The Evolution Of The Visual System In Primates

Jon H. Kaas

Prepared for:
The New Visual Neurosciences
Jack Werner and Leo Chalupa (Eds.)
MIT Press – 2013

Text 7,194 words
Refs 2,184 words

Figures: 6

Contact information:
Jon H. Kaas
Distinguished Professor
Department of Psychology
Vanderbilt University
PMB 407817
2301 Vanderbilt Place
Nashville, TN 37240-7817
Tele: 615-322-6029
Fax: 615-343-8449
e-mail: jon.h.kaas@vanderbilt.edu

Introduction

Compared to most mammals, primates are highly visual. While the over 350 species of primates vary in their behavioral adaptations and thus brain organizations, primates in general share a number of distinctive features of brain organization and of visual system organization. Thus, an experienced investigator, given any primate brain, can look at appropriately prepared brain sections and say: yes, this is a primate. Here we review the features of the visual system of primates that distinguish them from those of other mammals, consider the ways that visual systems of primates are known to vary, and suggest how the distinctive features of the visual systems of primates emerged in evolution and came to vary. To do this, we first outline the evolutionary history of primates, starting with early mammals, mention some overall features of primate brains that distinguish them from those of other mammals, and proceed to discuss the major components of the visual systems (the retina, visual thalamus, superior colliculus, and visual cortex) of primates in terms of what primates share and how primates vary.

What is special about primate brains?

Primate brains are different than the brains of other mammalian taxa, and many of these differences relate to the visual system and the emphasis on vision that characterize primates. An experienced comparative neuroanatomist can recognize a brain from being from one of the 350 or so primate species by its fissure pattern (always a lateral fissure and a calcarine fissure) and its expansive occipital and temporal regions (containing visual areas). In a series of brain sections, a distinctive pattern of lamination in the dorsal lateral geniculate (visual) nucleus most clearly identifies the brains as from a primate, but other features are also characteristic of primates.

A fundamental difference in primate brains compared to the brains of other mammals is the number of neurons they have, given the size of their brain (Herculano-Houzel et al., 2007). In general, species with larger brains have more neurons, and by implication, more computational power. However, the increase in neuron numbers with progressively larger brains in non-primate mammals is less than that for primates with a similarly sized brain. For example, a primate brain that is roughly the same size as that of a rodent has twice the number of neurons that are more densely packed than other mammals with progressively larger brains. This is partly a result of an increase in the average size of neurons in the brains of these non-primate mammals, but also because the ratio of glia and other cells per neuron increases in non-primates. As an example of this difference, the brain of a small monkey of about 16 grams has 1.5 billion neurons, while a

rodent brain of about the same size (18 grams) has only 0.9 billion neurons (Fig. 1). Even the largest rodent that ever lived, the now extinct South American rodent, phoberomus, at 700 kg (1540 lbs.) had a brain with only an estimated 7.5 billion neurons, while a human of 81 kg. (180 lbs) has a brain of about 86 billion neurons (Avzevedo et al., 2009). Elephants with brains three times the size of a human brain, nevertheless fall short with about half the number of at least cortical neurons as the human brain (Hart and Hart, 2007). Neuron densities are higher in primate brains because neurons on average are smaller, although primates also have a great range of neuron sizes, shapes, and functions (Sherwood and Hof, 2007). This seems to be especially the case in neocortex, where primary visual cortex, V1, has very small neurons in layer 4, hence the name, koniocortex. Yet, there are also a few very large pyramidal neurons (Meynert neurons). Because differences in neuron sizes and packing densities vary across visual areas and primate taxa (Collins et al., 2010), we return to this issue in the section on visual cortex.

In addition to differences in cellular composition, size and density, primate brains differ from the brains of other mammals in a number of other ways. First, although variable across the primate taxa, in general primates have more cortical areas compared to non-primate mammals, and this difference is particularly noted in the visual cortex where well-studied macaque monkeys are proposed to have more than 30 cortical fields (Felleman and Van Essen, 1991; Kaas, 1989. Second difference is that matched cortical areas in the two cerebral hemispheres tend to specialize in different ways, at least in the anthropoid primates with larger brains (Corballis, 2007). Obvious hemispheric differences in humans include left hemisphere specialization for language and handedness, but right hemisphere specializations for face recognition and other visual functions have been reported as well. Another important difference is in the size of the peripheral olfactory system, which has gotten relatively smaller and less emphasized in primates (Bhatnagar and Smith, 2007), while frontal and parietal networks for sensorimotor abilities have expanded greatly, and diversified for a variety of primate lifestyles.

Primate Evolution

Before considering the evolution of visual systems of primates in detail, it is useful to briefly outline the phylogenetic relationships of present-day primates and their close relatives, and how they evolved. Early mammals gave rise to the six major branches of present-day mammals including the early branches of the egg-laying monotremes, and the marsupials, which rear their young in a pouch of skin or a pseudo-pouch where they are attached to the nipples and hang like

a cluster of grapes. The four main branches of placental (eutherian) mammals diverged over 90 million years ago (Fig. 2). While carnivores such as domestic cats have long been used in studies of the visual system, and ferrets more recently, carnivores are not closely related to primates. As members of the Euarchontoglire superclade, primates are most closely related to tree shrews (Scandentia) and flying lemurs (Deromoptera). Despite this common name, flying lemurs glide, rather than fly, and they are not lemurs. Rodents and Lagomorphs are the other members of the Euarchontoglire superclade and thus more closely related to primates than carnivores. This relationship implies that if we are interested in inferring what the brains were like of the most recent non-primate ancestors of primates, we should look at the brains of tree shrews, flying lemurs (largely unavailable for study), rodents, and rabbits.

Early primates emerged as a branch of the Euarchontoglire superclade over 80 million years ago (Meredith et al., 2011). They diversified into several lines of archaic primates that became extinct, and the euprimates, which led to the present-day lemurs, lorises, and galagos, the visually specialized tarsiers, and the great radiation of anthropoid primates (New World monkeys, Old World monkeys, apes, and humans). Early primates were small and resembled present-day galagos and some of the lemurs in brain size relative to body size, although their brains were somewhat smaller than those of present-day prosimians. Their fossil remains indicate that they were likely nocturnal, and fed in the thin branches of bushes and trees on insects, small vertebrates, fruits, and buds (Ross and Martin, 2007). Feeding while positioned on thin, often moving branches and reaching for food implies that early primates had already evolved neural networks for exceptional visuomotor control of hand movements (Block and Boyer, 2002), one of the most distinguishing features of the behaviors of extant primates (Whishaw, 2003). While present-day prosimians are varied, and some are now diurnal, galagos and a few other prosimians, such as mouse lemurs, may have changed the least from the general body form and brain organization of early primates. Galagos are African primates that are the size of cats, or smaller, arboreal, nocturnal, and feed on fruits, gums, and insects. One line of early prosimian primate evolution led to present-day tarsiers and anthropoids. Tarsiers are highly specialized, small, nocturnal, visual predators of invertebrates and small vertebrates, and they apparently eat no plants. The earliest anthropoids, as well as the shared ancestors with tarsiers, were small, diurnal visual predators, with later stem anthropoids (monkeys) evolving larger body sizes, and diversified diets that included fruit, leaves, and other parts of plants. Many of these primates formed social groups, possibly as diurnal life made them less cryptic and more

dependent on others for protection and warnings. A line of anthropoid monkeys some 25-30 mya led to apes, which formed a successful radiation, occupying rainforest environments. One line of apes diverged 6-8 million years ago into a branch that led to modern chimpanzees and bonobos, and to bipedal primates - the hominins, including modern humans (de Sousa and Wood, 2007). Hominins probably emerged as one line of apes adapted to a drier climate with grassland and savannah. The early hominins, australopiths, roamed the earth about 5 million years ago. They were bipedal, but they retained skeletal features for climbing trees. Their brains were about the size of apes of similar body size. The genus Homo emerged about 2 million years ago with Homo habilis, followed 1.7 million years ago by Homo erectus, which spread out of Africa, and Homo sapiens, some 250,000 years ago. Other Homo species included Neanderthals, which died out only 35,000 years ago. There is evidence for an archaic hominin population from Siberia, the Denisovans, which also coexisted with modern humans (Skoglund and Jakobsson, 2011).

Extant primates constitute one of the most diversified taxonomic groups. It includes 14 families, over 350 species, and a range of body sizes from the 40-gram mouse lemur to the 200-kilogram male gorilla, a 5000-fold difference that is important as body size relates to brain size (Jerison, 1973). This variability in body and brain size makes a comparative study of primate brains a challenging task, especially since all members of the remarkable and rapid hominin radiation are now extinct except for us. Yet a wealth of recent studies has led to much progress, and a lot that can be inferred about the brains of unstudied species.

The Eye and the Retina

The eyes and retinas of modern primates reflect their ancestral condition as well as subsequent adaptations to new visual environments (Preuss, 2007). Ancestral primates were thought to be nocturnal (crepuscular), being most active during the dim light just after sunset and just before sunrise (Ross and Martin, 2007). Early primates, as well as extant primates, had large forward-facing eyes, which favored stereoscopic vision and produced a sharper image for central vision. Most extant strepsirhine primates have retained a nocturnal lifestyle, and their eyes have retained visual specializations for functioning in dim light. Thus, the retina lacks a fovea, and even in the central retina, there is a convergence of a number of receptors on bipolar cells to promote the detection of light. In addition, the back of the retina is lined with a tapetum, a reflecting layer absent in some modern prosimians (diurnal lemurs): this enables receptors to be stimulated by reflected as well as direct light. Also, the retinas of nocturnal prosimian primates are dominated

by rods, which are more sensitive than cones and responsive to a broader range of wavelengths. As for most mammals, strepsirhine primates have two types of cones, the short wavelength-sensitive or blue (S) cones, and the medium-to-long wavelength (green/red or M/L cones). The S-cone pigment has been lost in some nocturnal primates (lorises, galagos and owl monkeys) (Wikler and Rakic, 1990).

Tarsiers are haplorhine primates, as are anthropoid primates. The ancestors of tarsiers, in common with all anthropoid primates, were probably diurnal, resulting in the loss of the reflecting tapetum, an increase in the proportion of cones–to-rods, and a cone-dominated fovea, all adaptations for higher visual acuity in bright light. When the more immediate ancestors of tarsiers reverted to nocturnal life, they compensated for the lack of a tapetum by evolving very large eyes, and by adding rods to a degenerate fovea. Despite their nocturnal lifestyle, present day tarsiers retain a distribution of functional S cones (Hendrickson et al., 2000).

