

6.10 The Evolution of Parietal Areas Involved in Hand Use in Primates

L Krubitzer, Department of Psychology, Center for Neuroscience, University of California, Davis, CA, USA

E Disbrow, Department of Neurology, Center for Neuroscience, University of California, Davis; Department of Radiology, San Francisco, CA, USA

Submitted, 2005; Published by Elsevier Inc.

6.10.1	Introduction	184
6.10.2	Sensory Versus Association Cortex	184
6.10.3	Organization of Anterior Parietal Cortex in Primates (Areas 3b, 3a, 1, and 2)	186
6.10.4	Area 3b or S1	187
6.10.4.1	Functional Organization	187
6.10.4.2	Connections	191
6.10.5	Area 3a	195
6.10.5.1	Functional Organization	195
6.10.5.2	Connections	198
6.10.6	Area 1	198
6.10.6.1	Functional Organization	198
6.10.6.2	Connections	200
6.10.7	Area 2	200
6.10.7.1	Functional Organization	200
6.10.7.2	Connections	203
6.10.8	Posterior Parietal Area 5 in Primates	203
6.10.8.1	Functional Organization	203
6.10.8.2	Connections	204
6.10.9	Is Area 5 Homologous Across Mammals?	206
6.10.10	The Evolution of Anterior and Posterior Parietal Cortex	206
	References	208

Glossary

acallosal A neural pathway that does not project to the contralateral hemisphere and does not receive inputs via the corpus callosum. Such a region can be determined in studies of callosal connections by noting an absence of callosally projecting axon terminals in an otherwise terminal-rich area.

analogous A structure that has the same function. An analogous structure need not be homologous.

callosal A neural pathway that projects to the contralateral hemisphere via the corpus callosum. A callosal zone refers to a region of the cortex that receives inputs via the corpus callosum.

caudal Anatomical location – toward the tail.

contralateral A relative term referring to the opposite side of the brain or body.

deep receptors Peripheral receptor in the skin, muscles, or joints.

extrastriate Visual cortex that does not include V1 (striate cortex).

glabrous Regions of the skin lacking hairs, e.g., the pads of hands and feet.

homologous A structure that is inherited from a common ancestor. A homologous structure is not always analogous.

interdigitate To interweave two or more structures.

lateral Anatomical location – away from the midline of the brain or body.

medial Anatomical location – toward the midline of the brain or body.

myelin A material composed of lipids and lipoproteins that surrounds certain axons and functions as an electrical insulator. Myelin stains are often used to demarcate cortical areas and thalamic nuclei.

optokinetic Movement of the eyes when a moving visual stimulus is viewed.

rapidly adapting receptor A mechanoreceptor that responds to the initial presentation of a stimulus but stops responding or reduces its firing rate throughout the presentation of a sustained stimulus.

rostral Anatomical location – toward the rostrum or snout.

slowly adapting receptor A mechanoreceptor that responds throughout the presentation of a sustained stimulus.

topographic organization A feature of cortical organization in which adjacent points within a cortical field represent adjacent points on the sensory epithelium.

vibrissae Whiskers and/or stiff hair located on the face of an animal that often function as a tactile organ.

6.10.1 Introduction

Anthropocentric /, anθrɒpɪ'sentrik/. M19. [f. prec. + CENTRIC] Centering in humans; regarding humanity as the central fact of the universe (*The New Shorter Oxford English Dictionary*).

As a beginning for a review on areas of the primate brain involved in generating frames of reference and ultimately a sense of self, the definition of anthropocentrism may seem misplaced. Yet anthropocentrism is, paradoxically, central to this scientific endeavor: our fascination with ourselves is simultaneously the driving force behind our desire to understand biological organisms and the activities they generate (including anthropocentrism itself) and probably the largest stumbling block to achieve an objective understanding. That we are anthropocentric is without question. Indeed, when not actually pursuing activities necessary for our literal survival, we spend the majority of our time pursuing an understanding of ourselves. We strive to understand our uniqueness, our past, our future, how we behave together, how we behave individually, how we think, how we expend our resources, and how to determine if there is any other sentient being out there like us. These pursuits encompass a variety of disciplines such as psychology, sociology, philosophy, anthropology, history, and economics, to name a few. All of these disciplines are based on the premise that humans are radically different from other animals – that we abide by a different set of rules, that we are unconstrained by evolution, and that we have miraculously developed emergent properties, such as a mind, intelligence, language, and even a soul. While we poke fun at this egocentric drive that all of us possess and the anthropocentric nature of our institutions, we must concede that this magnificent sense of self is biologically driven. Specifically, there are regions of the neocortex that are involved in generating a sense of

our own body with respect to the world around us. These regions allow us to distinguish ourselves from external animate and inanimate objects and to interact with them via highly specialized morphological tools, such as our hands.

Despite this natural preoccupation with ourselves, and our need to understand how complexity has arisen in our species, many authors believe that it is more informative, when trying to appreciate our unique attributes with respect to other species, to examine similarities across groups, rather than trying to explain this uniqueness or variability in isolation. For example, are there similar principles of organization for all mammal brains? Once this question has been answered, then one can examine the departures from the common plan of organization to determine how these departures or modifications are achieved, and ultimately how they generate variable behavior like that described above for humans. A good illustration of this approach, and the focus of this review, is provided by an examination of the somatosensory areas of anterior and posterior parietal cortex in both primate and nonprimate mammals. These regions appear to have expanded in humans and are proposed to be associated with a number of sophisticated behaviors.

6.10.2 Sensory Versus Association Cortex

Traditionally, the mammalian neocortex has been divided into three broad categories: motor cortex, sensory cortex (including primary and second sensory fields such as S1, S2, V1, V2, A1, and R), and association cortex. This broad classification became popular in the middle part of the twentieth century, at which time electrophysiological mapping studies demonstrated that all mammals possessed

motor cortex and primary and second sensory cortices, and that primates in particular had a great deal of association cortex (Woolsey, C. N. and Fairman, D., 1946; Woolsey, C. N., 1958; see Kaas, J. H. and Collins, C. E., 2004, for review). Association cortex, as defined by modern textbooks, includes temporal, prefrontal, and posterior parietal cortex and is hypothesized to mediate complex behaviors such as perception, attention, cognition, and other high-level mental functions (Saper, C. B. *et al.*, 2000). The argument for defining cortex as association is somewhat circular and is based on the premise, which emerged from earlier mapping studies of Woolsey and colleagues, that the amount of cortex that could not be defined as unimodal sensory cortex in primates was relatively large compared to other mammals (Figure 1). Since primates were thought to be more cognitively complex than other mammals, this expanded cortex became associated with higher mental processes and was considered a primate phenomenon.

Unfortunately, the early mapping studies that provided support for these ideas were hampered by

technical difficulties such as suboptimal anesthetics, recording methods, and stimulation parameters, all of which made it difficult to elicit responses from neurons in cortex other than primary and secondary sensory fields. Despite these limitations, these early studies fostered several ideas regarding the human brain that still persist today. Probably the most noteworthy are that primary fields are evolutionarily older, and that association cortex is a new evolutionary phenomenon found mainly in human and nonhuman primates. Thus, association cortex is proposed to be the hallmark of human brain evolution.

These ideas were firmly entrenched for most of the twentieth century. Indeed, a number of psychologists still hold this view, and it is currently circulated as the reigning model in most popular textbooks (e.g., Carlson, N. R., 1998; Saper, C. B. *et al.*, 2000). However, work in the early 1970s by Allman J. M. and Kaas J. H. (1971; 1974; 1975; 1976) upended these traditional views by demonstrating in nonhuman primates that much of extrastriate cortex that was considered association cortex actually contained a number of unimodal visual fields (also see

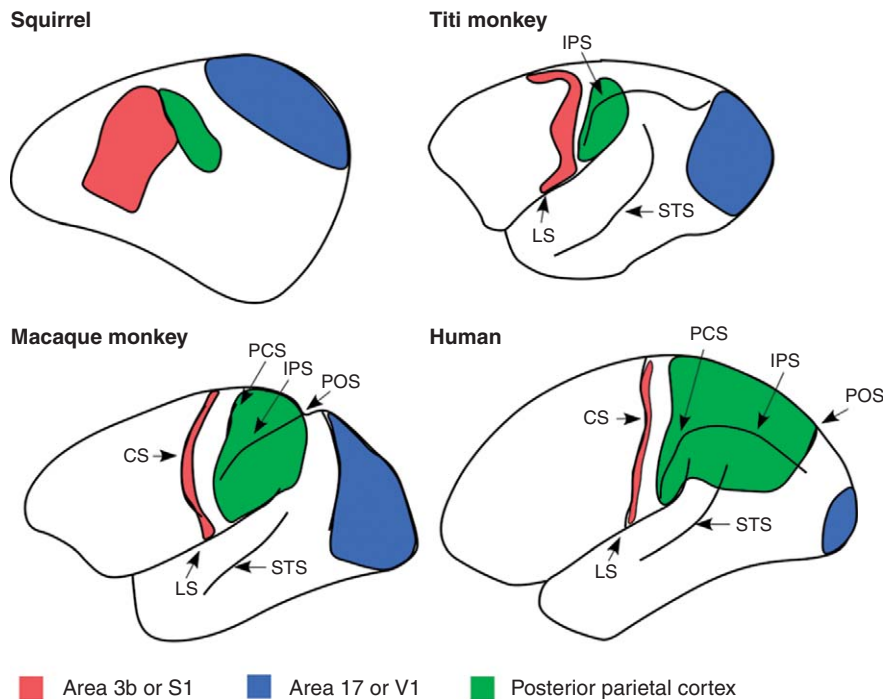


Figure 1 The location of association cortex (green) relative to the primary somatosensory area (red) and the primary visual area (blue) in four mammalian species. In mammals with a small neocortex, such as the gray squirrel, primary sensory areas occupy a relatively large portion of the cortical sheet. In mammals with a large neocortex such as monkeys, these primary sensory areas occupy relatively less cortex. In human primates, primary sensory areas occupy a very small portion of the neocortex, while association cortex, including posterior parietal cortex, occupies a large expanse of the cortical sheet.

Felleman, D. J. and Van Essen, D. C., 1991). Somewhat later, work in both somatosensory (Merzenich, M. M. *et al.*, 1978; Robinson, C. J. and Burton, H., 1980a; 1980b; Pons, T. P. *et al.*, 1985; Krubitzer, L. A. and Kaas, J. H., 1990; Krubitzer, L. *et al.*, 1995a) and auditory cortex (e.g., Imig, T. J. *et al.*, 1977; Hackett, T. A. *et al.*, 1998) demonstrated that parietal cortex and portions of temporal cortex that were thought to be association regions were occupied by somatosensory and auditory cortical fields, respectively (see Kaas, J. H. and Collins, C. E., 2004, for review).

Despite the ever-dwindling classical association cortex in primate brains (including human primates), there are still a few strongholds that seem indomitable, namely, prefrontal and posterior parietal cortex. Work on prefrontal cortex in humans demonstrates that it is involved in higher-order cognitive processes such as the ability to detect and respond to novel events, to discriminate internally motivated versus externally driven models of the world, and to “extract oneself from the present and fluidly move forward and backward in time” (p. 1319; Knight, R. T. and Graboweicky, M., 2000, for review). However, this region of cortex also has a number of visuomotor, olfactory, and limbic functions.

In humans, posterior parietal cortex is considered to be involved in coding the spatial location of objects within a particular frame of reference, both egocentric and extracentric (e.g., Mishkin, M. *et al.*, 1983; Behrmann, M., 2000; Robertson, L. C. and Rafal, R., 2000, for review). In nonhuman primates, posterior parietal cortex is divided into a number of cortical areas that are thought to be involved in visuospatial processing related to limb and hand use such as monitoring limb location during visually guided reaching and grasping, converting sensory locations into motor coordinates for intentional movement, and perceiving the movements of the body in extrapersonal space (Andersen, R. A. *et al.*, 1997; Snyder, L. H. *et al.*, 1997; Wise, S. P. *et al.*, 1997; Debowy, D. J. *et al.*, 2001; Andersen, R. A. and Buneo, C. A., 2002). Thus, much of the region traditionally defined as posterior parietal association cortex has actually evolved in primates as a consequence of and for the generation of specialized hand use rather than for general higher mental functions.

The following review will focus on several fields in anterior parietal cortex (areas 3a, 3b, 1, and 2) involved in processing somatic inputs from the skin, muscles, and joints, as well as one area of posterior parietal cortex (area 5) involved in manual dexterity,

bilateral coordination of the hands, intentional reaching and grasping, and interhemispheric transfer of information. We contend that our sense of self, or an internal representation of our body with respect to the external world, is a concrete characteristic common to all mammals. This internal representation is generated by interactions between visual, proprioceptive, and vestibular systems, all of which are intricately intertwined with the motor system. Such an interaction allows an individual to interface an internal representation of self with the external world via a particular morphological structure, such as a hand, thereby generating a sensorimotor feedback loop that allows one to distinguish self from nonself.

6.10.3 Organization of Anterior Parietal Cortex in Primates (Areas 3b, 3a, 1, and 2)

Somatosensory cortex in primates is divided into three major divisions: anterior parietal cortex, posterior parietal cortex, and cortex of the lateral sulcus (see Kaas, J. H. and Pons, T. P., 1988, for review). Each of these major divisions contains several cortical areas. Anterior parietal cortex includes the primary somatosensory area, S1, which corresponds to area 3b in primates (see Kaas, J. H., 1983, for review), area 3a, area 1, and area 2. Posterior parietal cortex has been subdivided differently by different investigators, but most would agree that at least one of these regions, area 5, processes somatic inputs. Finally, like posterior parietal cortex, cortex in the lateral sulcus has been subdivided differently by different investigators. Recently, our laboratory and others have examined this region of cortex using multiunit electrophysiological recording techniques and neuroanatomical tracing methods combined with architectonic analysis, and we have divided this cortex into several fields including the second somatosensory area, S2, the parietal ventral area, PV, the ventral somatosensory area, VS, and the rostroventral parietal area, PR (e.g., Krubitzer, L. A. and Kaas, J. H., 1990; Krubitzer, L. *et al.*, 1995a; Disbrow, E. *et al.*, 2002; 2003; Wu, C.-H. and Kaas, J., 2003).

In this chapter we focus only on somatosensory areas of the anterior and posterior parietal cortex. While several anterior parietal fields such as areas 3a, 3b, 1 and 2 are architectonically distinct in some primates, architectonic comparisons across species

are difficult to make for fields other than areas 3b and 3a. Ideally, the consideration of homology should be based on a number of criteria such as architecture, electrophysiological recording data, cortical and subcortical connections, and lesions to cortical fields and resultant behavioral deficits (Kaas, J. H., 1982). Indeed, determining homology based on architecture alone, in the absence of corroborative electrophysiological data, leads to too many inaccuracies in subdividing the neocortex and erroneous conclusions regarding the evolution of cortical fields. For this reason, the following review focuses primarily on electrophysiological recording studies, studies of connections and studies of lesions, rather than studies which only use architecture to subdivide the cortex.

Cortical fields

A1	primary auditory area
AIP	anterior intraparietal area
C1	caudal region 1
C2	caudal region 2
DSG	dysgranular zone
LIP	lateral intraparietal area
M1	primary motor area
MIP	medial intraparietal area
PM	parietal medial area
PP	posterior parietal cortex
PR	rostroventral parietal area
PV	parietal ventral area
R	rostral area
R1	rostral region 1
R2	rostral region 2
S1	primary somatosensory area
S2	secondary somatosensory area
S3	third somatosensory area
SMA	supplementary motor area
UZ	unresponsive zone
V1	primary visual area
VIP	ventral intraparietal area
VPZ	ventral posterior nucleus, recipient zone

Sulci

CS	central sulcus
IPS	intraparietal sulcus
LS	lateral sulcus
PCS	post central sulcus
POS	parietal occipital sulcus
STS	superior temporal sulcus

Thalamic nuclei

CL	central lateral nucleus
MG	medial geniculate nucleus
Pa	anterior pulvinar
PO	posterior nucleus
VL	ventral lateral nucleus
VP	ventral posterior nucleus

Vpi	ventral posterior nucleus, inferior division
VPI	ventral posterior nucleus, lateral division
VPm	ventral posterior nucleus, medial division
VPs	ventral posterior nucleus, superior division

Body parts

ch	chin
ck	cheek
dig	digits
D1	digit one
D2	digit two
D3	digit three
D4	digit four
D5	digit five
F or ft	foot
fa	forearm
fl	forelimb
fp	forepaw
gen	genitals
hl	hindlimb
hp	hindpaw
j	jaw
l	lip
nb	nail bed
ne	neck
sh	shoulder
sn	snout
t	toes
te	teeth
to	tongue
tr	trunk
ut	upper trunk
vib	vibrissae
w	wing
web	finger web
wr	wrist

Neuroanatomical directions

dor	dorsal
prox	proximal

6.10.4 Area 3b or S1

6.10.4.1 Functional Organization

The topographic organization of the primary somatosensory area, S1 or area 3b, has been described in a variety of primates including Old World macaque monkeys (Nelson, R. J. *et al.*, 1980); New World monkeys such as owl (Merzenich, M. M. *et al.*, 1978), squirrel (Sur, M. *et al.*, 1982), cebus (Felleman, D. J. *et al.*, 1983), spider (Pubols, B. and Pubols, L., 1971), titi (Padberg, J. P. *et al.*, 2005), tamarin (Carlson, M. *et al.*, 1986), and marmoset monkeys (Krubitzer, L. A. and Kaas, J. H., 1990); prosimian galagos (Sur, M. *et al.*, 1980); and humans (e.g., Penfield, W. and Rasmussen, T., 1968; Woolsey,

(Continued)

C. *et al.*, 1979; Fox, P. T. *et al.*, 1987; Moore, C. *et al.*, 2000; Blankenburg, F. *et al.*, 2003, for review; Hlushchuk, Y. *et al.*, 2003). In all primates investigated, area 3b forms a systematic representation of the contralateral body surface with the tail, genitals and feet represented most medially, followed by the representations of the hindlimb, trunk, forelimb, hand, face, and oral structures in a mediolateral progression (Figure 2).

Single unit studies demonstrate that neurons in area 3b have small receptive fields compared to other anterior parietal fields (e.g., Gardner, E., 1988) and along with optical imaging studies show that neurons are rapidly or slowly adapting to cutaneous stimulation (e.g., Sur, M. *et al.*, 1984; Chen, L. *et al.*, 2001) and respond to high-frequency stimulation (e.g., Lebedev, M. and Nelson, R., 1996), pressure, and flutter (Chen, L. *et al.*, 2001). In awake behaving monkeys, firing rates are modulated by contact with an object (DeBow, D. J. *et al.*, 2001), and neurons respond prior to wrist movements (Nelson, R. *et al.*, 1991). It is proposed that area 3b is involved in texture and form discrimination (Johnson, K. O. and Lamb, G. D., 1981; Chapman, C. E. and Ageranioti-Bélanger, S., 1991; Sinclair, R. J. and Burton, H., 1991; Ageranioti-Belanger, S. A. and Chapman, C. E., 1992; Tremblay, F. *et al.*, 1996; Jiang, W. *et al.*, 1997; DiCarlo, J. *et al.*, 1998; see Johnson, K. and Yoshioka, T., 2002, for review) as well as topographic tactile learning (e.g., Romo, R. *et al.*, 1998; 2000; Diamond, M. *et al.*, 2002, for review). While most researchers have examined the neural response to stimulation of the hand or have designed behavioral tasks associated with the hand, one group of studies examined the properties of neurons in area 3b in response to tongue and face movements (Lin, L.-D. *et al.*, 1994a; 1994b). These investigators found that neurons in area 3b (and area 1) increase their firing rate for preferred tongue directions and suggest that neurons in 3b and 1 provide sensory inputs to M1 necessary for generating coordinated tongue and facial movements. Such a homologous processing network in primates could form the basis, in a modified form, for the highly derived articulation behaviors that have evolved in humans.

