Chapter 3
The Evolution of Mammalian Brains from Early Mammals to Present-Day Primates

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Abstract The changes in brains as they evolved from early mammals to modern humans involved a great expansion of overall brain size and especially neocortex. Early mammals were small, and their small brains had a proportionately small cap of neocortex divided into approximately 20 functionally distinct areas. Numbers of areas and the size of the cortical sheet increased with the first primates and contained 40–50 cortical areas. Overall the six million years of the evolution of modern humans from early bipedal apes, brains evolved from a great ape size of 400 cc to roughly 1400 cc, with neocortex having an estimated 200 cortical areas occupying 80% of the brain. This cortical mass of 16 billion neurons, together with a high level of hemispheric specialization, appears to be critically involved in mediating the impressive cognitive abilities of modern humans.

Keywords Cortical areas • Thalamus • Marsupials • Monotremes • Prosimians • Monkeys • Apes • Humans

3.1 Introduction

The brains of the 5400 or so species of present-day mammals vary greatly in structure and function, especially at the level of the neocortex. Early mammals of 250 million years ago (mya) were cat or rat or even smaller in size (O'Leary et al. 2013; Rowe et al. 2011; Smith et al. 2010), and they had small brains with proportionately less neocortex than in most extant mammals (Kielan-Jaworowska et al. 2004; Rowe et al. 2011). Many of the early mammals were near the sizes of the smallest of extant mammals, meaning that they were near the lower limit in size for mammals (Schmidt-Nielson 1984), and evolved variations in body size were largely restricted

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to larger sizes (Cope's rule; Baker et al. 2015; Smith et al. 2010). Larger body sizes are generally associated with larger brains (Jerison 1973), and larger brains present more opportunities for the evolution of impressive variations. Most notably, larger brains within a clade have more neurons (e.g., Herculano-Houzel et al. 2007) and may have more cortical areas (Brodmann 1909; Kaas 2008; Van Essen et al. 2012a, b). However, even mammals with relatively small brains sometimes have specialized systems and areas that are impressively unique (Kaas 2011a). Modifications of the somatosensory system of the duck-billed platypus for mediating electroreception in addition to touch (Krubitzer et al. 1995) and the auditory system for echolocation in microbats (Covey 2005) are good examples. Here, we start with a reconstruction of the brains and especially the neocortex of early mammals, based on evidence from the fossil record and from comparative studies of the brains of extant mammals. Then, we consider the likely organization of the brains of placental mammals that are most closely related to primates, and the inferred organization of the brains of early primates, early anthropoid primates, and finally apes and humans. Thus, we closely follow a single line of mammalian evolution while necessarily neglecting other interesting lines and their outcomes. Yet, a focus on the evolution of modern human brains is quite justified, in part by our general interest in ourselves, and how we got here, and in part because this interest has generated a lot of relevant studies of how primate brains are organized.

3.2 Early Mammals

Early mammals evolved from one line of stem amniotes (those able to lay eggs on dry land), the synapsid clade that gave rise to early "mammal-like reptiles" and then early mammals some 200 or more mya, with only mammals as surviving members. The other surviving branch from stem amniotes, the sauropsid clade, gave rise to present-day reptiles and birds. The emergence of one part of the brain, the neocortex, has been considered a mammalian innovation, but that is not fully correct, as neocortex is homologous with the dorsal cortex of reptiles and wulst of birds (Butler and Hodos 2005). Yet, stem amniotes, some 340 mya, likely had something like the dorsal cortex of reptiles, which seems to have changed little in most reptiles while becoming a thick mass of neurons in birds. In contrast, over the course of the evolution of the synapsid ancestors of early mammals, the small, thin cap of forebrain dorsal cortex, likely consisting a single layer of pyramidal neurons with a scattering of small, mostly inhibitory neurons as in reptiles (Shepherd 2011), was transformed into the thick, multilayered neocortex that has been retained by all extant mammals. Other parts of cortex became the piriform (olfactory) cortex and the hippocampus of mammals.

The primitive neocortex presented a fantastic opportunity for further modification in the decedents of early mammals, as the laminar organization of neocortex allowed for the functional specialization and differentiation of layers, while modular specialization of sets of neurons across depth of cortex also added considerable flexibility (Kaas 2012). Most importantly, neocortex could be subdivided into an increasing number of cortical areas, the so-called organs of the brain (Brodmann 1909), as brains got bigger and had more neurons. The various specializations of these areas and the ability to process information in a series of steps from cortical area to cortical area permitted the evolution of cortical systems with impressive computational powers. The computational flexibility of neocortex suggests why the proportion of brains that consisted of neocortex increased in many lines of mammal evolution, as brains get bigger, and the large brains of humans are 80% neocortex (Hofman 1988; Azevedo et al. 2009; Herculano-Houzel 2012). Thus, much of this review is on the enlargement and areal organization of neocortex in evolution. Developmentally, neocortex emerges late, and extending the generation period of neocortical neurons has been a major mechanism of neocortical enlargement in evolution (Finlay and Darlington 1995).

Our present understanding of the organization of neocortex in early mammals depends on part on the inferences that can be made from the fossil record. The endocasts of skulls indicate that early mammals had small brains with little neocortex, but with relatively large olfactory bulbs and olfactory (piriform) cortex (Kielan-Jaworowska et al. 2004). These early mammals had small eyes and were likely nocturnal and feeding on insects and small vertebrates (e.g., Rowe et al. 2011). The small eyes promoted the nocturnal bottleneck theory (see Hall et al. 2012) that suggested a loss of adaptations for photopic vision. This perhaps resulted in a shift of the focus of visual processing from the optic tectum of reptiles and birds and the superior colliculus of mammals to the visual cortex of mammals (Diamond and Hall 1969). Major adaptations of these early mammals included the evolution of high-frequency hearing (Coleman and Boyer 2012; Allman 1999), the evolution of tactile vibrissae for the detection of nearby objects (Muchlinski 2010), and the domination of olfaction (Streidter 2005).