Early anthropoid primates (monkeys) retained the M/L and the S cones. The M/L gene is on the X chromosome, and different alleles for this gene emerged to produce pigments with slightly different sensitivities to wavelength. Thus, for some species of New World monkeys, females may have different alleles on each of their two X chromosomes, which produce two slightly different M/L. Having two classes of M/L cones as well as S cones allows some females to function somewhat as trichromats. The males, with only one X chromosome, remain dichromates. Whether this enables the females to better detect ripe fruit and other colored food is unknown. However, one group of New World monkeys, the howler monkeys (Jacobs et al., 1996), evolved a three-cone retina by duplicating the ancestral M/L pigment gene. Evolved differences in the wavelength sensitivities of the pigments of photoreceptors, which were produced by the duplicated genes on the same X chromosome allowed both males and females to have trichromatic vision. A common ancestor of all Old World monkeys independently duplicated the M/L gene to produce (green) M and L (yellow-green) pigment genes, and all species of catarrhine primates (Old World monkeys, apes and humans) are trichromats. In some humans, one of these genes may become non-functional, so that individuals are functionally dichromates. As these genes are on the X chromosome, this condition is more likely to exist in males (with only one X chromosome).

The intrinsic connections of the retina produce three main types of retinal ganglion cells. The midget ganglion cells for the parvocellular pathway (P), the much larger parasol ganglion cells for the magnocellular pathway (M), and the small ganglion cells of the koniocellular pathway (K). These neuronal streams from the retina are named after their targets in the parvocellular, magnocellular, and koniocellular layers of the dorsal lateral geniculate nucleus. The three types of ganglion cells appear to have homologues in other mammals, but their relative numbers and targets differ. In many species of the K and M classes (also called W and Y) dominate (Casagrande et al., 2007), while the P class (also called X) is small. In primates, the P class includes about 80 percent of the ganglion cells, and the K and M classes are each about 10 percent (Weller and Kaas, 1989). In many mammals, most ganglion cells of the retina project to the superior colliculus, but in primates only about 20 percent of the ganglion cells, the K and M cells project to the superior colliculus. However, nearly all ganglion cells project to the lateral geniculate nucleus, and most or all P cells appear to project exclusively to the lateral geniculate nucleus (Weller and Kaas, 1989). Thus, the role of the P (midget) ganglion cells has vastly changed in primate evolution compared to their non-primate ancestors, and the primary target of the retina has moved from the superior colliculus to the lateral geniculate nucleus as cortical processing of visual information became more important.

The Superior Colliculus

The superior colliculus is a laminated visual structure in the dorsal midbrain of all mammals. In other vertebrates, the superior colliculus is called the optic tectum, and it is the major structure for generating visual behavior. In primates, the superior colliculus is generally considered a visuomotor structure, although it provides visual inputs to the lateral geniculate nucleus (Harting et al., 1991) and pulvinar (Fig. 5) of the dorsal thalamus. In many mammals, the projections of the superior colliculus activate pulvinar neurons that provide an important second source of visual information to temporal visual cortex, thereby preserving some visual abilities after damage to primary visual cortex. Primates appear to be much more dependent on primary visual cortex for the activation of extrastriate cortex, suggesting that the role of the superior colliculus in perception has diminished. Other outputs of the superior colliculus are to groups of motor neurons in the brainstem that mediate eye and head movements, so that the eyes and central vision are directed toward objects of potential interest. Visual and other information reaches the superior colliculus via direct retinal projections (Kaas, 1978), and projections from visual and visuomotor areas of cortex (Baldwin and Kaas, 2012; Collins et al., 2005).

The projections of the retina to the superior colliculus in all examined primates (e.g., Lane et al., 1973) differ from all non-primate patterns in that only the “hemi-retinas” that are devoted to the contralateral visual hemifield project to each superior colliculus (Fig. 3). This pattern must have been present when the first primates evolved, but not much before, because tree shrews, rats, and rabbits (close relatives of primates) all have the more generalized condition that includes inputs from the complete retina of the contralateral eye (Kaas et al., 1974). It was once thought that megachiropteran (fruit) bats also had the primate pattern, and this was considered evidence that these bats might actually be primates (Pettigrew, 1986), but further study did not support this conclusion (Thiele et al., 1991). For other reasons, bats are now placed on the Laurasiatheria clade, and are no longer considered closely related to primates (Fig. 2). This primate specialization of only representing the contralateral hemifield in each superior colliculus likely relates to the emphasis on binocular and central vision that occurred in early primates.

The other major change that took place in the superior colliculus with the emergence of primates was a dramatic increase in the inputs from the ipsilateral eye, so that the major portion of the superior colliculus was responsive to both eyes. As the eyes rotated forward to create a large binocular visual field in the evolution of early primates, an increased input from the ipsilateral eye likely spread over most of the superior colliculus to terminate with a visuotopic pattern that matched that of the inputs from the contralateral eye. In present-day galagos, the contralateral retinal inputs to the superior colliculus terminate more superficially in the superficial gray layer of the superior colliculus than the inputs from the contralateral eye (Tigges and Tigges, 1970). In contrast, the retinal inputs from both eyes terminate at the same superficial level in New World and Old World monkeys, but in a patchy pattern so that terminations from the ipsilateral eye may alternate with those from the contralateral eye (Weller and Kaas, 1989). With either pattern, terminations from the ipsi and contra eyes are at least partially segregated.

Another variable feature of the superior colliculus is in the input from cortex. All mammals with functional visual cortex have projections from visual cortex to the superficial layers of the superior colliculus, but most non-primate mammals do not have the vast array of cortical visual areas present in primates (Felleman and Van Essen, 1991). Thus, the number of visual areas contributing inputs to the superior colliculus increased with the expansion and the expansion of the visual cortex and an increase in the number of visual areas in the ancestors of early primates.

Primates also differ from most non-primates in having a large region of posterior parietal cortex that is involved in visuomotor functions (Kaas et al., 2011), and these visuomotor areas project to the superior colliculus (Baldwin and Kaas, 2012; Collins et al., 2005). Although all primates have a frontal eye field where electrical microstimulation evokes eye movements, this field does not project strongly to the superior colliculus in prosimian galagos as it does in anthropoid primates. This observation suggests that significant visuomotor projections from frontal cortex to the superior colliculus were not present in early primates, but they emerged with the evolution of the diurnal ancestors of anthropoid primates.

The Visual Thalamus: the dorsal lateral geniculate nucleus and the pulvinar

The main visual structures of the dorsal thalamus of all mammals are the dorsal lateral geniculate nucleus, LGN, and the pulvinar complex. In primates, the target of almost all retinal ganglion cells is the LGN (Weller and Kaas, 1989). All primates have a laminated LGN that reflects a basic pattern of four main layers (Fig. 4). The two thinner ventral layers of large cells (the magnocellular layers) next to the optic track receive inputs from the M cells of the retina, while the two thicker dorsal layers of smaller cells (the parvocellular layers) receive inputs from the much more numerous P ganglion cells. The outer (external) layers of each pair receive inputs from the contralateral eye, and the inner (internal) layers receive inputs from the ipsilateral eye. However, there is some evidence for a modification of this pattern in tarsiers so that the external magnocellular layer receives inputs from the ipsilateral eye (Pettigrew et al., 1989). The K ganglion cells of the retina project to a distinct pair of koniocellular layers of small cells in the LGN of prosimian primates, and in other primates, project to a scattering of small cells between layers. The P-cell layers divide to form additional sublayers in the LGN of some of the New World monkeys, all of the Old World monkeys, and the great apes and humans.

In cats, the results of early studies of the response properties of retinal ganglion cells led investigators to define X, Y and W cell classes, which are very similar to the P, M, and K classes of primates, and likely represent homologous classes of cells in perhaps all mammals (Casagrande et al., 2007). Allowing for this premise, we can use comparative evidence to reconstruct the probable evolution of the laminar organization of the LGN from early mammals to present-day primates. Early mammals, as for many species of present-day mammals, likely had only weakly differentiated layers in the LGN (Kaas, 2007), with cryptic lamination revealed as a central pocket of inputs from the ipsilateral eye bordered on each side by tissue with inputs

from the contralateral eye (Fig. 4). The contra layer most distant from the optic tract likely had a mixture of P (X) and M (Y) retinal inputs, as did the central ipsi layer. The larger layer near the optic tract had K (W) retinal cell inputs, or a mixture of M (Y) and K (W) inputs, and was dominated by inputs from the contralateral eye, with some inputs from the ipsilateral eye, perhaps forming an ipsilateral region central in this layer, as in some rodents**.**

The closest relatives of primates, the tree shrews and flying lemurs, also have a laminated LGN, but they differ in the arrangement of inputs from the two eyes (Fig. 4). In addition, LGN layers in tree shrews segregate inputs from classes of ganglion cells in a different way than primates. Most notably, the neurons with P (X) and M (Y) retinal inputs are mixed in the same layers, while those P and M neurons that respond to light onset (ON cells) are in different layers than the layers that have neurons that respond to light offset (OFF cells). Thus, distinctly laminated LGNs evolved independently and differently in tree shrews, flying lemurs, and primates. The early primates likely evolved a basic four-layer pattern from a more generalized LGN, with some segregation of inputs by eye of origin and some segregation by type of input from ganglion cell classes. Specialized layers for K-cell inputs were probably part of this early pattern, but these layers were diminished or lost as diurnal primates emerged, so that LGN K cells were scattered between layers. Tarsiers did not regain K layers with a return to nocturnal life, but tarsiers and the only nocturnal monkey, the owl or night monkey, evolved a thick K-cell region, but not distinct K-cell layers, between the P and M layers. In anthropoid primates, the emphasis on diurnal vision resulted in a great increase in the proportion of the LGN devoted to P-cell inputs. These layers became thicker, especially in parts representing central vision, and they subdivided to form four or more P “layers” (actually partial layers or leaflets of layers). The appearance of four leaflets of P layers over the part of the LGN representing central vision, plus the two M layers led to the description of the LGN as having 6 layers. However, in apes and humans, even sub-leaflets of leaflets can be found and this would lead to an even greater number if counted as full layers. A more parsimonious interpretation is that the LGN of primates has two M cell layers, two P cell layers that sometimes subdivide, and various distributions of K cells that are more pronounced in nocturnal primates, where the distributions of K cells are sometimes recognized as forming layers.

