

Krubitzer L and Campi K. (2009) Neocortical Organization in Monotremes.
In: *Encyclopedia of Neuroscience*; Squire LR (Ed.), Volume 6 (pp. 51-59)
Oxford: Academic Press.

Neocortical Organization in Monotremes

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Introduction

Monotremes are a unique order of mammals that includes only three extant species: the duck-billed platypus (*Ornithorhynchus anatinus*), the short-billed echidna (*Tachyglossus aculeatus*), and the western long-billed echidna (*Zaglossus bruijnii*). Like other mammals, monotremes possess a segmented jaw, have three bones that comprise the middle ear, are warm blooded, and lactate. However, they have retained at least some characteristics of therapsid reptiles, such as laying eggs and the presence of a cloaca (in fact, the term 'monotreme' literally means 'single hole'). Although these animals are often referred to as primitive or ancestral, they are not the ancestors of all mammals. Instead, monotremes formed a very early radiation of mammals that originally evolved from early synapsids, which are considered to have been reptile-like mammals (Figure 1). Monotremes are of interest from a neurobiological perspective because it is thought that they may have retained features of brain organization that were present in the first mammals.

Of course any extant mammal is a compilation of both retained characteristics and newly derived features, and monotremes possess both general and specialized features of the body and the brain. For example, as determined by the fossil records, the first mammals appeared about 200 Ma (Figure 1), during the late Triassic or early Jurassic period, and are thought to have laid eggs; however, they were shrew-like animals that did not possess a bill, unlike the three extant monotreme species today. Thus, the distinct bill of the platypus and the unique bill and tongue of the echidna are newly derived features that are associated with navigation, mate selection, and prey capture, and these features are related to highly specialized lifestyles of these three species. This idea also holds true for features of brain organization. Studies of monotreme neocortex suggest that they have retained a number of general mammalian characteristics, as well as incorporated a number of newly derived features associated with their unique morphological specializations and behavior. This article describes the organization of somatosensory, visual, auditory, and motor cortex, as determined from architectonic analysis, electrophysiological recordings, and anatomical connection studies in two of the three extant

monotreme species, the duck-billed platypus and the short-billed echidna (to our knowledge, the neocortex of western long-billed echidna has not been examined). We will compare the neocortical organization in monotremes with that of other species to determine which features are common to all mammals. Such a comparison allows us to infer the organization of neocortex of early mammals.

Gross Brain Morphology

The brains of the platypus and the echidna are distinctly different from each other; the platypus has a smooth, relatively small brain (Figures 2(a) and 2(b)), and the echidna has a convoluted, large brain with commensurate expansion of the cortical sheet (Figures 2(c) and 2(d)). In the echidna, the major sulci of the brain are termed the α sulcus and the β sulcus (Figure 2(c)), and much of the cortical surface is buried within the fissures (Figure 2(d)). In the platypus, sensory cortical areas occupy the caudal two-thirds of the entire cortical sheet, and motor cortex occupies much of the remaining rostral cortex. Similarly, in the echidna, sensory cortex is located in the caudal portion of the neocortex, caudal to the α sulcus, and motor cortex is located just rostral to sensory cortex, between the α and β sulci. While there is very little cortex rostral to motor cortex in the platypus, in the echidna there is an enormous expansion of the cortical sheet rostral to motor cortex, the function of which is unknown.

The size of pyriform cortex also differs between the platypus and the echidna. The pyriform cortex is separated from the neocortex by the rhinal sulcus and is located lateral (ventral) to the neocortex. In the echidna, the relative size of pyriform cortex with respect to the neocortex is very large compared to the pyriform cortex of the platypus. As in many other mammals, the olfactory bulb of the platypus is smooth and relatively small; however, the olfactory bulb in the echidna is extremely large and contains a number of fissures. The increased size of pyriform cortex and the olfactory bulbs in echidnas may be related to the expansion of the frontal lobe (discussed in the section titled 'Multimodal and frontal regions of cortex').

Somatosensory and Electrosensory Cortex

Much of what is known about the organization of the neocortex in monotremes comes from studies of the somatosensory system. This is likely due

