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Evolution of the Large, Complex Sensorimotor Systems of Anthropoid Primates

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A cladistic approach was used to reconstruct the probable changes from the basic sensorimotor system of early mammals to the much more complex system of humans and other anthropoid primates. At the cortical level, early mammals had as few as 4-5 somatosensory areas and possibly no separate motor areas. Early primates already had 7-8 motor areas, and additional higher-order somatosensory areas in lateral and posterior parietal cortex. Anthropoid primates are further distinguished by more serial processing, 4 distinct fields in anterior parietal cortex, and more areas in posterior parietal cortex.

One can not attend a major sporting event or musical concert without marveling at the impressive sensorimotor skills that some individuals display. Such exceptional abilities obviously depend on a sensorimotor system that can be individualized and specialized to a remarkable degree as a result of training and practice. Each member of our species with a normal brain is capable of a great range of skillful behaviors, and each member has the potential of acquiring uncommon abilities that would be exceedingly difficult for the novice. Such abilities depend on our large sensorimotor systems, consisting of many complex interconnected components. Mammals with smaller brains and simpler systems appear to have only a limited range of sensorimotor abilities, although some have a few impressive skills. This review outlines the major steps that appear to have occurred in the evolution from a relatively simple sensorimotor system in early mammals to a much more complex and powerful system that emerged with the first anthropoid primates, and was further elaborated in subsequent lines of anthropoid evolution, especially the one leading to humans.

Current concepts on how the sensorimotor system evolved are not based on direct evidence from fossils, as brains do not fossilize and the endocasts of skulls provide little information about brains other than size and fissure patterns (Jerison, 1990). While fissure patterns do have some potential for revealing the proportions of regions of primary somatosensory cortex devoted to particular skin surfaces, such as the forepaw or hand (see Radinski, 1975), endocasts have not provided much relevant information about the organizations of early sensorimotor systems. Instead, deductions are made from information provided from studies of brain organization of extant species of mammals (see Kaas, 1995; Northcutt, 1995; Northcutt & Kaas 1995; Kaas & Preuss, 2002). Inferences about the course of brain organization based on present-day mammals rest on the assumption that the brains of these mammals constitute mosaics of primitive (ancestral) and derived

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(modern) features or characters. The cladistic approach of character analysis (Hennig, 1966) is considered to be an acceptable method for distinguishing primitive from derived features (that is, the direction of change from one state to another). In principle, the application of the method is simple. If all members of a clade (group of phylogenetically related species) have a character, the character was more likely inherited from a common ancestor than evolved independently in the lines leading to each species. The more species considered from a group, the more likely that an ancestral trait will be correctly identified. In practice, the method is difficult to apply in a fully adequate and effective manner to the task of revealing the courses of brain evolution in mammals. Characters are often difficult to identify as present or absent or having one form or another without (and even with) extensive experimental study, and brain states that require experimental discovery are rarely known for many species (see Kaas, 2002). Thus, inferences about brain evolution are generally based on observations from dangerously few species. The situation is especially serious when one studies primates, as many of the over 200 species of primates are unavailable for experimental study.

However, circumstances are not as limited as they may seem. All species are not equal as sources of information about brain evolution. A guided selection of specific species for extensive detailed study can provide more information than an unguided approach. Although the small brain of a hedgehog and the large brains of humans, elephants, and whales all are reasonably considered as mosaics of primitive and advanced characters, we do know from the fossil endocasts that small mammals with small brains and little neocortex evolved first, and not the other way around. Thus, many have considered the study of small-brained mammals as most relevant to the issue of understanding what the brains of early mammals were like, while studies of the moderately enlarged brains of modern-day prosimians may provide more inferences about the brains of early prosimian-like primates. This is the approach taken here. Of course, inferences based on few species, even if one considers them to be the most relevant species, are tentative, as they need the test of broader comparative studies.

Here we make inferences about the course of the evolution of the sensori-motor system from early mammals to modern humans. The somatosensory and motor divisions of this system can be considered as separate systems, as structures can be identified as mainly sensory or mainly motor. Yet, these two systems or divisions of a larger system work closely together so that somatosensory cortex also has motor functions, while motor cortex has sensory functions. For convenience and tradition, we refer to somatosensory and to motor systems, while considering them to be divisions of a larger, more complex sensorimotor system.

Early Mammals

Our inferences about how the sensorimotor systems of early mammals were organized are largely based on the results of experimental studies in small mammals with small brains and little neocortex. These mammals and their brains most closely resemble the body and brain sizes of early mammals as indicated by the fossil record. Recent reconstructions of the phyletic radiation of mammals recognize six

major clades or superorders (Springer & de Jong, 2001), and small-brained species continue to exist in each of these clades. A reasonable approach would be to compare the somatosensory systems of the small-brained species in all of these clades to see what they have in common, and propose that these common features have been retained from a common early mammalian ancestor. This approach, however, is limited by the existence of obvious specializations in some of the otherwise key species, and the lack of relevant studies on many of these species.

Of the six major clades of living mammals, the monotremes and marsupials merit special attention because they retain several key premammalian features. Most notably, both lack a corpus callosum as a source of communication between the two cerebral hemispheres, and monotremes continue to lay eggs, as did their reptilian ancestors. Marsupials evolved gestation, but not the ability for an extended gestation period like the placental mammals that constitute the other four superorders.

While it might seem logical to extensively consider the somatosensory systems of monotremes, they are a narrowly focused order with only two families (platypuses and echidnas), with each family consisting of only a few species. Because they are relatively rare and protected, there have been few experimental studies. The platypus has the smaller brain, but it has an extremely specialized somatosensory system, that includes an electroreception subsystem (Krubitzer, 1998; Krubitzer, et al., 1995). Both platypuses and echidnas devote an unusually large proportion of neocortex to the processing of somatosensory information, while having only a few cortical areas. In both monotremes, microelectrode recordings have identified a large primary area, S1, and a large additional field lateral to S1, that appears to be the parietal ventral area, PV, based on relative location and somatotopy. A belt of cortex just rostral to S1 is responsive to more intense stimuli, such as pressure and light taps on the skin. This area may be homologous to the rostral somatosensory belt, SR of opossums (see below).

Because their somatosensory systems are less obviously specialized, we might learn more from marsupials. We start with opossums, a vernacular name applied to a number of small marsupials of a family now native only to the New World. Quite similar marsupials are found in marsupial families of Australia, where they are referred to as possums. Opossums and possums are available for experimental study, and such studies have revealed quite a bit about their sensorimotor systems. Studies of the North American opossum (e.g., Beck et al., 1996) suggest that its somatosensory cortex consists of five major subdivisions (Figure 1). A primary area, S1 or the first somatosensory area , contains a systematic representation of the tactile receptors of the body. As in other mammals, light touch on the skin or the bending of hairs activates S1 in different regions, depending on the body part. The tail and hindlimb are represented most medially, while the forelimb and hand are represented more laterally. The activating inputs from the skin are relayed from a "dorsal-column-trigeminal complex" in the lower brainstem, composed of trigeminal (face), cuneate (forelimb), and gracile (hindlimb) subnuclei. These structures project contralateral to the ventroposterior (VP) nucleus of the thalamus (Figure 2). This systematic representation of the contralateral body surface is commonly divided into lateral (VPL) and medial (VPM) "nuclei" (more

