

15. Andreu MJ, Dávila JC, Real MA, Guirado S (1996) Intrinsic connections in the anterior dorsal ventricular ridge of the lizard *Psammotrochus algirus*. *J Comp Neurol* 372:49–58
16. Hoogland PV, Vermeulen-Vanderzee E (1995) Efferent connections of the lateral cortex of the lizard *Gekko gekko*: evidence for separate origins of medial and lateral pathways from the lateral cortex to the hypothalamus. *J Comp Neurol* 352:469–480
17. Hoogland PV, Vermeulen-Vanderzee E (1989) Efferent connections of the dorsal cortex of the lizard *Gekko gekko* studied with *Phaseolus vulgaris*-leucoagglutinin. *J Comp Neurol* 285:289–303
18. Martínez-García F, Amiguet M, Schwerdtfeger WK, Olucha FE, Lorente MJ (1990) Interhemispheric connections through the pallial commissures in the brain of *Podarcis hispanica* and *Gallotia stehlinii* (Reptilia, Lacertidae). *J Morphol* 205:17–31
19. Rodríguez F, López JC, Vargas JP, Gómez Y, Broglio C, Salas C (2002) Conservation of spatial memory function in the pallial forebrain of reptiles and ray-finned fishes. *J Neurosci* 22:2894–2903
20. Day LB, Crews D, Wilczynski W (2001) Effects of medial and dorsal cortex lesions on spatial memory in lizards. *Behav Brain Res* 118:27–42
21. Davies DC, Martínez-García F, Lanuza E, Novejarque A (2002) Striato-amygdaloid transition area lesions reduce the duration of tonic immobility in the lizard *Podarcis hispanica*. *Brain Res Bull* 57:537–541
22. Keating EG, Kormann LA, Horel JA (1970) The behavioral effects of stimulating and ablating the reptilian amygdala (*Caiman sklerops*). *Physiol Behav* 5:55–59

Evolution of Association Pallial Areas: Parietal Association Areas in Mammals

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Definition

Posterior parietal cortex is a large region of cortex that lies between somatosensory and primary cortices. In some mammals such as primates, it contains a number of cortical fields whose functions include coding the spatial location of objects within both egocentric and extrinsic frames of reference, and in generating an internal representation of the body that contributes to a “sense of self,” “body schema,” or “body image.” While the posterior parietal association areas are well developed in primates, likely in conjunction with specialized

hand use, some of these areas may be present in a primitive form in other mammals. A similarly located region of cortex has been identified in rodents, carnivores, hedgehogs, tenrecs, and opossums.