Studies in which area 3b has been lesioned in monkeys are consistent with single unit studies. For example, lesions in area 3b result in an inability to make discriminations of roughness, hardness, and angle of an object (Randolph, M. and Semmes, J., 1974). Other studies demonstrate that lesions in area 3b result in an inability to make static tactile discriminations (detection of edges), as well as tactile

discriminations that require movement, such as discriminating a many-sided object (Schwartz, A., 1983). While the studies of Lamotte R. H. and Mountcastle V. B. (1979) support these findings, the lesions in their study encompassed the entire postcentral gyrus, making it difficult to relate a particular deficit with a specific cortical area.

A primary somatosensory area has also been identified in a wide range of nonprimate mammals including monotremes (e.g., Krubitzer, L. *et al.*, 1995b), marsupials (e.g., Pubols, B. H. *et al.*, 1976; Beck, P. D. *et al.*, 1996; Huffman, K. *et al.*, 1999; Frost, S. B. *et al.*, 2000), and eutherians (e.g., Felleman, D. J. *et al.*, 1983; see Kaas, J. H., 1983; Chapin, J. K. and Lin, C.-S., 1984; Ledoux, M. S. *et al.*, 1987; Johnson, J. I., 1990; Catania, K. C. *et al.*, 1993; Krubitzer, L., 1995, for review). Like area 3b in primates, S1 or area 3b in other mammals is topographically organized with the foot represented most medially, followed by the representation of the trunk, forelimb, forepaw, and face in a mediolateral progression (Figure 3). While single units have been recorded in the barrel field of some rodents, a full description of work in barrel cortex is beyond the scope of this chapter. However, Diamond M. *et al.* (2002) propose that S1 in whisking rodents may be involved in topographic learning via the whiskers, as is the hand representation in area 3b in monkeys. For our purpose, it is important to note that not only is the gross topographic organization of S1 similar in all species examined, but also the types of systems-level modifications to S1, or the rules of change, are consistent across species.

Probably the most salient modification in S1 across species is the amount of neocortex that represents body parts associated with specialized use, which we term behaviorally relevant body surfaces. For example, animals such as the duck-billed platypus have evolved electrosensory receptors that run in parallel strips along the bill (Figure 4). Together with mechanosensory receptors, platypus use electrosensory receptors almost exclusively for prey capture, navigation, and most other activities (Scheich, H. *et al.*, 1986; Manger, P. R. and Pettigrew, J. D., 1995; see Krubitzer, L., 1998, for review). The importance of this morphological structure is reflected in the neocortical organization in that a large percentage of S1, and indeed most of the neocortex, is devoted to the representation of the bill (Krubitzer, L. *et al.*, 1995b). Other examples of cortical magnification of specialized morphology (Figure 3) include the nose representation of the star-nosed mole (Catania, K. C. *et al.*, 1993), the

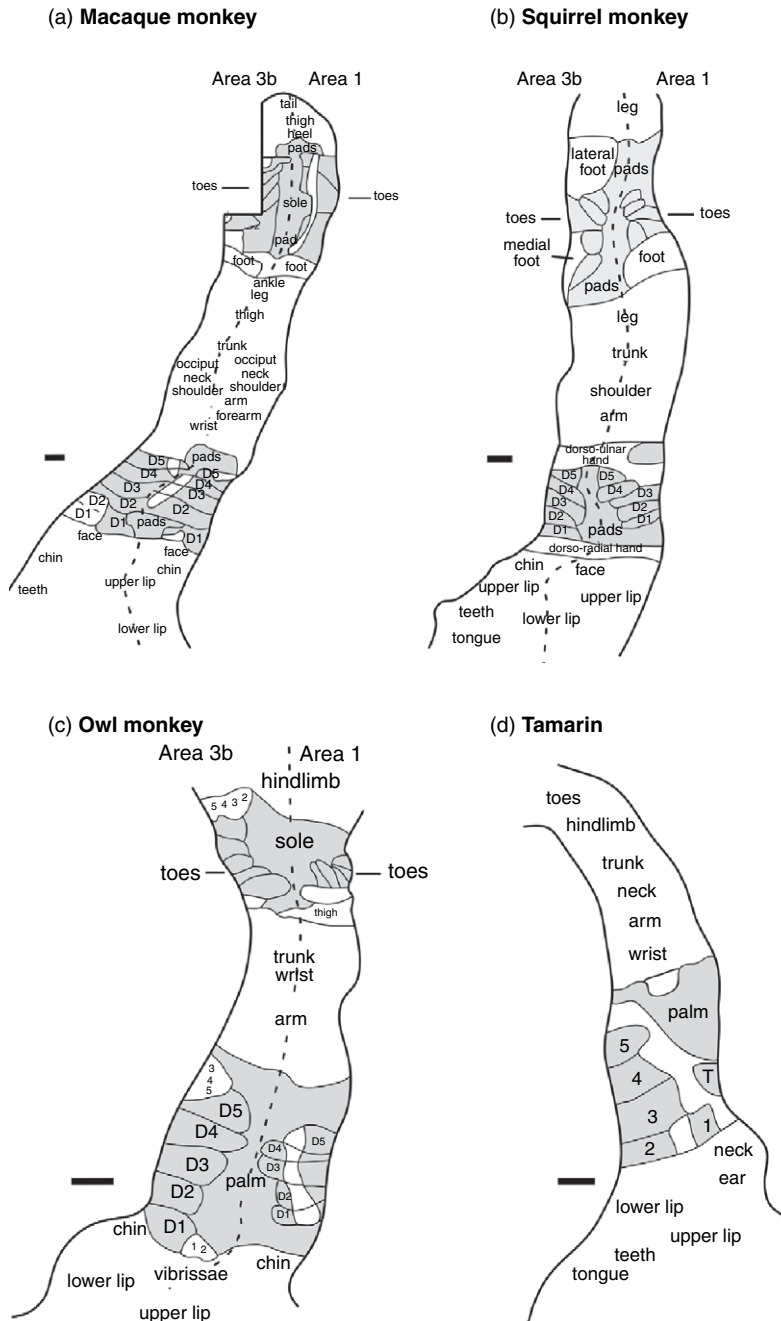


Figure 2 The topographic organization of the primary somatosensory area (S1 or 3b) and area 1 in New and Old World monkeys. Both areas 3b and 1 contain a systematic representation of the contralateral body surface and form mirror representations of each other. In some primates (a–c) area 1 is very well developed, while in other primates (d) area 1 has not been identified. We propose that area 1 coevolved with a well-developed, glabrous hand in some lineages. This is supported by the fact that tamarins have a more primitive hand with claws, compared to the other primates shown. (a) From Nelson, R. J., Sur, M., Felleman, D. J., and Kaas, J. H. 1980. Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis*. *J. Comp. Neurol.* 192, 611–643; (b) From Sur, M., Nelson, R. J., and Kaas, J. H. 1982. Representations of the body surface in cortical areas 3b and 1 of squirrel monkeys: comparisons with other primates. *J. Comp. Neurol.* 211, 177–192; (c) From Merzenich, M. M., Kaas, J. H., Sur, M., and Lin, C.-S. 1978. Double representation of the body surface within cytoarchitectonic areas 3b and 1 in “S1” in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.* 181, 41–74; (d) From Carlson, M., Huerta, M. F., Cusick, C. G., and Kaas, J. H. 1986. Studies on the evolution of multiple somatosensory representations in primates: the organization of anterior parietal cortex in the New World Callitrichid, *Saguinus*. *J. Comp. Neurol.* 246, 409–426.

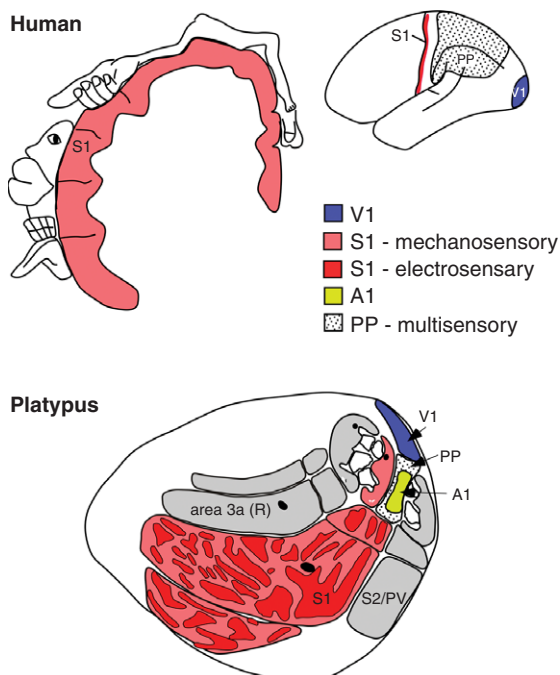


Figure 4 A schematic rendition that demonstrates the cortical magnification of behaviorally relevant body part representations in area 3b across different mammals. In humans, the hand, lips, and oral structure representations are magnified, while in platypus, the bill representation is magnified. Although such magnification occurs for different body part representations, the rules of modification of S1 are similar in both groups of mammals despite approximately 200 million years of independent evolution. This observation indicates that S1 is highly constrained in evolution. The schematic of the human is adapted from Penfield, W. and Rasmussen, T. 1968. Secondary Sensory and Motor Representation. In: Cerebral Cortex of Man. A Clinical Study of Localization of Function (Chapter VI), pp. 109–134. Hafner Publishing Company and the schematic of the platypus is adapted from Krubitzer L. *et al.* (1995).

for omnivorous feeding and for the articulation of species-specific sounds. Similarly, some primates have a relative enlargement of other body parts that are related to specialized use. For example, cebus and spider monkeys have an enlarged representation of their prehensile tail (Felleman, D. J. *et al.*, 1983; Pubols, B. and Pubols, L., 1971). While this magnification of S1 in different species is related to innervation density at the periphery (e.g., Lee, K. and Woolsey, T., 1975; Catania, K. C. and Kaas, J. H., 1997), recent evidence also indicates that the use, or the unique pattern of activity from peripheral sensory receptor arrays, also contributes to this

cortical magnification (Recanzone, G. H., 1992b; Catania, K. C. and Kaas, J. H., 1997; Xerri, C. *et al.*, 1996). It has been proposed that this magnification generates the high spatial resolution necessary for texture and form discriminations made with specialized structures (see Johnson, K. and Yoshiako, T., 2002, for review).

A second type of consistent modification that has evolved in a number of different lineages is the segregation of inputs from similar body parts into distinct isomorphs, or modules, defined electrophysiologically or histochemically (Figure 5). For example, in primates, rapidly adapting and slowly adapting inputs are segregated into separate clusters or bands within S1 (e.g., Sur, M. *et al.*, 1984; Chen, L. *et al.*, 2001), and the face representation is divided into myelin light and dense zones that segregate different portions of the face and oral structures (Krubitzer, L. A. and Kaas, J. H., 1990; Jain, N. *et al.*, 2001). In a number of rodents, inputs from the vibrissae are segregated into cortical barrels (Woolsey, T. A. and Van der Loos, H., 1970), in the star-nosed mole, nose follicles form isomorphs (Catania, K. C. *et al.*, 1993), and in the duck-billed platypus, electrosensory and mechanosensory inputs are segregated into interdigitating bands (Krubitzer, L. *et al.*, 1995b). The evolutionary and developmental significance of modules has been discussed previously (Krubitzer, L., 1995; Krubitzer, L., and Kahn, D., 2003). In brief, we hypothesize that modules represent a stage in the evolution of a cortical field and that selection for shorter connection length and/or increased speed of transmission has led to the aggregation of modules in different cortical fields and different species over time. If this is the case, then it suggests that a cortical field is actually a pattern of activation (connectivity) from a variety of sources including the thalamus and ipsilateral and contralateral hemispheres that shifts and redistributes across the cortical sheet within an individual lifetime (development) and across species over time (evolution).

6.10.4.2 Connections

The ipsilateral cortical connections of area 3b have been described in macaque monkeys (e.g., Jones, E. G. *et al.*, 1978; Pearson, R. C. A. and Powel, T. P. S., 1985; Shanks, M. F. *et al.*, 1985b; Juliano, S. *et al.*, 1990; Darian-Smith, C. *et al.*, 1993; Burton, H. and Fabri, M., 1995; Burton, H. *et al.*, 1995), New World titi monkeys (Coq, J. O. *et al.*, 2004; Padberg, J. P. *et al.*, 2005), marmosets (Krubitzer, L. A. and Kaas, J. H., 1990),

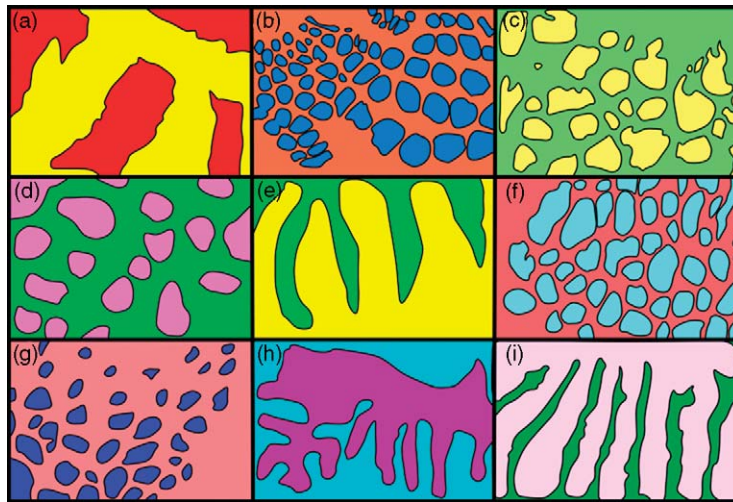


Figure 5 A schematic illustrating a second type of modification, modular organization, that has been observed in slices of flattened sensory cortex in a variety of different mammals. (a) Myelin bands in area 18 of squirrel monkeys; (b) the barrel field in S1 of rats; (c) modules in the insula of dolphin neocortex; (d) entorhinal clusters in macaque monkeys; (e) ocular dominance columns in monkeys; (f) entorhinal clusters in humans; (g) the barrel field in S1 of brush-tailed possums; (h) mechanosensory and electrosensory bands in S1 of duck-billed platypuses; and (i) nose follicle representation of S1 in star-nosed moles. This figure was adapted from Manger, P., Sum, M., Szymanski, M., Ridyway, S., and Krubitzer, L. 1998. Modular subdivisions of dolphin anterior insular cortex: does evolutionary history repeat itself? *J. Cogn. Neurosci.* 10(2), 153–166.

and prosimian galagos (Wu, C.-H. and Kaas, J., 2003). In these primates, restricted injections in area 3b result in a relatively tight distribution of connections predominantly with adjacent somatosensory cortical fields including areas 3a, cortex immediately caudal to area 3b (areas 1 and 2 in macaque monkeys, area 1/2 in New World monkeys and galagos), S2 (and PV where described), and primary motor cortex (Figure 6). In primates, thalamic connections of area 3b are predominantly from the ventral posterior nucleus, both VPM and VPI (e.g., Jones, E. G. *et al.*, 1979; Nelson, R. J. and Kaas, J. H., 1981; Mayner, L. and Kaas, J., 1986; Darian-Smith, C. *et al.*, 1990; Krubitzer, L. A. and Kaas, J. H., 1992; Rausell, E. and Jones, E. G., 1995; Coq, J. O. *et al.*, 2004; Padberg, J. and Krubitzer, L., 2006). However, sparse projections from VPI, VPs, and Pa have also been observed (e.g., Cusick, C. G. and Gould, H. J. I., 1990).

Both the cortical and subcortical connections of area 3b (S1) have been described in a number of mammals such as rodents (e.g., Wise, S. P. and Jones, E. G., 1976; Akers, R. M. and Killackey, H. P., 1978; Krubitzer, L. A. *et al.*, 1986; Chapin, J. K. *et al.*, 1987; Krubitzer, L. and Kaas, J., 1987; Koralek, K. A. *et al.*, 1990; Fabri, M. and Burton, H., 1991; Paperna, T. and Malach, R., 1991), carnivores (Alloway, K. D. and Burton, H., 1985; Barbaresi, P. *et al.*, 1987; Herron, P. and Johnson, J. I., 1987), and marsupials

(Beck, P. D. *et al.*, 1996; Elston, G. N. and Manger, P. R., 1999; see Johnson, J. I., 1990, for review). As in primates, S1 is densely connected with area 3a (R, UZ, and dysgranular cortex), M1, and S2/PV. The major thalamic projection to S1 is from VPI and VPM, and connections are also observed with the posterior nucleus, PO.

The total pattern of callosal connections of areas 3b, 1, 2, and 5 indicates that the hand representation of area 3b is almost completely acallosal in primates (e.g., Pandya, D. N. and Vignolo, L. A., 1968; Killackey, H. P. *et al.*, 1983; Shanks, M. F. *et al.*, 1985a; 1985b). Surprisingly, specific callosal connections of individual anterior parietal fields have only been described for a few species of primates (e.g., Manzoni, T. *et al.*, 1986; Krubitzer, L. A. and Kaas, J. H., 1990; Padberg *et al.*, 2005). In macaque monkeys it was found that while the hand representation of area 3b does not project to the hand representation of area 3b of the opposite hemisphere, it does project to S2 (e.g., Manzoni, T. *et al.*, 1986). In marmosets, electrophysiologically defined body part representations in area 3b are differentially interconnected across hemispheres. Myelin light portions of area 3b appear to be strongly interconnected, while myelin dense portions of area 3b are acallosal. Furthermore, as described in early studies, the hand representation of area 3b appears to be mostly acallosal. Area 3b is also

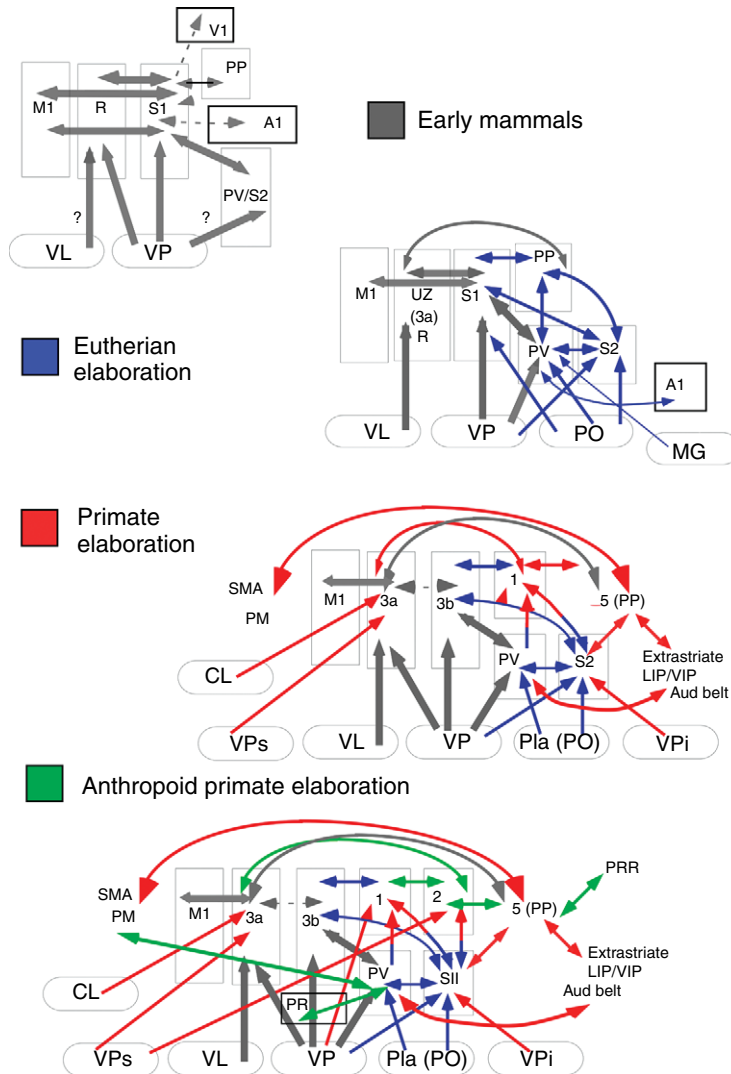


Figure 6 An overview of the cortical and thalamocortical connections of anterior parietal cortical fields, lateral sulcus fields, and posterior parietal area 5 in mammals. This figure is not an exhaustive overview of the connections of particular fields in different mammals. Rather, this figure depicts that particular patterns of connections can be identified in all groups of mammals due to retention from a common ancestor (gray arrows). Such connections are homologous. Additional connections arose later in mammalian evolution and have been added to this retained network in eutherian mammals (blue arrows). In different lineages, such as primates, these networks were further elaborated with the addition of new cortical areas, modules to existing cortical areas, and new thalamic nuclei. Such modifications to the neocortex make determining homologous areas and connection patterns difficult. Furthermore, these types of anatomical modifications suggest that homologous cortical fields may not be analogous (Figure 8).

interconnected with S2 and PV of the opposite hemisphere. Similar findings were reported in titi monkeys in which the hand representation was acallosal, and myelin light regions formed callosal zones in area 3b (Padberg *et al.*, 2004).