The small cap of neocortex that was revealed by the most favorable endocasts of the sculls of early mammals was likely subdivided into a small number of cortical areas, but the fossil record does not reveal these subdivisions. However, some of the major fissures of neocortex of mammals with large brains are sometimes revealed, and they may indicate aspects of functional organization (e.g., Radinsky 1976). Inferences about the internal anatomical and functional organizations of the neocortex and brains of early mammals are necessarily based on comparative studies of the brains of extant mammals. In that regard, the most informative studies are likely to be from mammals with small brains, and few obvious behavioral specializations, thus resembling early mammals (Kaas 2016). Common features of brain organization across members of the six major clades of the mammalian radiation likely reflect those that have been retained from early common ancestors (Kaas 2011b).

Comparative studies of the areal organization of neocortex have revealed a number of consistent features (Fig. 3.1). For example, all studied mammals have a primary somatosensory area, S1, including mammals with little neocortex (e.g., Catania et al. 1999). There is good evidence from many such mammals that narrow strips of cortex along the rostral and caudal borders of S1 have patterned connections with S1 and thus are somatosensory (e.g., Ebner and Kaas 2015). In addition,

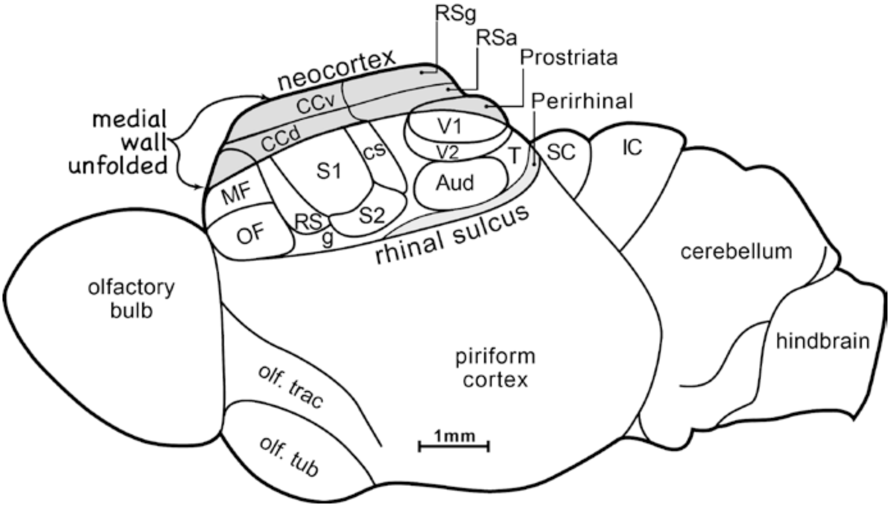

Fig. 3.1 The proposed organization of the neocortex of early mammals. Note the dominance of the large olfactory system, the small cap of neocortex that fails to cover the midbrain, and the lack of motor and premotor areas, as well as a lack of a corpus callosum. Somatosensory areas, with motor functions, included a primary area, S1; a second area, S2; possibly a parietal ventral area, PV; rostral and caudal somatosensory areas, RS and CS; possibly a gustatory area, G; and a small region of posterior parietal cortex. Visual areas included primary and second areas, V1 and V2, prostriata, and a temporal visual area, T. Prefrontal cortex included medial and orbital divisions, MF and OF. Cortex of the medial wall of the cerebral hemisphere included dorsal and ventral divisions of cingulate cortex, CCd and CCv, and granular and agranular divisions of retrosplenial cortex, RSq and RSa. A larger hippocampus (not shown) folded under from medial-caudal entorhinal cortex

the region of the second somatosensory area, S2, has been found to consist of two areas, S2, and parietal ventral area, PV, at least in most mammals (e.g., Remple et al. 2003; Beck et al. 1996). Thus, the neocortex of early mammals likely contained four or five somatosensory areas. While a gustatory region or area, G, has not been studied in many mammals, such an area likely existed in early mammals. All studied mammals also have a region of lateral cortex that responds to sounds and has the architectonic features of primary auditory cortex. However, it is not clear from the limited comparative evidence if early mammals had more than one primary area, as well as other auditory areas, as even small mice have several auditory areas (Kaas 2011c). Primary visual cortex, V1 or area 17, appears to be present in all or most mammals, although it can be reduced to a narrow strip of cortex with few or no visual function in mammals that live underground, such as the “blind” mole rat (Cooper et al. 1993). A second visual area, V2, a small visual area on the medial border of V1, area prostriata, and a visual portion of temporal cortex have all been widely identified across mammals (Rosa and Krubitzer 1999).

Only a few other cortical areas have been widely recognized across members of the major braches of the mammalian radiation. These areas include the architectonically distinct granular and agranular retrosplenial areas, RSa and RSag; dorsal and ventral subdivisions of cingulate cortex, CCd and CCv; and medial and orbital divisions of prefrontal cortex, MF and OF. The perirhinal cortex likely had functional divisions, and the endorhinal cortex was present next to the hippocampus. Overall, the early common ancestors of all extant mammals have roughly 20 cortical areas and possibly more. As the cap of neocortex of early mammals was small, and the proper functioning of any cortical area depends on being large enough to contain all the neurons needed for its function (Kaas 2000), early mammals had few cortical areas. However, some small extant mammals even appear to have lost some areas in comparison to ancestors (Catania et al. 1999).

