'developmental interdependence within the visual system could explain why, despite large interspecific variation, a common plan of visual organization is universally preserved in vertebrates'. Such interdependence might reflect a set of events that is regulated by a single gene (pleiotropy) or a limited population of genes. Thus, it is not possible to remove one event or function without altering the other events that are encoded by that gene. This type of construction necessarily constrains the evolution of the nervous system. As Miklos and colleagues said: 'Once there is multiple usage for any thing – be it gene, protein, circuit, or organ, compromise is inevitable and specific optimality is unachievable'. Therefore, the retino-geniculo-cortical pathway has not been eliminated, even in animals that do not
Fig. 1. Common features of cortical organization in mammals. The organization of cortical fields from six different mammals, as drawn on a flattened cortex. Although the relative size, shape, and internal organization of fields has been modified independently in different lineages, homologies can still be identified based on a number of criteria (see Box 1). Similar colors depict homologous fields, although evidence for some of the cortical subdivisions is still preliminary. Subdivisions of echidna cortex are drawn from Ref. 7, while those of the quoll are from Ref. 2 (auditory); and Ref. 3 and L. Knobitzer, unpublished observations (somatosensory visual). Subdivisions of the squirrel neocortex are from Ref. 4 (somatosensory and motor), Ref. 5 (auditory), and Ref. 6 (visual). Subdivisions of the flying fox are from Ref. 7 (visual), Refs. 8 and 9 (somatosensory), Ref. 10 (areas 21 and 41), and Ref. 11 (auditory). Subdivisions of the marmoset are drawn from Ref. 12 (visual), Refs. 13 and 14 (somatosensory), and Ref. 15, in the closely related tamir, Saginus (auditory). VI is estimated from echinodermic boundaries and patterns of connections. Subdivisions of the macaque monkey are taken from Ref. 16 (visuocortical), Ref. 16 (anterior parietal cortex), Ref. 17 (lateral somatosensory and visual), and Ref. 18 (auditory cortex). Medial wall at the top and nasolateral is to the right. For abbreviations, see Box 2.

Fig. 2. The organization of neocortices in higher primates. The visual cortex is depicted in red, the auditory cortex in blue, the somatosensory cortex in purple, and the motor cortex in yellow. For abbreviations, see Box 3.

and most species have modified existing sensory apparatuses and systems for enhancing stimulus detection, rather than creating new mechanisms of detection. Although a few species have added new sensory systems (for example, electroreception in the platypus), and magnetoreception in the Pacific dolphin), these have interfaced with existing neural systems, and do not claim exclusive corticotoric territory.