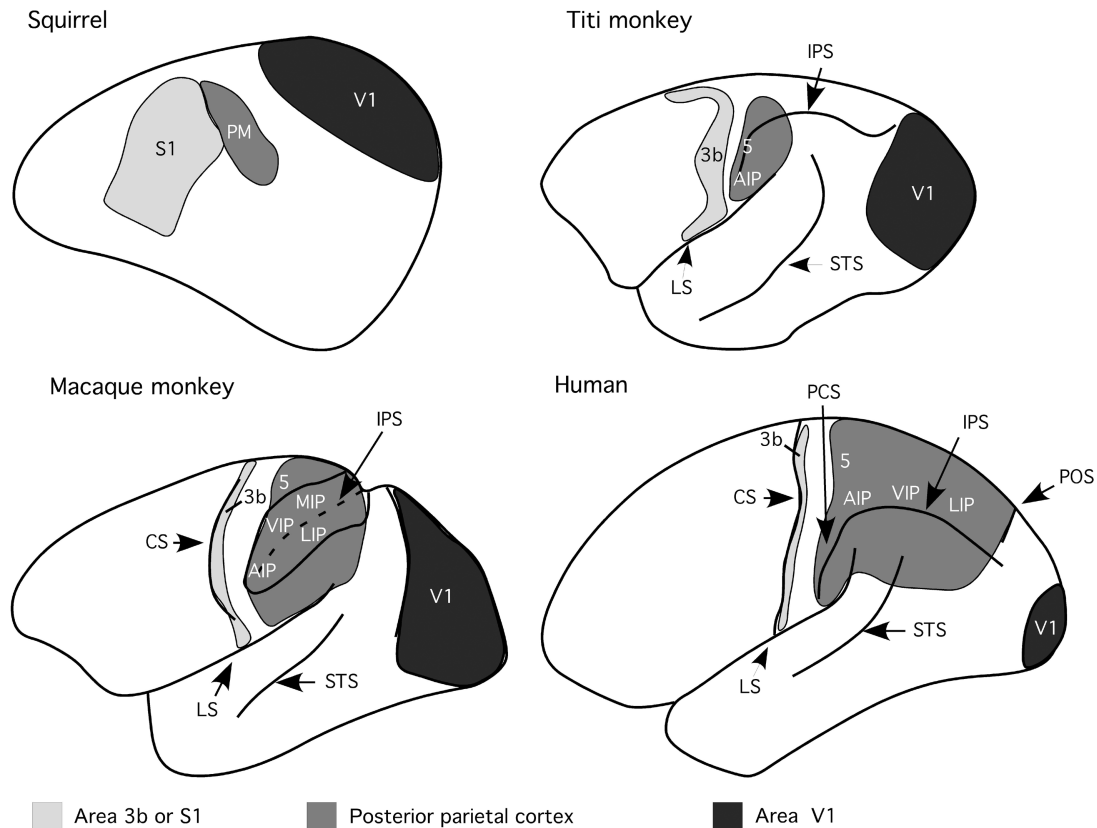
Characteristics

All mammals actively explore their environment with specialized body parts that contain unique arrangements of various types of sensory receptors. It has been proposed that the complex motor sequences involved in exploration require an internal representation of the body, a knowledge of what constitutes the body or self, and a knowledge of what constitutes the external world, which includes animate and inanimate objects (see [1]). The region of the neocortex that is thought to generate these complex abilities is the posterior parietal association cortex, which has greatly expanded in human and nonhuman primates. Because an internal representation of the body is necessary in order to interact appropriately with the external environment, it is likely that all mammals have portions of their brain devoted to generating such an internal representation. Unfortunately, little is known about posterior parietal association cortex in mammals other than primates and whether there are fundamental features of the mammalian neocortex that give rise to this internal framework or “sense of self.”

Introduction: Posterior Parietal Cortex as an Association Area

The neocortex is a uniquely mammalian structure that comprises a large portion of the brain and is responsible for the higher order sensory, perceptual, and cognitive behaviors. In several lines of descent such as primates, cetaceans, and elephants the neocortex has disproportionately expanded compared to the rest of the brain, and much of this expansion appears to be due to an increase in the number of higher-order association areas. Traditionally the mammalian neocortex has been divided into three broad categories including motor cortex, sensory cortex, and association cortex. Association cortex, as defined by many modern text books, includes temporal, prefrontal, and posterior parietal cortex, and is hypothesized to mediate complex behaviors such as perception, attention, cognition, and other high level mental functions. The definition of what constitutes association cortex is based on the premise, which emerged from earlier mapping studies of Woolsey [2] (e.g., 1958), that the amount of cortex that could not be defined as unimodal sensory cortex in primates was relatively large compared to other mammals (Fig. 1).

Because primates are thought to have a larger repertoire of higher level or cognitive behaviors than other mammals, this expanded cortex became associated with higher mental processes and was considered a primate phenomenon.



Evolution of Association Pallial Areas: Parietal Association Areas in Mammals. Figure 1 Illustrations of the location of posterior parietal cortex, PP (dark grey), in several different mammals including squirrels, non-human primates and humans. Although the relative location of PP, between S1 (light grey) and V1 (black), is maintained in the different species, the amount of cortex devoted to PP, and the number of subdivisions within PP has changed in different mammals. Further, this cortex has greatly expanded in anthropoid primates including macaque monkeys and humans.

However, the early mapping studies, which provided support for these ideas, were hampered by technical problems, which made it difficult to elicit responses from neurons in cortex other than primary and secondary sensory fields. Despite these limitations, these early studies generated several long held tenants regarding sensory and association cortex. Probably the most noteworthy was that primary fields are evolutionarily older, and that association cortex is a new evolutionary phenomenon found mainly in human and non-human primates. Thus, the expansion of association cortex was proposed to be the hallmark of human brain evolution.