properly, subnuclei) for the body and face, respectively. VP projects to S1, and at least two other areas (Figure 1), the second somatosensory area (S2), and the more recently discovered (Krubitzer et al., 1986) parietal ventral area (PV). Other ascending sensory pathways include afferents from muscle spindles, essential for motor control and position sense, which are kept separate at the level of the lower brain stem, and apparently at the level of the thalamus where they terminate adjacent to VP, possibly in a structure termed the posterior nucleus (Po) or medial Po (Pom). Pom projects to S1 and possibly to other subdivisions of somatosensory cortex.
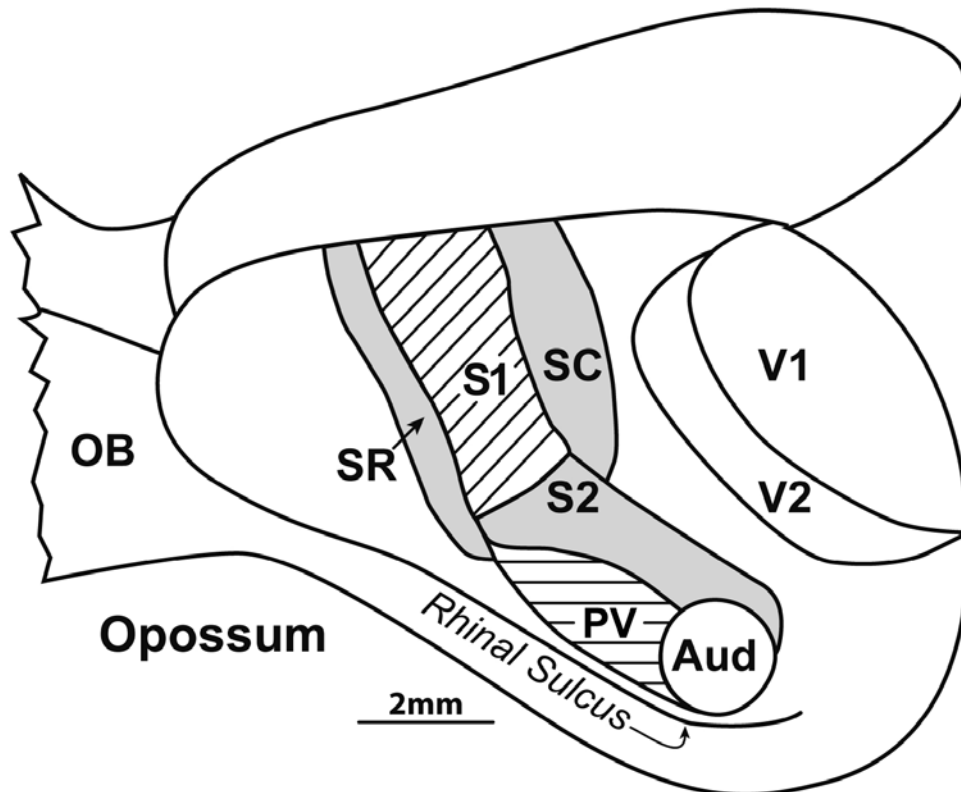

Figure 1. Cortical areas of the forebrain of the North American opossum (*Didelphis marsupialis*). In this dorsolateral view of the brain, the olfactory bulb (OB) and olfactory cortex below the rhinal sulcus occupy much of the forebrain. The rather small neocortex above the rhinal sulcus contains four somatosensory fields that have been defined by microelectrode recordings, architecture, and patterns of connections. These include a primary somatosensory area, S1, and second area, S2, a parietal ventral area, PV, and rostral (SR) and caudal (SC) bands of somatosensory cortex along the borders of S1. In addition there is at least one auditory field (Aud.) and at least two visual fields, the primary area (V1) and the second area (V2). There is no evidence for a separate motor area rostral to S1 and SR. Based on Beck et al, (1996)

The other major ascending somatosensory pathway in mammals is the spi-nothalamic system, which includes afferents sensitive to temperature, pain, touch and movement. The second order neurons in the spinal cord and brainstem relay to structures in the contralateral brainstem and thalamus, including the VP nucleus and adjoining portions of the thalamus. Thalamic projections include S1, S2 and PV, but it is not yet clear how or if functional subdivisions of this relay (pain, temperature,
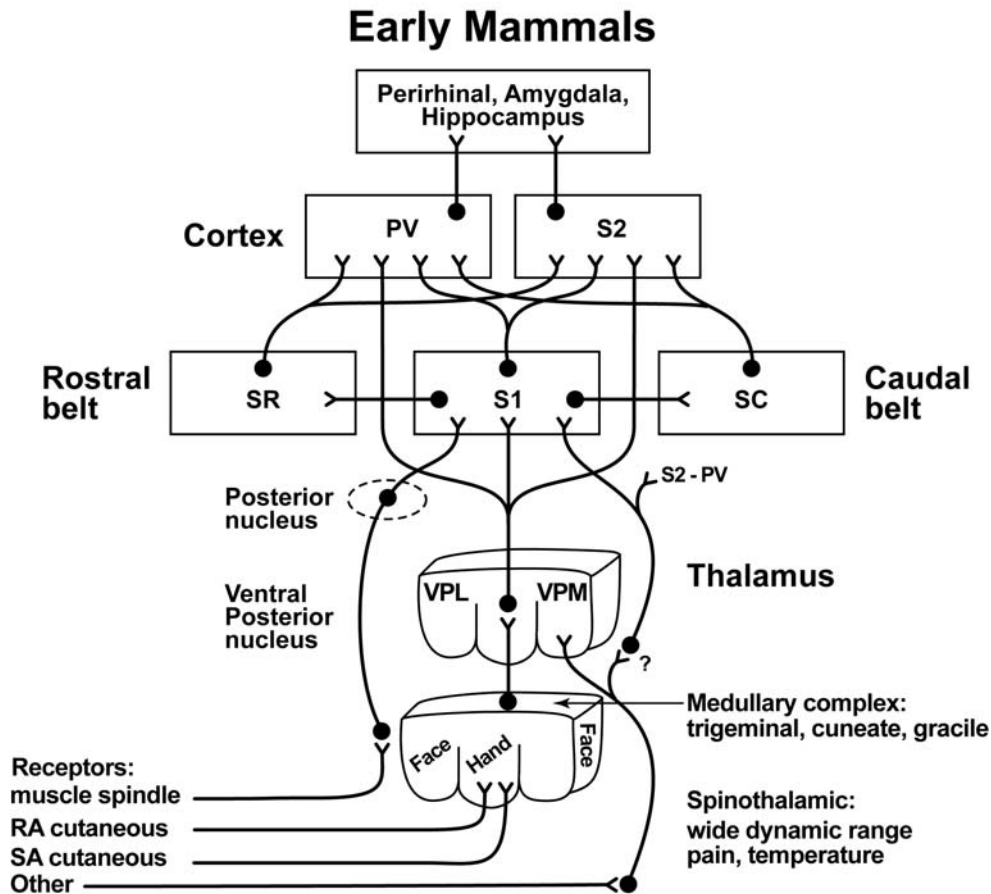
Figure 2. A schematic of the proposed organization of the somatosensory system of early mammals. The major somatosensory pathways include those from low threshold, rapidly conducting cutaneous afferents that are usually subdivided into rapidly adapting (RA) and slowly adapting (SA) classes, as well as the muscle spindle afferents for position sense. These afferents enter the spinal cord or brain stem and course in the dorsal columns or brain stem to subnuclei in the lower medulla with inputs from the face (trigeminal), forelimb (cuneate) or hindlimb (gracile). These subnuclei project via the medial lemniscus to the ventroposterior nucleus (VP), which also forms a systematic representation of the body. Within VP, the ventroposterior medial (VPM) and ventroposterior lateral (VPL) subnuclei, representing the face or body, respectively, are commonly distinguished. Muscle spindle receptors project to subnuclei adjacent to the trigeminal, cuneate, and gracile subnuclei in the medulla, and project via the medial lemniscus to the ventrolateral somatosensory thalamus, probably adjacent to VP in the posterior complex or nucleus. Other afferents from the skin (including those that are sensitive to a wide dynamic range of tactile stimuli into painful levels, and those sensitive to painful stimuli, or temperature) synapse in the spinal cord or brain stem on neurons that project contralaterally to form the spinothalamic tract. This tract terminates in and around VP. These somatosensory thalamic nuclei and regions project to subdivisions of somatosensory cortex (see fig 1 for abbreviations), which interconnect to form a processing network that interacts with structures involved in memory and stimulus evaluation (hippocampus, amygdala).

touch) are segregated in their terminations in cortex. Primates, for example, appear to have separate pain and temperature related nuclei in the thalamus (Craig et al., 1994) and pain and temperature-related areas in cortex near S2 (see Ostrowsky et al., 2002). Spinothalamic terminations in VP possibly conduct information about

stimulus intensity (wide dynamic range neurons) and modulate S1 activity. In rats and monkeys, the spinothalamic pathway does not provide above threshold activation of S1 (Jain et al., 1995; 1997). This may be the case for all mammals.