Species differences

While there appears to be a retained plan of neocortical organization, this plan has been altered in different lineages. Rodents represent a highly diverse group in terms of morphological and behavioural specialization, and they occupy a variety of niches. Despite common features, their neocortical organization also reflects these specializations. The highly visual, arboreal squirrel (Sciurus carolinensis) has a cone-like retina, a relatively large and well-laminated lateral geniculate nucleus, and a proportionately large visual cortex that includes areas VI, V3, and at least five additional extrastriate areas (Figs 1 and 3A). Much less cortex is devoted to processing somatosensory and auditory information. Murid rodents (families: Cricetinae and Muridae), such as the terrestrial hamster, rat and mouse, rely little on vision but their use of tactile information is extensive. The visual cortex in these species is relatively small and less complex in organization than that of other carnivores, whereas the somatosensory and auditory cortices have expanded greatly (Fig. 3B). The vibrissal representation alone approximates one-third of the total surface area of the neocortex. The subterranean pocket mouse (Thomomys) also has an expanded somatosensory cortex. However, unlike the murid gopher, a large representation of the plantar surface is specialized for the detection of tactile discriminations for predator evasion. The representation of the face and cheek pads is specialized for the detection of food, and large Australian marsupials, such as rodents, fill niches, and examination of their neocortex reveals that modifications to the retained plan of organization, although evolved independently, take the same form as those of rodents and the arboreal brush-tailed possum (Trichosurus vulpecula), a large region of cortex is devoted to processing somatosensory and auditory information.
Fig. 1. Common features of cortical organization in mammals. The organization of cortical fields from six different mammals, as drawn on a flattened cortex. Although the relative size, shape and internal organization of fields has been modified independently in different lineages, homologies can still be identified based on a number of criteria (see Box 1). Similar colours depict homologous fields, although evidence for some of the cortical subdivisions is still preliminary. Subdivisions of the echidna cortex are drawn from Ref. 1, while those of the rod are from Ref. 2 (auditory), and Ref. 3 and L. Krubitzer, unpublished observations (somatosensory visual). Subdivisions of the squirrel neocortex are from Ref. 4 (isomotor and somatosensory), Ref. 5 (auditory), and Ref. 6 (visual). Subdivisions of the monkey area 17 are from Ref. 7 (visual), Ref. 8 and 9 (somatosensory), Ref. 10 (area 3a and 4a), and Ref. 11 (auditory). Subdivisions of the chimpanzee cortex are taken from Ref. 12 (visual), Ref. 13 (isomotor and somatosensory), and Ref. 14, in the closely related tamarin, Saginus (auditory). VS is estimated from architectonic boundaries and patterns of connections. Subdivisions in the macaque monkey are taken from Ref. 15 (isomotor and visual), Ref. 16 (anterior parietal fields), Ref. 17 (lateral somatosensory fields) and lateral portions of anterior parietal cortex), and Ref. 18 (auditory cortex). Medial is at the top and rostral is to the right. For abbreviations, see Box 2.

and most species have modified existing sensory apparatuses and systems for enhancing stimulus detection, rather than creating new mechanisms of detection. Although a few species have added new sensory systems (for example, electroreception in the platypus16, and magnetoreception in the Pacific dolphin17), these have interfaced with existing neural systems, and do not claim exclusive cortical territory18.

Species differences

While there appears to be a retained plan of neocortical organization, this plan has been altered in different lineages. Rodents represent a highly diverse group in terms of morphological and behavioral traits. Although they occupy a variety of common features, their neocortex also reflects these specializations. The archerex is a small rodent (Scirius cuneculens) with retina19, a relatively large and well-developed cerebellar cortex19, and a proportionately large visual cortex that includes areas VIb, VIIb and visual areas 17, 18 and 19

Fig. 2. The organization of neocortex in highly derived species. Subdivisions of cortex in animals with sensory specializations such as the echolocating ghost bat, the electroreceptive platypus, and the star-nosed mole. More than half of the cortex of the ghost bat is involved in processing auditory information (black + Aud), while approximately two-thirds (including SI, PV, P, M and Rf) of cortex in the platypus is involved in processing inputs from the bill (either electroreceptors or mechanoreceptors, or both, red). In the star-nosed mole, visual cortex (V, yellow) is very small, and a large area of cortex is devoted to processing inputs from the nose. Despite the dramatic modifications in terms of size, internal organization, and the addition of modules in these species, components of a common plan of organization can still be identified (delineated in the same colour). Subdivisions of the ghost bat cortex are redrawn from Ref. 20 (somatosensory) and L. Krubitzer (unpublished observations) (visual and auditory). Subdivisions of the platypus cortex are redrawn from Ref. 1, and those of the star-nosed mole cortex are redrawn from Ref. 30. Medial is at the top and rostral is to the right. Scale bars, 1 mm.
Differences in the size or configuration, or both, of a retained cortical field are observed across mammals and across sensory and motor cortices. For example, SI in raccoons is relatively larger than in other carnivores, and the raccoon has a large expansion of the representation of the hand, such that individual digits are represented on separate gyri.\(^{25}\) This enlargement is related to the extensive use of tactile information from the glabrous hand for prey capture. The relative size and shape of SI in the flying fox and squirrel (Fig. 4A and C) is significantly different from that of monkeys (Fig. 4B and D). While the architec tonic appearance and mediolateral organization of SI is similar across species, details of the internal organization can be quite different. For example, in bats the rostrocaudal organization of the forelimb is reversed from that of most other species: the distal portion of the wing and digits are represented caudally, while more proximal portions of the digits, wing and forelimb are represented more rostrally.\(^{25,26}\) This is thought to be related to the difference in normal body orientation of bats compared with other animals.