The view of a hugely expanded association cortex in primates was upended by work in the early 1970s by Allman and Kaas [3] who demonstrated that much of extrastriate cortex in non-human primates that was considered to be association cortex actually contained a number of unimodal visual areas. Somewhat later, portions of parietal and temporal cortex previously thought to be association regions were similarly

reassigned as unimodal somatosensory and auditory cortical fields, respectively (see [4] for review). Although we now appreciate that much of the expanded neocortex in mammals such as primates actually contains sensory areas, there are still a few regions of the neocortex that are considered to be association areas, one of which is the posterior parietal cortex.

Posterior parietal cortex appears to be involved in coding the spatial location of objects within both egocentric and extrinsic frames of reference (e.g., [5]). Much of the region traditionally defined as posterior parietal association cortex has likely evolved in primates for the generation of specialized hand use, such as manual dexterity, bimanual coordination, and visually-guided reaching and grasping. Such behavior requires an internal representation of the body that allows some species-specific effector, such as the hand in primates, to interact with objects in their surroundings. This internal coordinate system of the body contributes to what has variously been termed “sense of self,” “body schema,” and “body image.” Currently it is unclear whether other mammals

possess neocortical areas homologous to the posterior parietal areas in primates.

Posterior Parietal Cortex in Primates

Posterior parietal cortex in primates is located within and around the intraparietal sulcus, approximately midway between primary visual cortex (V1) and primary somatosensory cortex (3b; Fig. 1). Most work on posterior parietal areas comes from studies in macaque monkeys. In these primates, posterior parietal fields including areas 5, 7, the medial intraparietal area (MIP), the lateral intraparietal area (LIP), and the ventral intraparietal area (VIP) are thought to be involved in visuospatial processing including monitoring limb location during visually guided reaching tasks, converting sensory locations into motor coordinates for intentional movement, and perceiving the movements of the body in extrapersonal space (e.g., [5–7]). Multiunit electrophysiological studies indicate that neurons in area 5 respond to stimulation of deep receptors of the contralateral and sometimes ipsilateral body, and that area 5 is dominated by the representation of the hand and forelimb, (Fig. 3; e.g., [8]).

Some posterior parietal areas, including area 5, are more densely connected with motor cortical fields than with somatosensory or visual cortical fields. (e.g., [6,8]; Rizzolatti et al., 1998). Indeed, recent work by Stepniewska et al. [9] has shown that posterior parietal association cortex has important motor functions. Microstimulation of rostral regions of posterior parietal cortex in galagos, including area 5, evoked what the authors term “ethologically significant behaviors.” These behaviors included defensive behavior, reaching, hand to mouth movements, and aggressive behaviors. It is apparent from these studies that posterior parietal areas may be specialized motor integrators that allow the internal or animal-centered states to interface with and explore the external world.

Work in posterior parietal cortex of other primates besides macaques is restricted to a few species, but most studies indicate that New World Monkeys and prosimians have significantly less posterior parietal cortex than Old World macaque monkeys (Fig. 1; [10]). Posterior parietal areas caudal to area 3b in galagos and marmosets are less extensive than those of macaques (e.g., [10,11]). Recent work in titi monkeys indicates that area 5 appears to be present, but the amount of cortex it occupies is relatively small compared to macaque monkeys [8]. One common feature of posterior parietal cortex, specifically area 5, in all primates, is an increased representation or cortical magnification of ecologically relevant effectors, such as the hand (Fig. 2).

Another feature that most primates share is dense connectivity between posterior parietal, motor, and premotor areas, and orbitofrontal cortex and the lateral posterior and lateral dorsal nuclei of the thalamus.

Posterior Parietal Cortex in Non-Primate Mammals

Although the organization of posterior parietal cortex, defined here as cortex caudal to primary somatosensory cortex (S1) and rostral to the second visual area (V2), is not well understood in most non-primate mammals, the existing data indicate that multimodal cortex is present in the same general region as posterior parietal cortex in primates (Fig. 3).