Callosal connections have been described for area 3b or S1 in rats (e.g., Wise, S. P. and Jones, E. G., 1976; Akers, R. K. and Killackey, H. P., 1978), mice (White,

E. L. and DeAmicis, R. A., 1977), cats (e.g., Ebner, F. F. and Myers, R. E., 1965; Caminiti, R. *et al.*, 1979; McKenna, T. M. *et al.*, 1981), raccoons (Ebner, F. F. and Myers, R. E., 1965; Herron, P. and Johnson, J. I., 1987), flying foxes (Krubitzer, L. *et al.*, 1998), rabbits (Ledoux, M. S. *et al.*, 1987), and tree shrews (Cusick, C. G. *et al.*, 1985; Weller, R. E. *et al.*, 1987; see Krubitzer, L. *et al.*, 1998, for review). As in primates,

there is a heterogeneity of callosal connectivity of different body parts that appear to be associated with use. For example, the representations of specialized body parts in area 3b are acallosal, and zones such as the unresponsive zone in squirrels, the dysgranular zone (septa) in rats, the heterogeneous zones of raccoons, and the myelin light area 1/2 interdigitations in flying foxes are rich in callosal connections, as is the unmyelinated region in monkeys. Thus, studies of callosal connectivity for all mammals investigated report that S1 contains callosal zones related to different body part representations often associated with distinct myelin light zones (Figure 7; see Krubitzer,

L. et al., 1998, for review). Body part representations associated with specialized use such as the barrels in rodents, lateral face representations in rabbits, and the hand representations in primates are devoid of callosal connections. Previous studies suggest that callosal free zones are the regions of cortex where thalamocortical afferents terminate (e.g., Wise, S. P. and Jones, E. G., 1976; Gould, H. J. I. and Kaas, J. H., 1981; Krubitzer, L. A. and Kaas, J. H., 1990; Krubitzer, *L. et al.*, 1998). It appears that selection for specialized peripheral morphology in the form of receptor-dense regions like finger tips also operates on cortical representations to both conserve discrete receptive

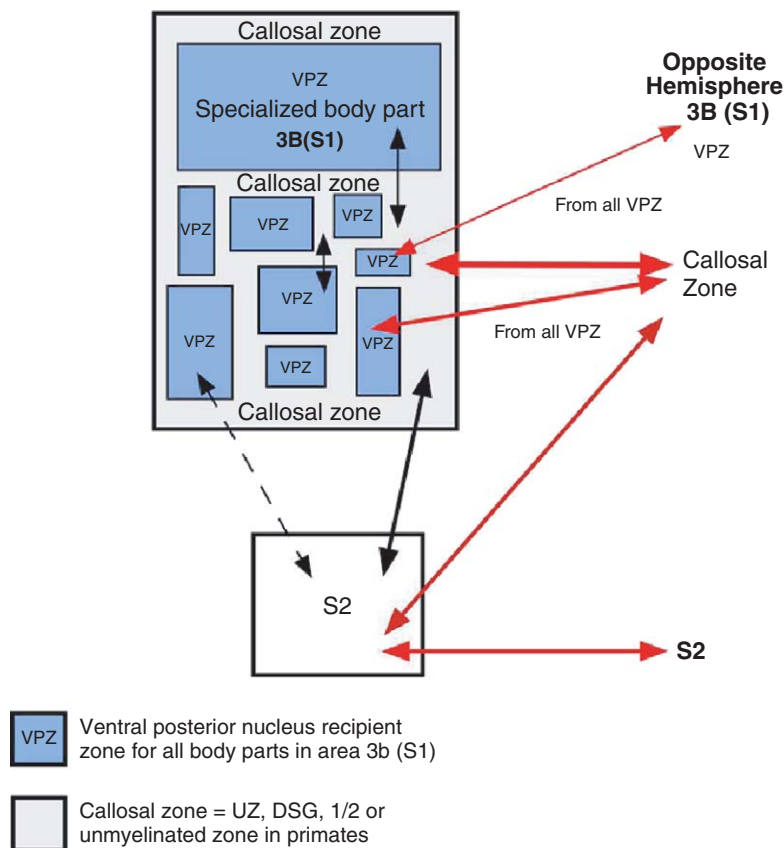


Figure 7 An illustration of the callosal connections of the primary somatosensory area (3b or S1) that depicts some common features of connectivity across all mammals. This figure demonstrates that area 3b appears to be modularly organized based on several important principles. First, S1 is broken into thalamocortical recipient zones (VPZ) and callosal recipient zones. Thalamocortical recipient zones of behaviorally relevant body parts (e.g., hand, bill, nose, and wing) are acallosal. Some of the VPZs have sparse callosal connections with VPZs in the opposite hemisphere and more dense connections to callosal zones in the opposite hemisphere. Finally, information from 3b can also reach the opposite hemisphere indirectly via S2. We and others propose that this type of organization evolved to maintain close intracortical connections between neurons in the same VPZ, uninterrupted by connections from the opposite hemisphere. This type of organization would allow for the maintenance of small receptive fields in neurons over a large region of cortex and would allow the integrity of sensory discriminations derived from inputs from behaviorally significant body parts to be maintained.

fields of neurons created by thalamocortical inputs and preserve neuroanatomical interactions between neighboring specialized skin regions. This conservation of thalamocortical inputs carrying information from specialized skin regions, and of short intrinsic cortical connections within the representation of these specialized skin regions, results in cortical zones or islands that are uninterrupted by callosal afferents (Herron, P. and Johnson, J. L., 1987; Ledoux, M. S. *et al.*, 1987; Krubitzer, L. *et al.*, 1998). We further suggest that in area 3b this type of connection labyrinth may be necessary to maintain the integrity of sensory discriminations derived from inputs from behaviorally significant body parts and as such constrains the evolution of S1.

Taken together, the data illustrate that there is a common organization of S1 across species and that modifications to this field take a similar form reflected as a magnification of the representation of specialized peripheral sensory morphology. How this magnification is related to specialized behavior is not clear, and why this mode of cortical specialization has emerged (compared to any number of potential types of modification) is not known. However, Kaas J. H. (1997) suggests that it is a byproduct of development that has been functionally optimized. Regardless of the functional significance of this magnification, comparative surveys demonstrate that the neocortex must be highly constrained since only a few modifications to S1, other than cortical magnification, have emerged. In addition to cortical magnification, the cortex has been modified to segregate subclasses of input, such as the segregation of rapidly adapting and slowly adapting inputs as well as the callosal and acallosal zones described above. Again, it is not understood why this feature has emerged independently in a number of different lineages, but it has been proposed that it reflects developmental contingencies and is therefore highly constrained (e.g., Krubitzer, L., 1995; Kaas, J. H., 1997; Krubitzer, L. and Kahn, D., 2003).

As with cortical organization, connections of S1 also have similar patterns across mammals. This homologous network may in part subservise similar functions, but it is likely that with the addition of new fields and connections (as in primates), and a reweighting of existing synaptic interactions, new functions or at least a species-specific refinement of particular behaviors is likely to have emerged (Figures 6 and 8). This observation, of course, implies that even for primary fields, direct extrapolation between nonhuman and human primates regarding function is problematic.

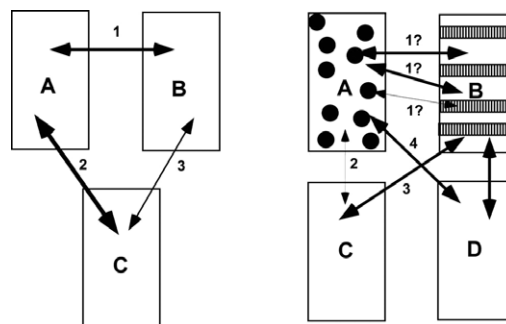


Figure 8 A theoretical rendition of the evolution of cortical fields and their connections. This figure illustrates the difficulties inherent in assigning homology across groups of mammals. It also illustrates the problems with making direct extrapolations regarding analogy of cortical fields, and their circuitry, between any groups of mammals (such as macaque monkeys and humans). Hypothetical cortical fields include field A, B, and C with connection patterns 1, 2, and 3 (*left*). When comparing cortical organization and connections across groups to determine homology, several problems arise. First, new cortical fields have been added in some groups (D). Second, modules may have been added to existing cortical fields (A and B). Third, the density of connections between fields may have changed (connection 2). Fourth, existing connections have been modified by the generation of modules (connection 1). Finally, new connections (4) have developed between retained fields (A) and new fields (D). All of these events are complicated by the fact that connection patterns are often used to determine homology between fields. Thus, even when one can convincingly determine the homology of cortical fields in different groups of animals, it is unlikely that homologous fields are strictly analogous.

6.10.5 Area 3a

6.10.5.1 Functional Organization

A representation of deep receptors of the contralateral body, termed area 3a, is located immediately rostral to area 3b. Area 3a was originally described as an architectonically distinct cortical field in humans by Vogt C. and Vogt O. (1919) but has since been described in a variety of mammals. The functional organization of area 3a in primates has been described for marmosets (Huffman, K. J. and Krubitzer, L., 2001a) and macaque monkeys (Krubitzer, L. *et al.*, 2004) in multiunit recording studies, and recently in humans using modern imaging techniques (Moore, C. *et al.*, 2000). These studies demonstrate that area 3a contains a topographically organized representation of deep receptors and musculature of the contralateral body that parallels that of area 3b (Figure 3) and ultimately receives input

from proprioceptors of the muscles and joints (Phillips, C. B. *et al.*, 1971; Schwarz, D. W. *et al.*, 1973; Heath, C. J. *et al.*, 1975; Hore, J. *et al.*, 1976; see Tanji, J. and Wise, S., 1981, for review). Single unit studies in awake monkeys report that neurons in area 3a modulate activity prior to wrist flexion and extension (Nelson, R., 1987) and are active under a variety of joint movements (Gardner, E., 1988). Neural activity in area 3a increases with maintained limb position and is modulated with the velocity of movement toward a limb position, as well as the ultimate position of the limb (Tanji, J., 1975; Wise, S. and Tanji, J., 1981). Furthermore, lateral portions of area 3a (termed 3aV) contain neurons that respond to vestibular stimulation (Guldin, W. O. *et al.*, 1992). Thus, area 3a in primates is a proprioceptive field that is closely involved in the kinetics of movement. This contention is supported by microstimulation studies in monkeys which demonstrate that body movements can be elicited by stimulating area 3a with very small currents (e.g., Stepniewska, I. *et al.*, 1993).

Studies in other mammals have identified a region of cortex just rostral to area 3b in which neurons respond to stimulation of deep receptors. In carnivores such as cats (e.g., Oscarsson, O. and Rosén, I., 1963; 1966; Oscarsson, O. *et al.*, 1966; Landgren, S. and Silfvenius, H., 1969; Zarzecki, P. *et al.*, 1978; Felleman, D. J. *et al.*, 1983), raccoons (Johnson, J. I. *et al.*, 1982; Feldman, S. H. and Johnson, J. I., 1988), and ferrets (Hunt, D. L. *et al.*, 2000), a region just rostral to area 3b exhibits a number of characteristics of area 3a in monkeys, such as neural response to stimulation of deep receptors, architectonic appearance, and gross topographic organization (Figure 3). This field has been termed area 3a in cats and ferrets and kinesthetic cortex in raccoons. In other mammals such as marsupials (see Huffman, K. *et al.*, 1999), rodents (see Slutsky, D. A. *et al.*, 2000, for review), insectivores (Krubitzer, L. *et al.*, 1997), and monotremes (Krubitzer, L. *et al.*, 1995b), these features are observed in a field just rostral to S1, termed the rostral field, R (Figure 9). In all of these mammals, this cortical area immediately rostral to S1 and caudal to area 4 contains a gross mediolateral organization that mirrors that of area 3b, although there is a great deal of variability across groups. Thus, all mammals have a cortical field located just rostral to area 3b that receives inputs from deep receptors of the contralateral body and is distinguished from motor cortex (area 4) based on a number of criteria including functional organization, neural stimulus preference, architectonic

distinctiveness, and when known cortical and subcortical connectivity. We propose that area 3a is homologous in all mammals.

As demonstrated for area 3b, there are several features of area 3a organization that have been consistently modified in different lineages, and these modifications appear to be more related to the use of behaviorally relevant body parts than in area 3b. For instance, when the topographic organization of area 3b is compared with that of area 3a in macaque monkeys, area 3b is observed to be more topographically precise, particularly for representations of the digits where every digit is represented in an exclusive cortical zone. This aspect of representation in area 3b has been observed in every primate examined regardless of the use of the hand or whether the primate in question has an opposable thumb. In contrast, in area 3a in macaque monkeys, exclusive cortical territory is devoted to the representation of D1 and D2, while digits 3 through 5 are represented together. In area 3a in marmosets, little if any cortical territory is devoted to the exclusive representation of a single digit. Digit representation in area 3a in the two species appears to parallel differences in use (Figure 3). Macaque monkeys have opposable thumbs and are highly skilled graspers who employ two general techniques. The first technique is to oppose D1 to D2 (precision grip), and the second technique is to oppose all four remaining digits to the palm (power grip; Welles, J. F., 1976; Roy, A. *et al.*, 2000). Marmoset monkeys, on the other hand, generally employ only a power grip, and their cortical representation in area 3a reflects this behavior. These observations suggest that in primates, area 3a emerges in development and evolution as a result of the actual use of the body part, and therefore, the motor system must play an important role in its construction.

Studies of the organization of area 3a in a variety of other species who use the hand quite differently than primates support this contention (Figure 3). For instance, the flying fox has a highly derived hand in which the digits have evolved membranes that span between them. This digit/membrane configuration functions as a whole unit, the wing, which is adapted for flight. Consequently, all digits form a single representation in area 3a, the wing, and there is no cortical territory that exclusively represents any one digit (Krubitzer, L. *et al.*, 1998), although such exclusive digit representation is present in area 3b in these mammals (Calford, M. B. *et al.*, 1985; Krubitzer, L. A. and Calford, M. B., 1992). Another interesting

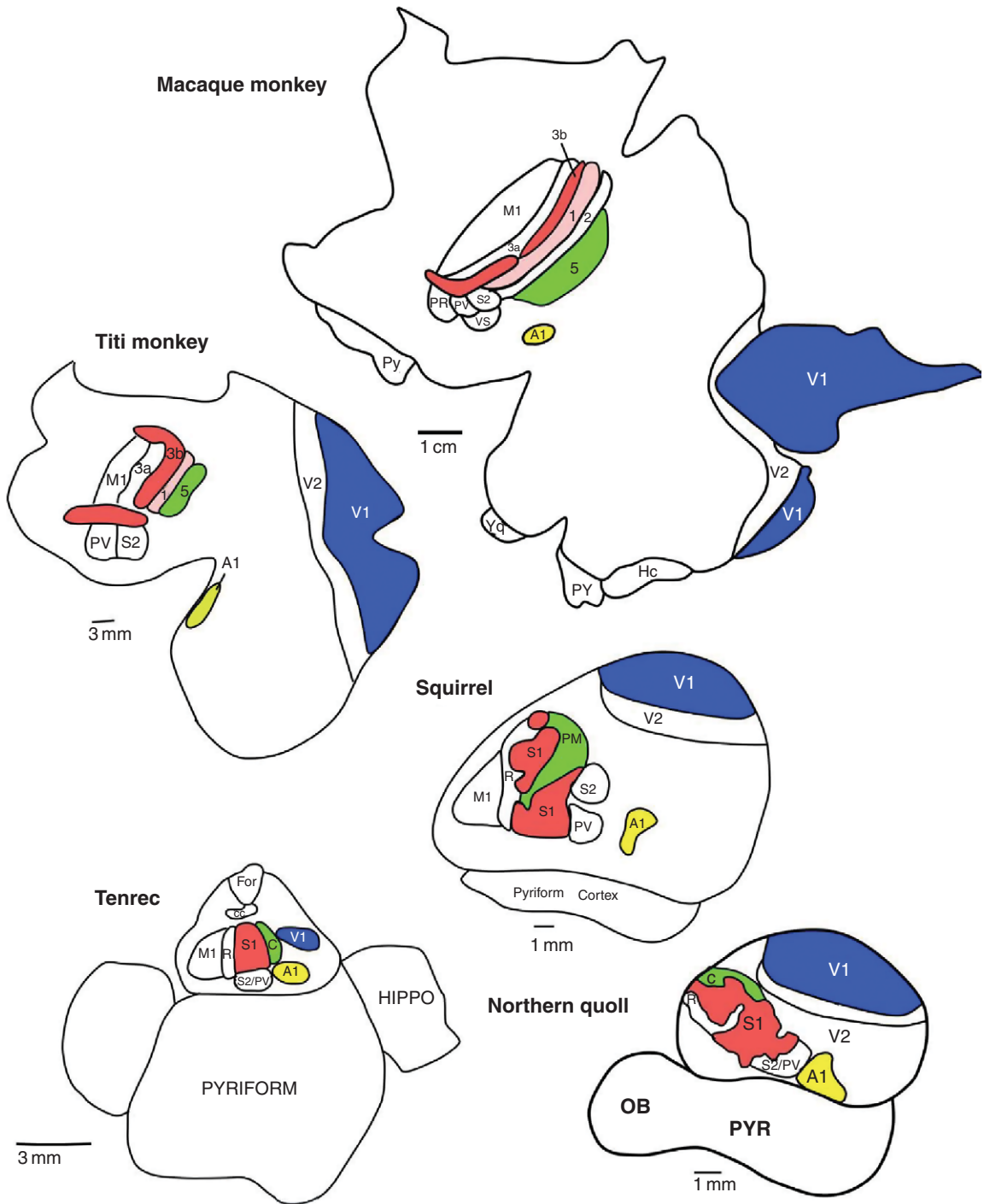


Figure 9 The organization of neocortex in several different mammals. This figure demonstrates that assigning homology of a cortical field based on the location of a particular field relative to another field is problematic. For instance, in mammals with large brains, such as macaque monkeys, area 1 is immediately caudal to area 3b, area 5 is close to the caudal boundary of area 1, and both are very far removed from V1 and V2. In mammals such as squirrels, cortex immediately caudal to area 3b, PM, is relatively close to V2 compared to macaque monkeys. In tenrecs, cortex immediately caudal to area 3b (S1) is also immediately adjacent to V1. If one were to assign homology based solely on location, this cortex in tenrecs could as easily be termed area 1 as it could be termed V2.

example of use-dependent organization of area 3a is the marsupial striped possum. This animal has a specialized D4 that it uses almost entirely to capture insects (Van Dyck, S., 1983). While exclusive cortical territory for all of the digits is observed in area 3b (with a magnification of D4), only D4 is represented in area 3a. Differences in use between members of the same species can produce a good deal of variability in the topographic organization of area 3a (e.g., Recanzone, G. H. *et al.*, 1992b), and this variability is even more pronounced across species due to specialized motor sequences or exaggerated behaviors that coevolved with specialized peripheral morphology and associated sensory receptor arrays (Krubitzer, L. *et al.*, 2004).