In opossums, S1 distributes sensory information to four other cortical areas, S2, PV, and bands of cortex immediately rostral (the rostral somatosensory area SR) and caudal (the caudal somatosensory area, SC) to S1 (Figure. 1). These four areas likely distribute information to other regions of cortex, but the distribution pattern is largely unknown. Areas PV and S2, at least, likely project to small bordering zones along the rhinal sulcus. These regions, and possibly S2 and PV, provide access to motivational and memory systems involving the amygdala and hippocampus.

What is missing from our description so far is any mention of the motor component of the sensorimotor system. This is not because the motor component is lacking, but it is surprisingly limited. Muscle spindle and other sensory information is relayed to the cerebellum, where it is relayed via the deep cerebellar nuclei to the ventral anterior thalamus. These cerebellar inputs appear to terminate on neurons in the ventral lateral (VL) thalamus, largely (or completely, as in placental mammals) rostral to VP (Walsh & Ebner, 1973). The motor thalamus is also defined by inputs from the globus pallidus of the basal ganglia, considered part of the extrapyramidal motor system, but the distribution of pallidal inputs to the thalamus of opossums is unclear. What is apparent is that there is no evidence for a separate motor area or motor areas of cortex that would serve as a target or targets for these motor-related thalamic relays.

Somatosensory areas have motor functions in all mammals, and this is clearly the case in opossums. Long ago, Lende (1963) noted that motor movements could be evoked by electrical stimulation of the S1 region in opossums. In addition, S1 and the S2 and PV regions contribute directly to motor control by projecting to movement-related neurons in the spinal cord and brainstem (Nudo & Masterton, 1990). Lende (1963) and subsequent investigators have been unable to identify any motor area in opossums rostral to S1 and SR in the position of primary motor cortex (M1) of placental mammals, or any of the premotor areas in frontal cortex of primates. The motor thalamus apparently relays to somatosensory cortex (Donoghue & Ebner, 1981), which thereby must mediate the cortical components of motor control for these mammals.

Whether this type of impoverished motor system reflects that of early mammals is uncertain. There is some limited, but unconvincing, evidence for a motor region rostral to S1 (and SR) in monotremes and some marsupials, and evidence for and against a separate motor area in members of a third major mammalian clade, Xenarthra (armadillos & sloths; see Beck et al., 1996, for review), so several possibilities remain, including the possibility that opossums and perhaps some other mammals simplified cortical organization by losing motor cortex. Another but unlikely possibility is that motor cortex exists, but has not been recognized. For now, we favor the third possibility that M1 and premotor areas do not exist in marsupials and monotremes, and did not exist in the first mammals, but emerged with the advent of placental (eutherian) mammals.

In contrast, there is much less doubt about the components of the

somatosensory system of opossums. The somatosensory system of North American opossums appears to be very similar to those in other opossums and small-brained marsupials (see Catania et al., 2000; Huffman et al., 1999; Elston & Manger, 1999).

The basic organization of the spinal cord and lower brainstem relays of somatosensory information have been retained in most or all extant mammals from reptilian ancestors, and some of the thalamic and even cortical components may have been as well. All studied mammals have a VP nucleus in the thalamus, with a relay to S1. S1, S2, PV and the rostral and caudal somatosensory belts, termed here SR and SC, have been defined in a wide range of mammals (e.g., Krubitzer et al., 1986, 1997; Krubitzer & Calford; 1992), including members of all but the Xenarthra superclade (armadillos, sloths, anteater) of mammals, where S1 has been defined, but evidence for other areas is yet lacking (see Johnson, 1990, for review). Another complication is that in some mammals only S2 (e.g., Catania et al., 1999) or PV (Krubitzer et al., 1995) has been identified. While the evidence for four or five areas in the wide range of small-brained mammals is convincing, there is little cortical space or evidence for additional somatosensory areas, other than in a narrow perirhinal region where several small areas may be related mainly to the amygdala and hippocampus. Thus, the provisional schematic of the somatosensory system of early mammals contains only a few cortical areas (Figure 2). While early mammals had a motor thalamus, defined by inputs from the cerebellum and basal ganglia, they may not have had a separate motor cortex.

Early Primates

Primates emerged as a branch of the Euarchontoglires superclade some 65-70 million years ago (Springer & de Jong, 2001). Other members of the superclade include rodents, lagomorphs, flying lemurs, and tree shrews. As flying lemurs are unavailable for experimental study, we know almost nothing about the organization of their sensorimotor system. However, tree shrews (Sur et al., 1980, 1981), rats (Li et al., 1990), and squirrels (Krubitzer et al., 1986; Slutsky et al., 2000), and possibly rabbits (Gould, 1986) appear to have the five basic somatosensory areas of opossums (areas S1, SR, SC, S2, and PV). These mammals also have a ventroposterior nucleus that project to both S1 and the more lateral areas, S2 and PV, so they are activated in parallel from the same thalamic relay (see Garraghty et al., 1991). In addition, these mammals have a primary motor area, M1, and there is some evidence for a second area, M2, which may be the supplementary motor area or the dorsal premotor area of primates (e.g., Li et al., 1990; Rouiller et al., 1993). The motor nuclei of the thalamus with cerebellar and pallidal inputs, are distinct. These are all features of the sensorimotor system that characterize members of the clade. The immediate ancestors of primates would have had these features of the sensorimotor system.

Early primates were small-bodied, nocturnal predators living on a mixture of insects, small vertebrates, leaf buds, and fruit (Ross, 1996). They lived in the tropical rainforests and depended on vision for detecting food. This involved the acquisition of the adaptive traits of a shorter snout, to reduce obstruction of frontal vision, and more forward facing eyes. Possibly to protect these eyes, visually guided

reaching and grabbing with the forelimb tended to replace grasping with the mouth. This placed emphasis on eye-hand coordination. The big toes and thumbs became opposable for grasping, and nails replaced claws (Bloch & Boyer, 2002). While vision was obviously emphasized, these adaptations in the limbs suggest that modifications of the sensorimotor system occurred.

Soon after the evolution of the first primates, three major branches emerged, the prosimians, tarsiers, and anthropoids. The prosimians diverged into the lemur, loris and galago lines, with considerable variability in their adaptations, especially for the lemurs. Yet, relatively small bodies, small brains, and a nocturnal life were maintained in most prosimians. In relative size and shape, prosimian brains have changed the least of the extant primates, from those of early primates (Radinsky, 1975).
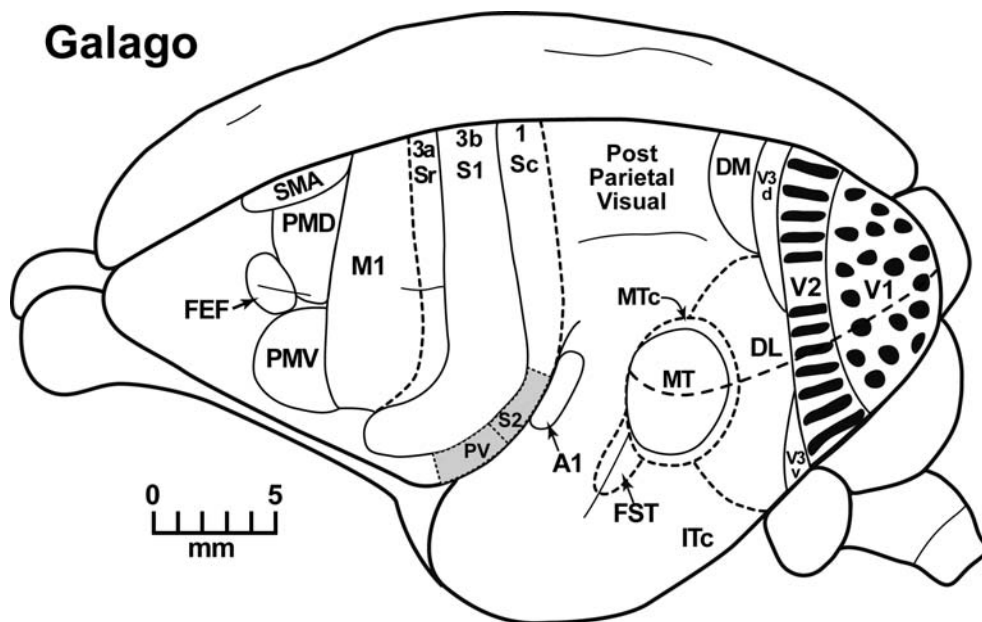