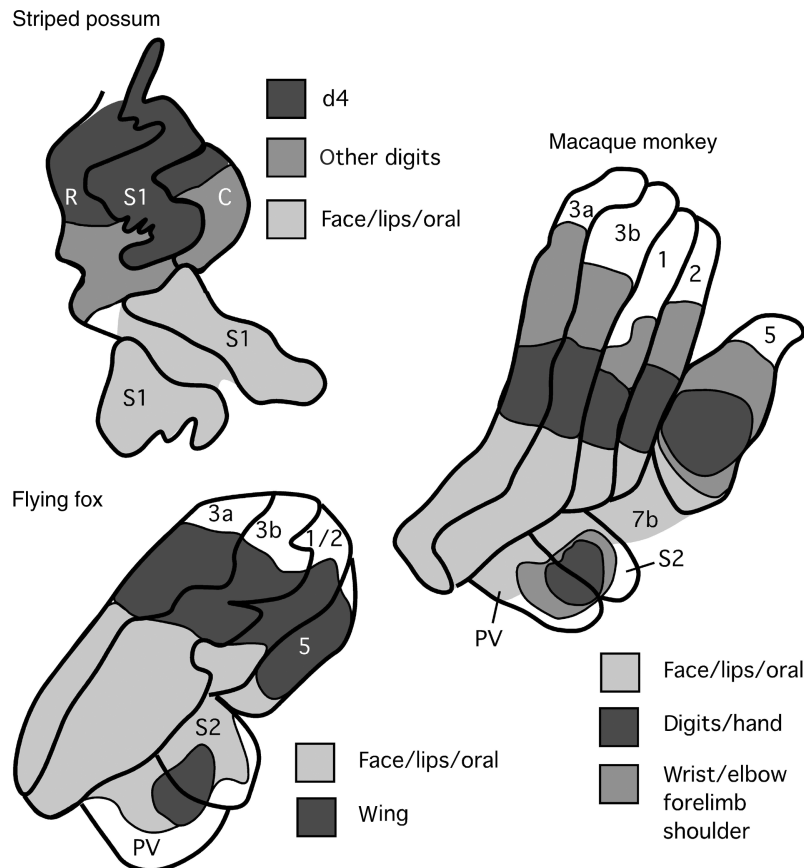
Recent studies in rodents demonstrate that they are capable of dexterous manipulations of objects (for review, Whishaw, [12] 2003). These manipulations include reaching for items in front of the animal, and using combinations of digits to hold and orient food items. It has been suggested that skilled forelimb movements may in fact be a phylogenetically old behavior that developed in early tetrapods (e.g., [12]). If this is the case, then the neural substrate for these skilled forelimb movements, which in primates appears to be posterior parietal cortex, must also be phylogenetically old, and should be observed in a wide range of mammalian species other than primates.

Studies of cortical regions in rodents that may be involved in these behaviors are limited to rats and squirrels. In rats, anatomical studies indicate that there is a posterior parietal area termed PPC (Fig. 3), and that thalamocortical connections of PPC originate from nuclei such as the lateral posterior and lateral dorsal nucleus (e.g., [13]). Homologous thalamic nuclei project to posterior parietal cortex in primates (e.g., [14]). In addition to projections from sensory areas of the neocortex, PPC in rats receives inputs from other association cortical areas such as the ventrolateral and medial orbital areas, and medial agranular cortex.

In squirrels, a region of cortex caudal to S1, termed the posterior medial (PM) area, is interconnected with S1 and contains neurons that respond to stimulation of deep receptors (Fig. 3). Further, PM/PPC is dominated by the representation of the forelimb (e.g., [15]). Based upon location, connections, and neural responsiveness, it seems likely that this region in rodents is involved in at least some of the intentional and skilled behaviors of the forepaw studied by Whishaw and colleagues.

In addition to primates and rodents, there is evidence that posterior parietal cortex has common features across all mammalian taxa (Fig. 3). For example, in carnivores such as ferrets, overlapping maps of visual and somatosensory responsiveness within a rostral posterior parietal zone have been described [16]. In cats, a zone of cortex caudal to area 3b contains neurons that respond to both deep and cutaneous somatosensory stimulation, and an area 5 similar to that observed in primates has been described (e.g., [17]).