3.3 Placental Mammals

Early mammals slowly started to diverge soon after they emerged, with the monotreme line separating from the marsupial plus placental line about 165 mya and the marsupials from the placentals some 130–150 mya (Bininda-Emonds et al. 2007; Nilsson et al. 2010). The four placental superorders (Afrotheria, Euarchontoglires, Laurasiatheria, and Xenarthra) separated about 100 mya, and most of the orders of extant mammals were established by 85 mya, with some members surviving the mass extinction event 65 mya. Overall, the major branches of the mammalian tree are old, the rate of change was often slow, and diversification rates were low until 55–50 mya (Bininda-Emonds et al. 2007). This is especially the case for anthropoid primates with New World monkeys, Old World monkeys, apes, and human lineages all emerging in the last 45 mya. This suggests that the brains of many mammalian species have not changed that much from those of early ancestors, while others have changed greatly within the last 40–50 million years. The comparative evidence is largely consistent with this scenario. However, an important advance was the evolution of the placenta, which allowed the embryonic development period for the brain to be greatly extended. This resulted in longer prenatal development times for the brain and reduced the need for the early development of neural mechanisms for postnatal functions. This advantage likely relates to the relatively great success of placental mammals over monotremes and marsupials. Placental mammals also had two major innovations in brain organization. First, only placental mammals have the corpus callosum, which first supplemented the functions of the anterior commissure, and then largely replaced them. Second, present evidence largely supports the conclusion that only placental mammals have a primary motor area, M1, and premotor cortex (e.g., Beck et al. 1996). It is not clear how motor cortex emerged, but the dysgranular cortex on the rostral border of S1 has important motor functions, as does S1 to a lesser extent (Young et al. 2012). Thus, motor cortex may have emerged as an elaboration of dysgranular sensorimotor cortex. The motor functions of neocortex in monotremes and marsupials appear to be mediated by somatosensory cortex (see Ashwell 2013).

While early mammals had roughly 20 or more cortical areas, and a similar number of nuclei in the dorsal thalamus, the architectonic differentiation of cortical areas, thalamic nuclei, and midbrain colliculi was poor. Little changed for most mammals, including early placental mammals. However, cellular and laminar specializations of cortical areas and subcortical nuclei occurred to varying extents independently in many different lines of mammalian evolution. The dorsal lateral geniculate nucleus, as a well-studied example, has poorly differentiated layers, and little variation in neuron sizes and features in most mammals, but markedly different patterns of lamination and neuron anatomy emerged in different lines of mammalian evolution as the importance of vision increased (see Kaas et al. 1972). Other examples of anatomical specializations of thalamic nuclei are illustrated by Jones (2007). These anatomical changes mean that the functions of some structures were substantially changed in some lines of evolution, while the structures themselves were retained from early common ancestors, and thus are homologous as structures.

3.4 The Brain of Early Primates

Primates are part of the Euarchontoglires superorder of placental mammals. Other Superorders of placental mammals include Xenarthra (e.g., sloths, armadillos), Afrotheria (e.g., elephants, tenrecs), and Laurasiatheria (e.g., cats, moles, and bats). Euarchontoglires include Glires (rodents and rabbits) and archontans (gliding lemurs, tree shrews, and primates). The primate line diverged from the other Euarchontoglires lines roughly 100 mya, and the last common ancestors of all present-day primates probably existed as early as 80 or more mya, although fossil evidence of primate evolution goes back only 55 mya or so (e.g., Steiper and Seiffert 2012). Thus, it is not clear when the morphological characteristic of modern primates first emerged. Modern primates have large brains relative to body size, and they have more parietal and temporal cortex, and parts of frontal cortex than other Archontoglires, and depend more on vision and less on olfaction (Martin 1990). The fossil record suggests that many of these brain changes emerged within the last 50 mys (e.g., Silcox et al. 2010). However, the earliest fossil primate already had grasping hands and feet with nails instead of claws and forward-facing eyes. These features are likely adaptations to living in the terminal branches of tropical trees where insects, buds, and fruits are available as food (Bloch and Boyer 2002). Their lifestyle placed an emphasis on the evolution of neural systems for processing visual inputs, especially in the aid of visual predation. Olfaction became less important. As related adaptations, early primates were small and nocturnal. Thus, the small mouse lemurs from the island of Madagascar have been considered as a “living model” of early primates (Gebo 2004). However, the brains of these 40–65 g primates have not been studied enough to provide an overview of their organization. Mouse lemurs are members of one branch of radiation of strepsirrhine primates. Besides the lemurs of Madagascar, other strepsirrhine primates include the loris of Southeast Asia and the galagos of Africa. Fortunately the organization of the forebrain of galagos has been

