

Karlen SJ and Krubitzer L. (2009) Marsupial Neocortex. In: *Encyclopedia of Neuroscience*; Squire LR (Ed), Volume 5 (pp. 671-679). Oxford: Academic Press.

Marsupial Neocortex

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Introduction

Although most of us are familiar with only a few species of marsupials, such as kangaroos, koalas, and opossums, there are actually hundreds of marsupial species. Like placental mammals, they are an extremely diverse group that has a number of behavioral specializations related to individual lifestyles. For example, there are marsupials that are terrestrial, arboreal, burrowing, and aquatic. Marsupials can be highly social, such as the striped possum, or solitary, such as the koala; they can be carnivorous, herbivorous, or omnivorous. This diversification is tied to the evolution of unique peripheral morphologies and highly specialized behaviors, both of which are related to alterations in overall brain size, neocortical organization, and connectivity.

In this article, we begin by examining the general lifestyle and morphological characteristics of all marsupials. We then describe the organization of somatosensory, visual, auditory, and motor cortex in marsupials. Finally, we discuss how alterations in the basic plan of organization are associated with specialized behaviors and individual lifestyles.

General Features of Marsupials

Marsupials represent one of three subclasses of mammals that include Prototherians (monotremes), Metatherians (marsupials), and Eutherians (placentals). Monotremes diverged early in evolution, and evidence from gene sequencing studies indicates that marsupials arose concurrently with placental mammals, approximately 180 Ma (Figure 1). The first marsupials are thought to have arisen in North or South America and subsequently migrated to Australia and Southeast Asia, possibly through Antarctica; however, an alternative theory suggests that marsupials may have arisen in Laurasia, somewhere in present-day Asia, and migrated to North America.

Extant marsupials have been subdivided into seven different orders, and more than 270 species have been identified (Figure 1). The exact phylogenetic relationship between marsupial orders is unresolved because different types of data result in conflicting phylogenetic relationships. In general, Didelphimorphia are considered to be the oldest order. This group is relatively homogeneous, and all species within this

order have relatively small brains with few cortical fields. The orders Paucituberculata and Microbiotheria are also found in the Americas, but very little is known about the organization of their neocortex. The remaining four orders are found in Australia, Tasmania, New Guinea, and neighboring islands, and they include most of the well-known marsupials.

Regardless of phylogeny, there are a number of features that all marsupials share. The most noted is the marsupium, or pouch, from which they derive their name. The marsupium varies between species from a closed pouch to a small, primal pouch or no pouch at all. Marsupials have a short gestation, between 8 and 42 days, and are born in an immature state. When born, they must make their way to the marsupium and attach to the mother's nipple in order to survive (Figure 2). Once in the pouch, the young animals reside there for the remainder of gestation.

Marsupial brains vary dramatically in size, shape, smoothness of the neocortical surface, and encephalization (the expected size of the brain relative to body size). For example, some marsupials have small, smooth brains with a small proportion of the brain devoted to the neocortex, whereas others have relatively larger, fissured brains with a larger proportion of the brain devoted to the neocortex (Figure 3). In terms of brain organization, perhaps the most notable feature of the forebrain is that marsupials (and monotremes) lack a corpus callosum. Instead, most interhemispheric communication occurs through the anterior commissure, which has been shown to be functionally equivalent to the corpus callosum in placental mammals.

Finally, all but three species of marsupials are nocturnal or crepuscular. This aspect of lifestyle is particularly interesting since all monotremes are nocturnal, suggesting that the common mammalian ancestor was nocturnal.

Somatosensory Cortex

The organization of somatosensory cortex has been studied in several species, all of which have a primary somatosensory area (S1) and a second somatosensory area (S2) located caudolateral to S1. The functional organization of S1 has been described using electrophysiological mapping techniques. In all species examined, S1 contains a complete and inverted representation of the contralateral body surface with the tail represented most medially, followed by the representation of the hindlimb, trunk, forelimb, forepaw, face, and oral structures in a medial to lateral progression. Most neurons in S1 respond to cutaneous