In marsupials such as the short tailed opossum, striped possum, native cat and Virginia opossum, a small multimodal band of cortex is present between S1 and V1, and is termed C or SC (e.g., [18,19]). Likewise in



Evolution of Association Pallial Areas: Parietal Association Areas in Mammals. Figure 2 The somatotopic organization of anterior (3a, 3b, 1 and 2) and posterior parietal area 5 in several species of mammals. Although some mammals have increased the number of somatosensory areas such as area 3a, 1 and 2 in primates, all mammals have similar features of organization of anterior and posterior parietal area. The most noteworthy feature here is an expanded representation of behaviorally relevant body structures (noted in different species by different shades of grey). These include D4 and oral structures in the striped possum, the wing and oral structures in the flying fox, and the hand, shoulder and oral structures in the macaque monkey.

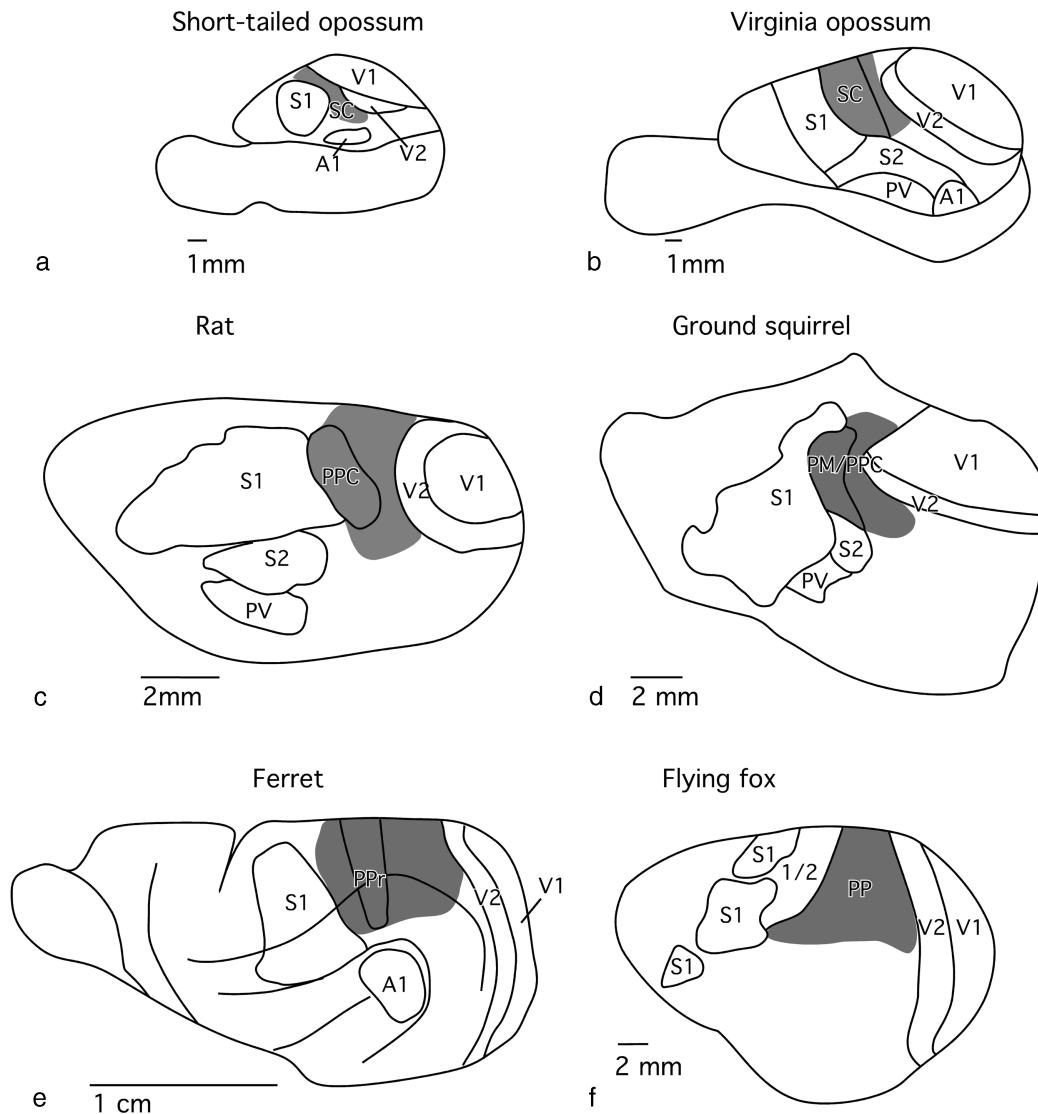
hedgehogs and tenrecs, a narrow band of cortex in the location of posterior parietal cortex has been identified, and neurons in this region respond to visual and/or to auditory stimulation, to stimulation of cutaneous somatosensory receptors (i.e., deflection of quills), and/or to visual stimulation [20]. Species such as the flying fox have a cortical field termed PP, which is immediately caudal to area 1/2. Neurons in PP respond to stimulation of deep receptors as well as to visual stimulation, and PP has connections with area 1/2 (e.g., [21]).