The generation of modules within cortical fields is another common modification to the plan of organization. Modules are defined here very globally as structural and physiological discontinuities within the limits of a classically defined cortical field (Fig. 3C). This heterogeneity within a field is reflected in architectonic appearance (including visualization using immunohistochemistry), neural-response properties, stimulus preference and connections. In the somatosensory system, modules are sometimes related to different ethological specializations to the periphery but are not always related directly to an obvious behavior (for example, barrels in cortex correspond to vibrissae but not necessarily to whisking behavior (Fig. 5A and D)).\(^{25,26}\) The nose of the star-nosed mole, and the bill of the platypus, has very large heterogeneous representations in the cortex (Fig. 5B and C) that are related to the distribution of inputs from specialized structures at the periphery. In the visual cortex of primates, modular organization for fields VI and VII (Fig. 5E), as well as other extrastriate areas (Fig. 5F), can be defined by patterns of connections, architectonic appearance or electrophysiological properties of neurons.\(^{25,26}\) Even in the absence of architectonic or physiological distinctions, connection patterns are patchy in their distribution within a cortical field, and reflect the heterogeneous nature of the cortex (Fig. 5G and H).

We propose that the ubiquity of modules across sensory systems and mammals suggests that they are generated by a set of similar mechanisms, and that the potential to generate modules is present in the common ancestor.

The addition of new cortical fields to the network is another means by which existing patterns of organization change. When comparing the neocortices of different species, a consistent observation is that species differ in the number of cortical fields devoted to a given sense.\(^{25,26}\) For example, the cortex of the echidna has several fields that appear to be homologous to fields that are described in macaque monkeys (for example, VI and SI, Fig. 1), however, while the echidna has only two visual areas, the macaque monkey is thought to have over 15 visual areas.\(^{25}\) The possible mechanisms that underlie addition of cortical fields are discussed below.

Finally, formation of modules, and the addition of new fields, is likely to result in a reweighting of connection patterns of the existing network (Fig. 6). For example, while field VI shows common patterns of connections in rodents and primates, including direct inputs from the lateral geniculate nucleus and outputs to field VII, other patterns of connections are different. Field VI in primates has acquired discrete modules that are related to processing colour, form and motion,\(^{25,26}\) and a number of extrastriate fields have been added. Unlike the interconnections between fields VI and primates arise from discrete modules within fields. Furthermore, while field VI in primates projects to several other extrastriate areas and connections do not appear to be homologous. Although cortical fields can be defined in different linesages, using the criteria outlined in Box 3, the types of modifications described above make it unlikely that the structures are analogous (Box 1). Indeed, despite the developmental events that produce such specialization, such modifications appear to be changing the retained network such that a wide range of diversity in sensory, behavioral and cognitive abilities is present. What are such changes accomplished? What are the mechanisms that are involved in module formation and changes in cortical-field configuration and function?

Theories of cortical evolution

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The generation of modules within cortical fields is another common modification to the retained plan of organization. Modules are defined here very globally as structural and physiological discontinuities within the limits of a classically defined cortical field (see Box 3). This heterogeneity within a field is reflected in architectonic appearance (including visualization using immunohistochemistry), neural-response properties, stimulus preferences and connections. In sensory systems, modules are sometimes present morphocortically in multiple lines (e.g., Fig. 5A and D). The nose of the beard, and the bill of the platypus, has very prominent representations in the cortex (C) that are related to the distribution of specialized structures at the periphery. Cortex of primates, modular organization and VI (Fig. 5E), as well as other extra (Fig. 5F), can be defined by patterns of architectonic appearance or electrophysiological properties of neurons. Even in the alectric or physiological distinctions, contours are patchy in their distribution across the field, and reflect the heterogeneous nature of the cortex (Fig. 5G and H).