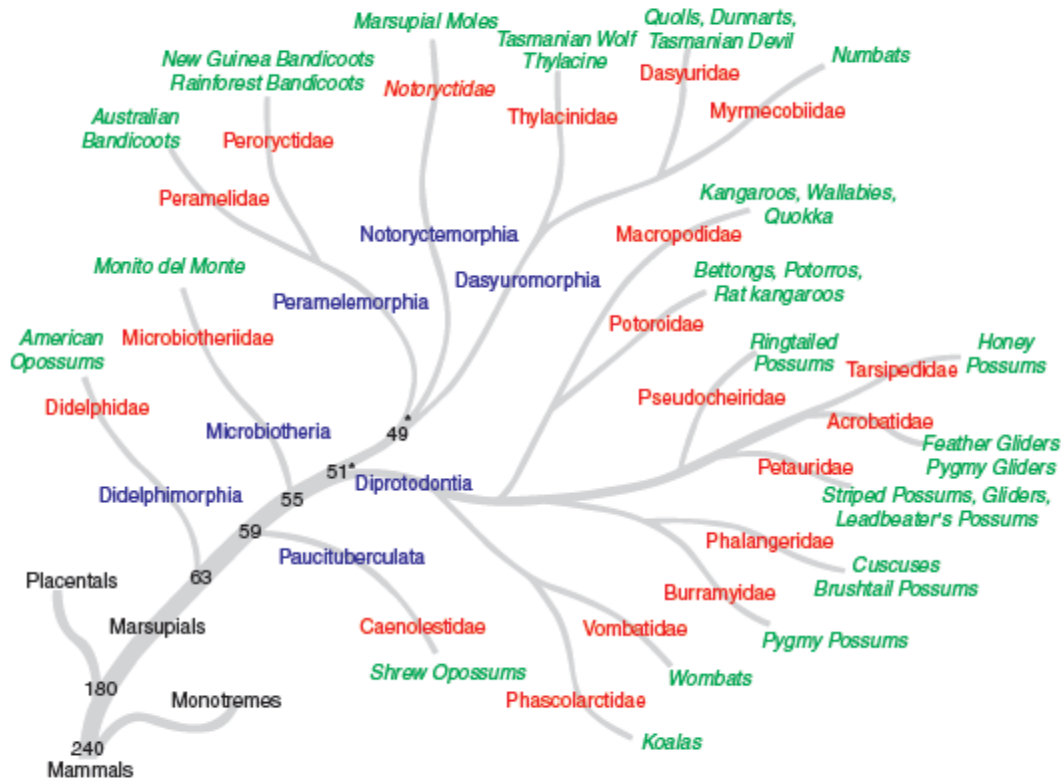


Figure 1 A phylogenetic tree illustrating the relationship between marsupials and other mammals. The seven extant marsupial orders are shown in blue, names of the families within each order are given in red, and examples of well-known species are in green. The timescale is in millions of years ago and is based on DNA sequence data from a 2004 study by Murphy et al. Asterisks indicate branch points that are ambiguous.



Figure 2 Marsupials are born at a very immature state, and they must make their way to the marsupium, or pouch, and attach to the mother's nipple in order to survive. (a) A litter of short-tailed opossums, a pouchless marsupial, on the day of birth. The immaturity of the young is evident in the embryonic developmental state of most of their body features and sensory organs (b). They are hairless, their eyes and ears are poorly developed, the hindlimbs and tail are stumps, and bone development is extremely immature. Only their olfactory system, their forelimbs, and, to a lesser extent, portions of the somatosensory system are developed at birth.

stimulation, and receptive fields for neurons are generally small, particularly on specialized morphological structures such as the vibrissae or forepaws.

In many instances, the specialized morphological structures are associated with unique behaviors. For example, the structure of the forepaw can vary dramatically between species from the spade-shaped

forepaw of the marsupial mole, used for digging, to the specially elongated fourth digit of the striped possum used to extract insects while foraging. The cortical representation of these specialized body parts in marsupials is generally enlarged in S1. This is called cortical magnification and is found in placental and monotreme mammals as well.