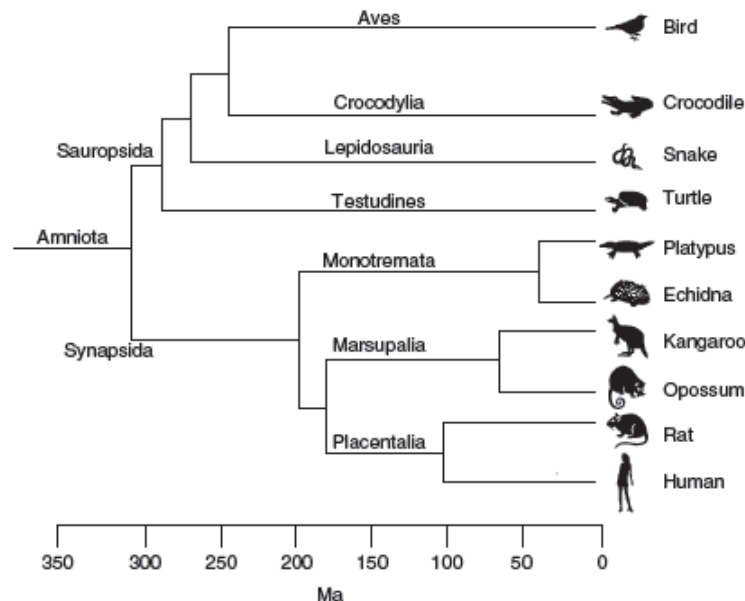


Figure 1 A cladogram depicting the phylogenetic relationships of reptiles, birds, and the three major groups of mammals, including monotremes. A large vertebrate group, the synapsids, arose more than 300 million years ago (Ma) and includes all mammals. Early synapsids are considered to be mammal-like reptiles that ultimately gave rise to the first mammals more than 200 Ma. Monotremes arose about 200 Ma, before the radiation of marsupials and placental mammals, approximately 180 Ma. Fossil records indicate that extant monotremes, which include the platypus and two species of echidnas, are highly derived, particularly in the structure of their bill, and in this respect do not resemble the first mammals.

to the unique morphological specialization of the bill, which is critical for the survival of these species and dominates the organization of the nervous system along the entire neuroaxis. Previous functional mapping studies have demonstrated that the somatosensory neocortex of both the platypus and the echidna is composed of three separate fields, a primary somatosensory area (S1 or area 3b), a rostral field (R), and a field just caudal to S1 that is in the position of the parietal ventral area (PV) in other animals (Figure 2).

The primary somatosensory area is a large field in both the platypus and the echidna and is topographically organized, with the tail and feet represented most medially, followed by the representation of the trunk, forelimbs, and face more laterally. In both the platypus and the echidna, the most striking feature of S1 is the bill representation, and in the platypus, neocortical specializations associated with their electroreceptive abilities are remarkable. Specifically, the platypus has evolved electroreceptive receptors that are located in a striped pattern down the bill and are interdigitated with the mechanosensory receptors, which are also arranged in stripes (Figure 3). Unlike electroreception in some electric fish, electroreception in the platypus is passive. Electroreceptive receptors enable the platypus to locate electrical signals

emitted from the muscle of small prey such as insects and crayfish, which generate electrical fields that can be as small as $20 \mu\text{V cm}^{-1}$. Unlike other mammals, the platypus uses electroreception combined with somatosensation (instead of vision, audition, and olfaction) for most daily activities, including navigation, mating, and feeding. Correspondingly, the bill representation comprises about 90% of S1. In cortex that has been sectioned tangentially and stained for cytochrome oxidase (CO), the bill representation of S1 stains heterogeneously, with CO light regions interdigitated with CO dark regions (Figure 3). These dark and light regions contain neurons responsive to mechanosensory and electroreceptive stimulation, respectively.

Like the platypus, the echidna also has an extremely large representation of the bill in S1. However, there are substantially fewer electroreceptors in the bill of the echidna (only a few hundred to 2000) compared with the 40,000 receptors found on the platypus bill. Thus, it is likely that electroreception is not used to the same extent in the echidna as it is in the platypus. Nevertheless, the echidna does use its bill and elongated tongue when foraging for termites and other insects, and this specialization is reflected in the organization of the somatosensory cortex. Most notably, the rostral 1 cm of the bill assumes the greatest amount

