

## 4.24 Hand Use and the Evolution of Posterior Parietal Cortex in Primates

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## Glossary

<i>3b</i>	Brodmann's area 3b, synonymous with S1.
<i>AIP</i>	Anterior intraparietal area.
<i>area 5</i>	Brodmann's area 5.
<i>area 7</i>	Brodmann's area 7.
<i>haptic shape perception</i>	Tactile sampling of a shape.
<i>LIP</i>	Lateral intraparietal area.
<i>MIP</i>	Medial intraparietal area.
<i>multimodal</i>	Neurons that respond to more than one type of sensory stimulus.
<i>PRR</i>	Parietal reach region.
<i>PV</i>	Parietal ventral area.
<i>retinotopy</i>	An ordered representation of the visual field in areas of the visual cortex.
<i>S1</i>	Primary somatosensory area.
<i>S2</i>	Secondary somatosensory area.
<i>saccade</i>	Rapid eye movements resulting in fixation from one point in the visual field to another.
<i>somatotopy</i>	An ordered representation of the skin surface in areas of the somatosensory cortex.
<i>VIP</i>	Ventral intraparietal area.

### 4.24.1 Introduction

What distinguishes humans from other primates? The most common answer to this question is language. Humans have a unique ability to communicate, and the organization and connectivity of the human brain reflect this specialty (see Primate Brain Evolution in Phylogenetic Context). We would argue that of equal importance is humans' ability to manipulate their environment with their hands. We are unparalleled in our facility to shape and influence our surroundings. As with the special skills associated with language production and comprehension, the

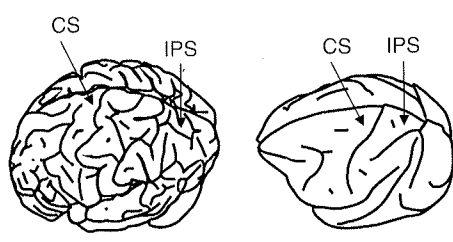
human brain has specific features of organization and connectivity underlying their remarkable manual abilities (see Neurological Specializations for Manual Gesture and Tool Use in Humans). One region involved with these abilities is the posterior parietal cortex.

The posterior parietal cortex consists of discrete areas that are proposed to perform different functions (Mountcastle *et al.*, 1975; Andersen *et al.*, 1997; Kalaska *et al.*, 1997; Snyder *et al.*, 1997; Graziano *et al.*, 2000; Gregoriou and Savaki, 2001). In macaque monkeys, the posterior parietal cortex has recently been subdivided into a number of cortical fields, including areas 5, 7 anterior intraparietal area (AIP), lateral intraparietal area (LIP), medial intraparietal area (MIP), ventral intraparietal area (VIP), and parietal reach region (PRR; Anderson *et al.*, 1997; Andersen and Buneo, 2002). Most studies of posterior parietal cortex in human and nonhuman primates examine its visual functions; however, this region also appears to be involved in visuospatial processing, including monitoring limb location during visually guided reaching (Mountcastle *et al.*, 1975; Lacquaniti *et al.*, 1995; Johnson *et al.*, 1996; Gregoriou and Savaki, 2001; Buneo *et al.*, 2002), and grasping (Taira *et al.*, 1990; Sakata *et al.*, 1995, 1998), converting sensory locations into motor coordinates for intentional movement (Andersen *et al.*, 1985; Battaglia-Mayer *et al.*, 2000), and perceiving the movements of the body in extrapersonal space (Andersen *et al.*, 1997; Snyder *et al.*, 1997). Further, the posterior parietal cortex is involved in saccadic eye movements (Colby *et al.*, 1996; Snyder *et al.*, 2000; see The Role of Vision in the Origin and Evolution of Primates), and the processing of visual and tactile shape and orientation information (Murata *et al.*, 2000; Taira *et al.*, 2000; Tsutsui *et al.*, 2001, 2002; see The Evolution of Sensory and

Motor Systems in Primates). There is also evidence that human posterior parietal cortex plays a role in shape perception (Faillenot *et al.*, 1997; Binkofski *et al.*, 1999a, 1999b; Kourtzi and Kanwisher, 2000; Amedi *et al.*, 2001; Bodegard *et al.*, 2001; Grefkes *et al.*, 2002). Thus, it appears that much of the region has evolved in primates as a consequence of, and for the generation of, specialized hand use.

While great strides have been made in understanding the organization and function of the posterior parietal cortex, there are difficulties associated with the study of this region. First, in the macaque monkey the designation of the location of various cortical fields is not consistent across laboratories (Cavada, 2001). Traditionally cortical fields are defined using several criteria. A cortical field is characterized by: (1) architectonic distinctiveness; (2) unique neural response properties; (3) unique connectivity; (4) a complete representation of the receptor surface; and (5) specific deficits after removal (Kaas, 1983). While criteria for defining a cortical field work well for primary fields such as 3b (S1) or S2 and parietal ventral (PV), they are not as useful for defining fields in the posterior parietal cortex. Traditional staining techniques are not adequate for distinguishing architectural boundaries of fields in posterior parietal cortex, and neural response properties are complex and often multimodal. Without clear anatomically defined borders, patterns of connectivity are difficult to determine, and fields appear to lack obvious visuo- or somatotopic organization, or even a complete representation of the receptor array (e.g., Colby and Duhamel, 1991).