Figure 3. A dorsolateral view of a galago (a small prosimian primate) brain showing somatosensory and motor areas. Somatosensory cortex includes a primary area, S1 (3b), and rostral (Sr) and caudal (Sc) somatosensory belts, that are likely to be homologous to areas 3a and 1 (or 1 plus 2), respectively, of monkeys. Lateral parietal cortex includes the second somatosensory area (S2), the parietal ventral somatosensory area (PV), and a parietal rostral area (PR). Cortex in the location of 7b is somatosensory and cortex in the region of the intraparietal sulcus (IPS) is involved in somatomotor and multisensorimotor functions. Motor areas include primary motor cortex (M1), a ventral premotor area (PMV), a dorsal premotor area (PMD), a supplementary motor area (SMA), and at least two cingulate motor areas in cortex of the medial wall (not shown). Primary (V1), secondary (V2), and other visual areas (V3, DL, DM, MT, MTc, FST, ITc; see Kaas, 2001 for description) are shown for reference.

The early ancestors of present-day tarsiers became diurnal, and then re-verted to a nocturnal life again, so they first acquired some specializations for daytime light levels, such as a fovea and the loss of a reflecting tapetum, and then had to respecialize for dim light by acquiring huge eyes, which compensate for the absence of a reflecting tapetum (Ross, 1996). The forebrain of tarsiers is dominated by specializations for visually detecting prey. Little is known about the sensorimotor

system, as tarsiers are not available for experimental studies. Yet, their brains have been studied histologically to reveal a ventroposterior nucleus (Simmons, 1982), a primary area of somatosensory cortex (identified by a layer of small cells; koniocellular cortex) and a presumptive primary motor area (identified by a nearly absent layer 4; agranular cortex).

The primate ancestors of anthropoid primates (monkeys, apes, and humans) were diurnal and emphasized vision. They diverged from the ancestors of tarsiers about 60 million years ago, and became more dependent on fruit eating (Ross, 1996). The use of the forepaws as hands became more important, and social groups often formed for predator protection. Only one branch of anthropoid primates, the owl monkey, diverted back to a nocturnal existence. The brains of anthropoid primates became proportionately larger, especially visual and sensorimotor portions of the forebrain. Some of the early African anthropoids somehow rafted over to the New World over 40 million years ago, where the New World radiation of monkeys occurred. Old World anthropoids divided into Old World monkeys and apes about 30-35 million years ago, and for a while the apes were a highly successful radiation. The break between the great apes and the lesser apes (e.g., gibbons) occurred some 20 million years ago, the chimpanzees and gorillas diverged about 15 million years ago, while the human and chimp lines separated quite recently, perhaps 7 million years ago (see Kaas & Preuss, 2002, for review).

Given that tarsiers are unavailable for experimental study and are highly specialized, our approach in reconstructing the sensorimotor system of early primates has been to compare present day prosimians, with small brains of ancestral proportions, with various monkeys. Of the prosimian radiation, African galagos have been most used in research, as they breed readily in captivity. Some of the subdivisions of the galago forebrain are shown in Figure 3.

The ascending somatosensory systems in galagos are rather generalized. As in other mammals (Figure 2), the dorsal column-trigeminal and the spinothalamic systems provide somatosensory inputs to the thalamus (Figure 4). The way that body surface receptors are represented in the dorsal column nuclei appears to conform to a generalized mammalian pattern, but this is uncertain for the gracile subnucleus that represents the hindlimb as this subdivision has not been extensively studied in mammals. What is clear is that the inputs to the cuneate subnucleus for the hand are more topographically ordered than those to the gracile subnucleus for the foot (Strata et al., 2003). This corresponds to the greater importance of the hand as a sensory surface in these and other primates.

At the level of the thalamus, three somatosensory nuclei can be identified, a ventroposterior nucleus (VP) with tactile inputs, a ventroposterior inferior nucleus (VPI), with spinothalamic inputs, and a ventroposterior superior nucleus (VPS) with inputs relayed from muscle spindles (Figure 4). There is evidence for a thin, poorly developed VPI nucleus in non-primate members of the superclade, but only primates have a distinct VPI. This nucleus projects broadly to somatosensory cortex, but to layers above layer 4 where its influence is likely to be modulatory. Projections to S2 and PV are the most dense. VP retains its generalized projection pattern (Figure 2) in that S1 receives the main projection, while activating inputs are also to S2 and PV (Wu et al., 1996). Thus, parallel projections from VP are capable, as in many

other mammals, of independently activating these three cortical areas (Garraghty et al., 1991). VP may also project to SC, and VPS may project to SR (as in anthropoid primates), but this is not yet known. The somatosensory thalamus also includes a posterior region just caudal to VP that also receives spinothalamic inputs, probably related to pain and temperature, but such nuclei have not been identified in prosimians, and cortical targets remain uncertain. Just dorsal to VP and medial to VPS, an anterior pulvinar is present, and this nucleus connects broadly to somatosensory cortex. The relationships of VPS and the anterior pulvinar to the posterior medial nucleus (Pom) of rats and other mammals (Figure 2) is uncertain, but the Pom of early mammals could have given rise to either or both nuclei in primates. Finally, the ventral lateral complex, exists rostral to VP, and is defined by inputs from the cerebellum and pallidum, and projections to motor (M1) and premotor cortex.
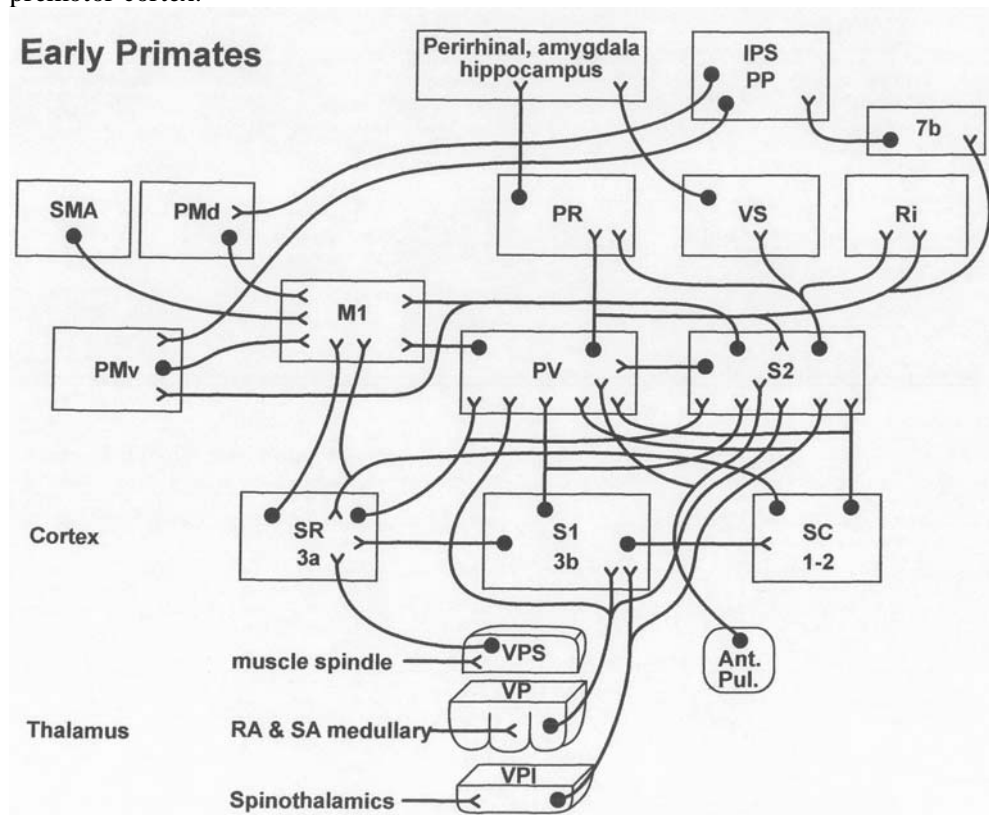