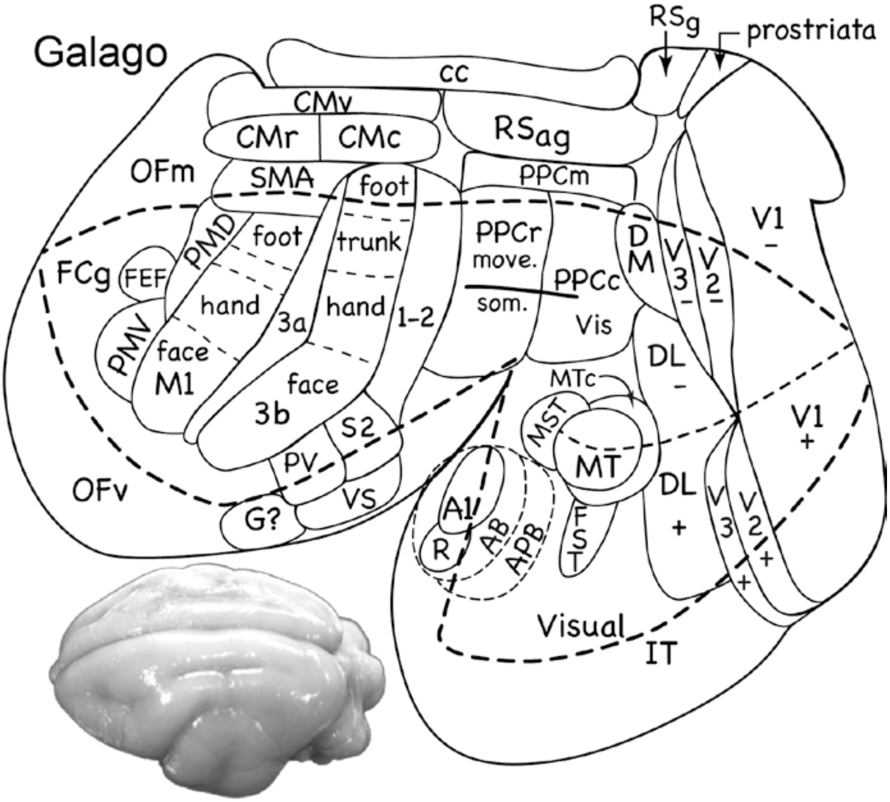

Fig. 3.2 Cortical areas on the flattened cortex of a galago, a strepsirrhine primate. Visual areas V1, V2, and prostriata have been retained from non-primate ancestors. Area V3, the dorsolateral visual area DL (V4); the dorsomedial visual area DM; the middle temporal visual area, MT; the MT crescent, MTc; the middle superior temporal area, MST; and the fundal area of the superior temporal sulcus, FST all appear to be primate innovations. Inferior temporal cortex, IT, likely has 4–5 subdivisions. The auditory core contains primary auditory cortex, A1, and a rostral area, R, as well as an auditory belt (AB) and a parabelt, APB. Somatosensory cortex includes S1 (area 3b), area 3a (see RS in Fig. 3.1), area 1 or 1 plus 2 (see CS in Fig. 3.1), S2 and PV, as well as a new ventral somatosensory area or areas, VS. A gustatory (taste) area (G) is likely; posterior parietal cortex, PPC, is large and divided into a caudal portion dominated by visual inputs, and a rostral portion with motor functions (see text). Motor cortex includes a primary motor area, M1; dorsal and ventral premotor areas, PMV and PMD; a supplementary motor area, SMA; a frontal eye field, FEF; and two or more cingulate motor areas, CMr and CMc. Retrosplenial cortex includes granular (RAg) and agranular (RSag) divisions. Medial and orbital divisions of frontal cortex, OFm and OFv, separate regions of granular prefrontal cortex, PFg, a primate innovation. The corpus callosum, CC, is new with placental mammals

extensively studied, allowing comparisons with the organization of the forebrains of New and Old World monkeys.

The known organization of the neocortex of galagos (Fig. 3.2) shows many of the characteristic features of primates of the closest relatives of primates that have been well studied, rats, mice, squirrels, and tree shrews. For the visual system, areas V1, V2, and prostriata have been retained, but modified from the organization in non-primate ancestors as inferred from present-day rodents and tree shrews. Thus, V1 has primate specializations that include sublaminar segregations in sublayers 4a and 4b of magnocellular and parvocellular classes of thalamic inputs and an orderly distribution of cytochrome oxidase ("blobs" (modules) in layer 3 (Casagrande and Kaas 1994). The grouping of cells that selectively respond to the orientation of visual bars and lines is a modular feature of V1 in primates that is shared with tree shrews but not with rodents (Van Hooser 2007). In galagos, V2 has a weak expression of band-like modules reflecting different processing streams that are more prominent in anthropoid primates (Collins et al. 2001). A third visual area, V3, has been found in galagos (Lyon and Kaas 2002) but not in rodents or tree shrews. Higher-order visual areas include the dorsolateral visual area, DL or V4; the dorsomedial visual area, DM; the middle temporal visual area MT; and the associated areas of the MT cortex (MTc, MST, FST). In addition, the inferior temporal region is visual, and it contains several visual areas that have not yet been well defined. In posterior parietal cortex, a region that greatly expanded in primates, caudal PPC is predominantly visual (Stepniewska et al. 2016). Most of these areas beyond V1 and V2 have no known homologues in non-primate mammals and are likely innovations that emerged in early primates. Subcortically, the superior colliculus of the midbrain has evolved to greatly increase the magnitude of the retinal inputs from the ipsilateral eye while losing the inputs from the temporal retina of the contralateral eye (Kaas 2014). These primates have a superior colliculus that represents the contralateral visual hemifield with inputs from both eyes rather than the whole retina of the contralateral eye as in non-primates. The dorsal lateral geniculate has been altered so that three classes of inputs from the retina are separated into the M (magnocellular), P (parvocellular), and K (koniocellular) layers in a pattern characteristic of primates and different from non-primates (Kaas et al. 1978; Kaas 2014; Casagrande 1994). Overall, visual cortex and subcortical visual structures have been greatly modified in primates and how these changes occurred as primates evolved from non-primate ancestors is not clear.

Much less is known about the organization of the auditory cortex and how it differs from other mammals, but there is evidence for at least two primary areas, A1 and rostral area R, of other primates (see Kaas 2011c), and for two regions of higher-level processing, the auditory belt (AB) and auditory parabelt (APB) cortex. Each of these regions is likely subdivided into functionally specialized areas, as for monkeys (Kaas and Hackett 2000), but this is not yet known. Multiple auditory areas have been identified in other mammals, such as cats and rats (Kaas 2011c). Multiple areas seem to have evolved in different clades, independently, at least in part, so it is not yet certain what areas and features of auditory cortex in primates are primate innovations.

Somatosensory cortex in galagos includes anterior, lateral, and posterior divisions of parietal cortex. Primary somatosensory cortex (S1) corresponds to area 3b of anthropoid monkeys, but it is not as well differentiated architectonically from adjoining cortex as in anthropoid primates (Sur et al. 1980). Yet, area 3b responds well to tactile stimuli, and it represents the contralateral body surface in a foot to face medial to lateral sequence. As in other primates, a narrow strip of dysgranular cortex, area 3a, exists in the rostral border of S1, which has both tactile and proprioceptive functions. Cortex along the caudal border of S1 has an orderly pattern of connections with S1, demonstrating a somatotopic representation parallel to S1, similar to that of area 1 of anthropoid primates. It is not yet clear if this cortex corresponds to area 1 alone or both areas 1 and 2 of anthropoid primates (Wu and Kaas 2003). Overall, this area 1, or area 1 plus area 2, resembles the cortex along the caudal border of S1 in rodents and tree shrews, more than the more distinct, and responsive, representations in areas 1 and 2 of monkeys. It seems likely that a single, poorly differentiated body representation evolved into area 1 and area 2 in early monkeys and that areas 1 and 2 were retained in all or most present-day anthropoids. Areas PV and S2 are just lateral to S1 (Wu and Kaas 2003), much as they are in rats and squirrels. Thus, these fields have been retained from non-primate ancestors. However, there is also evidence for another area or areas next to PV and S2, the ventral somatosensory area (VS) or areas (see Coq et al. 2004). This seems to be a primate innovation. A gustatory area, G, has not been well defined in galagos, but it likely exists in all mammals. Finally, the PPCr region contains a series of about eight small patches of cortex, we call domains, that have been defined by the complex movements produced by electrical stimulation (Stepniewska et al. 2009; Kaas and Stepniewska 2016). The separate domains evoked eye, protective arm, hand to mouth, reaching, running, and other complex movements when stimulated, and the domains are roughly arranged in a lateromedial sequence from head to foot. The domains appear to exist in all or most primates but not to this extent in the close relatives of primates. Thus they likely emerged with the expansion of posterior parietal cortex in early primates or their immediate ancestors.