6.10.5.2 Connections

There are several studies of the connections of area 3a in primates including macaque monkeys (e.g., Jones, E. G. *et al.*, 1978; Darian-Smith, C. *et al.*, 1993), squirrel monkeys (Guldin, W. O. *et al.*, 1992), and marmosets (Huffman, K. J. and Krubitzer, L., 2001a). These studies demonstrate that area 3a is densely connected with M1, SMA, area 2 (or cortex caudal to area 3b), S2/PV, cingulate cortex, insular cortex, and posterior parietal cortex (area 5; Figure 6). The surprising result from these previous studies is that area 3a has more numerous connections with motor and posterior parietal areas of the neocortex than with traditionally defined somatosensory areas. Studies of thalamic connections of area 3a in Old World (Jones, E. G. *et al.*, 1979; Darian-Smith, C. *et al.*, 1990) and New World monkeys (Akbarian, S. *et al.*, 1992; Huffman, K. J. and Krubitzer, L. A., 2001b) indicate that area 3a receives input from somatic nuclei such as the ventral posterior superior nucleus (VPs, VPLc of Jones, E. G. *et al.*, 1979; Friedman, D. and Jones, E., 1981 and Darian-Smith, C. *et al.*, 1993) and the anterior pulvinar (Pla), some of which (e.g., VPi, VPs, and VLc) are also associated with vestibular processing (e.g., Lang, W. *et al.*, 1979). Area 3a also receives input from nuclei associated with the motor system such as the ventral lateral (VL), ventral anterior (VA), and central lateral (CL) nucleus of the thalamus.

The cortical and subcortical connections of area 3a, or cortex in the location of area 3a, has only been described in a few mammals such as squirrels (Gould, H. J. *et al.*, 1989; dysgranular UZ), flying foxes (Krubitzer, L. *et al.*, 1998), cats (e.g., Avendano, C. *et al.*, 1992), and briefly for ferrets (e.g., Hunt, D. L.

et al., 2000). While there is variability in the patterns of cortical connections of area 3a across animals, there are consistent patterns of connections with motor cortex, areas of the lateral sulcus such as S2/PV, and with cortex immediately caudal to S1 (Figure 6; termed area 5, PP, 1/2, and C in different animals). Thalamic connections of the UZ/R region of squirrels (area 3a) were from nuclei situated rostral, dorsal, and caudal to VP and from the central medial nucleus (Gould, H. J. *et al.*, 1989).

As with 3b, in most studies, the total pattern of callosal connections of anterior parietal fields 3a, 3b, 1, and 2 has been examined rather than the specific connections of area 3a (e.g., Jones, E. G. and Powell, T. P. S., 1969a; Killackey, H. P. *et al.*, 1983; Shanks, M. F. *et al.*, 1985a). These studies suggest that like area 3b, the hand representation of area 3a is callosal. There are only a few studies of callosal connections of area 3a in primates and other mammals. In marmosets, specific connections of the hindlimb and forelimb representation in area 3a have been described (e.g., Huffman, K. J. and Krubitzer, L., 2001a). Interestingly, at least for the marmoset, the hand representation of area 3a does have callosal connections with the hand representation of area 3a in the opposite hemisphere. Furthermore, area 3a is callosally connected to areas M1 and SMA as well. Similar findings were demonstrated for the wing representation of the flying fox (Krubitzer, L. *et al.*, 1998).

Taken together, the data indicate that area 3a is a proprioceptive area that integrates somatic and vestibular inputs with the motor system. This cortical field is involved in the kinetics of movement (determining the load and force), in maintaining posture and limb position, and in regulating the velocity of limb movement.

6.10.6 Area 1

6.10.6.1 Functional Organization

A third somatosensory cortical field just caudal to area 3b, termed area 1, has been described in macaque monkeys and three species of New World monkeys including owl, squirrel, and cebus monkeys (Merzenich, M. M. *et al.*, 1978; Nelson, R. J. *et al.*, 1980; Sur, M. *et al.*, 1982; Felleman, D. J. *et al.*, 1983 respectively). Recent evidence indicates that area 1 is present in humans as well (e.g., Krause, R. *et al.*, 2001; Blankenburg, F. *et al.*, 2003). In some primates, such as macaques, squirrel monkeys, and owl monkeys, area

1 forms a mirror reversal representation of area 3b and contains a precise, topographically organized representation of the contralateral body surface, much like that of area 3b (Figure 2). As in area 3b, there is a magnification of the glabrous hand and oral structures, and receptive fields for neurons are small and limited to single digits. In other primates, only a rudimentary area 1 has been observed (e.g., titi monkeys, Coq, J. O. *et al.*, 2004; Padberg, J. P. *et al.*, 2005) or is absent under similar recording conditions (e.g., tamarins, Carlson, M. *et al.*, 1986; marmosets, Krubitzer, L. A. and Kaas, J. H., 1990; prosimian galagos, Sur, M. *et al.*, 1980). Although we and others have termed cortex caudal to area 3b 'area 1/2' in previous studies in marmoset monkeys (e.g., Krubitzer, L. A. and Kaas, J. H., 1990) and galagos (Wu, C.-H. and Kaas, J., 2003), this terminology was based solely on position with respect to area 3b, rather than any solid electrophysiological data. Indeed, in these species, cortex caudal to area 3b contains neurons that are either unresponsive to any type of sensory stimulation under the anesthetic conditions utilized or are inconsistently driven by stimulation of deep receptors or high-threshold cutaneous receptors of the contralateral body (Figure 11). Thus, area 1 is well developed in only a few primates including Old World macaque monkeys and a few New World monkeys. Given that these species have a well-developed glabrous hand compared to the clawed New World marmoset and tamarin monkeys, we hypothesize that this field coevolved with the highly specialized glabrous hand and is associated with sophisticated hand use.

Single unit studies demonstrate that like neurons in area 3b, neurons in area 1 are modulated by contact with an object (e.g., Debowy, D. J. *et al.*, 2001), are selective for motion across the skin, and are involved in edge orientation (e.g., Gardner, E., 1988). Furthermore, neurons in area 1 respond to noxious stimulation (Kenshalo, D. *et al.*, 2000). Lesions that are restricted to area 1 in primates demonstrate that animals are unable to discriminate between hard versus soft and rough versus smooth objects (Randolph, M. and Semmes, J., 1974; Carlson, M., 1981).

There is very limited evidence for an area 1 in other mammals. While investigators have subdivided cat cortex into architectonic areas 3a, 3b, 1, and 2 (e.g., Hassler, R. and Muhs-Clement, K., 1964), electrophysiological recording experiments in which this cortex was densely surveyed demonstrate that only a single representation of the contralateral body surface (area 3b or S1) resides in anterior parietal cortex

of the cat (e.g., Felleman, D. J. *et al.*, 1983). Although cortex caudolateral to area 3b has been electrophysiologically explored and termed S3 by Garraghty P. E. *et al.* (1987), these investigators propose that S3 may be homologous to S2 or PV in other mammals, rather than area 1. The data in ferrets are equivocal. Some laboratories report multiple cutaneous representations in anterior parietal cortex (termed C1, C2, R1, and R2; e.g., LeClerc, S. S. *et al.*, 1993), while others report that neurons in cortex caudal to area 3b respond to stimulation of deep receptors (Hunt, D. L. *et al.*, 2000). In the former study, only the snout representation was explored. It is not clear if indeed four separate cutaneous representations exist in ferrets since the mapping data were limited; or if they do exist, which of the four corresponds to area 3b and area 1. Finally, a field termed area 1/2 has been described for the flying fox (e.g., Krubitzer, L. A. and Calford, M. B., 1992). This region of cortex interdigitates with area 3b and contains neurons that respond to cutaneous stimulation of the contralateral body surface as well as islands of neurons that respond to stimulation of deep receptors. Like area 1 in primates, area 1/2 in the flying fox contains a complete representation of the contralateral body surface.

In all other mammals investigated, cortex caudal to area 3b contains neurons that respond to stimulation of deep receptors (Figure 11). For example, in rodents (Slutsky *et al.*, 2000), insectivores (Krubitzer, L. *et al.*, 1997), monotremes (Krubitzer, L. *et al.*, 1995b), and marsupials (Beck, P. D. *et al.*, 1996; Huffman, K. *et al.*, 1999), cortex immediately caudal to 3b contains neurons that respond to stimulation of deep receptors of the contralateral body, which are often multimodal (e.g., short-tailed possums and platypus). This field has been called the caudal field (C), the caudal somatosensory area (SC), the parietal medial field (PM), PPC, or area 1/2 in different mammals and has been proposed to correspond to posterior parietal cortex including area 5 or a combination of areas 1 and 2 (Reep, R. L. *et al.*, 1994; Krubitzer, L. *et al.*, 1997; 1998; Huffman, K. *et al.*, 1999; Slutsky, D. A. *et al.*, 2000, for review). Interestingly, studies in which the behavioral effects of lesions in PPC were examined in rats report that these animals have deficits in spatial attention and navigation (Kolb, B. *et al.*, 1994). Similar types of deficits are observed when posterior parietal cortex (rather than area 1) is lesioned in primates (see below).

It seems unlikely that cortex immediately caudal to area 3b in nonprimate mammals is homologous to area 1 in primates for three reasons. The first is that there are only two nonprimate mammals in which neurons in

cortex that adjoins area 3b at its caudal boundary respond to cutaneous stimulation, and this cortex has only been thoroughly explored in one of these species (e.g., flying fox). In all other mammals, cortex immediately caudal to 3b contains neurons that respond to stimulation of deep receptors that are often multimodal. Second, the location of an area 1 described in these animals as just caudal to S1 is not a conclusive indicator of homology because in small-brained mammals such as tenrecs and marsupial northern quolls, cortex immediately caudal to area 3b is also immediately rostral to V1 or V2 (Figure 9). Therefore, assigning homology based on position alone is problematic. Finally, prosimians, marmosets, and tamarins do not appear to have an area 1, which suggests that this field arose later in primate evolution and is therefore a purely primate phenomenon, with the cutaneous field immediately caudal to area 3b arising independently in flying foxes (and possibly ferrets, if area 1 does indeed exist in these animals), and serving different, although overlapping functions in these species (see below).

6.10.6.2 Connections

Highly restricted injections into electrophysiologically identified portions of area 1 have only been made in macaque monkeys (Pons, T. P. and Kaas, J. H., 1986; Burton, H. and Fabri, M., 1995; Burton, H. *et al.*, 1995) and titi monkeys (Coq, J. O. *et al.*, 2004; Padberg, J. P. *et al.*, 2005). Connections of area 1 in macaque monkeys are more broadly distributed than those in area 3b and are observed with areas 3b, 2, S2/PV, 5, AIP/7b, and sparsely with areas 3a, M1, and frontal cortex. Previous reports on connections of the architectonically defined area 1 with local parietal cortical areas support these electrophysiological studies (e.g., Jones, E. G. *et al.*, 1978; Vogt, B. A. and Pandya, D. N., 1978; Pearson, R. C. A. and Powell, T. P. S., 1985; Shanks, M. F. *et al.*, 1985b). In macaque monkeys, thalamocortical connections from electrophysiologically identified locations in area 1 indicate that like area 3b, area 1 receives the majority of its inputs from VP proper (e.g., Nelson, R. J. and Kaas, J. H., 1981; Pons, T. P. and Kaas, J. H., 1985). However, in New World titi monkeys, thalamocortical connections of area 1 are also from VL, Pa, and VPs (e.g., Padberg, J. and Krubitzer, L., 2006).

Examination of callosal connections of areas 3a, 3b, 1, and 2 indicates that the hand representation of area 1 is acallosal (e.g., Pandya, D. N. and Vignolo, L. A., 1968; Killackey, H. P. *et al.*, 1983; Shanks, M. F. *et al.*, 1985a; Conti, F. *et al.*, 1986). Recent work in titi

monkeys in our laboratory in which the injections in area 1 were made under electrophysiological guidance demonstrates sparse callosal connections for the hand representation in area 1 (Padberg, J. and Krubitzer, L., 2006). In this primate, area 1 was most densely interconnected with areas 5 and AIP/7 of the opposite hemisphere.

Connections, lesions, and single unit studies in macaque monkeys indicate that areas 3b and 1 in primates are involved in integrating local inputs from restricted portions of the glabrous hand necessary for fine tactile discriminations such as ascertaining object texture and form (Randolph, M. and Semmes, J., 1974; LaMotte, R. H. and Mountcastle, V. B., 1979; Carlson, M., 1981; Sinclair, R. J. and Burton, H., 1991; Ageranioti-Belanger, S. A. and Chapman, C. E., 1992; Jiang, W. *et al.*, 1997). We propose that area 1 is a recently evolved field restricted to primates, although some species (e.g., flying foxes) have independently evolved a cutaneous representation caudal to area 3b. The location of this field in flying foxes is similar to that of area 1 in primates, but comparative data and examination of behavior in this species indicate that it is unlikely that this area is homologous, or strictly analogous to area 1 in primates since flying foxes do not use their wings for making form and texture discriminations of objects. It is possible that this area arose with the modification of the distal forelimb for flight and is involved in making fine tactile discriminations regarding small changes in air pressure and velocity across the wing during flight.

6.10.7 Area 2

6.10.7.1 Functional Organization

The functional organization of area 2 has only been investigated in one species of nonhuman primate, the macaque monkey (e.g., Pons, T. P. *et al.*, 1985; Toda, T. and Taoka, M., 2001; 2002). In macaque monkeys, area 2 contains a complete representation of deep receptors of the contralateral body, and the gross mediolateral topography is much like that described for areas 3b and 1, although the somatotopic organization is not as precise. The representation of the hand and forelimb in area 2 is highly magnified, more so than in areas 3a, 3b, and 1 (Figure 10).

Studies of response properties of neurons in area 2 (e.g., Hyvärinen, J. and Poranen, A., 1978; Taoka, M. *et al.*, 1998; 2000; Iwamura, Y. *et al.*, 2002) report that neurons here respond well to stimulation of deep

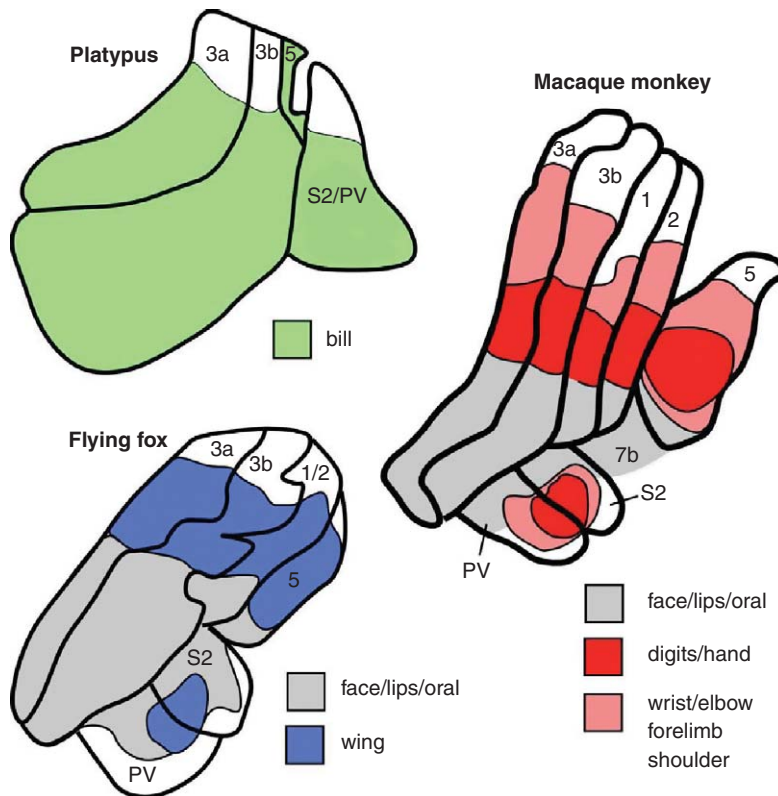


Figure 10 This figure demonstrates that parietal cortex obeys similar rules of construction regardless of which body part has been specialized. For example, the platypus has only three somatosensory areas and, we propose, a posterior parietal area (area 5). The three somatosensory areas are dominated by the representation of the bill, and area 5 exclusively represents the bill. In other groups, more cortical fields have been added between areas 3b and 5, such as areas 1 and 2 in macaque monkeys. These fields contain an enlarged representation of the hand and oral structures, as do 3b and 3a. Like the bill representation of area 5 in the platypus, area 5 in primates almost exclusively represents the hand. Even in species with a derived hand, such as the wing of the bat, similar principles of expansion and magnification are upheld.

receptors, although in some portions of area 2 neurons also responded to cutaneous stimulation (e.g., Pons, T. P. *et al.*, 1985; Ageranioti-Belanger, S. A. and Chapman, C. E., 1992), and may participate with areas 3b and 1 in texture discriminations (e.g., Salimi, I. *et al.*, 1999). Receptive fields for neurons in area 2 are relatively large (sometimes bilateral) when compared to areas 3b and 1 (e.g., Taoka, M. *et al.*, 2000; Iwamura, Y. *et al.*, 2002). In awake behaving monkeys, neurons in area 2 respond to both passive and active flexion of joints (Wolpaw, J., 1980; Gardner, E., 1988) and are facilitated or inhibited during grasping (Debowy, D. J. *et al.*, 2001). Furthermore, neuronal burst duration is correlated with arm movement duration (Burbaud, P. *et al.*, 1991), suggesting that area 2 directly participates in the online maintenance of movement. There is limited evidence for an area 2 in humans, and the organization and the subclass of receptors

represented appears to be similar to that of macaque monkeys (e.g., Moore, C. *et al.*, 2000). Lesions in macaque monkeys that include area 2 affect the animal's ability to discriminate object shape, size, and curvature (Randolph, M. and Semmes, J., 1974; Carlson, M., 1981). Furthermore, the animal is unable to make discriminations that require active exploration with the hands (Schwartz, A., 1983).