As with area 5 in primates, electrophysiological recording studies of posterior parietal cortex in other mammals indicate that there is an extreme magnification of ecologically relevant body parts (Fig. 2). For example, in rats and squirrels, this cortex is dominated by the representation of the forepaw. In marsupials such as the striped possum, with its specialized fourth digit, this cortex contains a large representation of D4 [19].

Another feature common to PPC and area 5 is that neurons in this region of cortex respond to stimulation of deep somatic receptors and often to visual stimulation as well. Finally, as in primates, in the few studies in which the connections of PPC have been investigated in non-primates, strong connections are observed with motor cortex, orbitofrontal cortex, and the lateral posterior and lateral dorsal nuclei of the thalamus.

The Evolution of Posterior Parietal Cortex

The presence of PPC in both New World and Old World monkeys, and a rudimentary form of PPC in most non-primate mammals studied suggests that this region of cortex arose early in mammalian evolution and has been retained in most or all species of this class (Fig. 4). If this is the case, then the long-held belief that PPC is a newly evolved region of cortex observed only in primates needs to be re-evaluated.

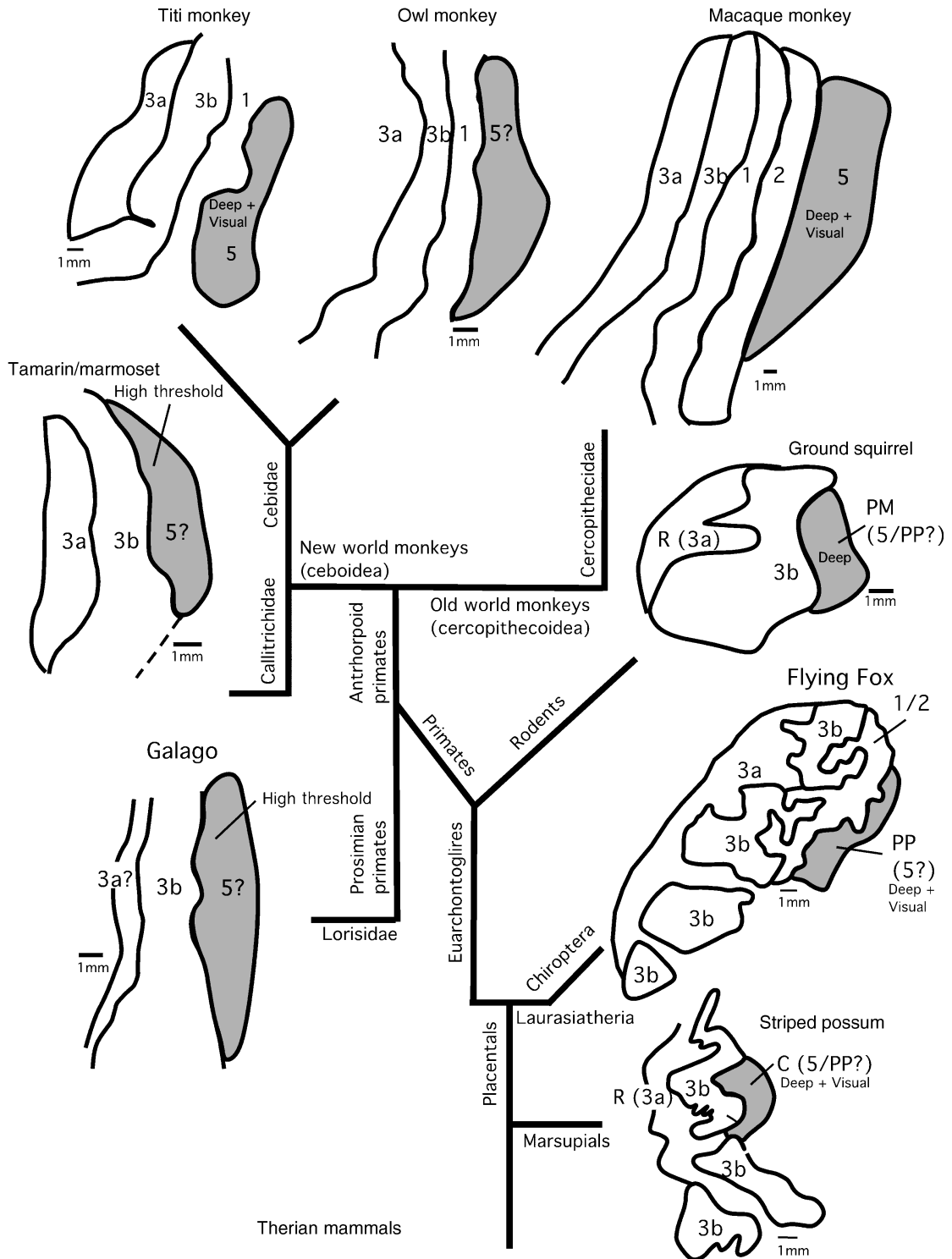


Evolution of Association Pallial Areas: Parietal Association Areas in Mammals. Figure 3 The location of the proposed homologue of PP (grey) in different non-primate mammals. In marsupials such as the short-tailed opossums (a) and the *Virginia opossum* (b) a field termed SC resides between S1 and V1 and neurons here are responsive to somatic and visual stimulation. In rodents such as rats (c) and ground squirrels (d) a field termed PPC and PR respectively is located just adjacent to S1 and as in marsupials, neurons in this region are responsive to visual and somatic stimulation. Posterior parietal cortex has been less well explored in other species such as ferrets (e) and flying foxes (f), but limited data indicate that these animals also have PP. Note that in small brained animals, PP is immediately adjacent to S1 and V1, and in mammals with larger brains such as ferrets, the PP does not appear to abut primary sensory areas.