We propose that the ubiquity of modules across sensory systems and mammals suggests that they are generated by a set of similar mechanisms, and that the potential to generate modules was present in the common ancestor. The addition of new cortical fields to the network is another means by which existing patterns of organization change. When comparing the neocortices of different species, a consistent observation is that species differ in the number of cortical fields devoted to a given sense. For example, the cortex of the echidna has several fields that appear to be homologous to fields that are described in macaque monkeys (for example, VI and SI, Fig. 1), however, while the echidna has only two visual areas, the macaque monkey is thought to have over 15 visual areas. The possible mechanisms that underlie addition of cortical fields are discussed below.

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Although cortical fields can be defined as homologous in different lineages, using the criteria that are outlined in Box 3, the types of modifications that are described above make it unlikely that they are strictly analogous. Indeed, despite the rigidity of some developmental events that produce common networks, such modifications appear to be capable of changing the retained network to such an extent that a wide range of diversity in sensory, perceptual, behavioural and cognitive abilities is possible. How are such changes accomplished? What are the mechanisms that are involved in module formation, and changes in cortical-field configuration and number?

Theories of cortical evolution

There is a number of theories to explain the addition of cortical fields in evolution. Lende proposed that early mammals had an overlapping sensory-motor amalgam that pulled apart gradually to form separate representations, while Ebenschen suggested that the nervous system increases in complexity by a process of parcellation. The latter theory of brain evolution promotes the idea that early brains were diffuse and basically undifferentiated and, through selective loss of connections, parcellated into multiple, differentiated aggregates or parts. Allman and Kaas suggested that existing cortical fields duplicate as a result of some genetic mutation, and these new fields acquire new connections and functions eventually. In a further elaboration of this theory, Kaas suggested that cortical fields might also evolve from existing fields through a process of gradual differentiation of a single field into two fields. According to Deacon, developmental changes in contextual events (for example, axon-target affinities, and timing) bias competitive interactions, and result in loss, addition, or replacement of connections (for a detailed review of theories of cortical-field evolution, see Ref. 58). Most theories of cortical-field evolution have been generated from the premise that early mammalian brains were diffusely organized and
Box 3. Subdividing the neocortex

In most modern approaches, the neocortex is subdivided into various compartments using a number of criteria. A cortical field is defined usually by an architectonic appearance that can be aligned with a complete representation of the sensory epithelium, as well as a unique pattern of connections. A range of histological techniques is now available, including myelin staining, enzymatic reaction and immunohistochemistry. This enables identification of cortical-field boundaries, as well as modules within fields. These histological techniques can be combined with electrophysiological recordings of multiple or single neurons so that 'map' of the sensory epithelium can be generated, and characteristics of individual neurons that are specific to specific features of cortical subdivisions be ascertained. These techniques can also be combined with anatomical tracing of connections, and a field's intrinsic, interhemispheric, interarchitectonic and subcortical connections determined.

However, any one cortical subdivision does not always fit all the defining criteria. For example, cortical fields are not always homogeneous in appearance (Fig. 3), nor do all neurons within a field possess similar response properties or stimulus preference. Observed connections of a given field might also differ depending on the presence of modules in some lineages. While the use of multiple criteria to subdivide the cortex helps to overcome this problem, such criteria still encourage us to view the cortex as static and composed of clearly separable parts, rather than as an evolving structure. The true nature of the cortex is dynamic, both within an individual's lifetime, and within a species over time.