Galagos also have a number of cortical motor areas that are shared with other primates (Wu et al. 2000). This includes a primary motor area (M1), ventral (PMV) and dorsal (PMD) premotor areas, frontal eye field (FEF), the supplementary motor area (SMA), and rostral, caudal, and ventral cingulate motor areas (CMA). The motor cortex of rodents (Young et al. 2012) and tree shrews (Remple et al. 2006) includes a primary area, M1, and at least one premotor area, and this is the likely pattern of motor cortex for all placental mammals. But additional motor areas appear to have been added with the evolution of early primates, especially of subdivisions of motor areas concerned with the control of hand and forelimb movements. In addition, small regions or domains where electrical stimulation of cortex evokes complex action specific movements exist in M1 and premotor cortex of galagos and likely all primates. These domains are functionally matched to domains of PPCr (Kaas and Stepniewska 2016). Other mammals may have similar domain-like subdivisions of M1 (e.g., Baldwin et al. 2017), but the types and numbers of such domains are different and fewer. The organizations of M1 and premotor cortex changed with the emergence of primates in that the numbers of domains increased, they were interconnected with functionally matched domains in a newly enlarged rostral region of posterior parietal cortex, and more domain were involved in producing movements of the forelimb and hand in such behaviors as grasping, hand to mouth, and protecting the head with an arm.

Other areas of cortex have been less explored in galagos and other prosimians, but these and all other primates have a granular region of prefrontal cortex that is thought to be an innovation of early primates (Preuss and Goldman-Rakic 1991). Areas of primary sensory cortex are characterized by having densely packed small neurons (granule cells) in layer 4 that are individually activated by only few inputs, thereby preserving this information for further processing. Motor areas, in contrast, are characterized by large pyramidal neurons that have large dendritic arbors that allow them to integrate information from many sources (Kaas 2000). The integration of many sources of information has long been considered to be an important feature of prefrontal cortex, and granular prefrontal cortex does have large pyramidal neurons with widespread dendritic arbors, especially in humans (Elston et al. 2006). So it is interesting that this cortex also is specialized for preserving the details of some of the inputs to small neurons of layer 4.

In summary, we see evidence for a remarkable reorganization of the brain in the ancestors of early primates, so that many changes or innovations occurred that were retained in galagos and most likely other prosimian primates, but also in monkeys and possibly all primates. Major changes involved the visual and motor systems, especially at the cortical level, where we see a sign of a greatly expanded role of neocortex, the “corticalization of function” that so characterizes the human brain (Herculano-Houzel et al. 2016). Comparative studies on the relatives of primates, rodents, and tree shrews don’t shed much light on when and how these remarkable changes occurred, but it is clear that most or all the these changes occurred after the divergence of Glires (rodents and lagomorphs) from archontans (tree shrews, gliding lemurs, and primates) and even after the divergence of the ancestors of primates from those of tree shrews some 85 mya.

3.5 The Brains of Early Monkeys

The early haplorhines or “dry-nosed” primates emerged as a branch from the strepsirrhine clade of “wet-nosed” primates over 60 mya (e.g., Murphy et al. 2004). An early branch of early haplorhines evolved into present-day tarsiers, while the other surviving anthropoid branches led to the more widespread New World monkeys (platyrrhines) and Old World monkeys (catarrhines), which eventually produced hominins (apes and humans). Early haplorhines were small and diurnal (Ni et al. 2013; Kay et al. 1997; Seiffert et al. 2010). The line leading to present-day tarsiers reverted back to being nocturnal, with appropriate modifications including extremely large eyes for their small head and body. Tarsiers feed in the fine branches and eat insects and small vertebrates as a specialized visual predator that eats no vegetable matter (Fleagle 1999). Not much is known about their brains, as experimental studies have been limited, but histological studies indicate that both the dorsal lateral geniculate nucleus and the pulvinar resemble those of monkeys in organization more than those of strepsirrhines (Collins et al. 2005; Wong et al. 2010). Primary visual cortex is remarkable in its relative size, 20–30% of neocortex, and its degree of histological differentiations into distinct layers and sublayers. However, these visual specializations in a small brain seem to have come at the cost of having less posterior parietal and prefrontal cortex.

Early monkeys diversified in Africa, with some rare individuals somehow rafting from Africa to South America, perhaps more than once, as early as 30–40 mya (Bond et al. 2015; Bloch et al. 2016). Studies of early African and South American primate fossils reveal similarities that have been lost (Bond et al. 2015; Seiffert 2012). However, these early monkeys had relatively larger brains than their strepsirrhine ancestors, with more neocortex and a more extensive temporal lobe. Early monkeys in both Africa and South America likely had dichromatic color vision, having just two classes of cone photoreceptors (as in most mammals), while surviving African anthropoids are trichromatic, having short, middle, and long wave sensitive cones. Trichromatic vision would seem to offer a considerable advantage in identifying colored fruits and buds as food in the dense arrays of leaves in tropical trees (Regan et al. 2001). As early monkeys diversified, many got larger and depended more on fruits, leaves, and buds for food. Most South American monkeys remained dichromats, while the placement of the gene for the long-wavelength gene on the X chromosome and a slight variation in the gene allowed some XX females to code for different cone pigments on each X chromosome and became trichromats, while all XY males remained dichromats (Jacobs 2008). However, one genus of large New World monkeys has both genes for longer-wave sensitivity pigments (medium and long) on each X chromosome, allowing all females and males to have trichromatic vision. Thus, the advantage of trichromatic vision evolved independently in New and Old World monkeys. This suggests that the independent changes in the retina induced comparable changes for the processing of color information in the visual systems of trichromatic New and Old World monkeys.