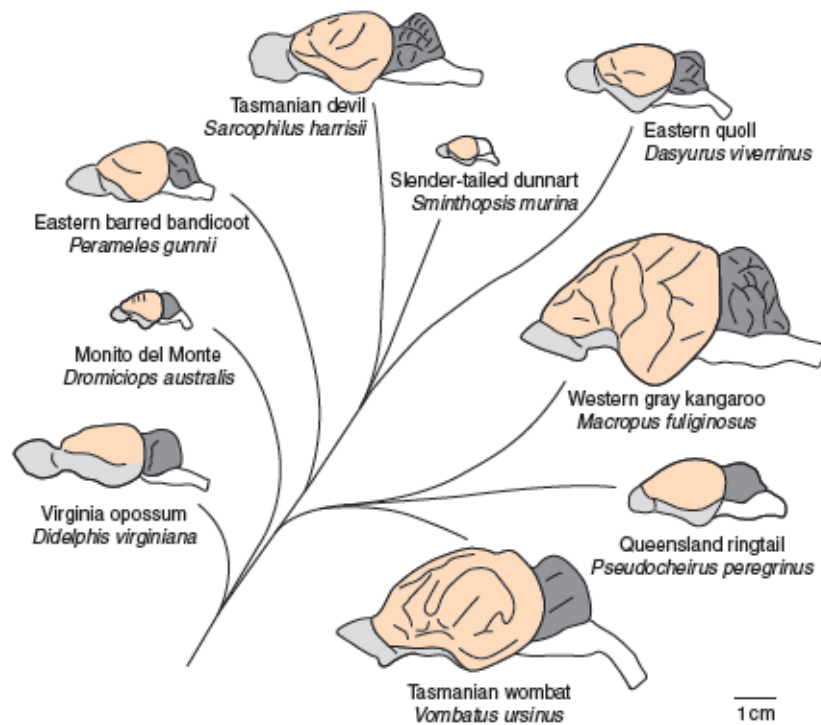


Figure 3 Lateral views of nine representative marsupial brains. Marsupial brains vary dramatically in their overall size; compare the brain of the Western gray kangaroo with that of the slender-tailed dunnart. The relative size of distinct brain areas also differs between species, such as the size of the olfactory bulb and pyriform cortex (gray), the size of the neocortex (light orange), and the size of the cerebellum (dark gray). Finally, the smoothness of the neocortical surface varies between species, such as the lissencephalic neocortex of the Virginia opossum versus the highly fissured neocortex of the Tasmanian wombat. Lines denote phylogenetic relationships between species; rostral is left and medial is up.

Caudolateral to S1 lies a second, smaller representation of the contralateral body surface called S2. This area has been electrophysiologically identified in all marsupials examined. As in placental mammals, S2 in marsupials contains a complete, noninverted representation of the contralateral body surface with the representation of the face and oral structures located adjacent to similar representations in S1. The forelimb and hindlimb representations are located progressively caudal, and the trunk and proximal body parts are represented medially. The receptive fields for neurons in S2 are larger than those for neurons in S1 and are often responsive to bilateral somatosensory stimulation and/or auditory stimulation. In many species, the S2 region actually contains two separate fields, a rostral field called the parietal ventral area (PV) and a caudal field termed S2. Both fields are somatotopically organized, and neurons in each field have large receptive fields.

Two other fields have been identified in the parietal cortex of several marsupial species; one field is rostral to S1, called the somatosensory rostral field (SR), and the other is caudal to S1, called the somatosensory

caudal field (SC). Neurons in both of these fields respond to stimulation of deep receptors or high-threshold cutaneous receptors. Because of similarities in location, stimulus preference, and patterns of connectivity, we have proposed that these areas correspond to fields that have been identified in other mammals, specifically that SR is homologous to area 3a of primates and flying foxes and that SC is homologous to the posterior parietal area (PP) in squirrels and posterior parietal cortex in rats. However, this hypothesis has not been tested.

Studies of corticocortical and thalamocortical connections of somatosensory cortex in marsupials are relatively restricted to the connections of S1. Corticocortical connections have been examined in the brush-tailed possum, Virginia opossum, white-eared opossum, short-tailed opossum, striped possum, and Northern quoll. In all animals, S1 has dense corticocortical connections with S2, PV, SR, SC, cortex immediately lateral to S1, and, in the brush-tailed possum only, motor cortex. S1 has sparse connections with cortex of the medial wall. Interhemispheric connections are restricted to S1, PV, and cortex lateral

to S1. Thalamocortical connections have been examined in the Virginia opossum, the brush-tailed possum, the Northern quoll, and the Tammar wallaby. In the Virginia opossum, thalamic connections with S1 arise predominantly from the ventroposterior nucleus (VP). Moderate projections are also from the ventrolateral nucleus (VL), the central intralaminar nucleus (CIN), the central lateral nucleus (CL), and the ventromedial nucleus (VM). Similar patterns of thalamocortical connectivity have been observed after injections into parietofrontal cortex (which contains S1) in the brush-tailed possum and the Northern quoll.

Taken together, the electrophysiological recording data and architectonic analysis indicate that two unimodal somatosensory fields are present in the neocortex of marsupials, S1 and S2. In some species, PV is clearly present as well. An additional field, SR, is associated with the somatosensory system but is also likely associated with motor processing. Likewise, the field caudal to S1, SC, is associated with somatosensory processing but may be homologous to one or more fields in the posterior parietal cortex of primates that are involved in sensorimotor integration.