Figure 4. A schematic of thalamic and cortical components of the sensorimotor system of early primates. Prosimian and anthropoid primates share the features shown. Only major feed-forward connections are indicated, and the nuclei of the motor thalamus are not included. Full patterns of connections for some of the areas have not been determined. Rapidly adapting (RA) and slowly adapting (SA) cutaneous afferents synapse in the lower brain stem and relay to the ventroposterior nucleus (VP). Muscle spindle afferents relay from the brain stem to the ventroposterior superior nucleus (VPS), while spinothalamic afferents terminate in the ventroposterior inferior nucleus (VPI) and other targets caudal to VP. The anterior pulvinar (ant. pul.) receives inputs from subdivisions of somatosensory cortex and projects back to these areas. The regions of 7b and retroinsular cortex (Ri) are not well defined. The cortex of region of the intraparietal sulcus (IPS) has several divisions with sensorimotor connections, but these have not been fully described. See fig.3 for abbreviations of somatosensory and motor areas.

The anterior somatosensory cortex of galagos closely conforms to the generalized mammalian plan (Wu et al., 2003). As in opossums, the anterior parietal cortex consists of three fields, S1, SR, and SC. In more lateral cortex, PV and S2 are apparent, but they are hidden in the upper bank of the lateral fissure, as in other primates. Galagos clearly have additional somatosensory cortex in this region as well, including a parietal rostral area, PR, possibly a parietal ventral area, PV, and a caudal area that may include regions corresponding to area 7b and retroinsular cortex of monkeys. These primates also have a region of posterior parietal cortex that resembles the cortex of intraparietal sulcus (IPS) of monkeys in that there are visual and somatosensory inputs, and projections to dorsal and ventral premotor areas of frontal cortex (Fang et al., 2001).

In summary, the basic organization of somatosensory cortex appears to have changed little from early mammals to early primates. Anterior parietal cortex of early primates continued to consist of only three distinct fields, although much more of these fields were devoted to processing information from the sensitive forepaw than in early mammals. As in early mammals, lateral cortex in early primates included PV and S2, and S1, S2 and PV were independently activated via VP. A major change in the organization of somatosensory cortex involved cortex lateral to S1. In the lateral fissure, a large somatosensory region emerged with several somatosensory areas in addition to S2 and PV. The second altered region is in posterior parietal cortex, where an intraparietal region of significant size emerged to mediate visuomotor and sensorimotor functions via visual, somatosensory, and other sensory inputs and outputs to premotor cortex. The pattern of cortical and subcortical organization in prosimian galagos reflects a pattern that likely has been retained from early primates.

The motor system of galagos has also been altered from that proposed for early mammals. The early ancestors of primates likely had a M1 and at least one premotor area, but motor cortex did not contain many areas, and motor areas were not well differentiated structurally. Galagos, in contrast, have a large primary area, M1, that has a large central region devoted to forepaw movements (Wu et al., 2002). However, locations in M1 that evoke movements of individual digits are rare in comparison with monkeys (e.g., Stepniewska et al., 1993). A ventral premotor area, PMV, is clear, and it is largely devoted to directing arm and hand movements in visual reach. The dorsal premotor area, PMD, is large, and electrical stimulation of PMD evokes a range of more complex movements. The supplementary motor area, SMA, is present and it represents body movements from the foot to the face in a caudorostral sequence. Two or three cingulate motor areas are evident in cortex of the medial wall of the cerebral hemisphere, and a frontal eye field is in dorsolateral frontal cortex, devoted to directing eye movements towards targets.

In summary, the motor system of galagos suggests that motor systems of early primates were much more complexly organized than motor systems of early mammals, as early primates had likely contained many or all of the cortical areas and thalamic nuclei of anthropoid primates. Nevertheless, the histological differentiation of M1 and other motor fields in galagos is not as pronounced as in monkeys, and the motor control of hand movements is not as precise. The motor system of galagos is one that likely emerged with the first primates, as the basic

components are also present in anthropoid primates. This more complex motor system may have allowed early primates to successfully compete for insect prey and other food in a nocturnal, arboreal, tropical environment.

Early Anthropoid Primates

Early anthropoid primates were monkeys. We can develop some concept of the common features retained by these primates by comparing New World (platyrrhine) and Old World (catarrhine) monkeys. The New World monkeys include the small marmoset monkeys and the more varied cebid monkeys that range in size from the smaller owl and squirrel monkeys with smaller brains with few fissures to the large spider and cebus monkeys with highly fissured, large brains. The Old World monkeys are generally large, with one group including macaque monkeys and baboons, and the other including the colobine monkeys.

Figure 5. A dorsolateral view of an owl monkey (a small New World monkey) brain showing somatosensory and motor areas. In these and other anthropoid primates, anterior parietal cortex clearly consists of four parallel representations in the areas 3a, 3b, 1 and 2. See figures 3 and 4 for abbreviations. The lateral sulcus has been opened to show the second somatosensory area, S2, the parietal ventral area, PV, the parietal rostral area, PR, and the ventral somatosensory areas, VS. As in Fig. 3, visual areas are shown for reference.

The somatosensory systems of New and Old World monkeys demonstrate some clear differences from those in prosimians (Kaas, 1993). First, anterior parietal cortex is generally well differentiated into four fields, typically numbered according to early architectonic descriptions as areas 3a, 3b, 1, and 2 (Figure 5). Each contains a parallel representation of body receptors, proceeding from the tail and hindlimb to the face, tongue and teeth in a mediolateral sequence. In all these monkeys, considerable portions of these areas (1/4 or more) are devoted to receptors in the hand. This is most pronounced in macaques, which skillfully use the hands,

and least pronounced in marmosets. In early electrophysiological studies, all four areas were included in S1, but only area 3b (S1 proper) is homologous with S1 of other mammals and S1 of prosimian primates (Kaas, 1983). Thus, we also refer to S1 of galagos as area 3b, although it does not have the distinctive koniocellular appearance of area 3b of anthropoid primates. Area 3a, just rostral to area 3b, is in the position of the rostral somatosensory belt (SR) of galagos, and SR of galagos, and likely nonprimates, is probably homologous with area 3a. Area 3a is characterized by a relay of muscle spindle receptor activity from the VPS of the thalamus. Caudal to area 3b, area 1 contains a second systematic representation of tactile receptors of the contralateral body surface, roughly organized as a mirror image of the representation in area 3b. Both areas 3b and 1 receive inputs from VP of the thalamus, in part (20%) from the same neurons (Cusick et al., 1985). Just caudal to area 1, a fourth strip-like area 2 is activated by muscle spindle receptors via projections from VPS, some of which are from the same neurons that project to area 3a (40%). Area 1 is highly dependent on projections from area 3b for activation (Garraghty et al., 1990), while area 2 gets cutaneous information from area 3b and 1, and, in some monkeys, sparsely from VP (Pons & Kaas, 1985). Areas 1 and 2 are well developed in most monkeys, but not in marmosets where area 1 is difficult to activate and there is no clear evidence for a separate area 2 (Krubitzer & Kaas, 1990). A reasonable assumption is that area SC of early primates differentiated into area 1 of monkeys, and area 2 was somehow added, but an alternative is that area SC differentiated into both areas 1 and 2. Marmosets, as an adaptation for their small size (Kaas, 2000), may have lost a distinct area 2. Area 1 and especially area 2 project to posterior parietal cortex, area 3a to motor cortex (M1), and all four areas project to S2 and PV (Kaas, 1993).