The comparative evidence on the relative sizes and types of LGN layers in primates is consistent with the view that the P system is critically involved in detailed vision, and in the use of cone

mediated sensitivities to color differences (Casagrande et al., 2007). Thus, P-cell information from the retina goes exclusively (or nearly so) to the LGN in anthropoid primates (Weller and Kaas, 1989). The smaller M system is used to detect change in the visual field, usually produced by object or self-motion. This retinal information goes to both the LGN and superior colliculus, likely via collateral branches of the same axons. The small K cell retinal output goes to both the LGN and superior colliculus via collaterals. Some K cells carry information from the short S-wavelength cones of the retina (White et al., 1998). K cell layers and neuron distributions in the LGN also receive projections from the superior colliculus (Harting et al., 1991), and they project both to layer 3 of primary visual cortex, but also to other extrastriate visual areas such as the middle temporal area, MT (Sincich et al., 2004; Stepniewska et al., 1999). These features suggest that the functions of the K cell system are quite distinct from those of the P and M cell systems. While the proportionately larger K cell layers and regions in nocturnal primates indicate that K cell inputs are likely important in vision in dim light, the roles of the K cell system in vision remain uncertain.

The other major visual structure of the dorsal thalamus is the pulvinar complex. It consists of several subdivisions or nuclei that are considered visual because they receive inputs from the superior colliculus or visual cortex, and project to visual cortex (Fig. 5). The pulvinar complex of primates has been traditionally divided into the inferior pulvinar, the lateral pulvinar and the medial pulvinar. The medial pulvinar is connected with multisensory and other regions of cortex, and is not considered to be a strictly visual structure. A proposed dorsomedial division of the lateral pulvinar is also not solely a visual structure. The pulvinar was once thought to be a part of the thalamus specific to primates, and this incorrect assumption is responsible for parts, or all, of the pulvinar complex being called the lateral posterior nucleus or nuclei in non-primate mammals.

Subdivisions or nuclei of the visual pulvinar in anthropoid primates have been revealed by differences in the expression of different substances (acetylcholinesterase, calbindin, glutamate transporters, cytochrome oxidase, etc.) and differences in connections, as well as by having different representations of the contralateral visual hemifield (Kaas and Lyon, 2007). All anthropoid primates appear to have the divisions of the visual pulvinar illustrated in Figure 5, but the relative sizes and positions of the nuclei differ. For example, nuclei projecting to primary visual cortex are proportionately larger in primates that are diurnal and have emphasized foveal

vision (i.e., nuclei more related to the ventral stream cortical processing). Unfortunately, the histological preparations, which have been so useful in revealing subdivisions of the visual pulvinar in anthropoid primates, have been less useful in prosimian primates, such that clear homologues of nuclei are less apparent (Wong et al., 2009). However, two large regions of the pulvinar in prosimian galagos that project to primary visual cortex (V1) appear to be homologous with the ventrolateral division of the lateral pulvinar (PLvl) and the central lateral division of the inferior pulvinar (PIcl) of anthropoids, while a caudal division of the pulvinar complex of galagos with inputs from the superior colliculus appears to be homologous to the posterior and central medial divisions of the inferior pulvinar of anthropoids. If so, the mediodorsal position of the caudal pulvinar in galagos is positioned much as the dorsal pulvinar nucleus is in tree shrews (Lyon et al., 2003) and the caudal pulvinar nucleus in squirrels (Baldwin et al., 2011). All these nuclei receive inputs from the superior colliculus and project to temporal visual cortex. Thus, we are beginning to be able to relate divisions of the pulvinar complex in primates to those of rodents and tree shrews, and infer how differences might have evolved. For now, it seems that a caudal nucleus in rodents, tree shrews, and galagos, and possibly many other mammals, is homologous to parts of the inferior pulvinar in anthropoid primates.

Visual Cortex

Early primates were characterized by a large expanse of visual cortex that was divided into a number of visual areas. Because the areal organization of visual cortex is not fully understood in any primate, much less in a range of primate species, only limited comparisons across members of the major branches of primate evolution are possible. Thus, the arrangement and number of cortical visual areas of early primates can only be inferred in part.

All primates have a large primary visual area, V1, which is rotated by the expansion of extrastriate visual cortex and posterior parietal cortex from its common caudal-dorsal position in other mammals to occupy the caudal pole of the hemisphere. As a result, much of V1 is on the ventral surface and medial wall of the hemisphere, and in the calcarine sulcus, a fissure found only in primates. Primary visual cortex in extant primates is approximately two to three times larger than would be expected for mammals of a similar body size, but V1 is smaller in prosimian primates than in simian primates of similar size. Primates tend to devote one-third to one-half of V1 to the first 10 degrees of central vision, with this expansion of central vision being more pronounced in diurnal primates (Rosa et al., 1997). All primates have a similar

projection pattern from LGN layers to V1 to that inputs from M layers terminate in a sub-layer of layer 4 that is external to the sub-layer with P layer inputs (Casagrande and Kaas, 1994). All primates appear to have a modular subdivisions of layer 3 such that a dot-like pattern of cytochrome oxidase (CO) dense "blobs," which receive afferents from the K cells of the LGN (Casagrande and Kaas, 1994), and non-blob surrounds (Preuss and Kaas, 1996) are visible. Tree shrews do not have the CO blob pattern, although myelin stains reveal a pattern of myelin-poor regions that are blob-like (Lyon et al., 1998). Both primates and tree shrews have orderly arrangements of orientation-selective neurons in V1 (Bosking et al., 1997). As this arrangement is not found in rodents, systematic arrays of orientation selective "columns" of neurons likely evolved in the common ancestors of tree shrews and primates. However, carnivores appear to have independently evolved an orderly arrangement of orientation-selective "columns" or modules in V1 (Kaschube et al., 2010).

Primates are unusual in that LGN inputs related to the contralateral and ipsilateral eyes tend to terminate in layer 4 of V1 in separate bands or clusters, forming the basis for the ocular dominance columns. However, the patterns created by the segregation of these inputs are quite variable across primate species, and even within a species (Adams and Horton, 2003)**.** Such variability likely reflects the interplay of changing neural activity patterns, the proportions of axon terminals related to each eye, and the chemical signals that guide termination patterns (Kaas and Catania, 2002). Ocular dominance columns, or bands, are not found in the closest relatives of primates (tree shrews, rodents and lagomorphs).

The major cortical outputs from V1 in all studied primates (Lyon and Kaas, 2001; Lyon and Kaas, 2002a; b; c) are in decreasing magnitudes to V2, V3, MT, and DM (Fig. 5). Most of the projections to MT are from deep layer 3 (3C, incorrectly identified as layer 4B in most studies; (see Casagrande and Kaas, 1994), while the middle of layer 3 (3B) provides most of the projections to the other cortical targets.

The laminar and sub-laminar specializations of V1 vary somewhat across primates, with layers being least distinct in prosimian primates and layers and sublayers being most distinct in tarsiers, where V1 occupies proportionately more neocortex than in any other primate (Collins et al., 2005). Humans have a specialization of a sub-layer of layer 3 that suggests a role in the magnocellular processing stream involved in motion analysis (Preuss et al., 1999). Across

primate taxa, V1 gets bigger with brain size, but only up to the great apes, as the much larger human brain has a V1 about the same size as in chimpanzees. Thus, the size of V1 relative to the rest of neocortex actually decreases in humans compared to other primates. Over a range of primate species from small prosimian brains to the large baboon brain, the ratio of V1 neurons to LGN neurons increases, so that as V1 increases in size, each LGN relay neuron relates to a larger number of V1 neurons. In addition, V1 of primates differs from V1 of other mammals by having more neurons for its size. Thus, V1 of primates has 3-4 times more densely packed neurons than other cortical areas. This difference is the least pronounced in prosimian galagos, more so in New World monkeys, even more in macaques and baboons (Collins et al., 2010). Such differences in neuron packing densities are not marked in non-primates. As high densities of small neurons provide a framework for preserving the details of visual scenes, V1 is specialized for detailed vision in all primates, with this feature much enhanced in Old World monkeys, apes and humans. In these anthropoids, even V2 has more densely packed neurons than most cortical areas.

Most of the outer border of V1, is formed by a narrow belt-like second visual area, V2, in all extant primates. This outer border of V1 represents the line of decussation of the retina (the zero vertical meridian), which corresponds to the full extent of the V1/V2 border. The rest of V1, corresponding to the temporal margin of monocular vision, is bordered by a small, poorly understood area, the prostriata (Rosa et al., 1997). Early primates, as in present-day nocturnal prosimians, devoted less of V1 to the representation of central vision. As a result, less of the border of V1 corresponded to the vertical meridian and a shared border with V2. Thus, V2 was less elongated than in extant diurnal primates.

In monkeys, V2 is characterized by a modular organization that is revealed by stains for CO as they mark alternating CO-dense and CO-light bands crossing the rostrocaudal extent of V2. The CO-dense bands appear to be of two types, “thick” and “thin”. Each of three types of bands is thought to have different connections with V1 modules and sublayers and with other visual areas (Hubel and Livingstone, 1987; Krubitzer and Kaas, 1990; Roe, 2004)**.** Such a pattern of modular organization is less apparent in prosimian primates, although CO-dense bands may be weakly apparent in favorable material (Preuss et al., 1993; Preuss and Kaas, 1996). However, modular differences in connections of V2 of galagos suggest that an anatomical framework for bands exists in V2 (Collins et al., 2001). Tree shrews also have a banding pattern of V1 connections in

V2 (Lyon et al., 1998; Sesma et al., 1984), but the functional significance of this segregation is not clear. These observations suggest that V2 had modular subdivisions in early primates, but the modules may have been less regular and distinct than in present-day simians. Nevertheless, a specific pattern of modular processing in V2 was part of the visual specializations of the primate branch of mammalian evolution.