Visual Cortex

The organization of the primary visual area (V1) has been examined using electrophysiological recording techniques in several different marsupials, including the Virginia opossum, the white-eared opossum, the big-eared opossum, the brush-tailed possum, the Tammar wallaby, the Northern quoll, and the short-tailed opossum. As in other mammals, V1 is located at the caudal pole of the occipital lobe and contains a complete visuotopically organized representation of the contralateral visual field. The representation of the upper visual field is located caudolaterally in cortex, the lower visual field representation is located rostromedially, the horizontal meridian bisects the upper and lower visual field representations, and the vertical meridian forms the rostromedial boundary of this field. Several studies have demonstrated that cortex immediately rostral to V1 contains neurons responsive to visual stimulation, and this area, called the second visual area (V2), has been mapped in detail in the Northern quoll. As in placental mammals, V2 contains a complete representation of the visual hemifield, with the vertical meridian represented at the caudomedial border of the field, adjacent to the vertical meridian border of V1. The horizontal meridian bisects the field and forms the rostromedial boundary of the field. The lower visual quadrant is represented rostromedially and the upper visual quadrant is represented caudolaterally.

In studies in which electrophysiological recordings were combined with architectonic analysis, V1 has been shown to be architectonically distinct from V2, and its appearance is similar to that described for V1 in placental mammals. In Northern quolls, V2 stains lightly for both myelin and cytochrome oxidase (CO), and in favorable preparations V2 is actually composed of heterogeneous light and dark patches in CO-stained tissue.

The cortical connections of V1 are similar in all species examined. For example, in the Virginia opossum, brush-tailed possum, mouse opossum, Tammar wallaby, big-eared opossum, and short-tailed opossum, V1 is densely connected with V2 (peristriate cortex), cortex just lateral to V2 in multimodal cortex (parietal cortex and PP), the caudotemporal area (CT), posterolateral peristriate cortex, and perirhinal cortex. Furthermore, the connections of V1 are not restricted to the representation of the vertical meridian, as is the case for a number of placental mammals. Instead, connections of V1 are found throughout V2 and CT of the ipsilateral hemisphere, although the connections with V2 are patchy and appear to be related to heterogeneities identified using CO stains. Studies of the overall pattern of commissural connections also demonstrate a patchy distribution with V1 and V2 of the opposite hemisphere, indicating that V2 may be modularly organized as it is in primates and other mammals.

Thalamocortical connections of V1 in marsupials are similar to those described in a number of placental mammals. In the brush-tailed possum, the Virginia opossum, the big-eared opossum, the Tammar wallaby, and the short-tailed opossum, the primary source of input to V1 is from the dorsal division of the lateral geniculate nucleus (LGd), with moderate inputs arising from the lateral posterior nucleus (LP). In the brush-tailed possum, the primary source of input to V2 is from LP, with sparse input from LGd. In the Virginia opossum, the lateral intermediate nucleus also projects sparsely to V2.

Taken together, the data indicate that visual cortex in marsupials contains at least two cortical areas, V1 and V2. Each field is topographically organized similar to that in placental mammals. Furthermore, features of neural response properties, histochemical appearance, cortical and subcortical connections, and even the presence of a modular organization are common for visual cortex across all mammals.

Auditory Cortex

Little is known about the number of auditory areas or the detailed organization of auditory cortex across marsupials. Most of what we do know comes from

work on two species, the Northern quoll (previously called the native cat) and the brush-tailed possum. In the Northern quoll, detailed maps of the primary auditory area (A1) have been generated, and these maps are tonotopically organized, as in placental mammals. Specifically, isofrequency bands run mediolateral in auditory cortex, with high frequencies represented rostrally and low frequencies represented caudally. In these animals, there is a disproportionate representation of high frequencies, and neurons in this high-frequency representation have very low thresholds. Studies of adult and juvenile Northern quoll vocalizations indicate that most adult vocalizations occur at the lower end of the hearing range, between 0.4 and 2 kHz, but that juveniles have calls within the peak frequencies of adult hearing, between 6 and 12 kHz. Furthermore, vocalizations and other sounds made by predators and prey of this species have a peak energy between 2 and 5 kHz and greater than 10 kHz, suggesting that the cortical magnification of high frequencies in the Northern quoll is important for predator and prey localization. Another auditory field just rostral to A1 was identified in the Northern quoll, but the data on this field were relatively sparse.

In the brush-tailed possum, the orientation of A1 is different than in other mammals in that high frequencies are represented dorsally and low frequencies are represented ventrally. However, as in the Northern quoll, the lowest thresholds for neurons in A1 in the brush-tailed possum fall between 12 and 21 kHz, similar to the range of frequencies used in vocalizations of the Virginia opossum.

Thalamocortical and corticocortical connections of auditory cortex have been examined in the Virginia opossum, the brush-tailed possum, and the Northern quoll. In all of these marsupials, the primary input to A1 is from the medial geniculate nucleus (MGN). Sparse projections also arise from the supragenulate nucleus. Since injections into different best frequency representations in the cortex produced discrete bands of label in MGN, the results indicate that projections from MGN to A1 are organized tonotopically.