A second significant change from the early primate type of organization was a loss of the direct VP thalamic inputs to S2 and PV (Figure 6) so that these areas became completely dependent on inputs from anterior parietal cortex for activation (Pons et al., 1987; Garraghty et al., 1990). Thus, processing in the somatosensory system became more serial and less parallel. This suggests that the depth of processing became more important than processing speed.

A third notable change in the system was that a considerable expansion of posterior parietal cortex occurred. This was the least pronounced in marmosets and nocturnal owl monkeys (Figure 5) and most pronounced in Old World macaque monkeys where six to eight distinct visuomotor and sensorimotor areas have been proposed for the cortex of the intraparietal sulcus and as many as 15-20 subdivisions of posterior parietal cortex with somatosensory functions are likely to exist (Lewis & Van Essen, 2000). In the intraparietal region, for example, ventral (VIP), lateral (LIP), medial (MIP), and anterior (AIP) sensorimotor areas have been described that appear to integrate visual, auditory, and somatosensory information to guide motor behaviors via projections to premotor and prefrontal cortex.

In motor cortex of simians, there is some evidence for functionally dividing an expanded M1 into rostral and caudal fields (Stepniewska et al., 1993), and subdividing the regions of ventral and dorsal premotor areas into a total of four fields (see Wu et al., 2000, for review). A presupplementary motor area has been proposed (e.g., Sakai et al., 2000) and prefrontal cortex has expanded and has

interconnections with premotor areas.

We do not yet know if New World and Old World monkeys have any marked differences in sensorimotor cortex that systematically distinguish these two groups. However, the proportional size of posterior parietal cortex is much less in some New World than Old World monkeys, and little is known about the organization of posterior parietal cortex in New World monkeys. As a puzzling subcortical difference, the representations of the hand (forepaw) in the cuneate nucleus differs in Old World macaques from New World monkeys and most other mammals in that the digits are ventral instead of dorsal (Florence et al., 1991). This ventral location for digit projections also appears to exist in humans. The functional significance of this change is uncertain.
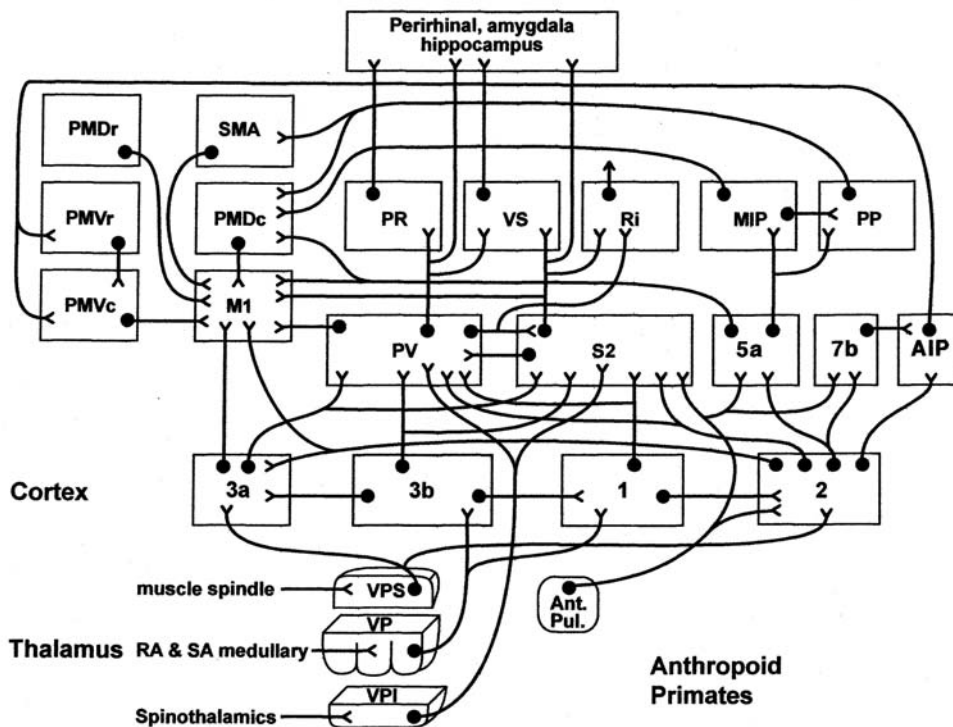

Figure 6. A schematic of the major thalamic and cortical components of the sensorimotor system of anthropoid primates (monkeys, apes, and humans). Compare with fig.4. The major difference from prosimian primates is that anterior parietal cortex has clearly differentiated into the four architectonic fields, 3a, 3b, 1 and 2. Posterior parietal (PP) cortex has enlarged, and in at least Old World monkeys, contains a number subdivisions of intraparietal cortex (the medial intraparietal area, MIP, and the anterior intraparietal area, AIP, are shown, but ventral, lateral, medial, and posterior areas are not). Rostral and caudal subdivisions of dorsal (PMDr and PMDc) and ventral (PMVr and PMVc) premotor cortex likely also existed in early prosimian primates (Fig 4). See figs. 2-5 for abbreviations.

Apes and Hominids

Much less is known about the brains of apes and humans because of the limitations on experimental studies in these primates. In addition, humans are the

only hominid still alive, so we know the course of hominid brain evolution only from the fossil record. What is clear is that our brains are nearly three times the size of the chimpanzee's, our nearest relative. In addition, we know from the endocasts of fossil skulls of hominids, that our presumptive ancestors of only 3 million years ago had brains the size of chimpanzee brains. The brains of hominids thereafter increased rapidly in size, especially over the last 2 million years, to the present large size (McHenry, 1994). This increase in size, by itself, has implications for brain organization, and thus for the organization of the human sensorimotor system.

As brains get bigger, certain design problems become more critical (see Kaas, 2000). In particular, connections between brain parts become longer as brains become bigger. Thus more and more of the brain is devoted to connections. As distance is time in the brain, a related problem is in speeding up conduction rates for neuron spikes to compensate for longer conduction distances. This is generally achieved by making axons thicker, and this results in large brains devoting proportionately more space to axons. Long connections, such as those between the two cerebral hemispheres became very costly in space occupied and in metabolic energy. Thus, one can expect selection pressure for brain changes that limit long connections and these costs. Probably for this reason, the human brain has a number of functions that are mediated largely in one cerebral hemisphere (the "lateralization" of function), as such lateralization reduces the need for long connections, between the hemispheres (Hopkins & Rilling, 2000).

Large brains, such as the human brain, tend to have larger cortical areas. Neurons within cortical areas are interconnected over short regions within the area by "lateral" intrinsic connections. To function in the same way, intrinsic connections would need to be longer and more numerous in larger areas, but this does not seem to occur. Thus, large areas are limited in the extent of their unifying intrinsic interactions because of the altered role of intrinsic connections. This suggests that the large human brain would not work very well if it were simply an enlarged version of an ape brain. However, there is clear evidence that our brains are not only larger, but different. Primary sensory areas such as S1 proper (3b) and V1 (area 17) can be identified histologically in human brains, and these areas have not increased in size as much as the neocortex increased in size. Thus, proportionately more neocortex is devoted to other cortical areas. A reasonable assumption is that our cortex has more cortical areas than our ancestors with smaller brains, as increasing the number of areas is a way of reducing the lengths of connections within and between areas (see Kaas, 2000).