Cortex immediately caudal to area 1 has been explored in a limited fashion in New World monkeys. Neurons in this region have been reported to be unresponsive to somatic stimulation, responsive only at the caudal border of area 1, or sometimes responsive to stimulation of deep receptors (Figure 11; e.g., Merzenich, M. M. *et al.*, 1978; Carlson, M. *et al.*, 1986; Huffman, K. J. and Krubitzer, L., 2001a). Thus, unlike macaque monkeys, it appears that New World monkeys do not possess an area 2. As noted above, cortex caudal to area 3b in nonprimate mammals contains

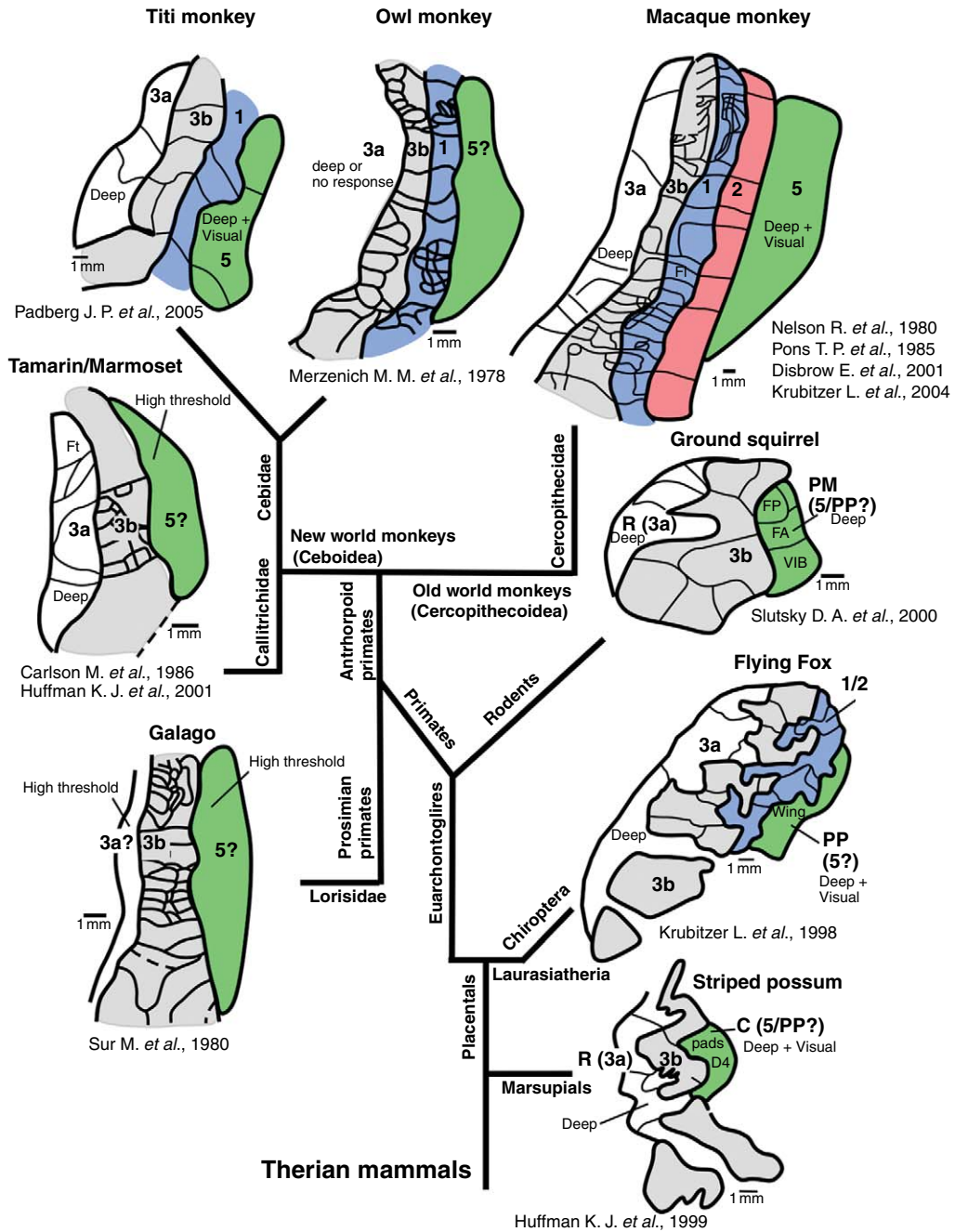


Figure 11 A simplified cladogram depicting the phylogenetic relationship of primates and other mammals and the organization of anterior and posterior parietal cortex in several species. Comparative data from these and other mammals indicate that early therian mammals possessed a primary somatosensory area (3b or S1, light gray), a rostral field (3a or R, white), and a caudal area (5 or PP, green). Some species, such as simian primates, have evolved a low-threshold cutaneous representation just caudal to 3b, termed area 1 (blue). Since area 1 has not been identified in other mammals, or even in prosimian primates, it is likely that area 1 evolved after the simian and prosimian divergence. Area 2 (orange) has only been identified in macaque monkeys. Comparisons across mammals indicate that areas 3a, 3b, and 5 are evolutionarily old fields and that new, unimodal somatosensory fields such as areas 1 and 2 evolved later in some lineages and are interspersed between existing fields (i.e., are not added hierarchically). We propose that areas 1 and 2 evolved with the modified morphology of the hand in anthropoid primates and that older, retained field, such as area 5, were modified both functionally and connectionally for sophisticated hand use. Phylogenetic relationships come from Murphy, W. J., Eizirik, E., O’Brein, S. J., Madsen, O., Scally, M., Douady, C. J., Teeling, E., Ryder, O. A., Stanhope, M. J., de Jong, W. W., and Springer, M. S. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294, 2348–2351 and Eisenberg, J. H. 1981. *The mammalian radiations: an analysis of trends in evolution, adaptation and behavior.* Continuum. Cortical organization of different species depicted here is taken from studies listed below each species.

neurons that respond to stimulation of deep receptors. While these regions could correspond to area 2 in these mammals and New World monkeys, it is also possible that they correspond to area 5. We suggest that this is the case based on several lines of evidence including the organization and magnification of representations in these fields, location relative to visual and somatosensory cortex, and the presence of neurons that also respond to stimulation of other sensory modalities (see below) but are often hard to drive under any given anesthetic condition (unlike neurons in area 2).

6.10.7.2 Connections

Studies of connections of area 2 in which injections were placed under electrophysiological guidance indicate that this field is connected with other somatosensory cortical areas such as 3b, 1, 3a, and S2, as well as with M1 and area 5 (Pons, T. P. and Kaas, J. H., 1985). Earlier studies of the connections of architectonically defined area 2 with local parietal cortical areas support these later studies (e.g., Jones, E. G. *et al.*, 1978). Area 2 receives thalamic input predominantly from VPs (VPLc of Friedman, D. and Jones, E., 1981) and the anterior pulvinar (Pa; Pons, T. P. and Kaas, J. H., 1985). The callosal connections of area 2 have only been described collectively with other anterior parietal fields. Unlike areas 3b and 1, the hand representation of area 2 does have callosal connections (see Manzoni, T., 1997). Taken together, all data indicate that area 2 is a proprioceptive area that is involved in the discrimination of shape and in the online maintenance of hand and forelimb movements necessary for reaching and grasping and is only present in Old World monkeys and humans (and likely great apes).

6.10.8 Posterior Parietal Area 5 in Primates

6.10.8.1 Functional Organization

Area 5 was first described as a very large cortical field that occupied the entire rostral bank of the IPS and much of the caudal postcentral gyrus (e.g., Brodmann, K., 1909). However, modern electrophysiological and anatomical studies indicate that area 5 is much smaller and resides in the middle of the rostral bank of the IPS and folds around the sulcal crown to spread onto the adjacent postcentral gyrus (e.g., Pons, T. P. *et al.*, 1985; Iwamura, Y., 2000, for

review). Most data pertaining to posterior parietal cortex, and to area 5 in particular, have been collected in macaque monkeys and recently in titi monkeys (Figure 11), with limited information available in humans (Culham, J. C. and Kanwisher, N. G., 2001). In all of these primates, area 5 is dominated by the representation of the hand and forelimb (Figure 10); neurons in area 5 have contralateral, ipsilateral, and bilateral receptive fields (particularly on the hand and forelimb), and most neurons respond to the stimulation of deep receptors of the skin and joints (e.g., Sakata, H. *et al.*, 1973; Mountcastle, V. B. *et al.*, 1975; Taoka, M. *et al.*, 2000; Iwamura, Y. *et al.*, 1994; 2002; Padberg, J. P. *et al.*, 2005; see Iwamura, Y., 2000, for review). Single unit studies in awake behaving macaque monkeys indicate that area 5 is involved in coordinating or programming intention of movement (Snyder, L. H. *et al.*, 1997; Debowy, D. J. *et al.*, 2001), in preshaping the hand before grasping an object (e.g., Debowy, D. J. *et al.*, 2001), and in generating body- or shoulder-centered, rather than eye-centered coordinates for reaching (Ferraina, S. and Bianchi, L., 1994; Lacquaniti, F. *et al.*, 1995; see Wise, S. P. *et al.*, 1997, for review). Furthermore, area 5 appears to be involved in the kinematics (e.g., spatiotemporal coordinates) rather than the kinetics (e.g., load and force of muscle) of reaching (see Kalaska, J. F., 1996; Wise, S. P. *et al.*, 1997, for review). The proposition that area 5 is involved in the kinematics of movement is in part supported by studies which demonstrate that a large proportion of neurons are active prior to an arm movement, that these neurons are direction-selective for arm movement, and that activity is dependent on the behavioral context in which the movement will occur (Burbaud, P. *et al.*, 1991).

Recent studies indicate that neurons in area 5 are involved in generating an internal representation of the body that can be modified by experience (Graziano, M. S. A. *et al.*, 2000). For example, neurons in area 5 can change their receptive field size and location when a limb used to perform a task is artificially extended with a tool (Iriki, A. *et al.*, 1996). Furthermore, Iriki A. and colleagues (2001) demonstrated that monkeys can be trained to recognize an image in a video monitor as part of their own body and that neurons in the IPS, in the location of what we consider to be area 5, change their visual receptive fields to incorporate changes in hand location and size, as viewed on the video monitor, into an internal frame of reference. In these studies, the position and the size of the visual receptive field was

modified with respect to modifications of the image in the monitor (e.g., expansions, contractions, and displacement of the hand). These investigators speculate that a symbolic representation of the self in humans has a precursor in monkeys that is latent and can be activated with training. We would argue that these monkeys always possess an internal frame of reference, much like that in humans, and that the experimenters devised a clever and objective way in which to evaluate this internal representation in a nonhuman mammal. We would further argue that such a representation is a critical characteristic of most living things and constitutes a sense of self. Thus, this sense of self is present in all mammals and the region of cortex we propose to be involved in generating this behavioral characteristic (area 5 or PP) is homologous across groups of mammals.

Our recent studies in New World titi monkeys, as well as preliminary findings in macaque monkeys, indicate that many neurons in area 5 can be driven by visual stimulation (Disbrow, E. A. *et al.*, 2001; Padberg, J. P. *et al.*, 2005; Figure 11). While responsiveness to visual stimulation has not been described in previous studies for area 5, the studies often did not test whether or not neurons would be responsive to visual stimulation. This issue of whether neurons in area 5 respond to visual stimulation is important for our discussion of the evolution of posterior parietal cortex in mammals, since as noted above, cortex immediately caudal to 3b in many primitive mammals contains neurons that respond to both somatic and visual stimulation.

There are several studies in which lesions, that include area 5, were made in posterior parietal cortex in monkeys. For example, studies in which unilateral lesions included areas 5, MIP, and 7b demonstrated that animals had deficits in coordinating arm velocity with hand velocity, that the postural relationship between the arm and wrist was disrupted, and that there were disruptions in coordinating the hand in shoulder-centered space (Rushworth, M. F. S. *et al.*, 1997). However, these lesions did not affect the range or velocity of movements or the hand's trajectory. In a related investigation in which areas 5, 7b, and MIP (which may have also included V6) were bilaterally ablated, the monkey had deficits in reaching to the same target under different starting positions (Rushworth, M. F. S. *et al.*, 1998). Finally, a study in green monkeys in which bilateral ablations were made to area V6A (but may have incorporated portions of area 5) demonstrated that monkeys showed a reluctance to move and had deficits in reaching,

grasping, and wrist orientation (Battaglini, P. P. *et al.*, 2002). While previous work on the effects of posterior parietal lesions on behavior are difficult to interpret because the size of the lesion was so large (e.g., Ettlenger, G. and Kalsbeck, J. E., 1962; Hartje, W. and Ettlenger, G., 1973; Brown, J. V. *et al.*, 1983), they do indicate that lesions to posterior parietal cortex result in nonvisually guided reaching deficits but spare roughness discrimination abilities (Brown, J. V. *et al.*, 1983; Murray, E. A. and Mishkin, M., 1984).

There are a number of studies in humans on the deficits that occur with insults to posterior parietal cortex. These studies indicate that the most severe deficit, termed spatial hemineglect, is in coding spatial location of objects within a particular frame of reference (see Robertson, L. C. and Rafal, R., 2000; Behrmann, M., 1999, for review). While the data suggest that there are several egocentric frames of reference, including that of the forelimb or shoulder, there are little data on areas of posterior parietal cortex that contribute to these frames of reference. Furthermore, in these studies, the lesions are extremely large and encompass a number of cortical areas, and it is difficult to interpret which area is associated with which aspect of the deficit.

6.10.8.2 Connections

There are only a few studies of connections of area 5 in the macaque monkey, and those that exist are limited in scope. For example, only one study used electrophysiological guidance to place injections in area 5, and in this study, only one injection in one animal was performed, and the injection spread into area 2 (Pons, T. P. and Kaas, J. H., 1986). Furthermore, only local connections, or connections in neighboring fields, were examined. This previous investigation demonstrated connections with areas 1, 7b, S2, M1, and premotor cortex, which is a subset of the connections we describe for area 5 in titi monkeys (Padberg, J. P. *et al.*, 2005). Early studies of connections of architectonically defined area 5 to local parietal cortical areas support these recent findings in macaques (e.g., Jones, E. G. and Powell, T. P. S., 1969b; Jones, E. G. *et al.*, 1978; Pandya, D. N. and Seltzer, B., 1982). In titi monkeys, area 5 connections are widespread compared to anterior parietal fields, and some of the strongest connections of area 5 are with motor and premotor cortex, the supplementary motor area, S2, PV, extrastriate visual areas, 7b, and cingulate cortex (Figure 6; Padberg, J. P. *et al.*, 2005). Studies of vestibular processing in human and

nonhuman primates indicate that cortex at the juncture of areas 5 and 7b projects to vestibular brainstem nuclei, contains neurons that respond to optokinetic and vestibular stimulation, and is interconnected with other areas of the neocortex that process vestibular information (Akbarian, S. *et al.*, 1988; Guldin, W. O. *et al.*, 1992; Akbarian, S. *et al.*, 1993; 1994; Brandt, T. and Dieterich, M., 1999; Lobel, E. *et al.*, 1999; see Guldin, W. and Grüsser, O.-J., 1998, for review).

Most studies that examine callosal connectivity have studied total patterns of connections of large regions of cortex (e.g., Karol, E. A. and Pandya, D. N., 1971; Killackey, H. P. *et al.*, 1983), or connections of several fields grouped together such as 3a, 3b, 1, 2, and 5 collectively (e.g., Jones, E. G. and Powell, T. P. S., 1969a; Boyd, E. H. *et al.*, 1971; Jones, E. G. *et al.*, 1975; Jones, E. G. *et al.*, 1979; Shanks, M. F. *et al.*, 1985a). A consistent observation is that area 5 receives callosal inputs throughout the field (i.e., including the hand representation). There is one study in which the connections of cortex in the location of area 5 were examined, although the location of the injection site was not verified electrophysiologically (Caminiti, R. and Sbriccoli, A., 1985). In this study in macaque monkeys, label in the hemisphere contralateral to that injected was observed throughout area 5, the supplementary motor area, 7b, and on the dorsal bank of the lateral sulcus (in the S2/PV region). Our recent studies in titi monkeys indicate that the hand representation of area 5 has dense callosal connections with the contralateral area 5 in the expected location of the hand representation (Padberg, J. P. *et al.*, 2005). Area 5 in titi monkeys is also connected with areas 7b/AIP, S2/PV, motor, premotor, and cingulate cortex, a finding similar to that of Caminiti R. and Sbriccoli A. (1985). Thus, area 5 is one of the few somatosensory cortical areas involved in integrating inputs between the hands and in the interhemispheric transfer of information necessary for limb and hand coordination.

This latter notion is supported by studies of the behavioral consequences of lesions to the posterior portions of the corpus callosum through which axons from posterior parietal cortex travel (Seltzer, B. and Pandya, D. N., 1983). For example, after lesions to the posterior portion of the corpus callosum, monkeys have deficits in intermanual transfer of information about shape, roughness, or size of an object (Manzoni, T. *et al.*, 1984; Hunter, M. *et al.*, 1976; Myers, R. E. and Ebner, F. F., 1976). However, if animals were allowed to view the manual task to be transferred, thus supplying visual input regarding the task to both

hemispheres, there was no noticeable deficit in information transfer across hemispheres (Kohn, B. and Meyers, R. E., 1969). Studies of tactile and tactuomotor transfer in humans who have undergone complete section of the corpus callosum or partial sections of the posterior portion of the corpus callosum indicate a number of abnormalities associated with transferring manual information regarding one hand to the opposite hemisphere. For example, complete section of the corpus callosum (Geffen, G. *et al.*, 1985) or a section in the portion of the callosum through which axons connecting the posterior parietal cortex of each hemisphere travel (Geffen, G. *et al.*, 1985; Risse, G. L. *et al.*, 1989), result in an inability to perform cross-localization, intermanual tasks (Geffen, G. *et al.*, 1985; Lassoode, M. *et al.*, 1986; Risse, G. L. *et al.*, 1989). Other studies demonstrate that with sections of the posterior corpus callosum, individuals cannot perform posture matching tasks (kinesthesia) in which they are required to match the position of one forelimb and hand with the opposite forelimb and hand in the absence of visual guidance (Risse, G. L. *et al.*, 1989). Finally, humans with sections of the corpus callosum performed poorly on the transfer of information regarding object shape, and the magnitude of the effect was dependent on the difficulty of the task (Lassoode, M. *et al.*, 1986). The studies described above in both human and nonhuman primates indicate that the connections between the posterior parietal cortex of each hemisphere, including area 5, transfer crucial information necessary for intermanual tactile learning and coordination of the hands.

Taken together, electrophysiological, connection, and lesion studies in nonhuman primates indicate that area 5 is involved in generating an egocentric, shoulder-centered frame of reference necessary for object exploration with the hands. Related abilities such as kinesthetic-visual matching, which may require an understanding of both object permanence and body part objectification, are proposed to be generated by regions in posterior parietal cortex (possibly area 5) in humans as well (see Mitchell, R. W., 2005, for review). This field also is involved in coordinating both hands to accomplish visually guided and perhaps nonvisually guided tasks and for interhemispheric transfer of information between the hands. While area 5 alone may not be responsible for generating an internal representation of the self, the activity of neurons in area 5 is coincident with tasks that require the animal to have such an internal representation, and receptive fields for neurons in

area 5 are modified in a manner consistent with alterations in the internal frame of reference.