Although ipsilateral cortical connections of A1 have not been described for any marsupial, dense projections from homotopic locations in A1 in the hemisphere contralateral to that injected have been described for both the brush-tailed possum and the Northern quoll. Furthermore, in the Northern quoll, A1 has been reported to connect ipsilaterally with the putamen and bilaterally with the lateral amygdala. Direct connections between the amygdala and A1 have not been reported for any placental mammal and may be a specialization of the Northern quoll or may represent a primitive pathway of mammals that was subsequently lost in placental mammals with the

addition of more auditory cortical fields. Support for the latter supposition comes from studies in marmoset monkeys which indicate that higher order auditory areas, such as the rostromedial field, have ipsilateral connections with the lateral amygdala.

Motor Cortex

The state of motor cortex in marsupials is contentious. The earliest experiments used gross electrical stimulation with unipolar and bipolar electrodes and demonstrated that motor cortex is located at the rostral pole of the neocortex, usually around the orbital sulcus. These experiments found that movements of individual body areas, such as the face, vibrissa, and forepaws, are represented progressively across the cortical surface; however, only half of the studies were able to find a clear representation of body areas posterior to the forepaws (i.e., the hindpaws and tail). Thus, for many years there was a debate as to whether marsupials had a motor representation of the lower body.

As techniques improved, several studies tried to address this issue. In 1939, Golby demonstrated the existence of a complete motor representation of the body at the rostral pole of the neocortex in the brush-tailed possum. Architectonic examination of cortex in this stimulated area confirmed that it corresponded to primary motor area (M1), as described in monotremes and placental mammals. Concurrently, Abbie demonstrated that body movements could be evoked at the far rostral pole of cortex in six different species of marsupials – the long-nosed bandicoot, the Tasmanian devil, the Eastern quoll, the brush-tailed possum, the red-necked wallaby, and the agile wallaby. His results demonstrated that motor cortex was topographically organized in all six species, although in the long-nosed bandicoot, the Tasmanian devil, and the Eastern quoll, the neocortex did not include a motor representation of the lower body. He concluded that there was probably no cortical motor representation of the lower body in the orders Peramelemorphia and Dasyuromorphia, but that there was a complete representation in the order Diprotodontia. Furthermore, he observed that the excitable cortex in all six species was coextensive with a larger layer IV, indicative of sensory cortex, which suggested that motor and somatosensory cortex overlapped.

In the early 1960s, Lende used more refined methods of cortical stimulation to explore sensory and motor cortex in the Virginia opossum and the wallaby. His results confirmed the presence of hindlimb and tail motor representation on the medial wall of the neocortex in both species (orders Didelphimorphia and Diprotodontia, respectively). Unlike earlier

marsupial studies, Lende demonstrated that these animals had a complete overlap of S1 and M1, which he called a sensory-motor amalgam. At the time, the results from his study were surprising but seemed to be in agreement with earlier data. These findings spurred a number of important ideas regarding cortical field evolution in mammals. Most notably, Lende proposed that marsupials represent a primitive state of cortical organization in which S1 and M1 are completely overlapping and that the evolution of this region is marked by a progressive separation of these fields in placental mammals, ultimately into two complete and separate sensory (S1) and motor (M1) representations (Figure 4(a)).

Early observations by Lende have been supported by several subsequent cortical stimulation studies in marsupials, including the brush-tailed possum, the white-eared opossum, and the short-tailed opossum. However, in the short-tailed opossum only movements of the jaw and vibrissae could be evoked in this sensory-motor amalgam. The finding that no other body part movements (particularly forepaw movements) could be evoked anywhere in the motor cortex of the short-tailed opossum is surprising in light of previous studies that demonstrated that dense corticospinal projections originate in S1.

Lende's hypothesis of a complete sensory-motor amalgam is not supported by all marsupial motor studies. In particular, in some marsupials there is a region of cortex located anterior to the proposed sensory-motor amalgam that does not respond to somatosensory stimulation and does not have connections with VP. Since these marsupials are in the order Diprotodontia, Haight and Neylon proposed that this order does not have a complete overlap of sensory and motor areas. Instead, they divided mammalian sensory motor organization into three types: (1) in placental mammals, S1 and M1 are completely separate and the body representations are mirror images of one another; (2) in marsupials and placental edentates, there is a complete overlap of S1 and M1, both with the same orientation; and (3) in monotremes, there is dual motor representation with one being coextensive with S1 and possessing the same orientation and the other occupying an anterior, mirrored position (Figure 4(b)). The partially separated S1/M1 in Diprotodontia and the fully separated S1 and M1 in placental mammals may represent evolutionary convergence.