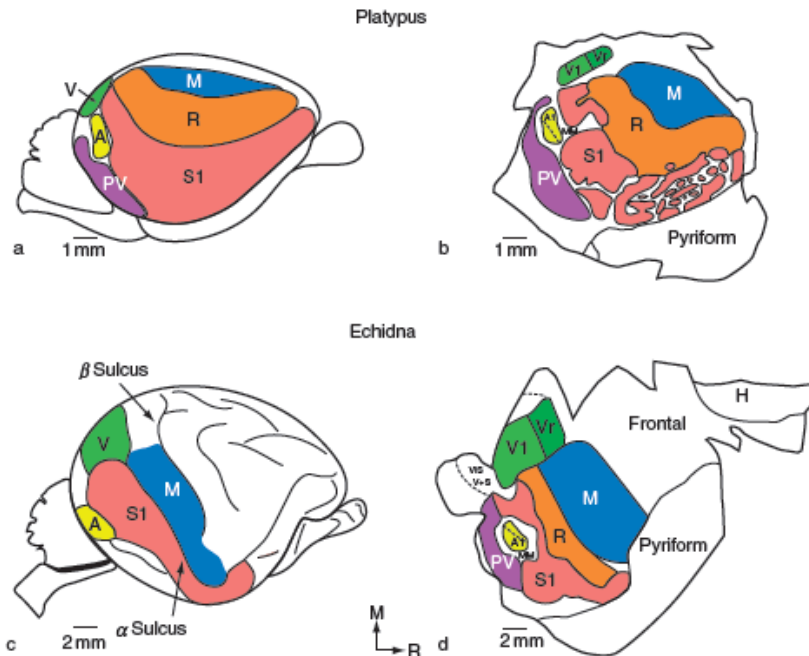


Figure 2 Gross brain morphology in the echidna and the platypus, depicting the location of sensory and motor areas (a,c), and flattened cortex depicting all the known sensory and motor areas of the cortex in each species (b,d). The echidna has a large, highly fissured, gyrencephalic brain, while the platypus has a smooth, lissencephalic brain. In the platypus, much of the entire neocortex is composed of the primary somatosensory area (S1), the rostral somatosensory field (R), the parietal ventral area (PV), and motor cortex (M). In the echidna, sensory cortex, including S1, is located caudally in the brain, and M is located between two major sulci, termed α and β . The rostral field (R) in echidnas is buried in the β sulcus. Primary sensory areas (S1, A, and V1) have been identified in both species. A small amount of cortex surrounding A has been identified as multimodal (MM). The relative amount of S1 cortex in the platypus is quite large, and most of this is occupied by the representation of the bill (see Figure 3). The echidna cortex is of particular interest because frontal cortex has undergone an extreme expansion, and such an expansion is not observed in the platypus. H, hippocampus; VIS, visual cortex; Vr, rostral visual field; V+S, visual and somatosensory cortex. Arrow directions M and R refer to medial and rostral, respectively.

of cortical space within the entire representation of the bill, and the receptive fields for neurons in this rostral representation are extremely small. As in the platypus, S1 in the echidna stains darkly for myelin, and architectonic analysis by Hassiotis and colleagues has demonstrated that S1 can be readily distinguished with acetylcholinesterase stains (AChE) and a monoclonal antibody reaction to neurofilament protein (SMI-32).

A second field, just rostral to S1, termed the rostral field (R), has been identified electrophysiologically and architectonically in both the platypus and the echidna. As in S1, R contains a complete representation of the contralateral body with a similar medial to lateral organization; however, neurons in R respond to stimulation of deep receptors whereas neurons in S1 respond to cutaneous stimulation. Like S1, R also contains an enlarged representation of the bill in both the platypus and the echidna. R can be distinguished from S1 architectonically because it stains lightly

for myelin and CO compared with S1. Furthermore, architectonic studies show that the laminar distribution of AChE in R is distinct from that of S1.

Finally, a cortical field just caudal to S1, termed PV, has been described in both the platypus and the echidna. This field contains a complete representation of the cutaneous receptors of the contralateral body that is distinct from the representation in S1. This field is in the relative position of PV described in other mammals and has a similar topographic organization. Within PV, the tail is represented medially, the hind limb is represented caudolateral to the tail, the forelimb is represented rostralateral to the tail, and the bill is represented lateral to these representations. Like S1 and R, there is an enormous magnification of the representation of the bill. Together, the bill representation in all three fields comprises approximately 64% of the entire cortical surface. Such magnification of a single body part is rarely seen in other mammals. PV, in both platypus and echidna