The outer border of V2 is bordered by V3 in all primates. The extent of V3 with its shared boundary with V2 was previously contentious in that some investigators considered ventral V3 as separate visual area (VP), differing from dorsal V3 by its lack of connections with V1 (Lyon and Connolly, 2011). But now there is compelling evidence for dorsal V3 and ventral VP being parts of the same visual area, with evidence of matching V1 connections to ventral and dorsal V3 in galagos, several species of New World monkeys, and macaques (Lyon and Kaas, 2001; Lyon and Kaas, 2002a; b; c; Lyon et al., 2002)**.** Given this broad distribution, early primates undoubtedly had a V3. However, there is no clear evidence yet for a V3 in tree shrews (Lyon et al., 1998), or in rodents and rabbits (Rosa and Krubitzer, 1999), so V3 may not have been present in the common ancestors of primates, tree shrews and rodents. This conclusion should be held cautiously, however, as further study could provide evidence for V3 in tree shrews and other mammals. As a primate-like V3 has been described in cats, this difference in distribution suggests that V3 in primates and cats evolved independently.

A similar conclusion relates to the evolution of the middle temporal visual area (MT). MT is easily identified in primates by its projection pattern from V1, dense myelination, retinotopic organization, and neurons that are dominated by a relay of the M-cell pathway though V1 (Casagrande and Kaas, 1994). This distinctive visual area has been found in galagos (Allman et al., 1973) and in all other studied primates, including humans, but not in tree shrews, rodents, or rabbits (Kaas, 1997). Because of this distribution, MT appears to be a visual area that first evolved with the early primates. Thus, cats are unlikely to have a homolog of MT, as is sometimes postulated.

Finally, in all primates, much of posterior parietal cortex is involved in processing visual information so that separate domains within this region can help plan, initiate, and guide adaptive movements of eyes, hands, and other parts of the body (Kaas et al., 2011). Some of these domains, including those for grasping, reaching, defense of the face and eye movements (Fig. 5)

have been defined by microstimulation in galagos, New World monkeys, and macaques, and they likely exist in all primates. Such movement domains do not appear to be present in posterior parietal cortex of tree shrews and rodents, which have very little posterior parietal cortex. Thus, this large region of cortex, with movement specific domains must have emerged in the immediate ancestors of the first primates. However, the region differs in organization and complexity, as primates differ in the skilled use of their hands, and more functional domains likely exist in humans than in prosimians and monkeys (Orban et al., 2006).

Toward a further understanding of how the human visual system evolved

Despite much progress, we are at the early stages of fully describing the organization of the human visual system, and we know little about the visual systems of apes. Members of the major branches of primate evolution cover a range of body and brain sizes, and they are specialized in various ways, so we can expect variations in the visual system within as well as across taxonomic groups. In Old World monkeys, over 30 visual areas have been proposed (Felleman and Van Essen, 1991), and these primates have greatly expanded regions of visual cortex in the temporal and parietal lobes compared to most New World monkeys and all prosimians. Quite possibly, Old World monkeys have more visual areas than most or all New World monkeys. Further increases in overall brain size and the total extent of visual cortex undoubtedly occurred in apes and in our early hominid ancestors. Possibly there was a further increase in the number of visual areas, but this is uncertain. What is clear from the fossil record is that our ancestors of only 3 million years ago had brains only slightly larger (600 – 800 cc) than those of present-day African apes (Kaas and Preuss, 2012), and these brains may have resembled those of African apes in general organization.

Over the last two million years, the brains of our ancestors increased rapidly in size to the present volume of about 1400 cc, but we know little about the structural changes in brain organization that occurred during that time. What is known from comparing human brains with those of apes is that the easily identified primary visual area increased only slightly in absolute size while occupying proportionately much less of the total neocortex. This observation is consistent with the conclusion that the number of cortical areas, including visual areas, has increased with the evolution of modern humans.

Changes in the numbers and sizes of cortical areas in primate evolution have functional consequences. The functions of cortical areas are altered as they change in size (Kaas, 2000). In smaller cortical areas, individual neurons are activated by a larger proportion of inputs. Thus, neurons in small cortical areas represent proportionally more of the inputs, and smaller cortical areas have intrinsic connections that cover more of the cortical area. These differences in connections make neurons in smaller areas more suitable for global comparisons as they have larger receptive field centers and surrounds. In contrast, large areas, such as V1, have mainly neurons that receive proportionally few of the inputs, as these neurons have smaller dendritic arbors (Elston, 2007). Thus, larger areas are good for processing the local detail of a stimulus, and smaller areas more broadly integrate information. This may be why the large human brain is not simply a larger version of a monkey brain. V1 and at least several other areas did not increase proportionately in size as brains became larger and new areas were likely added. Only a few visual areas would need to be large, and preserve detailed information about the visual scene while smaller visual areas could be specialized in various ways. The evolution of the complex human brain may have depended on the addition of gene copies that subsequently differentiated and acquired new functions (Ohno, 1970), possibly including those that increased the number of visual areas. The addition of new cortical areas allowed both added and original visual areas to differentiate, specialize, and mediate new capacities (Kaas, 1989).

Presently, we know that human brains are about three times as large as those of the African apes, but we still know very little about how human and ape brains differ structurally. Histochemical and traditional architectonic approaches can help identify nuclei and cortical areas that apes and humans have in common (Hackett et al., 2001; Qi et al., 2007), specialized features of those areas (Preuss et al., 1999), and possibly nuclei and areas unique to humans. The goal of determining the similarities and differences in cortical organization across primates has been expressed from the time of Brodmann (1909), but now we have powerful modern methods to add force to such studies.

Finally, much can be learned about the evolution of complex visual systems from theoretical approaches that examine scaling issues related to brain size (Herculano-Houzel, 2011), as well as from our growing understanding of the modes of brain development and how development can be altered in evolution (Molnár, 2011). Comparative studies of areal differences and similarities

in the histochemistry and patterns of gene expression of visual cortex of humans, apes and other primates are also of great value (Preuss et al., 2004; Takahata et al., 2011).

Figure Legends

1. Differences in the number of neurons in the brains of about the same size from a small monkey and a large rodent. Primates' brains of comparable sizes have more neurons than rodent brains, and this difference increases with greater brain size. This difference is even greater when neuron numbers are related to body size. The largest rodent that ever existed (now extinct) had a body size of 700 kg (1540 lbs.) while having an estimated 7.5 billion neurons, while the brain of an 81 kg (180 lb) human would have roughly 100billion neurons. These estimates are based on neuron scaling rules from Herculano-Houzel et al., (2007).

2. The emergence and radiation of the four major clades of placental (eutherian) mammals. In each clade, a few representative present-day species and other groups are listed. Primates are part of the Euarchontoglire radiation. The illustrated phylogenetic relationships suggest that inferences about the visual systems of early primates would be most productive when the visual systems comparisons are made with other members of the Euarchontoglire clade. Time on the left is in millions of years ago (mya). Based on Murphy et al., 2004.

3. All primates share a unique type of retinotopic organization in the superior colliculus. In all primates, the left superior colliculus receives superimposed inputs from the nasal hemiretina of the right (R) eye and the temporal hemiretina of the left (L) eye, resulting in a representation of the right hemifield that is largely binocular. The right superior colliculus (SC) has a comparable pattern of inputs from the left and right eyes. In other studied mammals, the complete retina of the contralateral eye projects to the superior colliculus, even though the temporal retina also projects ipsilaterally to the LGN, as in primates. The temporal retina may also project weakly to the ipsilateral superior colliculus in a species-variable manner. In nonprimate mammals, the superior colliculus represents the complete visual field of the contralateral eye, including the binocular part of the ipsilateral hemifield. LD, line of decussation of retinal projections to the two hemispheres. See Kaas and Preuss (1993).

4. Laminar patterns of the dorsal LGN in primates. The schematics are of the laminar patterns in brain sections cut across layers that are stacked like slices of bread from ventral (or along the optic tract) to dorsal (near the pulvinar). Early mammals had a simple pattern of LGN

lamination that segregated inputs from the ipsilateral retina in a central region between outer regions with inputs from the contralateral retina. All primates have a more elaborate pattern of four basic layers that evolved with the first primates. Close relatives of primates, tree shrews and flying lemurs, evolved different patterns of lamination. In flying lemurs, layers have been identified histologically and by having inputs from the contralateral (contra) or ipsilateral (ipsi) eye (Pettigrew et al., 1989). In tree shrews (Norton, 1982), microelectrode recordings suggest that M and P-cell (termed Y and X) inputs are mixed in the same layers, unlike primates, while ON and OFF ganglion cell inputs are segregated in different layers (Norton, 1982), unlike in primates. ON retinal ganglion cells respond to the onset of light in the receptive field center, while OFF cells respond to diming or offset of light. Other layers appear to have K-cell inputs. The basic primate pattern of lamination includes two parvocellular (P) and two magnocellular (M) layers, with the longer (for the monocular field) outer (external) layers receiving from the contralateral retina (PE, ME) and the shorter inner or internal layers (PI, MI) from the ipsilateral eye. Present-day tarsiers may have a modified pattern, as there is evidence that the two M layers have a reversed pattern of input in regard to eye of origin, so that ME receives input from the ipsilateral retina (Pettigrew et al., 1989). All prosimians have an extra pair of layers, the koniocellular layers (KE and KI). In other primates, K cells are scattered between layers where they do not form distinct layers. In many anthropoid primates, the parvocellular layers divide to form sublayers and leaflets of sublayers. In the diagram, the layers with input from the ipsilateral eye are shorter as they represent less of a contralateral visual hemifield (0°- 90°). Modified from Kaas et al., 1978.

5. Proposed subdivisions (nuclei) of the pulvinar complex which are likely common to most or all primates. Two large, retinotopically organized nuclei, the central lateral nucleus of the inferior pulvinar (PIcl) and the ventral lateral nucleus of the lateral pulvinar (PLvl) project to visual areas early in cortical processing (V1-V3) and areas in the ventral processing stream (caudal DL or V4 and caudal inferior temporal cortex), and are activated by inputs from early cortical areas. Two nuclei with dense inputs from the superior colliculus (SC), the posterior and central medial nuclei (PIp and PIcm) of the inferior pulvinar project to a collection of visual areas in the dorsal stream of visual processing (MT, dorsal and ventral divisions of FST, MST, MTc, DM or V3a, and rostral DL or rostral V4). Comparative evidence suggests that PIp and PIcm differentiated from a single caudal pulvinar nucleus, with superior colliculus inputs and projections to temporal cortex, in the non-primate ancestors of primates.