References

Fig. Dividing the neocortex by areas and modules. (A) A dorsal-lateral view of the neocortex of a mammal in which the neocortex is divided by area. (B) A more complete representation of cortical fields, and modules within these subdivisions, in a flattened view of the neocortex. Although fields such as VI do have sharp boundaries, the discovery of modules, defined architectonically, physiologically and functionally, in a number of visual (shades of grey) and somatosensory (shades of pink) areas has led to a reconsideration of cortical-field boundaries. In some cases, these boundaries are taken from Ref. c. Visual-field boundaries are taken from Ref. d, and auditory-field boundaries are from Ref. e. Scale bar, 2 mm. For abbreviations, see Box 2.

undifferentiated. However, recent observations in a variety of mammals whose ancestors branched off early in evolution do not support this contention.2,4-6 (Figs 3G–I, 5B–D and H), because some of the same mammals on whom these theories were founded have now been shown to have multiple, highly differentiated cortical fields.

Based on observations in our laboratory,1,4,9 we propose that cortical fields evolve by a process of initial invasion of new correlated inputs to the cortex (module formation), followed by a process of gradual aggregation of similar types of inputs. This process occurs in both directions so that partially aggregated groups might eventually aggregate further and form a new field, or might disperse or refract, or both, and form a more homogeneous arrangement. This process can stabilize in any lineage, so that the initial invasion might not aggregate or separate. The organization of anterior parietal fields in the grey-headed flying fox (Pteropus poliocephalus) represents an aggregation of inputs, as well as a partial segregation. Recently, a representation of deep inputs that form separate islands (area 2) within a representation of cutaneous inputs (area 1) has been identified.2 Although this field, which we call area 1/2, is embedded partially (Fig. 7C) in the primary somatosensory area, S1 and given the close relationship between primates and flying foxes, we propose that this field is a primitive form of areas 1 and 2 in primates. The second visual area, VII, in some primates (for example, Cebus apella) represents a more distinct aggregation stage (Fig. 7D) in that a representation of the visual hemifield occurs in the different modules (which also differ in architectonic appearance and connections) within the field.24 While it is tempting to consider these as intermediate stages of the aggregation process (as we have in the past), it would be inaccurate to do so. Extant species represent different frames of the evolutionary process, each containing cortical fields 'frozen' at a particular stage of initial invasion, aggregation or segregation. In any given extant mammal, a field might be at one particular stage, while a homologous field in another mammal might be at a different stage. The number of invasions, aggregations and segregations that have occurred in the evolution of a particular field within a given lineage is unknown.

Our theory implies that cortex is performing similar computations across its extent, and it is the unique pattern of inputs from the thalamus, and ipsilateral and contralateral cortical fields, that defines a cortical field.7 (Fig. 7). These patterns are capable of changes over many generations, resulting in the evolution of new patterns of activation (modules and fields), and a reweighting of existing afferent and efferent connections of these networks.

The mechanisms that are involved in module formation, cortical-field changes, and cortical-field addition are not well understood, and there is a continuing debate on how cortical fields are specified in development.10-12 It is proposed that the thalamus is the driving force of these changes, and the developing cortex is to a large extent multipotential13-16. For example, small changes in the timing of events (heterochrony) in, or the addition of new cells to, the developing thalamus might cause disconnections between neural groups therein, and result in significant changes in the size, number and internal organization of the cortical fields that are generated by these thalamic inputs. Based on studies of thalamocortical development in rats, a similar hypothesis has been proposed previously by Blakemore and Molnar.17

Regardless of proposed mechanisms that underlie cortical-field evolution, most observations indicate that new fields evolve from existing ones. Thus, theories that regard the development of the neocortex should take into account that the developing nervous system is also evolving nervous system. New fields are being interposed between retained fields, and retained fields are undergoing modifications in size, configuration, location, and patterns of connections. Thus, the study of cortical-field evolution is the study of the evolution of development, and development is a series of events upon which acts both within the developing organism18 and later upon the postnatal animal. Comparative studies suggest that some evolution must be restricted, since common
cortex