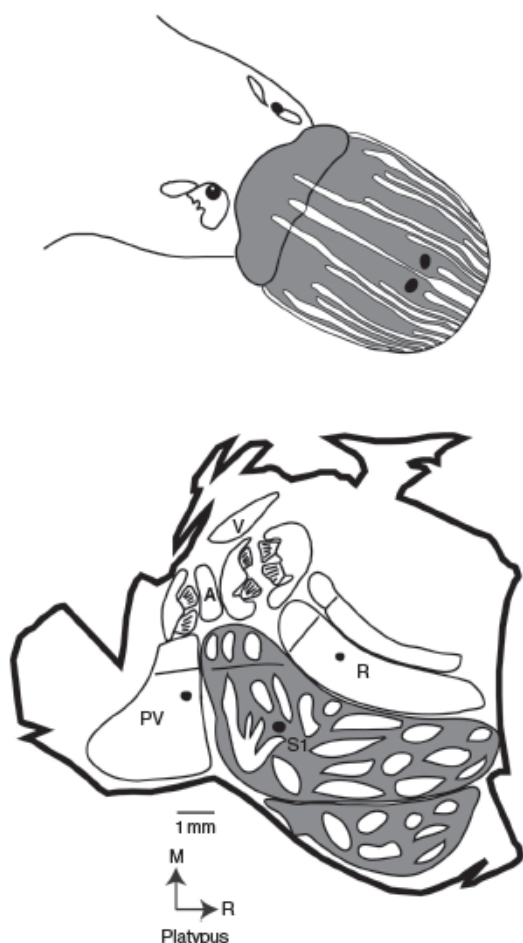


Figure 3 An illustration of the platypus (above), depicting the location of electrosensory receptors (white stripes) on its bill. The enormous size of the bill representation within the three separate somatosensory fields in the platypus neocortex (below) reflects the importance of the bill for survival behaviors. Within the primary somatosensory area (S1), mechanosensory receptors (shaded regions), interdigitate with the representation of electrosensory receptors. See [Figure 2](#) for abbreviations.

brain sections, stains moderately for myelin, and architectonic analysis in the echidna indicates that PV can be readily distinguished from S1 with a number of different stains, including AChE, parvalbumin, and SMI-32.

Anatomical studies have been done only in the echidna. Specifically, degeneration studies by Welker and Lende and neuroanatomical tracer studies by Ulinski have demonstrated that the major projection from the thalamus to S1 is from the ventral posterior nucleus. Cortical area R also receives input from the ventral posterior nucleus. Cortical connection experiments have shown that S1 has dense connections

with R and PV, moderate connections with motor cortex, and sparse connections with visual cortex.

Taken together, the architectonic, electrophysiological, and anatomical data indicate that three somatosensory fields are present in the platypus and the echidna: S1, R, and PV. All these fields have a greatly magnified representation of the bill, and in the platypus, S1 modules associated with electrosensory reception have been identified.

Visual Cortex

Relatively little is known about the organization of visual cortex in monotremes. In the platypus, studies of visual cortex organization are rare, but the limited data that exist from electrophysiological recording studies demonstrate that two fields are present, a caudal (Vc) and rostral (Vr) visual field ([Figure 4\(a\)](#)). The caudal visual field, Vc, contains neurons that are responsive only to visual stimulation. Although the visuotopic organization of this field is not as precise as in other mammals, Vc contains a representation of both the upper and lower central visual hemifield. Because neurons in Vc respond vigorously to visual stimulation and have relatively smaller receptive fields than neurons in Vr, this field may be homologous to V1, as described in other mammals. The rostral visual field, Vr, contains a representation of the visual hemifield; however, neurons in this field have larger receptive fields and respond less vigorously to visual stimulation. Architectonic analyses of these fields indicate that both are coextensive with a darkly myelinated zone, although Vc is slightly less myelinated than Vr.

In the echidna, early evoked potential studies by Lende demonstrated that visual cortex is located just medial to somatosensory cortex, and this has been confirmed in more-recent microelectrode recording studies by Krubitzer. Cortex in which neurons are responsive to visual stimulation has been subdivided into two and sometimes three distinct fields on the basis of architectonic analysis and anatomical connections. For example, architectonic analysis by Hassiotis and colleagues is consistent with electrophysiological recording studies by Lende and by Krubitzer and demonstrates that there is a visual field representation in the position of V1 which can be readily distinguished from the surrounding fields using myelin stains and AChE reactivity. Based on architecture, these investigators also distinguish a second field rostromedial to V1 that may correspond to V2 in other mammals. Furthermore, injections placed in the caudolateral portion of this field (which may be V1 plus the rostral area as defined by Hassiotis and colleagues; and Vc plus Vr as defined in