The dorsal medial nucleus of the lateral pulvinar (PLdm) has frontal and parietal lobe connections, while the medial pulvinar (PM) has connections with frontal, cingulate, insular, and temporal cortex. Based on Kaas and Lyon, 2007.

6. Proposed subdivisions of visual cortex in a prosimian primate (galago). Other areas are included for reference. A dorsolateral view of a galago brain is on the lower left. On the upper right, the cortex from the left hemisphere has been flattened so that subdivisions on hidden surfaces are visible. The dashed line on the flattened cortex outlines cortex that is visible on a dorsolateral view of the intact hemisphere. The areas shown here are common to all studied primates, and likely existed in the first primates. The primary visual area, V1, is characterized by a distribution of cytochrome oxidase (CO) dense patches of cortex known as blobs. These appear to exist in all primates, but not the close relatives of primates tree shrews and rodents). The second visual area, V2, has a sequence of myelin-dense bands crossing the width of the area. In anthropoid primates, these bands are of two functional types, thin and thick, bands are only weakly apparent in prosimian primates. V2 is bordered by a narrow V3. Other areas common to primates include the dorsolateral visual area, DL, also known as V4, the middle temporal visual area, MT, the MT crescent (MTc), the fundal area of the superior temporal sulcus (FST), the medial superior temporal area (MST), and the dorsal medial visual area, DM. The caudal half of posterior parietal cortex (PPC) is primarily visual, but functional subdivisions are unknown. The rostral half is visual and somatosensory, with subdivisions (domains) for guiding grasping (G), defense (D), reaching (R), and other movement sequences. The frontal eye field (FEF) is involved in eye movements. Inferior temporal (IT) cortex is visual, but functional subdivisions are unknown. Prostriata is a visual area common to mammals. Motor areas include primary motor cortex (M1) ventral (PMV) and dorsal (PMD) premotor cortex, the supplementary motor area (SMA) and ventral (CMv), rostral (CMr) and caudal (CMc) cingulate motor areas. Somatosensory areas include areas 3a, 3b, 1 (or 1 plus 2) of Brodmann, the second area (S2), the parietal ventral area (PV), a ventral somatosensory area (VS), and a proposed gustatory (G?) area. Auditory areas include primary (A1) and rostral (R) auditory areas, and the auditory belt (AB) and parabelt (PB). Retrosplenial cortex includes granular (RSg) and agranular (RSag) areas. Frontal cortex includes granular frontal cortex (gFC) and ventral (OFv) and medial (OFm) orbital frontal areas.

References

Adams, D. L., & Horton, J. C. (2003). Capricious expression of cortical columns in the primate brain. *Nat Neurosci, 6*, 113-114.

Allman, J. M., Kaas, J. H., & Lane, R. H. (1973). The middle temporal visual area (MT) in the bushbaby (*Galago senegalensis*). *Brain Res., 57*, 197-202.

Avzevedo, F. A. C., Carvalho, L. R. B., Grinberg, L. T., Farfel, J. M., Ferretti, R. E. J., Leite, R. E. P., et al. (2009). Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain. *J Comp Neurol, 513*, 532-541.

Baldwin, M. K. L., & Kaas, J. H. (2012). Cortical projections to the superior colliculus in prosimian galagos (Otolemur garnetti). *J Comp Neurol, Dec. 15 [Epub ahead of print]*.

Baldwin, M. K. L., Wong, P., Reed, J. L., & Kaas, J. H. (2011). Superior colliculus connections with visual thalamus in grey squirrels (Sciurus carolinensis): Evidence for four subdivisions within the pulvinar complex. *J Comp Neurol, 519*(6), 1071-1094.

Bhatnagar, K. P., & Smith, T. D. (2007). The vomeronasal organ and its evolutionary loss in catarrhine primates. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of Nervous Systems* (Vol. 4, pp. 142-152). London: Elsevier.

Block, J. I., & Boyer, D. M. (2002). Grasping primate origins. *Science, 298*, 1606-1610.

Bosking, W. H., Zhang, Y. M., Schofield, B., & Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. *J Neurosci, 17*(6), 2112-2127.

Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrhinde*. Leipzig: Barth.

Casagrande, V. A., & Kaas, J. H. (1994). The afferent, intrinsic, and efferent connections of primary visual cortex in primates. In A. Peters & K. Rockland (Eds.), *Cerebral Cortex, Vol. 10* (Vol. 10, pp. 201-259). New York: Plenum Press.

Casagrande, V. A., Khaytin, I., & Boyd, J. (2007). The evolution of parallel visual pathways in the brains of primates. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of the Nervous Systems* (Vol. 4, pp. 87-108). London: Elsevier.

Collins, C. E., Airey, D. C., Young, N. A., Leitch, D. B., & Kaas, J. H. (2010). Neuron densities vary across and within cortical areas in primates. *Proc Natl Acad Sci U S A, 107*(36), 15927-15932.

Collins, C. E., Lyon, D. C., & Kaas, J. H. (2005). Distribution across cortical areas of neurons projecting to the superior colliculus in New World monkeys. *Anat Rec, 285A*, 619-627.

Collins, C. E., Stepniewska, I., & Kaas, J. H. (2001). Topographic patterns of V2 cortical connections in a prosimian primate (Galago garnetti). *J Comp Neurol, 431*, 155-167.

Corballis, M. C. (2007). Evolution of hemispheric specialization of the human brain. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of Nervous Systems* (Vol. 4, pp. 379-396). London: Elsevier.

de Sousa, A., & Wood, B. (2007). The hominin fossil record and the emergence of the modern human central nervous system. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of Nervous Systems* (Vol. 4, pp. 291-336). London: Elsevier.

Elston, G. N. (2007). Specialization of the neocortical pyramidal cell during primate evolution. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of Nervous Systems* (Vol. 4, pp. 191-242). London: Elsevier.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex, 1*, 1-147.

Hackett, T. A., Preuss, T. M., & Kaas, J. H. (2001). Architectonic identification of the core region in auditory cortex of macaques, chimpanzees, and humans. *J Comp Neurol, 441*, 197-222.

Hart, B. L., & Hart, L. A. (2007). Evolution of the elephant brains: a paradox between brain size and cognitive behavior. In J. H. Kaas & L. A. Krubitzer (Eds.), *Evolution of Nervous Systems* (Vol. 3, pp. 491-497). London: Elsevier.

Harting, J. K., Huerta, M. F., Hashikawa, T., & Van Lieshout, D. P. (1991). Projections of the mammalian superior colliculus upon the dorsal lateral geniculate nucleus: organization of tectogeniculate pathways in nineteen species. *J Comp Neurol, 304*, 275-306.

Hendrickson, A., Djajadi, H. R., Nakamura, L., Possin, D. E., & Sajuthi, D. (2000). Nocturnal tarsier retina has both short and long/medium-wavelength cones in an unusual topography. *J Comp Neurol, 424*(4), 718-730.

Herculano-Houzel, S. (2011). Not all brains are made the same; new views on brain scaling in evolution. *Brain Behav and Evol, 78*, 22-36.

Herculano-Houzel, S., Collins, C. E., Wong, P., & Kaas, J. H. (2007). Cellular scaling rules for primate brains. *Proc Natl Acad Sci U S A, 104*, 3562-3567.

Hubel, D. H., & Livingstone, M. S. (1987). Segregation of form, color, and stereopsis in primate area 18. *J Neurosci, 7*, 3378-3415.

Jacobs, G. H., Neitz, M., Deegan, J. F., & Neitz, J. (1996). Trichromatic colour vision in New World monkeys. *Nature, 382*, 156-158.

Jerison, H. J. (1973). *Evolution of the Brain and Intelligence*. New York: Academic Press.

Kaas, J. H. (1978). Organization of visual cortex in primates. In C. R. Noback (Ed.), *Sensory Systems of Primates* (pp. 151-179). New York: Plenum Press.

Kaas, J. H. (1989). Why does the brain have so many visual areas? *J Cogn Neurosci, 1*, 121-135.

Kaas, J. H. (1997). Theories of visual cortex organization in primates. In K. S. Rockland, J. H. Kaas & A. Peters (Eds.), *Cerebral Cortex: Extrastriate Cortex in Primates* (Vol. 12, pp. 91-125). New York: Plenum Press.

Kaas, J. H. (2000). Why is brain size so important: Design problems and solutions as neocortex gets bigger or smaller. *Brain and Mind, 1*, 7-23.

Kaas, J. H. (2007). The evolution of the dorsal thalamus in mammals. In J. H. Kaas & L. A. Krubitzer (Eds.), *Evolution of Nervous Systems* (Vol. 3, pp. 500-516). London: Elsevier.

Kaas, J. H., & Catania, K. C. (2002). How do features of sensory representations develop? *Bioessays, 24*(4), 334-343.

Kaas, J. H., Gharbawie, O. A., & Stepniewska, I. (2011). The organization and evolution of dorsal stream multisensory motor pathways in primates. *Front Neuroanat, 5*(34), 1-7.

Kaas, J. H., Harting, J. K., & Guillery, R. W. (1974). Representation of the complete retina in the contralateral superior colliculus of some mammals. *Brain Res, 65*(2), 343-346.

Kaas, J. H., & Lyon, D. C. (2007). Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. *Brain Res Rev, 55*(2), 285-296.

Kaas, J. H., & Preuss, T. M. (2012). Human Brain Evolution. In L. R. Squire (Ed.), *Fundamental Neuroscience, 4th* . San Diego: Academic Press.

Kaschube, M., Schnabel, M., Löwel, S., Coppola, D. M., White, L. E., & Wolf, F. (2010). Universality in the evolution of orientation columns in the visual cortex. *Science, 330*, 1113-1116.

Krubitzer, L. A., & Kaas, J. H. (1990). Convergence of processing channels in the extrastriate cortex of monkeys. *Vis Neurosci, 5*, 609-613.

Lane, R. H., Allman, J. M., Kaas, J. H., & Miezin, F. M. (1973). The visuotopic organization of the superior colliculus of the owl monkey (Aotus trivirgatus) and the bush baby (Galago senegalensis). *Brain Res, 60*(2), 335-349.