While all mammals, including primates, appear to have regions of the neocortex associated with generating an internal frame of reference, in primates, new sensory areas such as anterior parietal fields 1 and 2 (Fig. 4) have been added, new connections have formed, and existing posterior parietal cortical areas associated with visually guided hand use have been elaborated.

All of these factors may ultimately have led to the emergence of a more refined internal representation of

self and increased the ways in which this internal representation interacts with objects in extra-personal space via the hands. Thus, the evolution of multiple sensory areas and an expansion of cortex devoted to hand use may be the hallmark of primate evolution. This species-specific internal representation is not a property that emerged in anthropoid primates alone but is a dynamic sensorimotor loop that all mammals possess in a derived form based on their morphological



Evolution of Association Pallial Areas: Parietal Association Areas in Mammals. Figure 4 A cladogram depicting the phylogenetic relationship of different species and the location of posterior parietal area 5 (grey) relative to anterior parietal fields. Note that in New World and Old World monkeys such as titi, owl and macaque monkeys, new sensory areas have been interspersed between evolutionary older fields such as 3b (S1) and posterior parietal areas (PP or area 5).

distinctions and distribution of sensory receptors. In primates and some rodents, the morphology in question is that of the hands and the behaviors associated with the use of the hands to explore and interact with the external environment. In other mammals, exploratory behavior may involve morphological structures such as a snout, bill, or nose follicle. Regardless of the effector organ, all of these behaviors require an internal frame of reference and specialized motor programs that allow efficient interface between the effector and the external world. Studies of connections as well as electrophysiological recording data indicate that PPC does have strong interconnections with motor areas of the cortex. This suggests that the motor system plays a critical role in generating an internal frame of reference which enables all animals to distinguish self from non-self, an attribute traditionally delegated solely to association cortex in primates.