Neurophysiological recordings of multiple or single neurons of the sensory epithelium, and characteristics of individual neurons to specific features of the stimulus can be measured. These techniques can also be combined with tracing of connections, and a field’s hemispheric, interhemispheric and subcortical connections determined. Each cortical subdivision does not always prescribe criteria. For example, cortical fields are never present in appearance (Fig. 7), and Fig. 7 suggests even when present, similar processes or stimuli are for preferred. Neurons in a given field might differ depending on a module of modules in some string while the more complex strategies of the cortex help to organize events. Such strategies still encourage us to see a static and composed of more or less as an evolving structure. The cortex is dynamic, both within and individual under a variety of spaces over time.

Fig. 3. Architectonically and anatomically defined modules in the neocortex in different sensory systems and different species. A, Incert (A-P; K); B, lenticular (G and H; P) microcircuits of cortex that have been flattened and cut parallel to the cortical surface, illustrating the discontinuities within cortical fields. (Cortex, including S and T, is bordered by processes for sucrose dehydrogenase and an array of dendritic processes). Neurons are observed in the vibrissae representation, as well as for representations of the vibrissae and whiskerpad in the CCO (CCO) dense representations of individual appendages (1-11). The nose of the striped mole are depicted. (C) The CC light and dense organization of the latt representation of S in the plateus in electrocochlear-neurons and mechanisms are inputs, respectively. (D) Myelin light and dark-staining regions in HC are related to connections from extrastriate visual areas. (F) In macaques, myelin light and dark-staining regions in HC are related to patterns of cortical connections. (H) Myelin light and dark-staining regions in the HC are related to connections from extrastriate visual areas. (I) Patchy interhemispheric connections via the anterior commissure are also observed in species (L. Krubitzer, unpublished observations). Scale bars, 1 mm.
neocortex and, therefore, its evolution. To understand how cortical fields evolve, and how organisms increase in perceptual and behavioral complexity, it is necessary to determine what triggers the addition and modification of cortical fields under rather rigid constraints.

Concluding remarks

Comparative analyses help generate hypotheses of cortical-field development, and enable some questions regarding cortical-field evolution to be answered. Specifically, are species differences really so different? Because differences in the neocortex consistently take the form of module formation, changes in cortical-field size, internal organization and number, and changes in connection patterns, it is likely that such alterations are generated from similar mechanisms. These mechanisms were probably present very early in mammalian evolution, and it is hypothesized that future changes will be shaped by similar mechanisms. Indeed, while the product in a given lineage of several million years of further evolution cannot be predicted exactly, which features are likely to be retained, the types of modification that are likely to occur, and what will not happen can be predicted with some certainty. By contrast, the amount of phenotypic variation that simple modifications confer is remarkable, especially since these changes might occur with little change to the genome. Thus, the restricted patterns of organization that have evolved in extant species, with minor, consistent, and often predictable modifications, can generate exceedingly variable behavioral, perceptual and cognitive abilities in mammals.

We patronize them for their incompleteness, for their tragic fate of having taken form so far below ourselves. And therein we err, and greatly err. For the animal shall not be measured by man. In a world older and more complete than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear. They are not brethren; they are not underlings; they are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth.

Beston, 1949 (Ref. 66)
Selected references

45. Weller, W.L. (1972) Brain Res. 3, 11-24
60. Roe, A.W. et al. (1990) Science 250, 818-820
64. Rakic, P. (1986) Science 231, 170-176

Acknowledgements
The author thanks Roan Twinn, Jon Clancy, Jack Pettigrew, Sheree Florence and Mike Callow for their helpful comments on this manuscript, and Gay Elton for technical assistance.

Work in the author’s laboratory was supported by the Australian Research Council.

with ourselves in the net of life and take the rivers of the splendid and the earth.

Bosten, 1949 (Ref. 66)