Lyon, D. C., & Connolly, J. D. (2012). The case for primate V3. *Proc R Soc B*, 279, 625-633.

Lyon, D. C., Jain, N., & Kaas, J. H. (1998). Cortical connections of striate and extrastriate visual areas in tree shrews. *J Comp Neurol, 401*(1), 109-128.

Lyon, D. C., Jain, N., & Kaas, J. H. (2003). The visual pulvinar in tree shrews I. Multiple subdivisions revealed through acetylcholinesterase and Cat-301 chemoarchitecture. *J Comp Neurol, 467*(4), 593-606.

Lyon, D. C., & Kaas, J. H. (2001). Connectional and architectonic evidence for dorsal and ventral V3, and dorsomedial area in marmoset monkeys. *J Neurosci, 21*(1), 249-261.

Lyon, D. C., & Kaas, J. H. (2002a). Connectional evidence for dorsal and ventral V3, and other extrastriate areas in the prosimian primate, Galago garnetti. *Brain Behav Evol, 59*, 114-129.

Lyon, D. C., & Kaas, J. H. (2002b). Evidence for a modified V3 with dorsal and ventral halves in macaque monkeys. *Neuron, 33*, 453-461.

Lyon, D. C., & Kaas, J. H. (2002c). Evidence from V1 connections for both dorsal and ventral subdivisions of V3 in three species of New World monkeys. *J Comp Neurol, 449*, 281-297.

Lyon, D. C., Xu, X., Casagrande, V. A., Stefansic, J. D., Shima, D., & Kaas, J. H. (2002). Optical imaging reveals retinotopic organization of dorsal V3 in New World owl monkeys. *Proc Natl Acad Sci U S A, 99*(24), 15735-15742.

Meredith, R. W., Janecka, J. E., Gatesy, J., Ryder, O. A., & Fisher, C. A. (2011). Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science, 334*, 521-524.

Molnár, Z. (2011). Evolution of cerebral cortical development. *Brain Behav and Evol, 78*, 94-107.

Ohno, S. (1970). *Evolution of Gene Duplication*. New York: Springer.

Orban, G. A., Claeys, K., Nelissen, K., Smans, R., Sunaert, S., Todd, J. T., et al. (2006). Mapping the parietal cortex of human and non-human primates. *Neuropsychologia, 44*, 2647-2667.

Pettigrew, J. P. (1986). Flying Primates? Megabats have the advanced pathway from eye to midbrain. *Science, 231*, 1304-1306.

Pettigrew, J. P., Jamieson, B. G. M., Robson, S. K., Hall, L. S., McNally, K. I., & Cooper, H. M. (1989). Phylogenetic relations between microbats, megabats and primates. *Proc Trans R Soc Lond, Sci B Biol Sci, 325*, 489-539.

Preuss, T. M. (2007). Primate brain evolution in phylogenetic context. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of Nervous Systems* (Vol. 4, pp. 1-34). Oxford: Elsevier.

Preuss, T. M., Beck, P. D., & Kaas, J. H. (1993). Areal, modular, and connectional organization of visual cortex in a prosimian primate, the slow loris (Nycticebus coucang). *Brain Behav Evol, 42*(6), 321-335.

Preuss, T. M., Cáceres, M., Oldham, M. C., & Geschwind, D. H. (2004). Human brain evolution: insights from microarrays. *Nat Rev Genet, 5*, 850-860.

Preuss, T. M., & Kaas, J. H. (1996). Cytochrome oxidase 'blobs' and other characteristics of primary visual cortex in a lemuroid primate, *Cheirogaleus medius*. *Brain Behav Evol, 47*(2), 103-112.

Preuss, T. M., Qi, H., & Kaas, J. H. (1999). Distinctive compartmental organization of human primary visual cortex. *Proc Natl Acad Sci U S A, 96*(20), 11601-11606.

Qi, H. X., Preuss, T. M., & Kaas, J. H. (2007). Somatosensory areas of the cerebral cortex: Architectonic characteristics and modular organization. In E. Gardner & J. H. Kaas (Eds.), *The Senses, A Comprehensive Reference* (Vol. 6, pp. 143-169). London: Elsevier.

Roe, A. W. (2004). Modular complexity of area V2 in the macaque monkey. In J. H. Kaas & C. E. Collins (Eds.), *The Primate Visual System* (pp. 109-138). Boca Raton: CRC Press.

Rosa, M. G. P., Casagrande, V. A., Preuss, T., & Kaas, J. H. (1997). Visual field representation in striate and prostriate cortices of a prosimian primate (Galago garnetti). *J Neurophysiol, 77*, 3193-3217.

Rosa, M. G. P., & Krubitzer, L. A. (1999). The evolution of visual cortex: where is V2? *TINS, 22*, 242-248.

Ross, C. F., & Martin, R. D. (2007). The role of vision in the origin and evolution of primates. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of Nervous Systems* (Vol. 4, pp. 59-78). London: Elsevier.

Sesma, M. A., Casagrande, V. A., & Kaas, J. H. (1984). Cortical connections of area 17 in tree shrews. *J Comp Neurol, 230*(3), 337-351.

Sherwood, C. C., & Hof, P. R. (2007). The evolution of neuron types and cortical histology in apes and humans. In J. H. Kaas & T. M. Preuss (Eds.), *Evolution of Nervous Systems* (Vol. 4, pp. 355-378). London: Elsevier.

Sincich, L. C., Park, K. F., Wohlgemuth, M. J., & Horton, J. C. (2004). Bypassing V1: a direct geniculate input to area MT. *Nat Neurosci, 7*, 1123-1128.

Skoglund, P., & Jakobsson, M. (2011). Archaic human ancestry in East Asia. *Proc Natl Acad Sci U S A 108*(45), 18301-18306.

Stepniewska, I., Qi, H. X., & Kaas, J. H. (1999). Do superior colliculus projection zones in the inferior pulvinar project to MT in primates? *Eur J Neurosci, 11*(2), 469-480.

Takahata, T., Shukla, R., Yamamori, T., & Kaas, J. H. (2011). Differential expression patterns of striate cortex enriched genes among Old World, New World, and prosimian primates. *Cereb Cortex*, [E-pub ahead of print Nov. 7, 2011], doi:10.1093/cercor/bhr308.

Thiele, A., Vogelsang, M., & Hoffman, K. P. (1991). Pattern of retinotectal projection in the megachiropteran bat (Rousettus aegyptiacus) *J Comp Neurol, 314*, 671-683.

Tigges, M., & Tigges, J. (1970). The retinofugal fibers and their terminal nuclei in Galago crassicaudatus. *J Comp Neurol, 138*, 87-102.

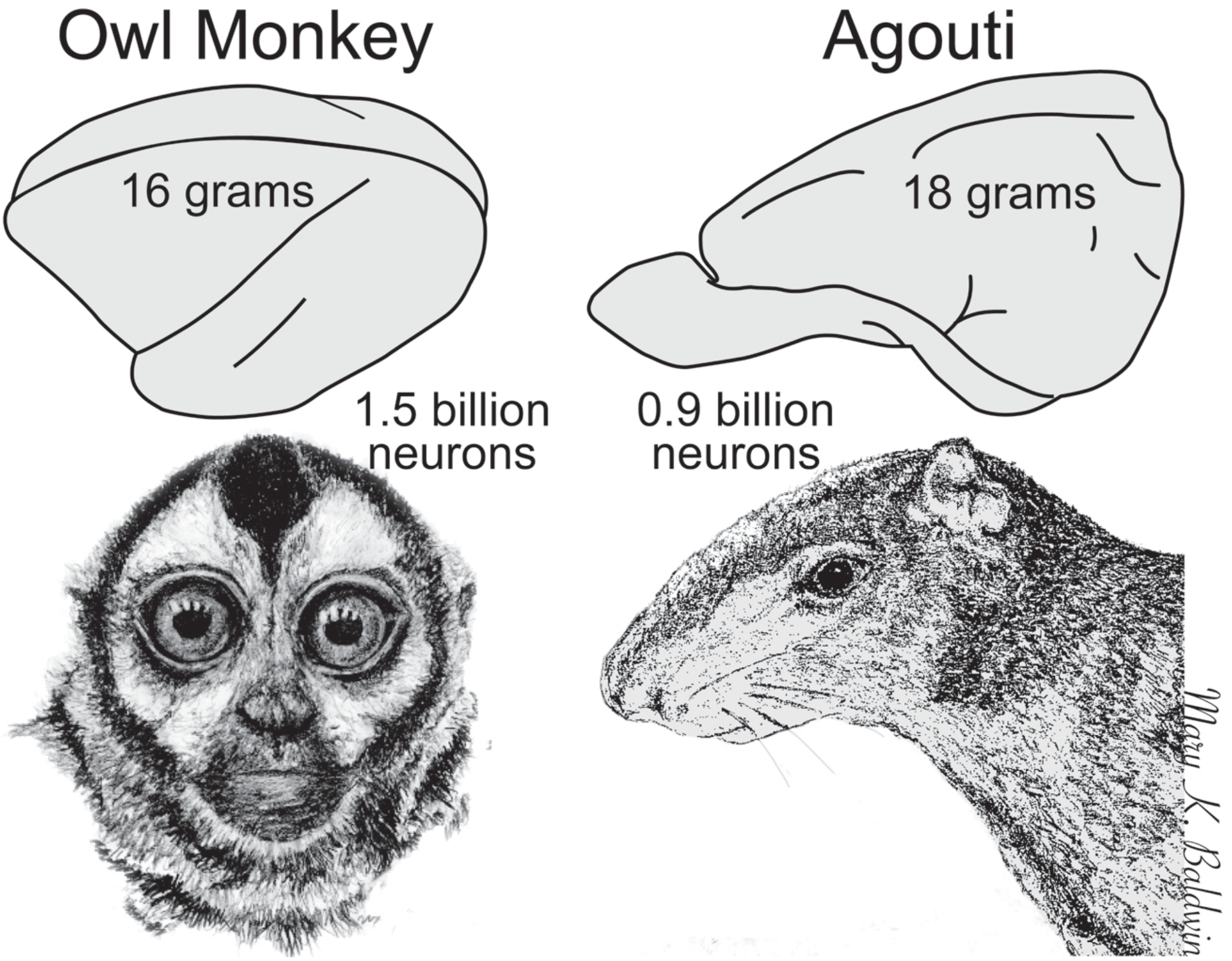
Weller, R. E., & Kaas, J. H. (1989). Parameters affecting the loss of ganglion cells of the retina following ablations of striate cortex in primates. *Vis Neurosci, 3*, 327-349.