6.10.9 Is Area 5 Homologous Across Mammals?

Throughout the text we intimated that cortex caudal to area 3b or S1 in nonprimate mammals is homologous to area 5. Although traditionally cortex immediately caudal to 3b is considered to be area 1 in nonprimate mammals such as cats, the predominant evidence for this traditional view is that this presumptive area is immediately caudal to area 3b. Furthermore, there is a tendency to make the cat somatosensory system both homologous and analogous to the primate somatosensory system, despite the fact that cats have a derived forepaw that is not used in a fashion analogous to that of the hand of primates. Indeed, [Johnson J. I. \(1990\)](#) states in his comparative analysis of mammal somatosensory cortex:

Doubtless due to the great number of investigations rather than the specializations of the species, no less than five distinct somatic sensory areas have been identified and formally numbered in cat neocortex. (p. 399)

It should be noted that in a number of species in which cortex caudal to area 3b has been mapped, this cortex is rostrally adjacent to V2 (which would make it V3 if one were to assume homology based solely on relative location; [Figure 9](#)). As noted above, cortex immediately caudal to 3b, and immediately rostral to V1 or V2, has been explored using electrophysiological recording techniques in a variety of mammals and has been termed C, PP, PM, or SC. Like area 5 in primates, there is an extreme magnification of particular body parts, such that a complete representation of the body surface is often not present ([Figures 10 and 11](#)). For example, in murine rodents, this cortex is dominated by the representation of the vibrissae and in squirrels by the representation of the forepaw. In marsupials such as the striped possum, with its specialized fourth digit, this cortex represents only D4. Also like area 5 and unlike areas 1 and 2, neurons in this cortex often respond to visual stimulation as well as to stimulation of deep receptors. Species such as the flying fox have a cortical field immediately caudal to 3b in which neurons respond to cutaneous and deep stimulation, termed area 1/2 (see above). Just caudal to this region, a cortical field in which

neurons respond to the stimulation of deep receptors as well as to visual stimulation has been described and termed the posterior parietal cortex or PP ([Krubitzer, L. A. and Calford, M. B., 1992](#)). While studies of connections of this caudal region of cortex in a variety of mammals would allow us to more accurately infer homology, we believe that most evidence supports the hypothesis that this field (termed C, SC, PM, and PP) is more like area 5 in primates than like area 1 or 2.

6.10.10 The Evolution of Anterior and Posterior Parietal Cortex

All mammals examined have a primary somatosensory area, S1 or 3b, in which the organization clearly reflects specializations of peripheral morphology, innervation density of peripheral receptors, and use. Furthermore, there appears to be a basic pattern of interconnections with several cortical and subcortical areas, suggesting that there is a network that has been inherited from a common ancestor but modified in different lineages with the evolution of peripheral morphology, as well as with the addition of new cortical fields and thalamic nuclei to the network. ([Figures 6 and 8](#)). While one would like to speculate as to the function of S1, most single unit recording studies in awake behaving animals and/or lesions of S1 have been done in primates, namely, macaque monkeys. Thus, these data must be interpreted with caution when discussing other species since homologous fields need not be analogous. In primates, area 3b appears to be involved in texture and form discrimination, and such discriminations are made with the glabrous hands. Although the representation of the oral structures in area 3b of primates is greatly magnified, suggesting some behavioral specialization related to the mouth, most studies only examine response to stimulation of the hand, or the activity of neurons in area 3b during discriminations made with the hand. If S1 serves as a general-purpose processor of cutaneous inputs necessary for fine discriminations using a morphologically distinct and specialized structure for a particular animal, then one would expect different magnifications of different body parts for different animals. One would also expect that the greatest variability within a species would be for the specialized body part that is used extensively, such as the hand (e.g., [Merzenich, M. M. et al., 1987](#)) and lips ([Cusick, C. G. et al., 1986](#)) of

primates, versus a less actively used body part such as the trunk, which appears to be the case.

Like area 3b, area 3a appears to be part of a common plan of cortical organization in all mammals (Figure 11). Area 3a is a proprioceptive area involved in integrating somatic and vestibular inputs (at least in primates) with the motor system to generate specialized behavior that allows the animal to maximally interface receptor-dense morphological structures (e.g., hand, nose, and bill) with an external object or animal to be explored. Such a sensorimotor interface likely contributes to an enlarged representation of a specialized peripheral structure not only in area 3a, but also in all anterior parietal fields. While the body part in question may be different for different animals, the same rules of modification are implemented in all mammals.

The presence of an area 1 or a rudimentary area 1 in several New World primates and macaque monkeys, and what appears to be the absence of area 1 in marmosets, tamarins, prosimian galagos, as well as other mammals, indicates that this cortical field arose later in primate evolution (Figure 11). We believe that the most parsimonious explanation for the observations made about anterior parietal cortex in a variety of primates is that in early primates, areas 3b and 3a were present. A rudimentary area 1 arose after the simian and prosimian divergence, and this was lost or greatly reduced in some lineages (e.g., Callitricidae), retained in a primitive form in some lineages (e.g., titi monkeys), or became well developed in some lineages (e.g., squirrel monkeys and macaque monkeys), possibly with the evolution of the hand and consequent tactile abilities associated with hand use. It should be noted that the two species of New World monkey (tamarins and marmosets) that do not possess an area 1 have a modified hand with claws used to a large extent for climbing, and to a lesser extent for tactile discrimination.

The functional organization of area 2 has only been investigated in one species of nonhuman primates, the macaque monkey (Pons, T. P. *et al.*, 1985). While cortex immediately caudal to area 1 has been explored in New World monkeys and prosimian galagos, neurons in this region have been reported to be unresponsive to somatic stimulation, responsive only at the caudal border of area 1, or sometimes responsive to the stimulation of deep receptors, features generally associated with area 5 in macaque monkeys. Thus, if one relies on electrophysiological mapping data, it appears that New World monkeys do not possess an area 2 (e.g., Padberg, J. P. *et al.*, 2005;

Figure 11). It is tempting to postulate that area 2 arose or coevolved with the emergence of an opposable thumb and is related to the behaviors associated with using a variety of grips for tactile exploration and identification.

The presence of an area 5 in both New World and Old World monkeys, and a rudimentary form of area 5 (posterior parietal cortex) in most mammals studied, suggests that this posterior parietal field arose early in evolution and has been retained in most or all mammals (Figure 11). While area 5 may be a homologous cortical area in all mammals, the addition of new areas, such as 1 and 2, and new connections likely promotes new functions of this cortical field in primates (Figures 6 and 8). For example, PM in squirrels and PP in flying foxes may be homologous to area 5 in primates, but not strictly analogous. Much like the magnification of behaviorally relevant body parts in area 3b, in area 5 these representations and associated functions are magnified to the extreme in particular lineages. An important point of these observations in primate and nonprimate mammals is that cortical fields are not added in a functional hierarchy in evolution but rather are interspersed between existing fields. Indeed, we believe that the data indicate that areas 3a and 3b and 5 are evolutionarily old fields and that areas 1 and 2 are recent primate phenomenon, likely associated with sophisticated hand use.

With respect to the ideas put forward in the beginning of this chapter regarding the evolution of association cortex, we propose a modified scenario based on data in a variety of other mammals. In primates, unimodal somatosensory cortex has expanded with the addition of areas 1 and 2. Posterior parietal area 5 in primates, although homologous to area 5 in other mammals, has undergone a number of changes including a magnification of the hand and forelimb representation, the preponderance of neurons active under different reaching and grasping paradigms, and the broad distribution of ipsilateral and contralateral connections of the hand and limb representation with proprioceptive, limbic, and motor cortex (Figure 6). All of these features are coincident with the evolution of the hand and opposable thumb in a number of primates, as well as with a larger repertoire of grips and manual and bimanual hand configurations (Napier, J., 1960; 1962; Welles, J. F., 1976). A reasonable hypothesis is that anterior parietal cortex in primates has expanded as a result of sophisticated hand use, which distinguishes primates, and humans in particular, from other

mammals. An evolutionary old cortical area, area 5, has been modified due to the addition of these new anterior parietal fields and the evolution of highly derived manual behavior. Thus, modification of homologous cortical fields (area 5), and the addition of new unimodal cortical fields (e.g., areas 1 and 2) devoted to hand use, is one of the hallmarks of human brain evolution.

The evolution of sophisticated, visually guided, hand use and the addition of anterior parietal fields and the elaboration of posterior parietal cortical areas associated with this behavior may ultimately have led to the emergence of a more refined and species-specific internal representation of self, and an increased number of permutations of how this internal representation can interact with objects in extrapersonal space via the hands. It should be noted that this species-specific internal representation is not a static, enigmatic property that emerged in anthropoid primates alone but is a dynamic sensorimotor loop that all mammals possess in a derived form based on their morphological distinctions and distribution of sensory receptors. Studies of connections as well as electrophysiological recording data indicate that the motor system is a critical component for distinguishing self from nonself, an attribute traditionally delegated solely to association cortex. It follows then that any discussion of an internal representation of self and how an individual distinguishes itself from nonself should incorporate the motor system in this more than human phenomenon.

Acknowledgements

This work was supported by an NINDS grant (R01-NS035103-11) and McDonnell Foundation grant to Leah Krubitzer.

References

- Ageranioti-Belanger, S. A. and Chapman, C. E. 1992. Discharge properties of neurones in the hand area of primary somatosensory cortex in monkeys in relation to the performance of an active tactile discrimination task. II. Area 2 as compared to areas 3b and 1. *Exp. Brain Res.* 91, 207–228.
- Akbarian, S., Berndt, K., Grusser, O.-J., Guldin, W., Pause, M., and Schreier, U. 1988. Responses of single neurons in the parietoinsular vestibular cortex of primates. *Ann. N. Y. Acad. Sci.* 545, 187–202.
- Akbarian, S., Grusser, O. J., and Guldin, W. O. 1992. Thalamic connections of the vestibular cortical fields in the squirrel monkeys (*Saimiri sciureus*). *J. Comp. Neurol.* 326, 423–441.
- Akbarian, S., Grusser, O. J., and Guldin, W. O. 1993. Corticofugal projections to the vestibular nuclei in squirrel monkeys: further evidence of multiple cortical vestibular fields. *J. Comp. Neurol.* 332, 89–104.
- Akbarian, S., Grusser, O.-J., and Guldin, W. 1994. Corticofugal connections between the cerebral cortex and brainstem vestibular nuclei in the macaque monkey. *J. Comp. Neurol.* 339, 421–437.
- Akers, R. M. and Killackey, H. P. 1978. Organization of corticocortical connections in the parietal cortex of the rat. *J. Comp. Neurol.* 181, 513–538.
- Allman, J. M. and Kaas, J. H. 1971. A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res.* 31, 85–105.
- Allman, J. M. and Kaas, J. H. 1974. A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*). *Brain Res.* 81, 199–213.
- Allman, J. M. and Kaas, J. H. 1975. The dorsomedial cortical visual area: a third tier area in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Res.* 100, 473–487.
- Allman, J. H. and Kaas, J. H. 1976. Representation of the visual field on the medial wall of the occipital-parietal cortex in the owl monkey. *Science* 191, 572–576.
- Alloway, K. D. and Burton, H. 1985. Homotypical ipsilateral cortical projections between somatosensory areas I and II in the cat. *Neuroscience* 14, 15–35.
- Andersen, R. A. and Buneo, C. A. 2002. Intentional maps in posterior parietal cortex. *Annu. Rev. Neurosci.* 25, 189–220.
- Andersen, R. A., Snyder, L. H., Bradley, D. C., and Xing, J. 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu. Rev. Neurosci.* 20, 303–330.
- Avendano, C., Isla, A. J., and Rausell, E. 1992. Area 3a in the cat. II. Projections to the motor cortex and their relations to other corticocortical connections. *J. Comp. Neurol.* 321, 373–386.
- Barbaresi, P., Fabri, M., Conti, F., and Manzoni, T. 1987. D-[³H]Aspartate retrograde labelling of callosal and association neurones of somatosensory areas I and II of cats. *J. Comp. Neurol.* 263, 159–178.
- Battaglini, P. P., Muzur, A., Galletti, C., Skrap, M., Brovelli, A., and Fattori, P. 2002. Effects of lesions in area V65 in monkeys. *Exp. Brain Res.* 144, 419–422.
- Beck, P. D., Pospichal, M. W., and Kaas, J. H. 1996. Topography, architecture, and connections of somatosensory cortex in opossums: evidence for five somatosensory areas. *J. Comp. Neurol.* 366, 109–133.
- Behrmann, M. 2000. Spatial Reference Frames and Hemispatial Neglect. In: *The New Cognitive Neurosciences* (ed. M. Gazzaniga), pp. 651–666. MIT Press.
- Blankenburg, F., Ruben, J., Meyer, R., Schwiemann, J., and Villringer, A. 2003. Evidence for a rostral-to-caudal somatotopic organization in human primary somatosensory cortex with mirror-reversal in areas 3b and 1. *Cereb. Cortex* 13, 987–993.
- Boyd, E. H., Pandya, D. N., and Bignall, K. E. 1971. Homotopic and nonhomotopic interhemispheric cortical projections in the squirrel monkey. *Exp. Neurol.* 32, 256–274.
- Brandt, T. and Dieterich, M. 1999. The vestibular cortex, its locations, functions, and disorders. *Ann. N. Y. Acad. Sci.* 871, 293–312.
- Brodman, K. 1909. Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien Dargestellt auf Grund des Zellenbaues. Barth.
- Brown, J. V., Ettlinger, G., and Garcha, H. S. 1983. Visually guided reaching and tactile discrimination in the monkey: the effects of removals of parietal cortex soon after birth. *Brain Res.* 267, 67–79.

- Burbaud, P., Doegle, C., Gross, C., and Bioulac, B. 1991. A quantitative study of neuronal discharge in areas 5, 2 and 4 of the monkey during fast arm movements. *J. Neurophysiol.* 66, 429–443.
- Burton, H. and Fabri, M. 1995. Ipsilateral intracortical connections of physiologically defined cutaneous representations in areas 3b and 1 of macaque monkeys: projections in the vicinity of the central sulcus. *J. Comp. Neurol.* 355, 508–538.
- Burton, H., Fabri, M., and Alloway, K. 1995. Cortical areas within the lateral sulcus connected to cutaneous representations in areas 3b and 1: a revised interpretation of the second somatosensory area in macaque monkeys. *J. Comp. Neurol.* 355, 539–562.
- Caiford, M. B., Graydon, M. L., Huerta, M. F., Kaas, J. H., and Pettigrew, J. D. 1985. A variant of the mammalian somatotopic map in the bat. *Nature* 313, 477–479.
- Caminiti, R. and Sbriccoli, A. 1985. The callosal system of the superior parietal lobule in the monkey. *J. Comp. Neurol.* 2237, 85–99.
- Caminiti, R., Innocenti, G. M., and Manzoni, T. 1979. The anatomical substrate of callosal messages from SI and SII in the cat. *Brain Res.* 35, 295–314.
- Carlson, M. 1981. Characteristics of sensory deficits following lesions of Brodmann's areas 1 and 2 in the postcentral gyrus of *Macaca mulatta*. *Brain Res.* 204, 424–430.
- Carlson, N. R. 1998. *Physiology of Behavior*, 6th edn. Allyn and Bacon.
- Carlson, M., Huerta, M. F., Cusick, C. G., and Kaas, J. H. 1986. Studies on the evolution of multiple somatosensory representations in primates: the organization of anterior parietal cortex in the New World Callitrichid, *Saguinus*. *J. Comp. Neurol.* 246, 409–426.
- Catania, K. C. and Kaas, J. H. 1997. Somatosensory fovea in the star-nosed mole: behavioral use of the star in relation to innervation patterns and cortical representation. *J. Comp. Neurol.* 387, 215–233.
- Catania, K. C., Northcutt, R. G., Kaas, J. H., and Beck, P. D. 1993. Nose stars and brain stripes. *Nature* 364, 493.
- Chapin, J. K. and Lin, C.-S. 1984. Mapping the body representation in the SI cortex of anesthetized and awake rats. *J. Comp. Neurol.* 229, 199–213.
- Chapin, J. K., Sadeq, M., and Guise, J. L. U. 1987. Corticocortical connections within the primary somatosensory cortex of the rat. *J. Comp. Neurol.* 263, 326–346.
- Chapman, C. E. and Ageranoti-Bélanger, S. 1991. Discharge properties of neurons in the hand area of primary somatosensory cortex in monkeys in relation to the performance of an active tactile discrimination task. I. Areas 3b and 1. *Exp. Brain Res.* 87, 319–339.
- Chen, L., Friedman, R., Ramsden, B., LaMotte, R., and Roe, A. 2001. Fine-scale organization of S1 (area 3b) in the squirrel monkey revealed with intrinsic optical imaging. *J. Neurophysiol.* 86, 3011–3029.
- Conti, F., Fabri, M., and Manzoni, T. 1986. Bilateral receptive fields and callosal connectivity of the body midline representation in the first somatosensory area of primates. *Somatosens. Res.* 3, 273–289.
- Coq, J. O., Qi, H., Collins, C. E., and Kaas, J. H. 2004. Anatomical and functional organization of somatosensory areas of the lateral fissure of the new world titi monkey (*Callicebus moloch*). *J. Comp. Neurol.* 476, 363–387.
- Culham, J. C. and Kanwisher, N. G. 2001. Neuroimaging of cognitive functions in human parietal cortex. *Curr. Opin. Neurobiol.* 11, 157–163.
- Cusick, C. G. and Gould, H. J. I. 1990. Connections between area 3b of the somatosensory cortex and subdivisions of the ventroposterior nuclear complex and the anterior pulvinar nucleus in squirrel monkeys. *J. Comp. Neurol.* 292, 83–102.
- Cusick, C. G., MacAvoy, M. G., and Kaas, J. H. 1985. Interhemispheric connections of cortical sensory areas in tree shrews. *J. Comp. Neurol.* 235, 111–128.
- Cusick, C. G., Wall, J., and Kaas, J. 1986. Representations of the face, teeth and oral cavity in areas 3b and 1 of somatosensory cortex in squirrel monkeys. *Brain Res.* 370, 359–364.
- Darian-Smith, C., Darian-Smith, I., Burman, K., and Ratcliffe, N. 1993. Ipsilateral cortical projections to areas 3a, 3b, and 4 in the macaque monkey. *J. Comp. Neurol.* 335, 200–213.
- Darian-Smith, C., Darian-Smith, I., and Cheema, S. S. 1990. Thalamic projections to sensorimotor cortex in the macaque monkey: use of multiple retrograde fluorescent tracers. *J. Comp. Neurol.* 299, 17–46.
- Debowy, D. J., Ghosh, S., Ro, J. Y., and Gardner, E. P. 2001. Comparison on neuronal firing rates in somatosensory and posterior parietal cortex during prehension. *Exp. Brain Res.* 137, 269–291.
- Diamond, M., Harris, J., and Petersen, R. 2002. Sensory Learning and the Brain's Body Map. In: *The Somatosensory System, Deciphering the Brain's Own Body Image* (ed. R. Nelson), pp. 183–195. CRC Press.
- Dicarlo, J., Johnson, J. K., and Hsiao, S. 1998. Structure of receptive fields in area 3b of primary somatosensory cortex in the alert monkey. *J. Neurosci.* 18, 2626–2645.
- Disbrow, E., Litinas, E., Recanzone, G., Padberg, J. P., and Krubitzer, L. A. 2003. Cortical connections of the parietal central area and the second somatosensory area in macaque monkeys. *J. Comp. Neurol.* 462, 382–399.
- Disbrow, E., Litinas, E., Recanzone, G., Slutsky, D., and Krubitzer, L. A. 2002. Thalamocortical connections of the parietal ventral area (PV) and the second somatosensory area (S2) in macaque monkeys. *Thalamus Relat. Syst.* 1, 289–302.
- Disbrow, E. A., Murray, S. O., Roberts, T. P., Litinas, E. D., and Krubitzer, L. A. 2001. Sensory integration in human posterior parietal area 5. *Soc. Neurosci. Abst.* 27, 511–526.
- Ebner, F. F. and Myers, R. E. 1965. Distribution of corpus callosum and anterior commissure in cat and raccoon. *J. Comp. Neurol.* 124, 353–356.
- Eisenberg, J. H. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation and behavior. *Continuum.*
- Elston, G. N. and Manger, P. R. 1999. The organization and connections of somatosensory cortex in the brush-tailed possum (*Trichosurus vulpecula*): evidence for multiple, topographically organized and interconnected representations in an Australian marsupial. *Somatosens. Mot. Res.* 16, 312–337.
- Ettlinger, G. and Kalsbeck, J. E. 1962. Changes in tactile discrimination in visual reaching after successive and simultaneous bilateral posterior parietal ablations in the monkey. *J. Neurol. Neurosurg. Psychiatry* 25, 256–268.
- Fabri, M. and Burton, H. 1991. Topography of connections between primary somatosensory cortex and posterior complex in rat: a multiple fluorescent tracer study. *Brain Res.* 538, 351–357.
- Feldman, S. H. and Johnson, J. I. 1988. Kinesthetic cortical area anterior to primary somatic sensory cortex in the raccoon (*Procyon lotor*). *J. Comp. Neurol.* 277, 80–95.
- Felleman, D. J. and Van Essen, D. C. 1991. Distributed hierarchical processing in primate cerebral cortex. *Cereb. Cortex* 1, 1–47.
- Felleman, D. J., Wall, J. T., Cusick, C. G., and Kaas, J. H. 1983. The representation of the body surface in S-I of cats. *J. Neurosci.* 3, 1648–1669.