New World monkeys evolved into roughly 125 species of various body sizes ranging from the 100–250 g of species of marmosets to the 11–12 kg sizes of howler monkeys. One New World monkey, the owl monkey reverted back to nocturnal living, while others remained diurnal. Old World monkeys are found in Africa and Asia and are generally as large or larger than the New World monkeys. There are over 85 species of Old World monkeys in two major subfamilies, the cercopithecines with cheek pouches for storing food and colobines with adaptations for feeding on leaves (Fleagle 1999). As early monkeys were small, the brains of some of the smaller New World monkeys likely reflect more of the organizations of the brains of early monkeys. Larger monkeys have larger brains, with proportionally more neocortex (Chaplin et al. 2013) and more neurons (Herculano-Houzel et al. 2007), and they likely have more cortical areas (Changizi and Shimojo 2005). The presence of larger brains with proportionally more neocortex implies an increase in the “corticalization of function” (Herculano-Houzel et al. 2016).

The most commonly studied brains of New World monkeys include those of squirrel monkeys, owl monkeys, and marmosets. The brains of the larger cebus and spider monkeys have been studied much less. As most studies have focused on aspects of cortical organization, and the areal organization of cortex is subject to major changes in evolution, our emphasis here remains on the cortex. However,

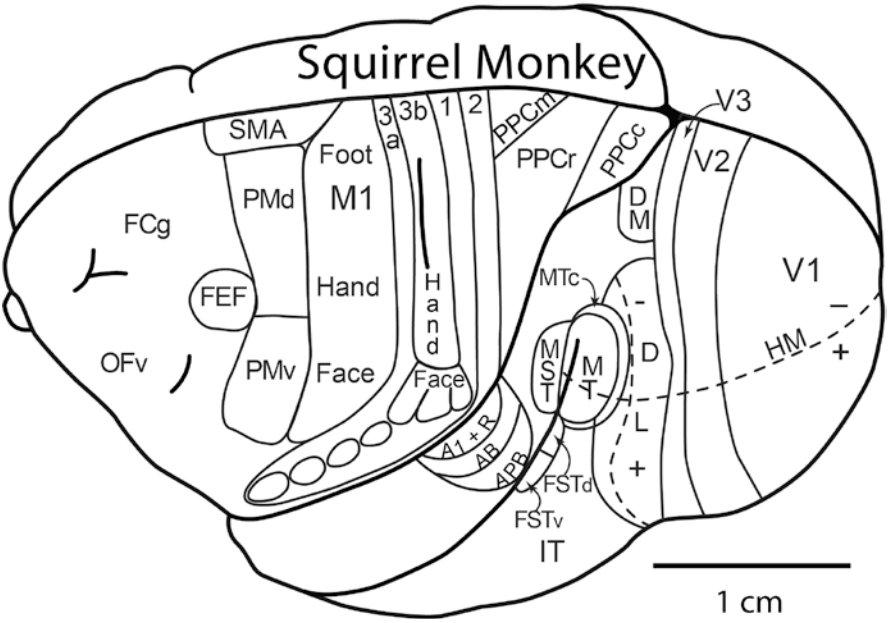

Fig. 3.3 Some of the cortical areas of a squirrel monkey shown on a dorsolateral view of the left cerebral hemisphere. All of the areas of the galago (Fig. 3.2) are present in monkeys, but there is proportionately more neocortex; somatosensory area 2 is distinct from area 1; the ventral somatosensory area is clearly divided into two areas (not shown); visual area FST has dorsal and ventral divisions; and granular frontal cortex, FCg, PPC, and IT cortex have expanded. See Fig. 3.2 for abbreviations and conventions

outside of the primary sensory and motor areas, identifying cortical areas is a difficult process, and many uncertainties and differences of opinion remain. However, the evidence supports the conclusion that even the smaller of the New World monkeys have more cortical areas than strepsirrhine primates, and this means more cortical areas are available for serial processing, and more diversity in cortical specializations is possible.

The proposed areal organization of the neocortex of a squirrel monkey is illustrated in Fig. 3.3. The full number of cortical areas is difficult to estimate as large regions of cortex have been relatively unexplored with experimental procedures, although architectonic features and patterns of connections have been used to define additional areas. The cortex with predominately visual function occupies most of the caudal half of the cortex and includes the visual areas of strepsirrhine primates but likely more areas. The dorsolateral visual area, DL or V4, appears to be subdivided into rostral and caudal halves, with DLr having more connections with the "action" or "dorsal" stream of visual processing, and DLc more connected with the "object identification" or "ventral" processing stream (Kaas and Lyon 2007). The FST region is also divided into dorsal and ventral areas, FSTd with dense connections with MT, and FSTv with dense connections with MTc

(Kaas and Morel 1993). There is clear evidence for V3 (Kaas et al. 2001), although this interpretation has been questioned (e.g., Rosa et al. 2005). The New and Old World monkeys (except owl monkeys) are diurnal, and the amount of cortex devoted to the ventral stream of cortical processing (Ungerleider and Haxby 1994; Goodale and Milner 1992), including a uncertain number of inferior temporal (IT) visual areas, is expanded for better identifying objects including faces for social primates (Ku et al. 2011; Tsao et al. 2008; Hung et al. 2015). The emphasis on visual object identification starts subcortically, with 80% of the retinal ganglion cells projecting to only the parvocellular layers of lateral geniculate nucleus (Weller and Kaas 1989) that activate the cortical ventral stream. Only about 10% of the ganglion cells project to the magnocellular layers, to provide the primary source of visual information for the dorsal "action" stream involving the MT cortex, DM, and much of posterior parietal cortex.