Like cortical stimulation studies, neuroanatomical studies indicate that S1 and M1 in marsupials are partially overlapping, but the data are equivocal with respect to the completely overlapping sensory-motor amalgam. For example, in the Virginia opossum, projections from VL (associated with the motor system), VP (associated with the somatosensory

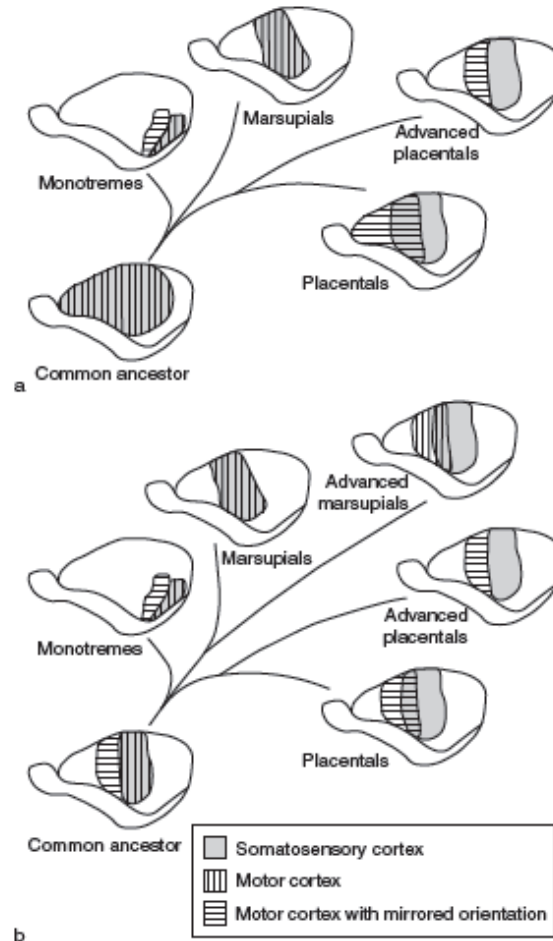


Figure 4 A diagram of the two prominent hypotheses on the evolution of sensory-motor cortex in mammals. (a) In 1969, Lende proposed that marsupials represent a primitive state of cortical organization in which S1 and M1 are completely overlapping and that the evolution of this region is marked by a progressive separation of these fields in placental mammals, ultimately into two complete and separate sensory (S1) and motor (M1) representations. (b) In 1979, Haight and Neylon proposed that there are three types of sensory motor organization. In monotremes (and potentially the common ancestor), there is dual motor representation with one being coextensive with S1 and possessing the same orientation and the other occupying an anterior, mirrored position. In placental mammals, S1 and M1 are completely separate and the body representations are mirror images of one another. In marsupials and placental edentates, there is a complete overlap of S1 and M1, both with the same orientation.

system), and CIN (associated with convergent somatic and cerebellar input) all converge on S1. Furthermore, the projections of VL are restricted to S1, supporting the idea of a completely overlapping sensory-motor amalgam. On the other hand, in the brush-tailed possum, thalamocortical projections appear to fall into three distinct zones. Cortex at the far rostral pole receives inputs from the mediodorsal

nucleus, generally associated with frontal cortex in placental mammals. Agranular cortex just caudal to this frontal region and rostral to S1, in the location of M1 in placental mammals, receives input predominantly from VL and less dense inputs from VP. Projections to S1, as described previously, are predominantly from VP and the posterior nucleus and sparsely from VL. Furthermore, comparative studies in which retrograde tracers were injected into the spinal cord of a number of different mammals indicate that the major source of spinal input from the cortex is similar in all mammals investigated, including several marsupial species. Specifically, there are two or three corticospinal projection zones (termed A, B, and C) that all mammals have, at least in part. One of these projection zones (A) appears to correspond to somatosensory and motor cortex. Although no direct correlations were made, projection zone A in the Virginia opossum and the short-tailed opossum appears to be restricted to somatosensory cortex, whereas this same projection zone in rodents and primates has a rostral extension into the location of motor cortex.

When considered together, results from cortical stimulation and neuroanatomical studies in marsupials are somewhat conflicting. Early cortical stimulation studies in marsupials indicate that motor cortex is at most partially overlapping with somatosensory cortex, whereas later studies indicate that motor cortex is completely overlapping with somatosensory cortex, but only in certain species. These differences could be due to techniques used, anesthetic effects, and species differences. For instance, studies in which the data appear to support a complete overlap were performed in two relatively primitive species, the Virginia opossum and the short-tailed opossum, both from the order Didelphimorphia. Furthermore, the restriction of thalamic projections from motor nuclei of the thalamus to S1 was observed only in the Virginia opossum. Thus, it may be that the order Didelphimorphia represents a more primitive state, and that modern Australian radiations have evolved motor cortex organization that more closely resembles that of most placental mammals.