- Ferraina, S. and Bianchi, L. 1994. Posterior parietal cortex: functional properties of neurons in area 5 during an instructed-delay reaching task within different parts of space. *Exp. Brain Res.* 99, 175–178.
- Fox, P. T., Burton, H., and Raichle, M. E. 1987. Mapping human somatosensory cortex with positron emission tomography. *J. Neurosurg.* 67, 34–43.
- Friedman, D. and Jones, E. 1981. Thalamic input to areas 3a and 2 in monkeys. *J. Neurophysiol.* 45, 59–85.
- Frost, S. B., Milliken, G. W., Plautz, E. J., Masterton, R. B., and Nudo, R. J. 2000. Somatosensory and motor representations in cerebral cortex of a primitive mammal (*Monodelphis domestica*): a window into the early evolution of sensorimotor cortex. *J. Comp. Neurol.* 421, 29–51.
- Gardner, E. 1988. Somatosensory cortical mechanisms of feature detection in tactile and kinesthetic discrimination. *Can. J. Physiol. Pharmacol.* 66, 439–454.
- Garraghty, P. E., Pons, T. P., Huerta, M. F., and Kaas, J. H. 1987. Somatotopic organization of the third somatosensory area (SIII) in cats. *Somatosens. Res.* 4, 333–357.
- Geffen, G., Nilsson, J., and Quinn, K. 1985. The effects of lesions of the corpus callosum on finger localization. *Neuropsychologia* 23, 497–514.
- Gould, H. J. I. and Kaas, J. H. 1981. The distribution of commissural terminations in somatosensory areas I and II of the grey squirrel. *J. Comp. Neurol.* 196, 489–504.
- Gould, H. J., 3rd, Whitworth, R. H., Jr., and LeDoux, M. S. 1989. Thalamic and extrathalamic connections of the dysgranular unresponsive zone in the grey squirrel (*Sciurus carolinensis*). *J. Comp. Neurol.* 287, 38–63.
- Graziano, M. S. A., Cooke, D. F., and Taylor, C. S. R. 2000. Coding the location of the arm by sight. *Science* 290, 1782–1786.
- Guldin, W. and Grusser, O.-J. 1998. Is there a vestibular cortex? *Trends Neurosci.* 21, 254–259.
- Guldin, W. O., Akbarian, S., and Grusser, O. J. 1992. Cortico-cortical connections and cytoarchitectonics of the primate vestibular cortex: a study in squirrel monkeys (*Saimiri sciureus*). *J. Comp. Neurol.* 326, 375–401.
- Hackett, T. A., Stepniowska, I., and Kaas, J. H. 1998. Subdivisions of auditory cortex and ipsilateral cortical connections of the parabelt auditory cortex in macaque monkeys. *J. Comp. Neurol.* 394, 475–495.
- Hartje, W. and Ettlinger, G. 1973. Reaching in light and dark after unilateral posterior parietal ablations in the monkey. *Cortex* 9, 346–354.
- Hassler, R. and Muhs-Clement, K. 1964. Architectonic construction of the sensorimotor and parietal cortex in the cat. *J. Hirnforsch.* 20, 377–420.
- Heath, C. J., Hore, J., and Philips, C. G. 1975. Inputs from low threshold muscle and cutaneous afferents of hand and forearm to areas 3a and 3b of baboon's cerebral cortex. *J. Physiol. (Lond.)* 257, 199–227.
- Herron, P. and Johnson, J. I. 1987. Organization of intracortical and commissural connections in somatosensory cortical areas I and II in the raccoon. *J. Comp. Neurol.* 257, 359–371.
- Hlushchuk, Y., Forss, N., and Hari, R. 2003. Distal-to-proximal representation of volar index finger in human area 3b. *NeuroImage* 21, 696–700.
- Hore, J., Preston, J. B., and Cheney, P. D. 1976. Responses of cortical neurons (areas 3a and 4) to ramp stretch of hindlimb muscles in the baboon. *J. Neurophysiol.* 39, 484–500.
- Huffman, K. J. and Krubitzer, L. 2001a. Area 3a: topographic organization and cortical connections in marmoset monkeys. *Cereb. Cortex* 11, 849–867.
- Huffman, K. J. and Krubitzer, L. A. 2001b. Thalamo-cortical connections of areas 3a and M1 in marmoset monkeys. *J. Comp. Neurol.* 435, 291–310.
- Huffman, K., Nelson, J., Clarey, J., and Krubitzer, L. 1999. The organization of somatosensory cortex in three species of marsupials, *Dasyurus hallucatus*, *Dactylopsila trivirgata*, and *Monodelphis domestica*: neural correlates of morphological specializations. *J. Comp. Neurol.* 403, 5–32.
- Hunt, D. L., Slutsky, D. A., and Krubitzer, L. A. 2000. The organization of somatosensory cortex in the ferret. *Soc. Neurosci. Abst.* 26, 243.13.
- Hunter, M., Maccabe, J. J., and Ettlinger, G. 1976. Intermanual transfer of tactile training in the monkey: the effects of bilateral parieto-prestriate ablations. *Neuropsychologia* 14, 385–389.
- Hyvärinen, J. and Poranen, A. 1978. Receptive field integration and submodality convergence in the hand area of the post-central gyrus of the alert monkey. *J. Physiol.* 283, 539–556.
- Imig, T. J., Ruggero, M. A., Kitzes, L. M., Javel, E., and Brugge, J. F. 1977. Organization of auditory cortex in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.* 171, 111–128.
- Iriki, A., Tanaka, M., and Iwamura, Y. 1996. Coding of modified body schema during tool use by macaque postcentral neurons. *NeuroReport* 7, 2325–2330.
- Iriki, A., Tanaka, M., Obayashi, S., and Iwamura, Y. 2001. Self-images in the video monitor coded by monkey intraparietal neurons. *J. Neurosci. Res.* 40, 163–173.
- Iwamura, Y. 2000. Bilateral receptive field neurons and callosal connections in the somatosensory cortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 355, 267–273.
- Iwamura, Y., Iriki, A., and Tanaka, M. 1994. Bilateral hand representation in the postcentral somatosensory cortex. *Nature* 369, 554–556.
- Iwamura, Y., Tanaka, M., Iriki, A., Taoka, M., and Toda, T. 2002. Processing of tactile and kinesthetic signals from bilateral sides of the body in the postcentral gyrus of awake monkeys. *Behav. Brain Res.* 135, 185–190.
- Jain, N., Qi, H.-X., Catania, K., and Kaas, J. 2001. Anatomic correlates of the face and oral cavity representations in the somatosensory cortical area 3b of monkeys. *J. Comp. Neurol.* 429, 455–468.
- Jiang, W., Tremblay, F., and Chapman, C. E. 1997. Neuronal encoding of texture changes in the primary and the secondary somatosensory cortical areas of monkeys during passive texture discrimination. *J. Neurophysiol.* 77, 1656–1662.
- Johnson, J. I. 1990. Comparative Development of Somatic Sensory Cortex. In: *Cerebral Cortex* (eds. E. G. Jones and A. Peters), pp. 335–449. Plenum.
- Johnson, K. O. and Lamb, G. D. 1981. Neural mechanisms of spatial tactile discrimination: neural patterns evoked by Braille-like dot patterns in the monkey. *J. Physiol.* 310, 117–144.
- Johnson, K. and Yoshioka, T. 2002. Neural Mechanisms of Tactile Form and Texture Perception. In: *The Somatosensory System, Deciphering the Brain's Own Body Image* (ed. R. Nelson), pp. 73–101. CRC Press.
- Johnson, J. I., Ostapoff, E.-M., and Warach, S. 1982. The anterior border zones of primary somatic sensory (SI) neocortex and their relation to cerebral convolutions, shown by micromapping of peripheral projections to the region of the fourth forepaw digit representation in raccoons. *Neuroscience* 7, 915–936.
- Jones, E. G. and Powell, T. P. S. 1969a. Connexions of the somatic sensory cortex of the rhesus monkey II contralateral cortical connexions. *Brain* 92, 717–730.
- Jones, E. G. and Powell, T. P. S. 1969b. Connexions of the somatic sensory cortex of the rhesus monkey: I. Ipsilateral cortical connections. *Brain* 92, 477–502.
- Jones, E. G., Burton, H., and Porter, R. 1975. Commissural and cortico-cortical "columns" in the somatic sensory cortex of primates. *Science* 190, 572–574.

- Jones, E. G., Coulter, J. D., and Hendry, S. H. C. 1978. Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. *J. Comp. Neurol.* 181, 291–348.
- Jones, E. G., Wise, S. P., and Coulter, J. C. 1979. Differential thalamic relationships of sensory-motor and parietal cortical fields in monkeys. *J. Comp. Neurol.* 183, 833–882.
- Juliano, S., Friedman, D., and Eslin, D. 1990. Corticocortical connections predict patches of stimulus-evoked metabolic activity in monkey somatosensory cortex. *J. Comp. Neurol.* 298, 23–39.
- Kaas, J. H. 1982. The segregation of function in the nervous system: why do the sensory systems have so many subdivisions? *Contrib. Sens. Physiol.* 7, 201–240.
- Kaas, J. H. 1983. What, if anything, is SI? Organization of first somatosensory area of cortex. *Physiol. Rev.* 63, 206–230.
- Kaas, J. H. 1997. Topographic maps are fundamental to sensory processing. *Brain Res. Bull.* 44(2), 107–112.
- Kaas, J. H. and Collins, C. E. 2004. The Resurrection of Multimodal Cortex in Primates: Connection Patterns that Integrate Modalities. In: *Handbook of Multisensory Processing* (eds. G. Calvert, C. Spence, and B. E. Stein), MIT Press. pp. 285–293.
- Kaas, J. H. and Pons, T. P. 1988. The somatosensory system of primates. *Comp. Primate Biol.* 4, 421–468.
- Kalaska, J. F. 1996. Parietal cortex area 5 and visuomotor behavior. *Can. J. Physiol. Pharmacol.* 74, 483–498.
- Karol, E. A. and Pandya, D. N. 1971. The distribution of the corpus callosum in the rhesus monkey. *Brain* 94, 471–786.
- Kenshalo, D., Iwata, K., Sholas, M., and Thomas, D. 2000. Response properties and organization of nociceptive neurons in area 1 of monkey primary somatosensory cortex. *J. Neurophysiol.* 84, 719–729.
- Killackey, H. P., Gould, H. J. I., Cusick, C. G., Pons, T. P., and Kaas, J. H. 1983. The relation of corpus callosum connections to architectonic fields and body surface maps in sensory motor cortex of new and old world monkeys. *J. Comp. Neurol.* 219, 384–419.
- Knight, R. T. and Graboweky, M. 2000. Prefrontal Cortex, Time and Consciousness. In: *The New Cognitive Neurosciences* (ed. M. Gazzaniga), pp. 1319–1330. MIT Press.
- Kohn, B. and Myers, R. E. 1969. Visual information and intermanual transfer of latch box problem solving in monkeys with commissures sectioned. *Exp. Neurol.* 23, 303–309.
- Kolb, B., Buhrmann, K., McDonald, R., and Sutherland, R. J. 1994. Dissociation of the medial prefrontal, posterior parietal, and posterior temporal cortex for spatial navigation and recognition memory in the rat. *Cereb. Cortex* 4, 664–680.
- Koralek, K. A., Olavarria, J., and Killackey, H. P. 1990. Areal and laminar organization of corticocortical projections in rat somatosensory cortex. *J. Comp. Neurol.* 299, 133–150.
- Krause, R., Kurth, R., Ruben, J., Schwiemann, J., Villringer, K., Deuchert, M., Moosmann, M., Brandt, S., Wolf, K., Curio, G., and Villringer, A. 2001. Representational overlap of adjacent fingers in multiple areas of human primary somatosensory cortex depends on electrical stimulus intensity: an fMRI study. *Brain Res.* 899, 36–46.
- Krubitzer, L. 1995. The organization of neocortex in mammals: are species differences really so different? *Trends Neurosci.* 18, 408–417.
- Krubitzer, L. 1998. What can monotremes tell us about brain evolution? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 353, 1127–1146.
- Krubitzer, L. A. and Calford, M. B. 1992. Five topographically organized fields in the somatosensory cortex of the flying fox: microelectrode maps, myeloarchitecture, and cortical modules. *J. Comp. Neurol.* 317, 1–30.
- Krubitzer, L. and Kaas, J. 1987. Thalamic connections of three representations of the body surface in somatosensory cortex of grey squirrels. *J. Comp. Neurol.* 265, 549–580.
- Krubitzer, L. A. and Kaas, J. H. 1990. The organization and connections of somatosensory cortex in marmosets. *J. Neurosci.* 10, 952–974.
- Krubitzer, L. A. and Kaas, J. H. 1992. The somatosensory thalamus of monkeys: cortical connections and a redefinition of nuclei in marmosets. *J. Comp. Neurol.* 319(1), 123–140.
- Krubitzer, L. and Kahn, D. 2003. Nature vs. nurture: an old idea with a new twist. *Prog. Neurobiol.* 70, 33–52.
- Krubitzer, L., Clarey, J., Tweedale, R., and Calford, M. 1998. Interhemispheric connections of somatosensory cortex in the flying fox. *J. Comp. Neurol.* 402(4), 538–539.
- Krubitzer, L., Clarey, J., Tweedale, R., Elston, G., and Calford, M. 1995a. A redefinition of somatosensory areas in the lateral sulcus of macaque monkeys. *J. Neurosci.* 15, 3821–3839.
- Krubitzer, L., Huffman, K. J., Disbrow, E., and Recanzone, G. 2004. Organization of area 3a in macaque monkeys: contributions to the cortical phenotype. *J. Comp. Neurol.* 471, 97–111.
- Krubitzer, L., Künzle, H., and Kaas, J. 1997. Organization of sensory cortex in a madagascan insectivore, the tenrec (*Echinops telfairi*). *J. Comp. Neurol.* 379, 399–414.
- Krubitzer, L., Manger, P., Pettigrew, J., and Calford, M. 1995b. The organization of somatosensory cortex in monotremes: in search of the prototypical plan. *J. Comp. Neurol.* 351, 261–306.
- Krubitzer, L. A., Sesma, M. A., and Kaas, J. H. 1986. Microelectrode maps, myeloarchitecture, and cortical connections of three somatotopically organized representations of the body surface in the parietal cortex of squirrels. *J. Comp. Neurol.* 250, 403–430.
- Lacquaniti, F., Guigon, E., Bianchi, L., Ferraina, S., and Caminiti, R. 1995. Representing spatial information for limb movement: the role of area 5 in monkey. *Cereb. Cortex* 5, 391–409.
- LaMotte, R. H. and Mountcastle, V. B. 1979. Disorders in somesthesia following lesions in parietal lobe. *J. Neurophysiol.* 42, 400–419.
- Landgren, S. and Silfvenius, H. 1969. Projection to cerebral cortex of group I muscle afferents from the cat's hind limb. *J. Physiol.* 200, 353–372.
- Lang, W., Büttner-Ennever, J. A., and Büttner, U. 1979. Vestibular projections to the monkey thalamus: an autoradiographic study. *Brain Res.* 177, 3–17.
- Lassonde, M., Sauerwein, H., Geoffroy, G., and DèCarie, M. 1986. Effects of early and late transection of the corpus callosum in children. *Brain* 109, 953–967.
- Lebedev, M. and Nelson, R. 1996. High-frequency vibratory sensitive neurons in monkey primary somatosensory cortex: entrained and non-entrained responses to vibration during the performance of vibratory-cued hand movements. *Exp. Brain Res.* 111, 313–325.
- Leclerc, S. S., Rice, F. L., Dykes, R. W., Pourmoghadam, K., and Gomez, C. M. 1993. Electrophysiological examination of the representation of the face in the suprasylvian gyrus of the ferret: a correlative study with cytoarchitecture. *Somatosens. Motor Res.* 10, 133–159.
- Ledoux, M. S., Whitworth, R. H., and Gould, H. J. I. 1987. Interhemispheric connections of the somatosensory cortex in the rabbit. *J. Comp. Neurol.* 258, 145–157.
- Lee, K. and Woolsey, T. 1975. A proportional relationship between peripheral innervation density and cortical neuron number in the somatosensory system of the mouse. *Brain Res.* 99, 349–353.
- Lin, L.-D., Murray, G., and Sessle, B. 1994a. Functional properties of single neurons in the primate face primary