References

- Krubitzer L, Disbrow E (2007) The evolution of parietal areas involved in hand use in primates. In: Kaas J, Gardner E (eds) *The senses: a comprehensive reference*, vol 5, Somatosensation, Academic Press, Oxford
- Woolsey CN (1958) Organization of somatic sensory and motor areas of the cerebral cortex. In: Harlow HF, Woolsey CN (eds): *Biological and biochemical bases of behavior*. University of Wisconsin Press, Madison, pp 63–82
- Allman JM, Kaas JH (1971) A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res* 31:85–105
- Kaas JH, Collins CE (2004) The resurrection of multimodal cortex in primates: connection patterns that integrate modalities. In: Calvert G, Spence C, Stein BE (eds) *Handbook of multisensory processing*. MIT Press, Cambridge
- Peseran B, Nelson MJ, Andersen RA (2006) Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron* 51:125–134
- Kalaska JF (1995) Parietal cortex area 5 and visuomotor behavior. *Can J Physiol Pharmacol* 74:483–498
- Fogassi L, Luppino G (2005) Motor functions of the parietal lobe. *Curr Opin Neurobiol* 15:626–631
- Padberg J, Disbrow E, Krubitzer L (2005) The organization and connections of anterior and posterior parietal cortex in titi monkeys: do new world monkeys have an area 2? *Cereb Cortex* 15:1938–1963
- Rizzolatti G, Luppino G, Matelli M (1998) The organization of the cortical motor system: new concepts. *Electroenceph clin Neurophysiol* 106:282–296
- Stepniewska I, Fang PC, Kaas JH (2005) Microstimulation reveals specialized subregions for different complex movements in posterior parietal cortex of prosimian galagos. *Proc Natl Acad Sci USA* 102(13):4878–4883
- Huffman KH, Krubitzer L (2001) Area 3a: topographic organization and cortical connections in marmoset monkeys. *J Comp Neurol* 435:291–310
- Whishaw IQ (2003) Did a change in sensory control of skilled movements stimulate the evolution of the primate frontal cortex? *Behav Brain Res* 146:31–41
- Reep RL, Chandler HC, King V, Corwin JV (1994) Rat posterior parietal cortex: topography of corticocortical and thalamic connections. *Exp Brain Res* 100:67–84
- Yeterian EH, Pandya DN (1985) Corticothalamic connections of the posterior parietal cortex in the rhesus monkey. *J Comp Neurol* 237:408–426
- Slutsky DA, Manger PR, Krubitzer L (2000) Multiple somatosensory areas in the anterior parietal cortex of the California ground squirrel (*Spermophilus beecheyii*). *J Comp Neurol* 416:521–539
- Manger PR, Masiello I, Innocenti GM (2002) Areal organization of the posterior parietal cortex of the ferret (*Mustela putorius*). *Cereb Cortex* 12:1280–1297
- Dykes RW, Rasmusson DD, Hoeltzell PB (1980) Organization of primary somatosensory cortex in the cat. *J Neurophysiol* 43:1527–1546
- Beck PD, Pospichal MW, Kaas JH (1996) Topography, architecture, and connections of somatosensory cortex in opossums: Evidence for five somatosensory areas. *J Comp Neurol* 366:109–133
- Huffman K, Nelson J, Clarey J, Krubitzer L (1999) The organization of somatosensory cortex in three species of marsupials, *Dasyurus hallucatus*, *Dactylopsila trivirgata*, and *Monodelphis domestica*: Neural correlates of morphological specializations. *J Comp Neurol* 403:5–32
- Krubitzer LA, Künzle H, Kaas JH (1997) Organization of sensory cortex in a Madagascan insectivore, the tenrec (*Echinops telfairi*). *J Comp Neurol* 379:399–414
- Krubitzer LA, Calford MB, Schmid LM (1993) Connections of somatosensory cortex in megachiropteran bats: the evolution of cortical fields in mammals. *J Comp Neurol* 327:472–506

Evolution of Auditory System in Anamniotes

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Definition

The ascending auditory system comprises the receptor apparatuses, sensory ganglia and central pathways that detect and convey auditory stimuli into and through the brain. It is not known whether jawless fishes (lampreys and hagfishes) hear. Across jawed vertebrates, the auditory system exhibits diversity in its auditory receptors and central nuclei but a common pattern of organization of its central ascending pathways (Fig. 1). Jawed fishes hear using ► **otolith endorgans** – the saccule, lagena and utricle – and the non-otolithic macula neglecta may