The number of areas in the sensorimotor system of humans is uncertain. However, we do know that humans have the four subdivisions of anterior parietal cortex, areas 3a, 3b, 1 and 2, each containing a representation of contralateral body receptors (see Kaas, 1993). It is likely that the proportions of the areas that are devoted to inputs from the digit tips have increased in hominid evolution, given the important role of this sensory surface. There is also good evidence for the existence of S2 and PV in cortex of the lateral fissure of humans (Disbrow et al., 2000), as well as a specific pain center in insular cortex of the lateral fissure (Ostrowsky et al., 2002). Posterior parietal cortex is particularly expansive, and a number of new sensorimotor areas may have emerged in this region (see Vanduffel et al., 2002). In

addition, frontal lobe regions for motor functions may have enlarged, increased in number, and become more focused on guiding arm, hand, and digit movements, as our motor skills are so impressive (e.g., Susman, 1994). Yet, these suppositions lack proper experimental support. We need to know much more about human brains, and about those of our closest relatives, chimpanzees.

Summary

Early mammals had small bodies and proportionally small brains with little neocortex. Judging from the results of experimental studies on extant mammals with little neocortex, this cortex was subdivided into only a few areas or "organs of the brain" in early mammals. Besides at least one auditory field, and possibly three visual areas, sensorimotor cortex included a primary somatosensory area, and adjoining belt-like sensorimotor fields along the caudal (SC) and rostral (SR) borders of S1. The second (S2) and parietal ventral (PV) somatosensory areas were just lateral to S1. These fields had both sensory and motor functions, and it remains uncertain if a separate primary motor area existed, as it now does in all placental mammals.

This basic organization of somatosensory cortex appears to have been retained with little modification in early primates. The SR belt of early mammals is likely homologous with area 3a of anthropoid primates, while SC has characteristics of both area 1 and area 2. In contrast, early primates had an elaborate motor system with a primary motor area and several premotor, supplementary, and cingulate motor areas.

Early monkeys had differentiated areas 3a, 3b, 1, and 2 in anterior parietal cortex. Processing in somatosensory cortex had become more serial so that S2 and PV were no longer activated independently from the thalamus but depended on inputs from S1 (area 3b). The poorly understood region of posterior parietal cortex between area 2 and visual cortex was much larger, and it was probably involved in using visual, auditory, and somatosensory information to form and relay instructions about hand and eye movements to premotor areas. Thus, posterior parietal cortex expanded in conjunction with the emergence of distinct premotor areas.

Little is known about precisely how early apes and then hominids differed from early monkeys, but their brains were much bigger, and premotor cortex and posterior parietal cortex became proportionally larger. It seems likely that these regions became more differentiated in structure and function, adding sensorimotor skills, and especially for the forelimb.

In the larger hominid brains, some of the longer cortical connections, especially between the two hemispheres, became reduced in relative number, and specializations of each hemisphere started to emerge as modular and local processing were emphasized to reduce the need for large numbers of long cortical connections.

References

Beck, P. D., Pospichal, M. W., & Kaas, J. H. (1996). Topography, architecture, and connections of somatosensory cortex in opossums: evidence for five somatosensory areas. *Journal of*

Comparative Neurology, **366**, 109-133.

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

Catania, K. C., Lyon, D. C. Mock, O. B., & Kaas, J. H. (1999). Cortical organization in shrews: evidence from five species. *Journal of Comparative Neurology,* **410**, 55-72.

Catania, K. C., Jain, N., Franca, J. G., Volchan, E., & Kaas, J. H. (2000). The organiza-tion of somatosensory cortex in the short-tailed opossum (*Monodelphis domestica*). *Somatosensory Motor Research,* **7**, 39-51.

Cusick, C. G., Steindler, D. A., & Kaas, J. H. (1985). Corticocortical and collateral tha-lamocortical connections of postcentral somatosensory cortical areas in monkeys: A double labeling study with wheat germ agglutinin (WGA) conjugated to horseradish peroxidase and radiolabeled WGA. *Somatosensory Research*, **3**, 1-31.

Craig, A. D., Bushnell, M. C., Zhang, E. T., & Blomquist, A. (1994). A thalamic nucleus specific for pain and temperature sensation. *Nature*, **372**, 770-773.

Disbrow, E., Roberts, T., & Krubitzer, L. (2000). Somatoptic organization of cortical fields in the lateral sulcus of Homo sapiens: Evidence for SII and PV. *Journal of Comparative Neurology*. **418**, 1-21.

Donoghue, J. P., & Ebner, F. F. (1981). The organization of thalamic projections to the parietal cortex of the Virginia opossum. *Journal of Comparative Neurology,* **198**, 365-388

Elston, G. N., & Manger, P. R. (1999). The organization and connections of somatosen-sory cortex in the brush-tailed possum (*Trichosurus vulpecula*): evidence for multiple, topographi-cally organized and interconnected representations in an Australian marsupial. *Somatosensory Motor Research,* **16**, 312-337.

Fang, P. C., Stepniewska, I., & Kaas, J. H., (2001). Ipsilateral cortical connections of the Premotor cortex in prosimian primates (*Galago garnetti*). *Society for Neuroscience Abstracts*, **27**, 825.3.

Florence, S. S. J., Wall, J. T., & Kaas, J. H. (1991). Central projections from the skin of the hand in squirrel monkeys. *Journal of Comparative Neurology*, **311**, 563-578.

Garraghty, P. E., Florence, S. L., & Kaas, J. H. (1990). Ablations of areas 3a and 3b of monkey somatosensory cortex abolish cutaneous responsivity in area 1. *Brain, Research*, **528**, 165-169.

Garraghty, P. E., Pons, T. P., & Kaas, J. H. (1991). Ablations of areas 3b (S-1 proper) and 3a activation of the first and second somatosensory areas in prosimian primates and tree shrews. *Journal of Comparative Neurology*, **310**, 1-11.

Garraghty, P. E., Pons, T. P., & Kaas, J. H. (1996). Ablations of areas 3b (S1 proper) and 3a of somatosensory cortex in marmosets deactivate the second and parietal ventral somatosensory areas. *Somatosensory Motor Research*, **7**, 125-135.

Gould, H. J. (1986). Body surface maps in the somatosensory cortex of rabbit. *Journal of Comparative Neurology,* **243**, 207-234.

Hennig, W. (1996). *Phylogenetic Systematics*. Urbana, IL: University of Illinois Press.

Hopkins, W. D. & Rilling, J. K. (2002). A comparative MR study of the relationship be-tween neuroanatomical asymmetry and interhemispheric connectivity in primates: Implications for the evolution of functional asymmetries. *Behavioral Neuroscience,* **114**, 739-748.

Huffman, K. H., Nelson, J., Clarey, J., & Krubitzer, L. (1999). The organization of soma-tosensory cortex in three species of marsupials: neural correlates of morphological specializations. *Journal of Comparative Neurology,* **403**, 5-32.

Jain, N., Florence, S. L. & Kaas, J. H. (1995). Limits on plasticity in somatosensory cor-tex of adult rats: Hindlimb is not reactivated after dorsal column section. *Journal of Neurophysiol-ogy*, **73**, 1537-1546.

Jain, N., Catania, K. C., & Kaas, J. H. (1997). Deactivation and reactivation of somato-sensory cortex after dorsal spinal cord injury. *Nature*, **386**, 495- 498.

Jerison, H. H. (1990). Fossil evidence on the evolution of neocortex. In Cerebral Cortex. In E. G. Jones & A. Peters (Eds.), *Comparative structure and evolution of cerebral cortex, Vol. 8A* (pp. 285-310). New York: Plenum Press

Johnson, J. I. (1990) Comparative development of somatic sensory cortex. In E. G. Jones & A. Peters (Eds.), *Cerebral cortex* (pp. 335-449). New York: Plenum Press

Kaas, J.H. (1983) What, if anything, is SI? Organization of first somatosensory area of

cortex. *Physiological Review,* **6**, 206-231.

Kaas, J. H. (1993). The functional organization of somatosensory cortex in primates. *Annuals of Anatomy,* 175, 509-518.

Kaas, J. H. (1995). The evolution of isocortex. *Brain, Behavior and Evolution*, **46**,187-196.

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. (2002). Convergences in the modular and areal organization of the forebrain of mammals: Implications for the reconstruction of forebrain evolution. *Brain, Behavior and Evolution*, **59**, 262-272.