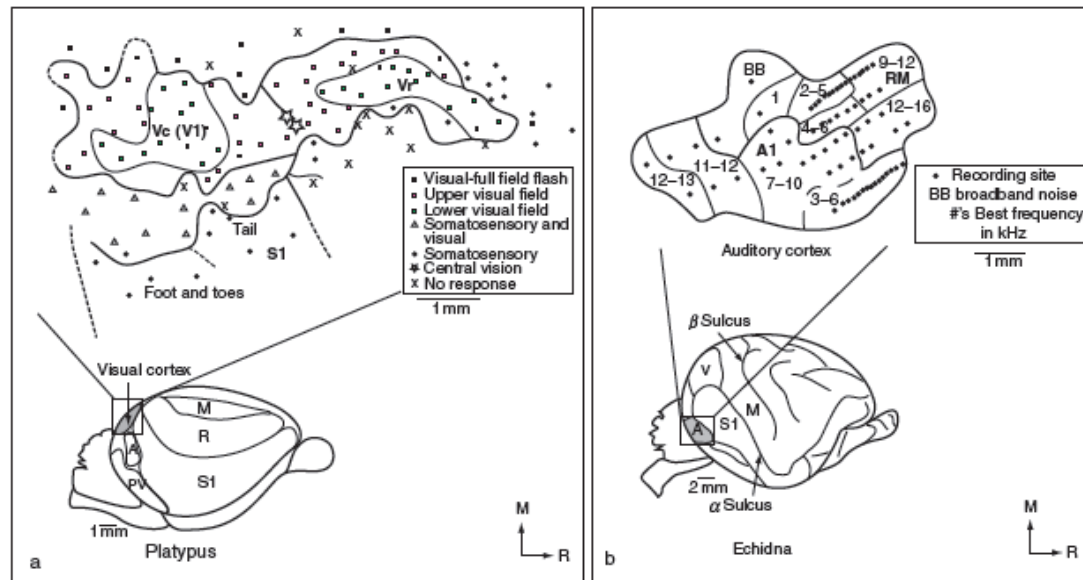


Figure 4 The functional organization of visual cortex in the platypus (a) and auditory cortex in the echidna (b). For both, the illustration at the top is an enlarged drawing of the area in the inset in the whole brain below. (a) Although the data are limited to a few platypus, there appear to be two representations of the contralateral hemifield. There is a caudal field, which appears to be homologous to V1 described in other mammals, and a rostral field, which may correspond to V2 in other mammals. On the basis of their location, these are termed Vc and Vr, respectively. (b) There appear to be two auditory fields in the echidna. In the caudolateral field, frequencies are represented from high caudally to low rostrally in isofrequency bands, much like A1 in other mammals. Because of the similarities between this field and the primary auditory area described in other mammals, we have termed this field A1. A rostromedial field (RM) is also present, in which frequencies are represented from low to high in a caudal to rostral progression. See [Figure 2](#) for abbreviations.

platypus) resulted in labeled cells and axon terminals immediately around the injection site, in cortex far rostral to the injection site, and in cortex lateral to the injection site. Finally, limited architectonic analysis and anatomical connection studies show that the cortex located caudal to the darkly myelinated V1, which has been previously demonstrated to contain neurons responsive to visual stimulation, has reciprocal connections with V1.

On the basis of cortical connections, architectonic analysis, and electrophysiological recordings in the platypus and the echidnas, it appears that at least two and possibly three fields exist in visual cortex. One of these fields, based on architecture, appears to be homologous to V1 described in other mammals. However, thalamocortical connections of visual cortex suggest that major differences exist between visual cortex in monotremes and other mammals.

Thalamocortical connections of visual cortex have been examined only in the echidna by Welker and Lende. Using degeneration methods, these investigators found that lesions in visual cortex resulted in degeneration of a nucleus that they termed the occipital pole region (OP) of the thalamus. This is different from other mammals in which the major source

of input to V1 is the lateral geniculate nucleus (LGN). In a previous review we proposed several alternative interpretations of their result. The first is that the lesioned region may not have been V1, as other data described above indicate; at least two and possibly three fields exist in this region. A second possibility is that the LGN was misidentified, although this seems unlikely since most other investigators who examined the architecture of the thalamus in monotremes place the LGN in the same location as did Welker and Lende. Third, it is possible that OP corresponds to the pulvinar in other mammals and that connections have been altered in marsupial and placental mammals. Finally, it is possible that none of the visual areas defined in the platypus and the echidna correspond to V1 and that V1 and its unique pattern of connectivity evolved later in marsupial and placental mammals. Support for the latter two hypotheses (that OP corresponds to the pulvinar and that V1 is a more recently evolved cortical field in marsupials and placental mammals) comes from studies of retinal projections in the echidna. These studies demonstrate that the superior colliculus, rather than the poorly differentiated OP, receives the majority of input from the retina.

Taken together, the data indicate that at least two and possibly three visual fields are present in monotremes, but the connections of these fields in monotremes appear to be somewhat different from those in other groups of mammals. It is uncertain whether this difference is a reflection of a primitive form of brain organization present in the common ancestor or whether these differences represent derivations of animals that have reduced visual pathways and rely very little on vision.

Auditory Cortex

The location of auditory cortex in both the platypus and the echidna was described in early evoked potential studies by Lende and by Bohringer and Rowe, respectively, and in more-recent microelectrode recording studies by Krubitzer. In the platypus, early studies indicated that auditory cortex completely overlaps visual cortex; however, recent studies have provided evidence for a small region of cortex, just caudal to the medial portion of S1 and lateral to V1, in which neurons respond solely to auditory stimulation (Figure 4(b)). Architectonic analysis of this cortex demonstrates that this field, which appears to be homologous to A1, stains darkly for myelin. A small belt of cortex immediately surrounding auditory cortex in the platypus contains neurons responsive to more than one modality.