The evolutionary changes in the somatosensory system have been less pronounced. The hand representation in primary somatosensory cortex in New and Old World monkeys is somewhat enlarged, and area 1 is more powerfully driven by touch. Area 2 is also highly responsive to touch, as well as muscle and limb movement. Some of the large spider and cebus New World monkeys have a highly sensitive glabrous pad on the end of their prehensile tail, which serves as an extra limb and has a large representation in somatosensory cortex (Felleman et al. 1983). This is an innovation that is restricted to one line of evolution in New World monkeys.

The larger brains of most Old World monkeys, and perhaps the larger New World monkeys, may have more cortical areas (Changizi and Shimojo 2005; Kaas 2008), but this depends on how they are defined and the types of evidence. Thus, much certainty exists. One recent estimate is that macaque monkeys have 140 areas (Van Essen et al. 2012a), but this may be an underestimate. For comparison, a recent atlas of the small marmoset brain portrays just over 100 cortical areas (Paxinos et al. 2012). However, as this estimate is largely based on architectonic distinctions, it may be an overestimate. In evaluating these estimates, it is important to consider how many neurons would be needed to mediate the proposed functions of an area and what the minimal size of that area might be (Kaas 2000). Some of the proposed cortical areas appear to be too small to be realistic. In addition, modular features of cortex can produce connectional and architectonic differences that are similar to those expressed by areas and thus may be confused with areas.

In summary, the evolved changes in the brains of early to recent monkeys include elaborations of parts of the visual system that enhanced the ability to recognize objects and the faces of individuals in highly social monkeys. This involved an elaboration of the classes of retinal ganglion cells that provided detailed spatial vision and trichromatic color vision and a great expansion of the ventral stream of visual processing. There was also an expansion of parts of the motor and sensory cortex devoted to forepaw use, as more kinds of plant food were used, and food processing with hands and teeth was more needed. As larger species with larger brains emerged, these larger brains provided more capacity, the possibility of more serial processing, and the further specializations of systems, nuclei, and cortical areas.

3.6 The Evolution of Apes and Ape Brains

Apes emerged in East Africa from a line of large bodied catarrhine monkeys some 25–30 mya (Andrews 2015). These monkey-like apes were arboreal, but also partly terrestrial, as suggested by their large size. Their larger sizes and correspondingly larger brains allowed them to compete with monkeys for high-quality food, territory, and stable supplies, such as figs (Jablonski et al. 2000). For a time, the ape radiation was very successful, and they spread to adjoining parts of Europe and Asia. In seasonal climates, the acquired ability to store fat reserves may have become important. Ultimately, the longer maturation times that resulted in slower rates of reproduction, together with the higher energy costs of larger bodies and brains, put apes at a comparative disadvantage with monkeys in times of environmental instability. Apes disappeared from much of their former range. However, the line of African great apes gave rise to a branch leading to present-day gorillas 8 or more mya, the chimpanzee-bonobo line 5–6 mya (producing chimpanzees and bonobos within the last 2 mya), and the line of bipedal hominins that led to modern humans. The last common ancestor of humans and chimpanzees most closely resembled modern chimpanzees in that it was not yet completely bipedal, had a high degree of sexual dimorphism, likely used tools; and probably nested in trees for safety (Andrews 2015). Our ancestors diverged by becoming predominantly bipedal, thus freeing the hands for tool use, food transport, and infant care, with no significant change in brain size. Hominin brains remained in the 400–500 cm^3 range until about 2 mya.

Studies of the brains of the extant great apes provide an opportunity to understand what the brains of our extinct hominin relatives were like. Because of limits on the types of studies that are possible, much of what is known about the brains of apes comes from histological studies of brains obtained after death. As expected some of the sensory and motor areas that have been identified by multiple criteria in monkeys have been identified histologically in chimpanzees. V1 or area 17 in chimpanzees has the distinctive laminar appearance of monkeys, but differs in not having a dense cytochrome oxidase band in the middle of layer 3 (Brodmann's layer 4A), and thus resembles area 17 of human brains in that way (Preuss et al. 1999). This suggests that inputs from the lateral geniculate nucleus have been reduced or eliminated from this sublayer, an interpretation consistent with anatomical results (Tigges and Tigges 1979). Thus, the substrate for processing visual inputs has been modified in great apes with different modifications occurring in humans. What these modifications mean functionally is not yet clear. Area 17 of chimpanzees is larger than in macaque monkeys, as the sheet of neocortex is extremely large, but area 17 is proportionally less of the total of neocortex, suggesting that more cortical areas exist or that other areas have disproportionally enlarged. As in Old World monkeys and humans, area 17 of chimpanzees is divided in layer 4 by broad, distinctive, ocular dominance columns (Tigges and Tigges 1979). Clear evidence for other visual areas, V2, V3, DM, MT, etc., of monkey visual cortex is lacking, but all these areas, and more, one are expected to exist in apes. It is clear that V1 and nearby visual areas, V2 and V3, have high neuron packing densities, as in other primates (Collins et al. 2016).