The Evolution of Cortical Fields in Marsupials and Other Mammals

Comparative studies of sensory and motor neocortex in a number of marsupials indicate that despite differences in lifestyle, size, and phylogeny, all marsupials share a common plan of cortical organization (Figure 5). For somatosensory cortex, S1 and S2 are present in all marsupials investigated, as well as in placental and monotreme mammals. This suggests that these fields arose very early in mammalian

evolution and were retained in all lineages. Three other somatosensory fields (PV, SR3a, and SC/PP) have been identified in several marsupials, although in some species these fields are more primitive and poorly developed, such as in the Virginia opossum and the short-tailed opossum (Figures 5(a) and 5(b)). As in marsupials, area 3a in placental mammals is well developed in some species, such as primates, and poorly developed in other species, such as mice. Similarly, PP is present in placental mammals but has been greatly expanded in primates into a large area with numerous cortical fields. The presence of these fields in both marsupials and placentals, but not in monotremes (the presence of a separate S2 and PV in monotremes is unresolved), indicates that these fields arose after the monotreme radiation.

For visual cortex, V1 and V2 have been identified in all marsupial and placental mammals studied, indicating that both fields were present in the common ancestor. However, V2 is less well developed in some species than in others. V1 has been identified in monotremes, but V2 does not appear to be present in this group. This suggests that V2 arose after the monotreme radiation.

Although less work has been done on the organization of auditory cortex, A1 has been identified (electrophysiologically and/or architectonically) in all marsupials investigated, as well as in placental and monotreme mammals. The ubiquity of this field in all subclasses indicates that it was present in the earliest common ancestor.

Finally, the status of motor cortex in marsupials is contentious. However, when all data are examined it appears that two types of organization exist. The first type is represented in primitive marsupials, such as the order Didelphimorphia. In these animals, there appears to be a complete sensory-motor overlap in that S1 is coextensive with M1. In more advanced marsupials, such as the order Diprotodontia, S1 and M1 only partially overlap. The state of organization in the common ancestor of all mammals is difficult to deduce from existing data. However, when comparing data across species, we believe that the common ancestor had a complete sensory-motor overlap. In the three species of extant monotremes, which are highly derived, these fields became distinct. In early marsupials, this overlap was inherited from the common ancestor, and in some advanced marsupial lineages these fields have become more distinguished and now only partially overlap. We propose that in early placental mammals a sensory-motor overlap existed, and it still exists for some primitive groups such as insectivores. In other groups, such as rodents, these areas are partially separated, and in some groups, such as primates, these areas have completely separated.

Although similarities exist in the organization of the cortex across all mammalian species, there are several