- somatosensory cortex. I. relations with trained orofacial motor behaviors. *J. Neurophysiol.* 71, 2377–2390.
- Lin, L.-D., Murray, G., and Sessle, B. 1994b. Functional properties of single neurons in the primate face primary somatosensory cortex. II relations with different directions of trained tongue protrusion. *J. Neurophysiol.* 71, 2391–2400.
- Lobel, E., Kleine, J., Leroy-Willig, A., Van de Moortele, P.-F., Le Bihan, D., Grusser, O.-J., and Berthoz, A. 1999. Cortical areas activated by bilateral galvanic vestibular stimulation. *Ann. N. Y. Acad. Sci.* 871, 313–323.
- Manger, P. R. and Pettigrew, J. D. 1995. Electoreception and feeding behaviour of the platypus. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 347, 359–381.
- Manger, P., Sum, M., Szymanski, M., Ridyway, S., and Krubitzer, L. 1998. Modular subdivisions of dolphin anterior ensular cortex: does evolutionary history repeat itself? *J. Cogn. Neurosci.* 10(2), 153–166.
- Manzoni, T. 1997. The callosal connections of the hierarchically organized somatosensory areas of primates. *J. Neurosurg. Sci.* 41, 1–13.
- Manzoni, T., Barbaresi, P., and Conti, F. 1984. Callosal mechanism for the enter hemispheric transfer of hand somatosensory information in the monkey. *Behav. Brain Res.* 11, 155–170.
- Manzoni, T., Conti, F., and Fabri, M. 1986. Callosal projections from area SII to SI in monkeys: anatomical organization and comparison with association projections. *J. Comp. Neurol.* 252, 245–263.
- Mayner, L. and Kaas, J. 1986. Thalamic projections from electrophysiologically defined sites of body surface representations in areas 3b and 1 of somatosensory cortex of cebus monkeys. *Somatosens. Res.* 4, 13–29.
- McKenna, T. M., Whitsel, B. L., Dreyer, D. A., and Metz, C. B. 1981. Organization of cat anterior parietal cortex: relations among cytoarchitecture, single neuron functional properties, and interhemispheric connectivity. *J. Neurophysiol.* 45, 667–697.
- Merzenich, M. M., Kaas, J. H., Sur, M., and Lin, C.-S. 1978. Double representation of the body surface within cytoarchitectonic areas 3b and 1 in “SI” in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.* 181, 41–74.
- Merzenich, M. M., Nelson, R. J., Kaas, J. H., Stryker, M. P., Jenkins, W. M., Zook, J. M., Cynader, M. S., and Schoppmann, A. 1987. Variability in hand surface representations in area 3b and 1 in adult owl and squirrel monkeys. *J. Comp. Neurol.* 258, 281–296.
- Mishkin, M., Ungerleider, L. G., and Macko, K. A. 1983. Object vision and spatial vision: two cortical pathways. *Trends Neurosci.* 6, 414–417.
- Mitchell, R. W. 2005. Mirrors and Matchings: Limitation from the Perspective of Mirror-Self Recognition, and Why the Parietal Region Is Involved in Both. In: *Spatial Perception, Spatial Cognition* (eds. F. Dolins and R. W. Mitchell). Cambridge University Press (in press).
- Moore, C., Stern, C., Corkin, S., Fischl, B., Gray, A., Rosen, B., and Dale, A. 2000. Segregation of somatosensory activation in the human rolandic cortex using fMRI. *J. Neurophysiol.* 84, 558–569.
- Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., and Acuña, C. 1975. Posterior parietal association cortex of the monkey: command functions for operations within intrapersonal space. *J. Neurophysiol.* 38, 871–908.
- Murphy, W. J., Eizirik, E., O’Brein, S. J., Madsen, O., Scally, M., Douady, C. J., Teeling, E., Ryder, O. A., Stanhope, M. J., de Jong, W. W., and Springer, M. S. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294, 2348–2351.
- Murray, E. A. and Mishkin, M. 1984. Relative contributions of SII and area 5 to tactile discrimination in monkeys. *Behav. Brain Res.* 11, 67–83.
- Myers, R. E. and Ebner, F. F. 1976. Localization of function in corpus callosum: tactual information transmission in *Macaca mulatta*. *Brain Res.* 103, 455–462.
- Napier, J. 1962. The evolution of the hand. *Sci. Am.* 207, 56–61.
- Napier, J. R. 1960. Studies of the hands of living primates. *Proc. Zool. Soc. Lond.* 134, 647–657.
- Nelson, R. 1987. Activity of monkey primary somatosensory cortical neurons changes prior to active movement. *Brain Res.* 406, 402–407.
- Nelson, R. J. and Kaas, J. H. 1981. Connections of the ventroposterior nucleus of the thalamus with the body surface representations in cortical areas 3b and 1 of the cynomolgus macaque, *Macaca fascicularis*. *J. Comp. Neurol.* 199, 29–64.
- Nelson, R., Smith, B., and Douglas, V. 1991. Relationship between sensory responsiveness and premovement activity of quickly adapting neurons in areas 3b and 1 of monkey primary somatosensory cortex. *Exp. Brain Res.* 84, 75–90.
- Nelson, R. J., Sur, M., Felleman, D. J., and Kaas, J. H. 1980. Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis*. *J. Comp. Neurol.* 192, 611–643.
- Oscarsson, O. and Rosen, I. 1963. Projection to cerebral cortex of large muscle-spindle afferents in forelimb nerves of the cat. *J. Physiol.* 169, 924–945.
- Oscarsson, O. and Rosen, I. 1966. Short-latency projections to the cat’s cerebral cortex from skin and muscle afferents in the contralateral forelimb. *J. Physiol.* 182, 164–184.
- Oscarsson, O., Rosen, I., and Sulg, I. 1966. Organization of neurones in the cat cerebral cortex that are influenced from group I muscle afferents. *J. Physiol.* 183, 189–210.
- Padberg, J. and Krubitzer, L. 2006. Thalamocortical connections of anterior and posterior parietal cortical areas in New World titi monkeys. *J. Comp. Neurol.* 497, 416–435.
- Padberg, J. P., Disbrow, E., and Krubitzer, L. 2005. The organization and connections of anterior and posterior parietal cortex in titi monkeys: do New World monkeys have an area 2? *Cereb. Cortex* 15, 1938–1063.
- Pandya, D. N. and Seltzer, B. 1982. Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. *J. Comp. Neurol.* 204, 196–210.
- Pandya, D. N. and Vignolo, L. A. 1968. Interhemispheric neocortical projections of somatosensory areas I and II in the rhesus monkey. *Brain Res.* 7, 300–303.
- Paperna, T. and Malach, R. 1991. Patterns of sensory intermodality relationships in the cerebral cortex of the rat. *J. Comp. Neurol.* 308, 432–456.
- Pearson, R. C. A. and Powell, T. P. S. 1985. The projection of the primary somatic sensory cortex upon area 5 in the monkey. *Brain Res. Rev.* 9, 89–107.
- Penfield, W. and Rasmussen, T. 1968. Secondary Sensory and Motor Representation. In: *Cerebral Cortex of Man. A Clinical Study of Localization of Function* (Chapter VI), pp. 109–134. Hafner Publishing Company.
- Phillips, C. B., Powell, T. P. S., and Wiesandanger, M. 1971. Projections from low threshold muscle afferents of hand and forearm to area 3a of baboon’s cortex. *J. Physiol.* 217, 419–446.
- Pons, T. P. and Kaas, J. H. 1985. Connections of area 2 of somatosensory cortex with the anterior pulvinar and subdivisions of the ventroposterior complex in macaque monkeys. *J. Comp. Neurol.* 240, 16–36.
- Pons, T. P. and Kaas, J. H. 1986. Corticocortical connections of area 2 of somatosensory cortex in macaque monkeys: a

- correlative anatomical and electrophysiological study. *J. Comp. Neurol.* 248, 313–335.
- Pons, T. P., Garraghty, P. E., Cusick, C. G., and Kaas, J. H. 1985. The somatotopic organization of area 2 in macaque monkeys. *J. Comp. Neurol.* 241, 445–466.
- Pubols, B. and Pubols, L. 1971. Somatotopic organization of spider monkey somatic sensory cerebral cortex. *J. Comp. Neurol.* 141, 63–76.
- Pubols, B. H., Pubols, L. M., DePette, D. J., and Sheely, J. C. 1976. Opossum somatic sensory cortex: a microelectrode mapping study. *J. Comp. Neurol.* 165, 229–246.
- Randolph, M. and Semmes, J. 1974. Behavioral consequences of selective subtotal Ablations in the postcentral gyrus of *Macaca mulatta*. *Brain Res.* 70, 55–70.
- Rausell, E. and Jones, E. G. 1995. Extent of intracortical arborization of thalamocortical axons as a determinant of representational plasticity in monkey somatic sensory cortex. *J. Neurosci.* 15, 4270–4288.
- Recanzone, G. H., Merzenich, M. M., Jenkins, W. M., Grajski, K. A., and Dinse, H. R. 1992b. Topographic reorganization of the hand representation in cortical area 3b of owl monkeys trained in a frequency discrimination task. *J. Neurophysiol.* 67, 1031–1056.
- Reep, R. L., Chandler, H. C., King, V., and Corwin, J. V. 1994. Rat posterior parietal cortex: topography of corticocortical and thalamic connections. *Exp. Brain Res.* 100, 67–84.
- Risse, G. L., Gates, J., Lund, G., Maxwell, R., and Rubens, A. 1989. Interhemispheric transfer in patients with incomplete section of the corpus callosum. *Arch. Neurol.* 46, 437–443.
- Robertson, L. C. and Rafal, R. 2000. Disorders of visual attention. In: *The New Cognitive Neurosciences* (ed. M. Gazzaniga), pp. 633–649. MIT Press.
- Robinson, C. J. and Burton, H. 1980a. Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory, and granular insula of *M. fascicularis*. *J. Comp. Neurol.* 192, 69–92.
- Robinson, C. J. and Burton, H. 1980b. Somatotopographic organization in the second somatosensory area of *M. fascicularis*. *J. Comp. Neurol.* 192, 43–67.
- Romo, R., Hernandez, A., Zainos, A., Brody, C., and Lemus, L. 2000. Sensing without touching: psychophysical performance based on cortical microstimulation. *Neuron* 26, 273.
- Romo, R., Hernandez, A., Zainos, A., and Salinas, E. 1998. Somatosensory discrimination based on cortical microstimulation. *Nature* 392, 387.
- Roy, A., Paulignan, Y., Farné, A., Joffrais, C., and Boussaoud, D. 2000. Hand kinematics during reaching and grasping in macaque monkey. *Behav. Brain Res.* 117, 75–82.
- Rushworth, M. F. S., Johansen-Berg, H., and Young, S. A. 1998. Parietal cortex and spatial-postural transformation during arm movements. *J. Neurophysiol.* 79, 478–482.
- Rushworth, M. F. S., Nixon, P. D., and Passingham, R. E. 1997. Parietal cortex and movement. *Exp. Brain Res.* 117, 311–323.
- Sakata, H., Takaoka, Y., Kawarasaki, A., and Shibutani, H. 1973. Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Res.* 64, 85–102.
- Salimi, I., Brochier, T., and Smith, A. 1999. Neuronal activity in somatosensory cortex of monkeys using a precision grip. II. Responses to object texture and weights. *J. Neurophysiol.* 81, 835–844.
- Saper, C. B., Iversen, S., and Frackowiak, R. 2000. Integration of Sensory and Motor Function: The Association Areas of the Cerebral Cortex and the Cognitive Capabilities of the Brain. In: *Principles of Neural Science* (eds. E. R. Kandel, J. H. Schwartz, and R. M. Jessel), pp. 349–380. McGraw-Hill Companies Inc.
- Scheich, H., Langner, G., Tidemann, C., Coles, R. B., and Guppy, A. 1986. Electroreception and electrolocation in platypus. *Nature* 319, 401–402.
- Schwartz, A. 1983. Functional relationship between somatosensory cortex and specialized afferent pathways in the monkey. *Exp. Neurol.* 79, 316–328.
- Schwarz, D. W., Deeck, L., and Fredrickson, J. M. 1973. Cortical projections of group I muscle afferents to areas 2, 3a, and the vestibular field in the rhesus monkey. *Exp. Brain Res.* 17, 516–526.
- Seltzer, B. and Pandya, D. N. 1983. The Distribution of posterior parietal fibers in the corpus callosum of the rhesus monkey. *Exp. Brain Res.* 49, 147–150.
- Shanks, M. F., Pearson, R. C. A., and Powell, T. P. S. 1985a. The callosal connexions of the primary somatic sensory cortex in the monkey. *Brain Res. Rev.* 9, 43–65.
- Shanks, M. F., Pearson, R. C. A., and Powell, T. P. S. 1985b. The ipsilateral cortico-cortical connexions between the cytoarchitectonic subdivisions of the primary somatic sensory cortex in the monkey. *Brain Res. Rev.* 9, 67–88.
- Sinclair, R. J. and Burton, H. 1991. Neuronal activity in the primary somatosensory cortex in monkeys (*Macaca mulatta*) during active touch of textured surface gratings: responses to groove width, applied force, and velocity of motion. *J. Neurophysiol.* 66, 153–169.
- Slutsky, D. A., Manger, P. R., and Krubitzer, L. 2000. Multiple somatosensory areas in the anterior parietal cortex of the California ground squirrel (*Spermophilus beecheyii*). *J. Comp. Neurol.* 416, 521–539.
- Snyder, L. H., Batista, A. P., and Andersen, R. A. 1997. Coding of intention in the posterior parietal cortex. *Nature* 386, 167–170.
- Stepniewska, I., Preuss, T. M., and Kaas, J. H. 1993. Architectonics, somatotopic organization, and ipsilateral cortical connections of the primary motor area (M1) of owl monkeys. *J. Comp. Neurol.* 330, 238–271.
- Sur, M., Nelson, R. J., and Kaas, J. H. 1980. Representation of the body surface in somatic koniocortex in the prosimian *Galago*. *J. Comp. Neurol.* 189, 381–402.
- Sur, M., Nelson, R. J., and Kaas, J. H. 1982. Representations of the body surface in cortical areas 3b and 1 of squirrel monkeys: comparisons with other primates. *J. Comp. Neurol.* 211, 177–192.
- Sur, M., Wall, J. T., and Kaas, J. H. 1984. Modular distribution of neurons with slowly adapting and rapidly adapting responses in area 3b of somatosensory cortex in monkeys. *J. Neurophysiol.* 51, 724–744.
- Tanji, J. 1975. Activity of neurons in cortical area 3a during maintenance of steady postures by the monkey. *Brain Res.* 88, 549–553.
- Tanji, J. and Wise, S. 1981. Submodality distribution in sensorimotor cortex of the unanesthetized monkey. *J. Neurophysiol.* 45, 467–481.
- Taoka, M., Toda, T., Iriki, A., Tanaka, M., and Iwamura, Y. 2000. Bilateral receptive field neurons in the hindlimb region of the postcentral somatosensory cortex in awake macaque monkeys. *Exp. Brain Res.* 134, 139–146.
- Taoka, M., Toda, T., and Iwamura, Y. 1998. Representation of the midline trunk, bilateral arms, and shoulders in the monkey postcentral somatosensory cortex. *Exp. Brain Res.* 123, 315–322.
- Toda, T. and Taoka, M. 2001. The complexity of receptive fields of periodontal mechanoreceptive neurons in the postcentral area 2 of conscious macaque monkey brains. *Arch. Oral Biol.* 46, 1079–1084.
- Toda, T. and Taoka, M. 2002. Integration of the upper and lower lips in the postcentral area 2 of conscious macaque monkeys (*Macaca fuscata*). *Arch. Oral Biol.* 47, 449–456.

- Tremblay, F., Ageranioti-Belanger, S. A., and Chapman, C. E. 1996. Cortical mechanisms underlying tactile discrimination in the monkey. I. Role of primary somatosensory cortex in passive texture discrimination. *J. Neurophysiol.* 76, 3382–3403.
- Van Dyck, S. 1983. *The Complete Book of Australian Mammals*. Angus and Robertson.
- Vogt, B. A. and Pandya, D. N. 1978. Cortico-cortical connections of somatic sensory cortex (areas 3, 1 and 2) in the Rhesus monkey. *J. Comp. Neurol.* 177, 179–192.
- Vogt, C. and Vogt, O. 1919. *Allgemeinere ergebnisse unserer hirnforschung*. *J. Psychol.* (Leipzig) 25, 279–462.
- Welker, W. I. and Seidenstein, S. 1959. Somatic sensory representation in the cerebral cortex of the raccoon (*Procyon lotor*). *J. Comp. Neurol.* 111, 469–501.
- Weller, R. E., Sur, M., and Kaas, J. H. 1987. Callosal and ipsilateral cortical connections of the body surface representations in SI and SII of tree shrews. *Somatosens. Res.* 5, 107–133.
- Welles, J. F. 1976. A comparative study of manual prehension in anthropoids. *Saugetierkundliche Mitteilungen* 24, 26–38.
- White, E. L. and DeAmicis, R. A. 1977. Afferent and efferent projections of the region in mouse Sml cortex which contains the posteromedial barrel subfield. *J. Comp. Neurol.* 175, 455–481.
- Wise, S. P. and Jones, E. G. 1976. The organization and postnatal development of the commissural projection of the rat somatic sensory cortex. *J. Comp. Neurol.* 168, 313–344.
- Wise, S. and Tanji, J. 1981. Neuronal responses in sensorimotor cortex to ramp displacements and maintained positions imposed on hindlimb of the unanesthetized monkey. *J. Neurophysiol.* 45, 482–500.
- Wise, S. P., Boussaoud, D., Johnson, P. B., and Caminiti, R. 1997. Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. *Annu. Rev. Neurosci.* 20, 25–42.
- Wolpaw, J. 1980. Correlations between task-related activity and responses to perturbation in primate sensorimotor cortex. *J. Neurophysiol.* 44, 1122–1138.
- Woolsey, C. N. 1958. *Organization of Somatic Sensory and Motor Areas of the Cerebral Cortex*. University of Wisconsin Press.
- Woolsey, C. N. and Fairman, D. 1946. Contralateral, ipsilateral, and bilateral representation of cutaneous receptors in somatic areas I and II of the cerebral cortex of pig, sheep, and other mammals. *Surgery* 19, 684–702.
- Woolsey, T. A. and Van der Loos, H. 1970. The structural organization of layer IV in the somatosensory region (SI) of the mouse cerebral cortex: the description of a cortical field composed of discrete cytoarchitectonic units. *Brain Res.* 17, 205–242.
- Woolsey, C., Erickson, T., and Gilson, W. 1979. Localization in somatic sensory and motor areas of human cerebral cortex as determined by direct recording of evoked potentials and electrical stimulation. *J. Neurosurg.* 51, 476–506.
- Wu, C.-H. and Kaas, J. 2003. Somatosensory cortex of prosimian galagos: physiological recording, cytoarchitecture, and corticocortical connections of anterior parietal cortex and cortex of the lateral sulcus. *J. Comp. Neurol.* 457, 263–292.
- Xerri, C., Coq, J. O., Merzenich, M. M., and Jenkins, W. M. 1996. Experience-induced plasticity of cutaneous maps in the primary somatosensory cortex of adult monkeys and rats. *J. Physiol. (Paris)* 90, 277–287.
- Zarzecki, P., Shinoda, Y., and Asanuma, H. 1978. Projection from area 3a to the motor cortex by neurons activated from group I muscle afferents. *Exp. Brain Res.* 33, 269–282.

Further Reading

- LaMotte, R. H. and Acuña, C. 1978. Defects in accuracy of reaching after removal of posterior parietal cortex in monkeys. *Brain Res.* 139, 309–326.
- Recanzone, G. H., Merzenich, M. M., and Jenkins, W. M. 1992a. Frequency discrimination training engaging a restricted skin surface results in an emergence of a cutaneous response zone in cortical area 3a. *J. Neurophysiol.* 67, 1057–1070.
- Rosa, M., Gattass, R., and Soares, J. 1991. A quantitative analysis of cytochrome oxidase-rich patches in the primary visual cortex of cebus monkeys: topographic distribution and effects of late monocular enucleation. *Exp. Brain Res.* 84, 195–209.
- Savaki, H. E., Kennedy, C., Sokoloff, L., and Mishkin, M. 1993. Visually guided reaching with the forelimb contralateral to a “blind” hemisphere: a metabolic mapping study in monkeys. *J. Neurosci.* 13, 2772–2789.
- Xerri, C., Merzenich, M., Jenkins, W. M., and Santucci, S. 1999. Representational plasticity in cortical area 3b paralleling tactual-motor skill acquisition in adult monkeys. *Cereb. Cortex* 9, 1047–3211.
- This work was originally submitted in 2005 and since then several relevant studies have been published which could not be incorporated into the text of the current chapter. These include:
- Berryman, L. J., Yau, J. M., and Hsiao, S. S. 2006. Representation of object size in the somatosensory system. *J. Neurophysiol.* 96, 27–39.
- Fitzgerald, P. J., Lane, J. W., Thakur, P. H., and Hsiao, S. S. 2006. Receptive field (RF) properties of the macaque second somatosensory cortex: RF size, shape, and somatotopic organization. *J. Neurosci.* 26, 6485–95.
- Fitzgerald, P. J., Lane, J. W., Thakur, P. H., and Hsiao, S. S. 2006. Receptive field properties of the macaque second somatosensory cortex: representation of orientation on different finger pads. *J. Neurosci.* 26, 6473–84.
- Padberg, J., Franca, J. G., Cooke, D. F., Soares, J. G., Rosa, M. G., Fiorani, M. Jr, Gattass, R., and Krubitzer, L. 2007. Parallel evolution of cortical areas involved in skilled hand. *J. Neurosci.* 27, 10106–15.
- Wang, X., Zhang, M., Cohen, I. S., and Goldberg, M. E. 2007. The proprioceptive representation of eye position in monkey somatosensory cortex.