There is also good architectonic evidence for areas 3a, 3b, 1, and 2 of anterior parietal cortex of chimpanzees (Qi et al. 2008). These areas are arranged in a rostrocaudal sequence from the depth of the central sulcus as they are in monkeys and humans, and they are very similar in architectonic appearance across these primates. Other somatosensory areas such as S2, PV, and VS likely exist but have not been demonstrated. In monkeys, primary auditory cortex consists of a distinctive core of three auditory areas, A1, a rostral area, R, and a rostrotemporal area, RT. A similar core region has been identified by architectonic criteria in chimpanzees, and the identifying features are very similar to those that identify the core in macaque monkeys and human (Hackett et al. 2001). However, it is not yet certain if this core is divided into three primary areas in macaques or if adjoining belt and parabelt auditory regions are functionally organized as in macaques (Kaas and Hackett 2000). Motor cortex organization, at least for primary and secondary motor areas, also seems to be similar in apes and macaques (Woolsey et al. 1960; Bailey et al. 1950; Grunbaum and Sherrington 1901). And a recent neuroimaging study of brain regions activated during grasping revealed a frontoparietal network similar to that of macaques, including presumed homologues of the anterior intraparietal area, AIP, and ventral premotor area of macaques (Hecht et al. 2015). In addition, a study using diffusion tensor imaging (DTI) to reveal the connections of the arcuate fasciculus in primates has suggested that these connections are more similar to those in macaque than in humans (Rilling et al. 2008). However, the chimpanzee brain is not simply a more-than-three-times larger macaque brain. Structural changes in brain organization have occurred, but they are as of yet understood in only a limited way. The proportionally smaller primary sensory and motor areas, for example, suggest that the cortical sheet of chimpanzees is divided into more cortical areas, allowing more steps in cortical processing and greater specialization of cortical areas. Chimpanzees also have marked asymmetries in the gross anatomy of the two cerebral hemispheres, suggesting that different anatomical specializations for hand use and other functions exist as do in humans (Gannon et al. 1998; Hopkins and Cantalupo 2004; Gilissen and Hopkins 2013). As for humans, chimpanzees are predominately right handed (Hopkins et al. 2004).

3.7 The Evolution of the Brains of Modern Humans

The fossil record indicates that the early hominins that diverged from the line that gave size to chimpanzees and bonobos some 6–7 mya were much like early members of the branch that led to chimpanzees and bonobos (Crompton et al. 2008; Robson and Wood 2008). However, these apes adjusted to woodlands that were subject to climate fluctuations and became drier and mixed with grasslands. It became adaptive for these apes to expand their home range for feeding and increase the range of food items in their diet. Walking on two legs allowed these early ancestors to cover more territory, see further and more clearly, and use their forelimbs to carry food to a safe place. Increasingly bipedalism allowed the hand and feet to differently specialize to great advantage. Bipedalism occurred early in hominin evolution, about 6 mya, while the once expected great increase in brain sizes did not occur until 2 mya, and then brain sizes increased from ape size (400 cc) in *Australopithecus* to more than double in early *Homo erectus*, to roughly 1400 cc of modern humans. Over the last 2.5 million years, the hand became increasingly modified from a great apelike beginning to a human hand in ways that would promote tool use (Tocheri et al. 2008). Ancestors from the time of *Homo erectus* spread from Africa to Asia and Europe but retreated or were wiped out with climate change and ice ages. Our species, *Homo sapiens*, emerged about 200,000 years ago in Africa, after a near extinction during a major ice age (Takahata et al. 1995). The evolution of the big human brains provided impressive cognitive and social skills, tool use, and technology and the ability through culture to expand and occupy highly difficult environments. The costs of these big brains include the amount of energy it takes to maintain them, the long developmental period to make them, and maintaining the capacity to store large amounts of (cultural) information. The high-energy cost of the big brains of our ancestors could only be meet by cooking or otherwise processing food, abilities that go back as far as 1.5–2 million years (Wrangham 2009; Herculano-Houzel 2016). The long development time for the bigger brains of our ancestors, resulting in later reproduction in life, was compensated for in a large part by a reduced mortality rate, a longer life span, shorter times between births, and the help of others in child care.

Large brains are important in that they have more neurons, the basic computational units of brains. But for cognition, large numbers of neurons need to be in the neocortex, as elephants have a three-times-larger brain than humans, but fewer neurons in the neocortex (16 billion, humans; 5.6 billion, elephants; Herculano-Houzel 2016). Proportionally more of the neurons in elephants are in the cerebellum, which has important functions, but we largely attribute our cognitive abilities to neocortex. Primates have an advantage over other mammals as primate brains maintain similar levels of neuron packing densities as from smaller to bigger brains, while other mammals have reduced neuronal densities as their brains get bigger (Herculano-Houzel et al. 2007). Additionally, we devote about 80% of the mass of our brains to neocortex (Azevedo et al. 2009; for review see Hofman 2014). Another important factor is where cortical neurons are concentrated. While the results of early studies suggested that neuron densities are the same across all cortices and across mammalian clades, except for a doubling of neurons in primary visual cortex of primates, this is far from the case. As shown most clearly in neuron counts per mm^2 of cortical surface for over 700 squares of cortex in a chimpanzee, neuron densities vary three to fourfold across cortical areas and regions. Neuron counts were very high in primary visual cortex and high in secondary visual areas and in auditory and somatosensory areas but also in frontal granular cortex (Collins et al. 2016). Low neuron packing densities were found in motor and premotor cortex. Similar differences in neuron packing exist in other primates and appear to exist in neocortex of humans (Gabi et al. 2016). Neuron packing densities decrease with increases in average neuron size, and larger neurons sum more inputs. Thus, we can assume that smaller neurons of sensory areas and of frontal granular cortex have the important role of preserving much of the information in their inputs, while the larger neurons of motor areas sum many inputs to best provide motor commands. Another factor that greatly contributes to the impressive abilities of the human brain (Tomasello 2014; Passingham 2008) is the great increase in the numbers of cortical areas and, thus, the steps available for cortical processing (Pinker 2009). These new areas have been added to association cortex, the cortex devoted to higher-order processing. Outside of a few, cortical areas are hard to identify, and the absolute number in the neocortex of human is far from certain. Estimates vary (e.g., Kaas 2006; Van Essen et al. 2012b), but the number is likely over 200, perhaps 4 times more than in early primates. Thus, in both human postnatal development and evolution, the association regions of cortex have expanded most, while the sensory areas expanded little (Hill et al. 2010). Functional imaging studies in human are now starting to present evidence for cortical areas that are unique to humans (e.g., Peeters et al. 2009), in addition to those areas involved in language (e.g., Brauer et al. 2011). Finally, hemispheric specialization has been greatly enhanced in the evolution of modern humans, allowing systems and cortical areas of the two hemispheres to differentially specialize, reduce processing time, and increase the cognitive abilities of humans (Corballis 2007; Van Essen et al. 2012b; Ringo et al. 1994; Brown and Kosslyn 1993).

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