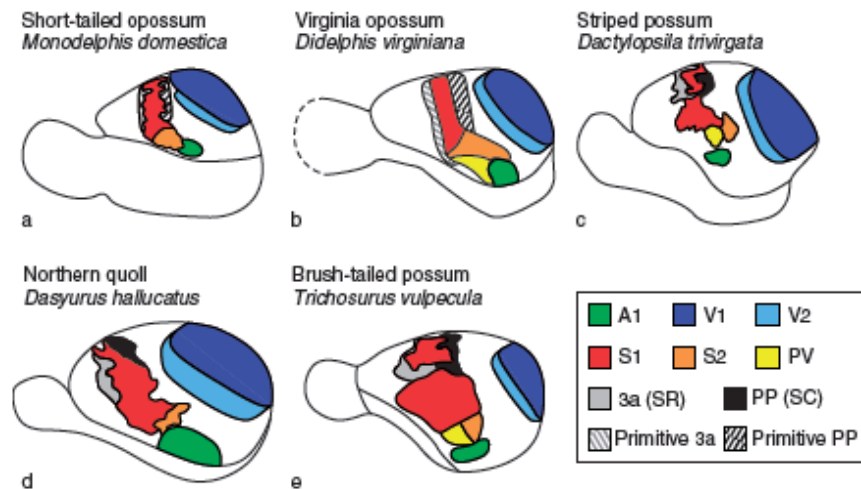


Figure 5 A summary of sensory neocortical organization in five marsupial species. Somatosensory areas S1 (red) and S2 (orange) have been identified in all marsupials (a–e) and all mammals. In some species, S2 has been subdivided into S2 and PV (yellow; (b, c, e). Two additional fields, 3a (gray) and PP (black), have also been identified (a–e), although in some species, such as the short-tailed opossum (a) and the Virginia opossum (b), these fields are more primitive (primitive 3a (gray striped) and primitive PP (black striped)). Visual areas V1 (dark blue) and V2 (light blue) have been identified in all marsupials (a–e); however V2 has only been fully described in the Northern quoll (d). Similarly, the primary auditory area A1 (green) has been identified in all marsupials (a–e) and all mammals; however, it has only been described in detail in the Northern quoll and brush-tailed possum (d, e). Rostral is to the left; medial is up. (a) Based on Huffman KJ, Nelson J, Clarey J, and Krubitzer L (1999) Organization of somatosensory cortex in three species of marsupials. *Dasyurus hallucatus*, *Dactylopsila trivirgata*, and *Monodelphis domestica*: Neural correlates of morphological specializations. *Journal of Comparative Neurology* 403: 5–32; Frost SB, Milliken GW, Plautz EJ, Masterton RB, and Nudo RJ (2000) Somatosensory and motor representations in cerebral cortex of a primitive mammal (*Monodelphis domestica*): A window into the early evolution of sensorimotor cortex. *Journal of Comparative Neurology* 421: 29–51; Kahn DM, Huffman KJ, and Krubitzer L (2000) Organization and connections of V1 in *Monodelphis domestica*. *Journal of Comparative Neurology* 428: 337–354. (b) Beck PD, Pospichal MW, and Kaas JH (1996) Topography, architecture, and connections of somatosensory cortex in opossums: Evidence for five somatosensory areas. *Journal of Comparative Neurology* 366: 109–133. (c) Huffman KJ, Nelson J, Clarey J, and Krubitzer L (1999) Organization of somatosensory cortex in three species of marsupials. *Dasyurus hallucatus*, *Dactylopsila trivirgata*, and *Monodelphis domestica*: Neural correlates of morphological specializations. *Journal of Comparative Neurology* 403: 5–32. (d) Rosa MG, Krubitzer LA, Molnar Z, and Nelson JE (1999) Organization of visual cortex in the Northern quoll, *Dasyurus hallucatus*: Evidence for a homologue of the second visual area in marsupials. *European Journal of Neuroscience* 11: 907–915. (e) Elston GN and Manger PR (1999) The organization and connections of somatosensory cortex in the brush-tailed possum (*Trichosurus vulpecula*): Evidence for multiple, topographically organized and interconnected representations in an Australian marsupial. *Somatosensory Motor Research* 16: 312–337 and Huffman KJ, Nelson J, Clarey J, and Krubitzer L (1999) Organization of somatosensory cortex in three species of marsupials. *Dasyurus hallucatus*, *Dactylopsila trivirgata*, and *Monodelphis domestica*: Neural correlates of morphological specializations. *Journal of Comparative Neurology* 403: 5–32.

differences in cortical field organization that relate to species-specific lifestyle. The first is a difference in the amount of cortex devoted to a particular sensory system. For example, in the Northern quoll (Figure 5(d)), visual cortex and auditory cortex are relatively large compared to the size of somatosensory cortex. This may be related to the Northern quoll's carnivorous lifestyle; it is an agile hunter and likely coordinates both auditory and visual information to capture prey. Conversely, the brush-tailed possum, which is a phalanger with a well-developed hand, typically eats leaves and flowers and has a larger somatosensory cortex than either visual or auditory cortex (Figure 5(e)). The second difference between species is the cortical magnification of behaviorally relevant sensory surfaces. For example, in the striped possum the representations

of the fourth digit and the tongue are relatively large compared to other body part representations within S1 and compared to similar representations in S1 of other species. In the striped possum, the fourth digit and the tongue are both used in their specialized feeding behavior. In the Tammar wallaby, one of only three diurnal marsupials, an enlarged representation of central vision is present within V1, as compared to the organization of V1 in nocturnal marsupials. Finally, high-frequency representations are relatively large in the Northern quoll, and these frequencies match the vocalization frequencies of predators and prey of this species.

The types of adaptations that have been made to cortical fields in marsupials are remarkably similar to those described in placental mammals. This is not

surprising given that marsupials, like placental mammals, have undergone significant radiations during evolution and have diversified greatly, particularly in Australia. This diversification consists of a wide array of morphological, behavioral, and cortical specializations. Many of the morphological and behavioral specializations are associated with patterns of activity (diurnal vs. nocturnal), habitat selection (arboreal, terrestrial, aquatic, or subterranean), and diet (carnivorous, herbivorous, omnivorous, or frugivorous). The similarities in cortical field organization indicate that there are large constraints imposed on evolving systems and that similar solutions to environmental challenges have independently emerged.

See also: Comparative Neurobiology: History; Evolution of Vertebrate Brains.

Further Reading

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