Whishaw, I. Q. (2003). Did a change in sensory control of skilled movements stimulate the evolution of the primate frontal cortex? *Behav Brain Res, 146*, 31-41.

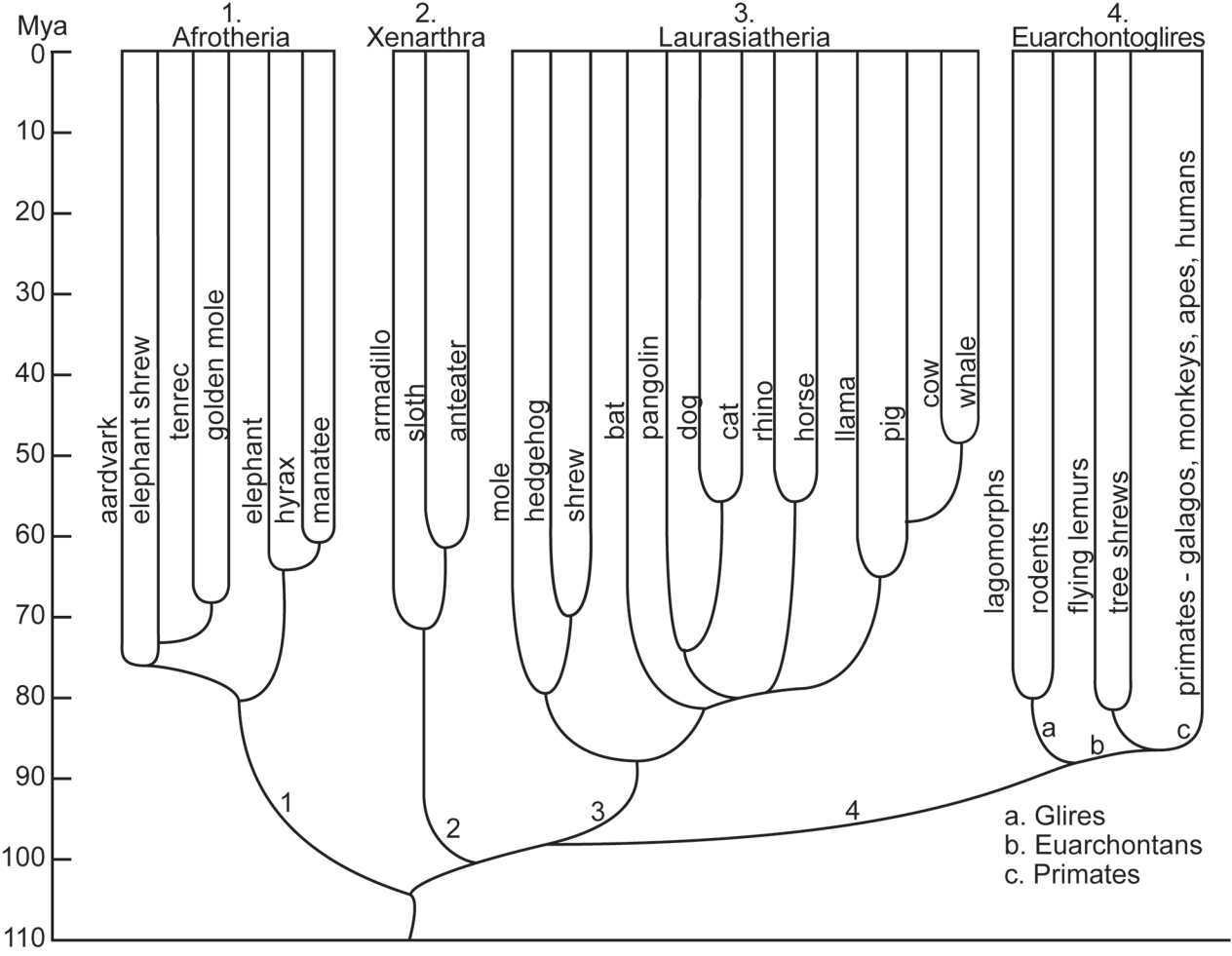
White, A. J., Wilder, H. D., Goodchild, A. K., Secfton, A. J., & Martin, P. R. (1998). Segregation of receptive field properties in the lateral geniculate nucleus of a New World monkey, the marmoset Callithrix jacchus. *J Neurophysiol, 80*, 2063-2076.

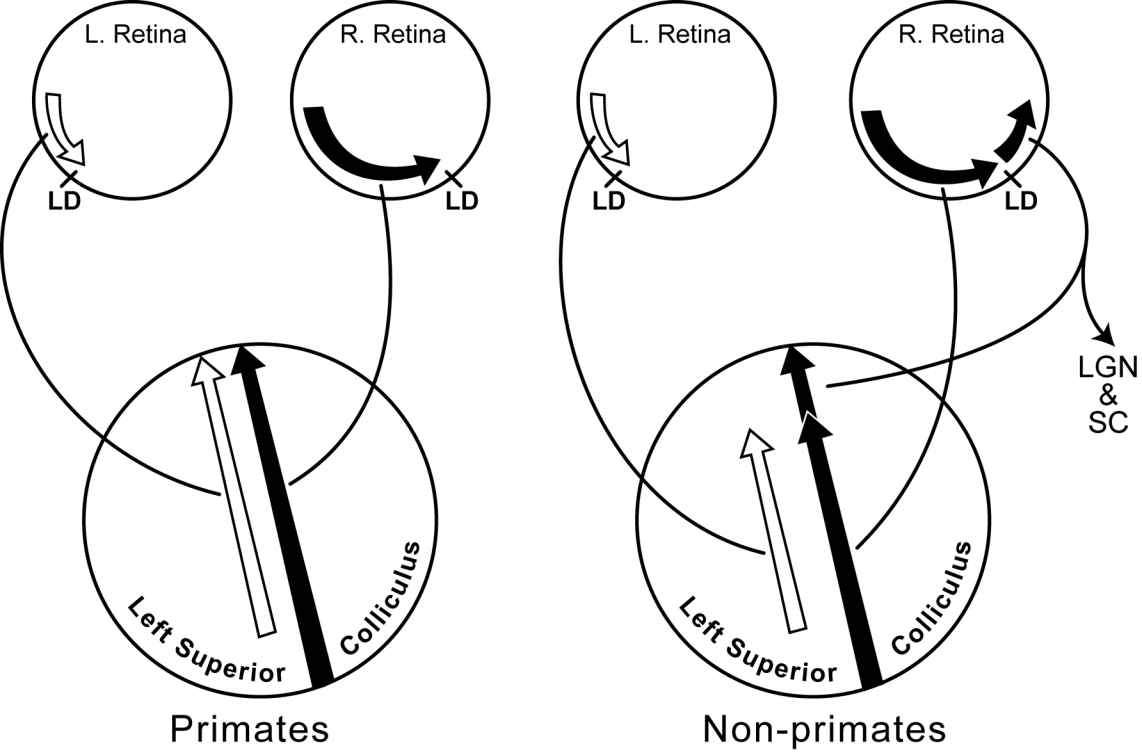
Wikler, K. C., & Rakic, P. (1990). Distribution of photoreceptor subtypes in the retina of diurnal and nocturnal primates. *J Neurosci, 10*, 3390-3401.

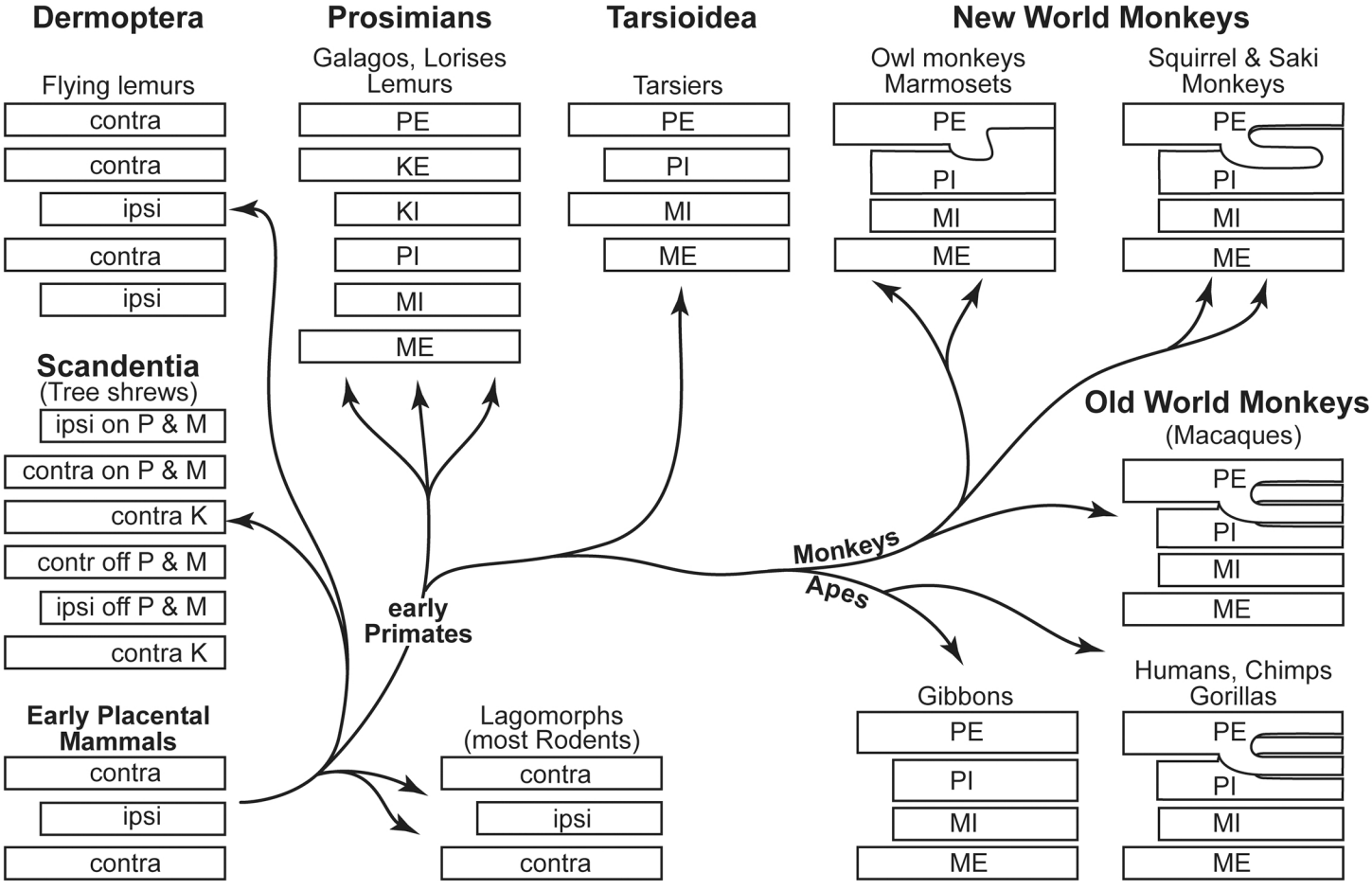
Wong, P., Collins, C. E., Baldwin, M. K., & Kaas, J. H. (2009). Cortical connections of the visual pulvinar complex in prosimian galagos (Otolemur garnetti). *J Comp Neurol, 517*(4), 493-511.