In the echidna, auditory cortex has been examined using electrophysiological recording procedures as well as architectonic analysis. Early functional mapping studies demonstrated that, as in the platypus, auditory cortex in the echidna is unimodal and is located just lateral to V1 and caudal to the medial portion of S1. In studies in which the neural response to pure tone frequencies was determined, the data show that two tonotopically organized fields are present: a rostromedial field, in which frequencies are represented from low frequencies caudally to high frequencies rostrally (Figure 4(b)), and a caudolateral field, in which low frequencies are represented rostrally and high frequencies are represented caudally. The internal organization of this caudal field suggests that it is homologous to A1, as described in other animals. Architectonic analyses of the auditory cortex in echidnas demonstrate that these auditory fields are darkly myelinated and that they are particularly distinct in AChE- and parvalbumin-stained tissue.

There are only a few studies of the anatomical connections of auditory cortex in monotremes, and these are limited to studies in the echidna. For example, Dann and Buhl demonstrated that auditory cortex has patchy connections with adjacent fields,

which may be other auditory fields. Degeneration studies of auditory cortex by Welker and Lende reported that lesions to auditory cortex result in degeneration of posterior regions of the thalamus, in the location of the medial geniculate nucleus (MG), although they did not specifically identify the MG nucleus architectonically.

Together, the data indicate that monotremes have a separate region of cortex that is devoted to processing unimodal auditory inputs. This cortex is architectonically distinct from surrounding cortex and receives inputs from posterior portions of the thalamus, likely MG. Limited electrophysiological and connection data in monotremes suggest that within this unimodal auditory region, two fields are present, one of which may be homologous to A1 described in other mammals.

Motor Cortex

Studies of motor cortex in monotremes began more than a century ago. In these early experiments, electrical stimulation of both the platypus and the echidna neocortex produced movement maps that were roughly topographically organized from foot to forelimb to face in a mediolateral progression. Subsequent studies by Lende and by Bohringer and Rowe confirmed these early findings and provided more details about the topography of motor cortex and its relationship to sensory cortical areas. In the platypus, it appears that almost all motor cortex completely overlaps somatosensory cortex, including what would be S1, R, and PV. In contrast, in the echidna, motor cortex appears to form a separate representation that may only partially overlap R. Architectonic studies in the echidna by Uliniski have illustrated that just rostral to cortical area R is a reduced layer IV and a very thick pyramidal cell layer (layer V), similar to area 4 or motor cortex described in other mammals. A recent architectonic analysis by Hassiotis and colleagues has confirmed this and has also identified a region of transitional cortex between M and R.

There are only a few studies on the anatomical connections of motor cortex in monotremes, and these are limited to studies of thalamocortical connections in echidnas. Degeneration studies by Goldby and by Welker and Lende demonstrate that the region of cortex defined as M1 (located between the α and β sulci) receives projections from the ventral lateral nucleus (VL) of the thalamus. However, it should be noted that the region of degeneration in these lesion studies was large and included posterior portions of the dorsal thalamus other than VL. These data are consistent with the idea that at least echidnas have a separate motor

cortex that receives input from the motor nucleus of the thalamus, as in other mammals.

Taken together, the data indicate that there may be two distinct types of motor cortex organization in monotreme neocortex. The first is a sensory–motor amalgam in which somatosensory and motor cortex are completely overlapping. This type of sensory–motor amalgam appears to be present in platypus and has been previously described by Lende in some marsupials. The second type of organization consists of a separate motor representation that is distinct from somatosensory cortex. This type of organization occurs in echidnas and is commonly observed in placental mammals. As in placental mammals, the primary source of input to motor cortex in echidnas is from VL of the thalamus.

Multimodal and Frontal Regions of Cortex

An interesting feature of cortical organization in both the platypus and the echidna is that the amount of nonspecific sensory cortex that resides between known unimodal sensory areas is extremely small. In both species, the small belt of cortex lateral to V1 and caudal to S1 and surrounding A1 contains neurons that respond to auditory and somatosensory stimulation, visual and auditory stimulation, or visual and somatosensory stimulation. In most other mammals, this region is somewhat larger, even in small-brained mammals, and is occupied by multimodal cortex (MM; cortex in which neurons respond to more than one modality). In primates, the geographic location of this region (termed posterior parietal cortex) has shifted away from auditory cortex with the expansion of the cortical sheet and is dramatically expanded and contains multiple cortical fields. The observation that sensory cortex in monotremes is dominated by primary sensory areas (S1, V1, and A1) and only one or two other fields devoted to processing sensory information for each sensory system, combined with the limited extent of multimodal or association cortex, suggests that unimodal sensory cortical areas emerged early in evolution. These data in monotremes, when compared with the neocortex of marsupial and placental mammals, suggest that association cortex, including regions of posterior parietal cortex, became increasingly differentiated, and in some groups of placental mammals such as primates, it came to occupy either as much cortical territory as unimodal sensory fields or more.