Kaas, J. H., & Lyon, D. C. (2001). Visual cortex organization in primates: theories of V3 and adjoining visual areas. *Program in Brain Research,* **134**, 185-295.

Kaas, J. H., & Preuss, T. M. (2002). *Human Brain Evolution. In* L. R. Squire, F. E. Bloom, M. J. Zigmond, S. K. McConnell, & N. C. Spitzer (Eds.), *Fundamental neurology,* 2nd Edition (pp. 1147-1166). San Diego, CA: Academic Press.

Krubitzer, L. A. (1998). What can monotremes tell us about brain evolution? *Philosophical Transactions of the Royal Society, London*, **B353**,1127-1146.

Krubitzer, L. A., & Calford, M. B. (1992). Five topographically organized fields in the somatosensory cortex of the flying fox. *Journal of Comparative Neurology, 371*, 1-30.

Krubitzer, L. A., & Kaas, J. H. (1990). The organization and connections of somatosensory cortex in marmosets. *Journal of Neurology*, **10**, 952-974.

Krubitzer, L. A., Sesma, M. A., & Kaas, J. H. (1986). Microelectrode maps, myeloarchitecture, and cortical connections of three somatotopically organized representations of the body surface in parietal cortex of squirrels *Journal of Comparative Neurology, 250*, 403-430.

Krubitzer, L. A., Manger, P. Pettigrew, J., & Calford, M. (1995). The organization of somatosensory cortex in monotremes: In search of the prototypical plan. *Journal of Comparative Neurology*, **351**, 261-306.

Krubitzer, L. A., Künzle, H., & Kaas, J. H.(1997). The organization of sensory cortex in a Madagascan insectivore, the tenrec (*Echinaps telfairi*). *Journal of Comparative Neurology, 379*, 399-414.

Lende, R. A. (1963). Cerebral cortex: a sensorimotor amalgam in the Marsupialia. *Science*, **141**, 395-403.

Li, X.-G., Florence, S. L., & Kaas, J. H. (1990). Areal distributions of cortical neurons projecting to different levels of the caudal brain stem and spinal cord in rats. *Somatosensory Motor Research*, **7**, 315-335.

McHenry, H. M. (1994). Tempo and mode in human evolutions. *Proceedings of the National Academy of Sciences USA,* **91**, 6780-6786.

Northcutt, R. G. (1995). The forebrain of gnathostomes: In search of a morphotype. *Brain, Behavior and Evolution*, **46**, 275-318.

Northcutt, R. G., & Kaas, J. H. (1995). The emergence and evolution of mammalian neocortex. *Trends in Neuoscience,* **18**, 373-379.

Nudo, R. J., & Masterton, R. B. (1990). Descending pathways to the spinal cord, III: Sites of origin of the corticospinal tract. *Journal of Comparative Neurology*, **296**, 559-583.

Ostrowsky, K., Magnin, J., Ryvlin, P., Ishard, J., Guenot, M., & Mauguiere, F. (2002). Representation of pain and somatic sensation in the human insula: a study of responses to direct electrical cortical stimulation. *Cerebral Cortex*, **12**, 376-385.

Picard, N., & Strick, P. L. (1996). Motor areas of medial wall: a review of their location and functional activation. *Cerebral Cortex,* **6**, 324-353.

Pons, T. P., & Kaas, J. H. (1985). Connections of area 2 of somatosensory cortex with the anterior pulvinar and subdivisions of the ventroposterior complex in macaque monkeys. *Journal of Comparative Neurology*, **240**, 16-36.

Pons, T. P., Garraghty, P. E., Friedman, D. P., & Mishkin, M. (1987). Physiological evidence forserial processing in somatosensory cortex. *Science*, **237**, 417-420.

Radinsky, L. (1975). Primate brain evolution. *American Scientist*, **63**, 656-663.

Ross, C. (1996). Adaptive explanation for the origins of the Anthropoidea (Primates). *American Journal of Primatology*, **40**, 205-230.

Rouiller, E. M., Moret, V., & Liang, F. (1993). Comparison of the connectional properties of The rat sensorimotor cortex: Support for the presence of a premotor or supplementary motor area. *Somatosensory Motor Research*, **10**, 269-289.

Sakai, S. T., Stepniewska, I., Qi, H.-X., & Kaas, J. H. (2000). Pallidal and cerebellum afferents to pre-supplementary motor area thalamocortical neurons in owl monkeys: A multiple labeling study. *Journal of Comparative Neurology,* **417**, 164 -180.

Simmons, R. M. T. (1982). The morphology of the diencephalons in the Prosimii. III. *The tarsioidea Journal of Hirnforsch*. **23**, 149-173.

Slutsky, D. A., Manger, P. R., & Krubitzer, L. (2000). Multiple somatosensory areas in the anterior parietal cortex of the California ground squirrel (*Spermophilus beecheyii*). *Journal of Comparative Neurology,* **417***,* 521-539.

Springer, M. S., & deJong, W. W. (2001). Which mammalian supertree to bark up. *Science,* **291**, 1709-1711.

Stepniweska, I., Preuss, T. M., & Kaas, J. H. (1993). Architectonics, somatotopic organization, and ipsilateral cortical connections of the primary motor area (M1) of owl monkeys. *Journal of Comparative Neurology*, **330**, 238-71.

Strata, F., Coq, J. O., & Kaas, J. H. (2003). The Chemo-and somatotopic architecture of the galago cuneate and gracile nuclei. *Neuroscience,* **116**, 831-850.

Striedter, G. F. (1998). Progress in the study of brain evolution: from speculative theories to testable hypotheses. *Anatomical Record (New Anatomist),* **253**, 105-112.

Sur, J., Nelson, R. J., & Kaas, J. H. (1978). The representation of the body surface in somatosensory area I of the grey squirrel. *Journal of Comparative Neurology,* **179**, 425-450.

Sur, M., Weller, R. E., & Kaas, J. H. (1980). The body surface representation in somatosensory area I of the tree shrew (*Tupaia glis*). *Journal of Comparative Neurology*, **194**, 71-95.

Sur, M., Weller, R. E., & Kaas, J. H. (1981). The organization of somatosensory area II in tree shrews. *Journal of Comparative Neurology*, **201**, 121-133.

Susman, R. L. (1994). Fossil evidence for early hominid tool use. *Science,* **265**,1570-1573.

Vanduffel, W., Fize, D., Peuskens, H., Denys, K., Sunaert, S., Todd, J. T., & Orban, G. A. (2002). Extracting 3D from motion: differences in human and monkey intraparietal cortex. *Science*, **298**, 413-415.

Walsh, T. M., & Ebner F. F. (1970). The cytoarchitecture of somatic sensory motor cortex in the opossum (*Didelphis marsupialis virginiana*): A Golgi study. *Journal of Anatomy*, **107**, 1-18.

Walsh, T. M., & Ebner, F. F. (1973). Distribution of cerebellar and somatic leminiscal projections to the ventral complex of the Virginia opossum. *Journal of Comparative Neurology*, **147**, 147-446.

Wise, S. P., Boussaound, D., Johnson, P. B. & Caminiti, R., (1997). Premotor and parietal cortex: cortical connectivity and combinatorial computations. *Annual Review of Neuroscience*, **20**, 25-42.

Wu, C. W., & Kaas, J. H. (2003). Somatosensory cortex of prosimian galagos: Physiological recording, cytoarchitecture and corticolcortical connections of anterior parietal cortex and cortex of the lateral sulcus. *Journal of Comparative Neurology*, **457**, 258-287

Wu, W. H. C., Beck, P. D., Kaas, J. H. (1996). Cortical and thalamic connections of the second somatosensory area, S2 in the prosimian primate,(*Galago garnetti*). *Society of Neuroscience Abstracts*, **22**, 107.

Wu, C. W., Bichot, N. P., & Kaas, J. H.(2000). Converging evidence from microstimulation, architecture, and connections for multiple motor areas in the frontal and cingulate cortex of prosimian primates. *Journal of Comparative Neurology,* **423**, 140-177.