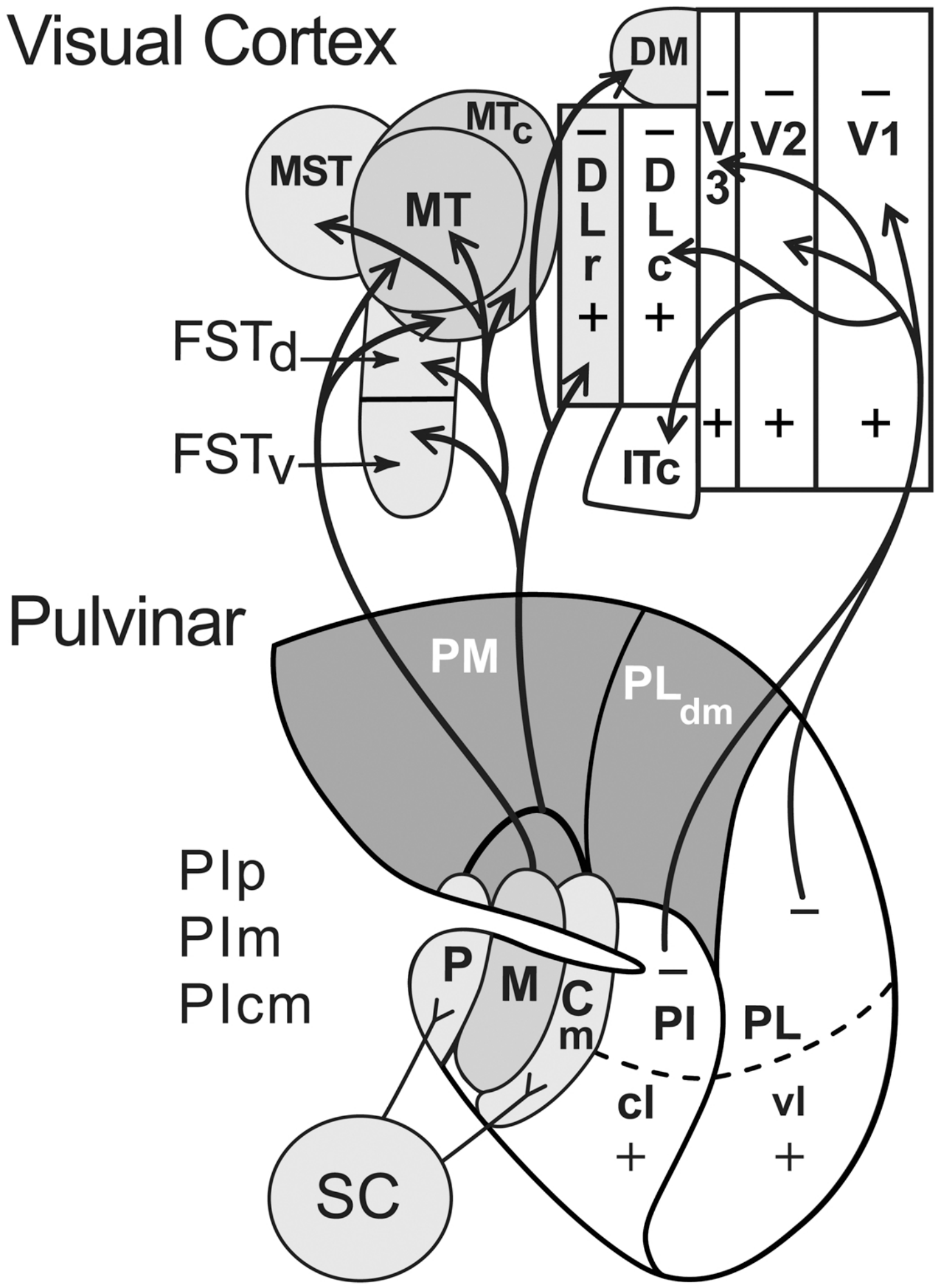

Owl Monkey
16 grams
1.5 billion
neurons
Agouti
18 grams
0.9 billion
neurons
Mary K. Baldwin

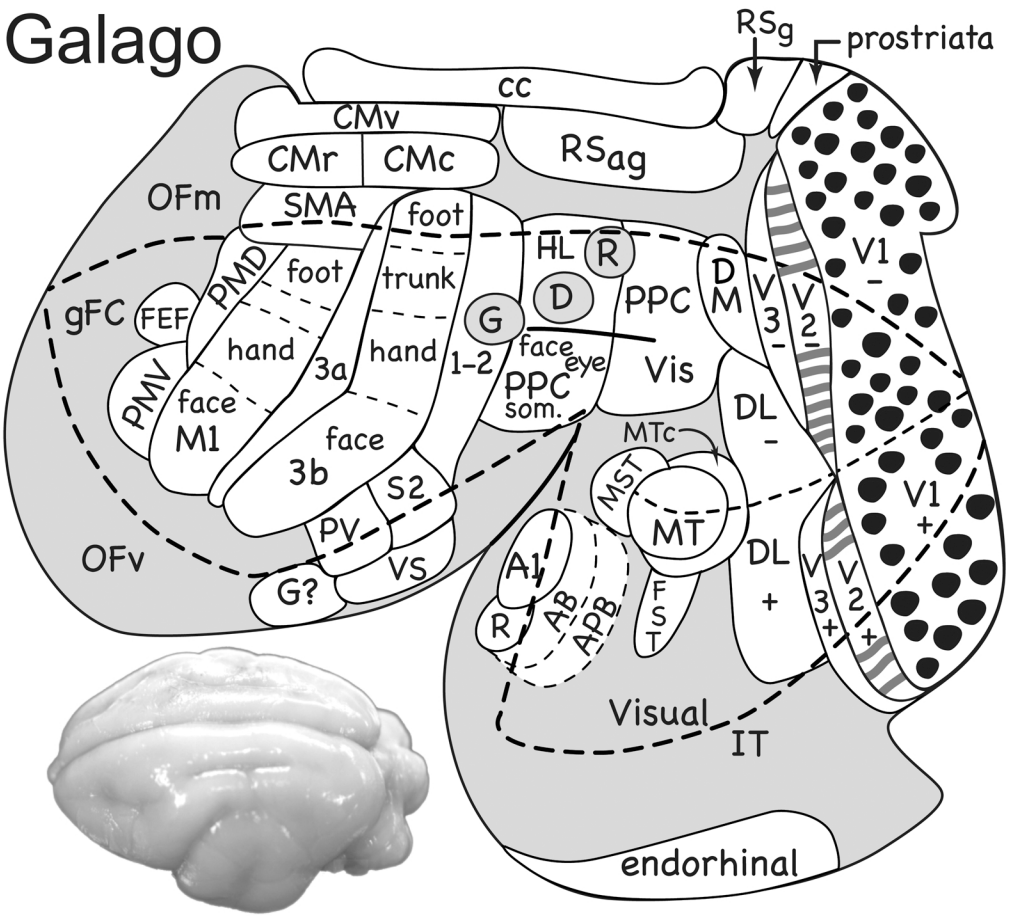
The Radiation of Placental Mammals




L. Retina
R. Retina
LD
LD
Left Superior
Colliculus
Primates
L. Retina
R. Retina
LD
LD
LGN
&
SC
Left Superior
Colliculus
Non-primates


Dermoptera
Flying lemurs
contra
contra
ipsi
contra
ipsi
Prosimians
Galagos, Lorises
Lemurs
PE
KE
KI
PI
MI
ME
Tarsioidea
Tarsiers
PE
PI
MI
ME
New World Monkeys
Owl monkeys
Marmosets
PE
PI
MI
ME
Squirrel & Saki
Monkeys
PE
PI
MI
ME
Scandentia
(Tree shrews)
ipsi on P & M
contra on P & M
contra K
contr off P & M
ipsi off P & M
contra K
Old World Monkeys
(Macaques)
PE
PI
MI
ME
early
Primates
Monkeys
Apes
Early Placental
Mammals
contra
ipsi
contra
Lagomorphs
(most Rodents)
contra
ipsi
contra
Gibbons
PE
PI
MI
ME
Humans, Chimps
Gorillas
PE
PI
MI
ME


Visual Cortex
DM
V1
V2
V3
MT
MST
MTc
DLr
DLc
FSTd
FSTv
ITc
Pulvinar
PM
PLdm
Plp
Plm
Plcm
P
M
C
m
PI
PL
cl
vl
SC


Galago
RSg
prostriata
cc
CMv
CMr
CMc
RSag
OFm
SMA
foot
HL
R
D
G
PPC
DM
V3
V2
V1
gFC
FEF
PMD
foot
trunk
hand
3a
hand
1-2
face
eye
Vis
PMV
face
M1
face
3b
PPC
som.
MTc
MST
MT
DL
S2
PV
VS
OFv
G?
A1
R
AB
APB
FST
Visual
IT
endorhinal