One of the most remarkable observations in the neocortex of the echidna is the enormous expansion of cortex rostral to motor cortex. This cortex contains neurons that are unresponsive to any mode of sensory stimulation, at least in anesthetized animals. Based

on the position of this area on the cortical sheet as well as patterns of projections from the mediodorsal nucleus of the thalamus, entorhinal cortex, amygdala, basal forebrain, pyriform cortex, substantia nigra, and the ventral tegmental areas, previous studies have proposed that this cortex is similar to prefrontal cortex in some mammals. However, the lack of the expanded frontal cortex in the platypus, as well as other mammals, including a variety of marsupial and placental mammals, which have only a very small region of cortex rostral to motor or sensory motor cortex, indicates that this expanded neocortex in the echidna arose independently and is a derivation of the echidna brain. Previously we proposed that the expansion of cortex rostral to motor cortex in echidnas might be associated with the elaboration of the olfactory system. As noted above, both pyriform cortex and the olfactory bulb in the echidna (Figure 2) are relatively large compared with its other brain structures and compared with these same structures in the platypus. Although olfaction has not been well studied in the echidna, it is possible that the expanded frontal cortex in the echidna is comparable to orbitofrontal cortex in other mammals and that it is related to the enhanced olfactory abilities of echidnas.

Comparisons with Other Mammals

While the organization of monotreme neocortex is interesting in and of itself, the importance of understanding cortical organization in monotremes is underscored when comparisons are made across all three mammalian lineages (monotremes, marsupials, and placentals). For example, as in other mammals, monotremes have undergone several modifications, which include a reconfiguration of sensory receptor morphology; expansions of cortex related to behaviorally relevant body parts, such as the bill representation in S1 and the expansion of frontal cortex in echidnas; and alterations in cortical connectivity. Similar modifications to the neocortex have been observed in marsupial and placental mammals, suggesting that the types of alterations made to evolving brains is highly constrained such that brain organization, even in distantly related species, often takes a similar form.

In addition to these modifications, a comparative analysis allows us to appreciate that there are a number of features of cortical organization that are similar in all three groups of mammals. First, there is a constellation of cortical fields that includes the primary sensory and motor areas (S1, V1, A1, and M1), as well as additional unimodal fields such as PV, R, Vr, and a second auditory field. Another interesting

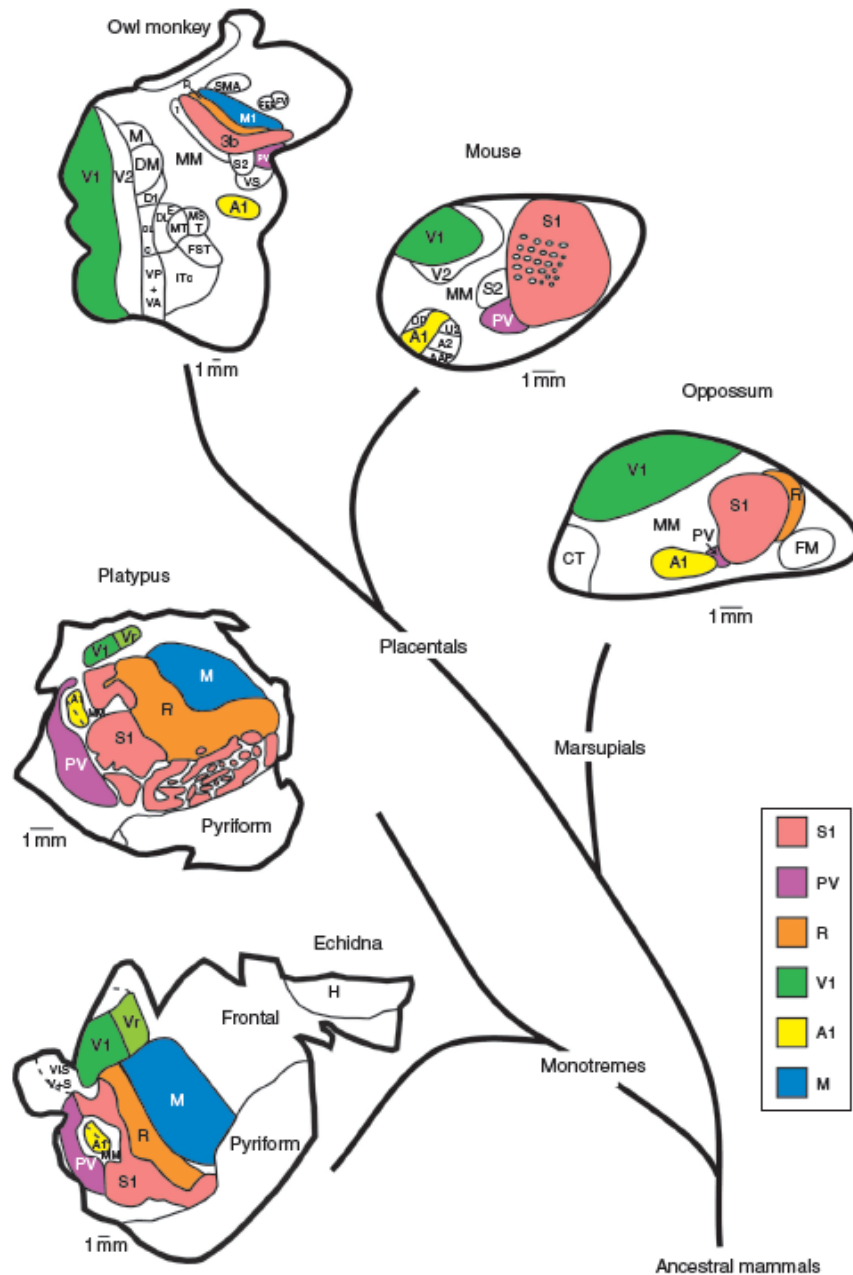


Figure 5 General phylogenetic relationship of the three major groups of mammals, and the cortical organization in representative mammals from each group. A comparative analysis indicates that all mammals have a constellation of cortical fields, including S1, R, PV, V1, A1, and two or three additional unimodal sensory areas. All mammals appear to possess either a separate motor area or a sensory-motor amalgam. Finally, all mammals have multimodal cortex. This type of analysis allows us to deduce the cortical organization of the common ancestor, which likely had these features of neocortical organization as well. Changes to the plan of cortical organization observed in different lineages include an expansion of the cortical representation of behaviorally relevant body surfaces, the expansion of the cortical sheet, the addition of new cortical fields, and alterations in connectivity. 1 and 3b are somatosensory areas; A and A1, auditory cortex; A2, second auditory area; AAF, anterior auditory field; C, caudal; CT caudal temporal field; DI, dorsal intermediate visual area; DL, dorsal lateral visual area; DM, dorsal medial visual area; FEF, frontal eye field; FM, frontal myelinated field; FST, fundal superior temporal area; FV, Frontal ventral visual eye field; ITC, caudal inferotemporal area; M, motor cortex; M1, primary motor area; MM, multimodal cortex; PV, parietal ventral areas; R, rostral somatosensory field; S1, primary somatosensory area; SMA, supplementary motor area; S2, second somatosensory area; U2, ultrasonic area; VA and VP, divisions of the ventral visual area; V1, visual cortex; V2, second visual area; Vr, rostral visual field; VS, ventral somatosensory area.

observation that can be made by comparing the cortical organization in monotreme, marsupial, and placental mammals is that there is more than one sensory field present for any given modality in all lineages. Until recently, it was believed that only primary sensory areas existed in monotremes. This notion led to the assumption that primary cortical fields are the evolutionarily oldest fields and that second and third sensory areas were added hierarchically in marsupial and placental mammals. The presence of at least three somatosensory fields, two visual fields, and two auditory fields in all mammals investigated suggests that the first mammals had two to three sensory areas for each modality and possibly a separate motor field as well. Thus, there is no clear evidence that primary cortical areas are phylogenetically older than other unimodal sensory areas.

Finally, a comparative analysis reveals that MM is present in all mammals, although its relative size and location is altered in different species. For instance, in monotremes, MM assumes a very small proportion of the neocortex and surrounds auditory cortex (Figure 5). In marsupials, MM has been identified just caudal to somatosensory cortex, lateral to visual cortex, and medial to auditory cortex. In placental mammals such as primates, this cortex has undergone a dramatic expansion and is composed of a number of cortical fields, although its location between visual, somatosensory, and auditory cortex is similar to that of MM in smaller-brained mammals such as mice. The presence of MM in all mammals investigated suggests that the first mammals had a small MM which was the forerunner of the more expanded posterior parietal cortex in marsupial and, particularly, placental mammals. This suggests that the potential for cross-modal integration of sensory inputs, which ultimately leads to the planning and execution of complex overt and covert behaviors, was present in a very primitive form in the common ancestor of all mammals.

See also: Auditory Cortex Structure and Circuitry; Auditory Cortex: Models; Marsupial Neocortex; Molecular Anatomy of the Mammalian Brain; Neocortex: Origins; Visual Cortical Models of Orientation Tuning.

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