These problems are compounded in humans by the striking anatomical differences between macaque monkey and human posterior parietal cortex. In the macaque, the intraparietal sulcus (IPS) is an easily identified relatively shallow sulcus just caudal to the central sulcus that runs in a mediolateral direction (Figure 1). In the human, the sulcal anatomy is quite different, with the bulk of the IPS running in a rostrocaudal direction, often with additional sulci in this region. While attempts have been made to draw



**Figure 1** Comparison of human (left) and macaque brains. Note the complexity of the region surrounding the IPS. CS, central sulcus. Scale bars: 1 cm.

parallels between work in macaques and humans (see Culham and Kanwisher, 2001, for review), comparisons are tentative at best. Further, human hand use diverges dramatically from that of macaque monkey hand use. Thus, the second difficulty in determining the organization and function of this region in humans comes from the lack of an animal model.

#### 4.24.2 Posterior Parietal Area 5

Because of the difficulties associated with identifying particular posterior parietal cortical fields in humans, we began our studies of this region by examining area 5. Several consistent features of area 5 have emerged from the monkey literature regarding its organization and receptive field characteristics. Area 5 is dominated by the representation of the hand and forelimb; neurons in area 5 have contralateral, ipsilateral, and bilateral receptive fields (particularly on the hand and forelimb), and most neurons respond to stimulation of deep receptors of the skin and joints (Mountcastle *et al.*, 1975; Pons *et al.*, 1985; Iwamura *et al.*, 1994, 2002; Taoka *et al.*, 1998, 2000; Iwamura, 2000). Single-unit studies in macaque monkeys indicate that area 5 is involved in intention of movement (Snyder *et al.*, 1997; Debony *et al.*, 2001), and the generation of body or shoulder rather than eye-centered coordinates for reaching (Ferraina and Bianchi, 1994; Lacquaniti *et al.*, 1995; see Wise *et al.*, 1997, for review). While this field has traditionally been considered a somatosensory area, our work in human (Disbrow *et al.*, 2001) and nonhuman (Padberg *et al.*, 2004, 2005) primates indicates that neurons in area 5 respond to visual stimulation as well.

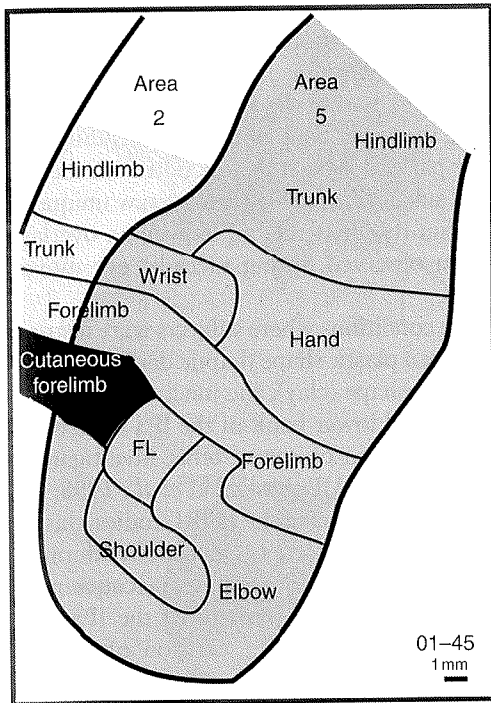
In our study of titi monkeys we used multiunit electrophysiological recording techniques in an anesthetized preparation to make several interesting observations about area 5 and the surrounding cortex (Padberg *et al.*, 2005). First, the field was dominated by the representation of the hand and forelimb. Second, neurons in area 5 respond to both deep somatic and visual stimulation. Finally, unlike anterior somatosensory fields in which the hand representation is mostly acallosal (Killackey *et al.*, 1983), area 5 receives interhemispheric input in the expected location of the hand representation. Dense label was also observed in area 7, S2/PV, and moderate label was observed in motor, premotor, extrastriate, and cingulate cortex.

Similarly, in preliminary studies of macaque monkeys, we examined responses to somatosensory and visual stimulation in area 5. As in the titi monkey we found that this region was dominated by a somatosensory representation of the hand and forelimb, and

that neurons at several sites within this representation also responded to visual stimulation (Figure 2). Injections placed into the forelimb representation of area 5 revealed connections with anterior parietal

and lateral somatosensory areas, additional regions of posterior parietal cortex, as well as M1, supplementary motor area (SMA), and anterior cingulate (Figure 3). These mapping and connectational data indicate that area 5 is involved in integrating visual and somatosensory inputs specifically relating to the hand, and may be generating a motor output for visually guided reaching behaviors.

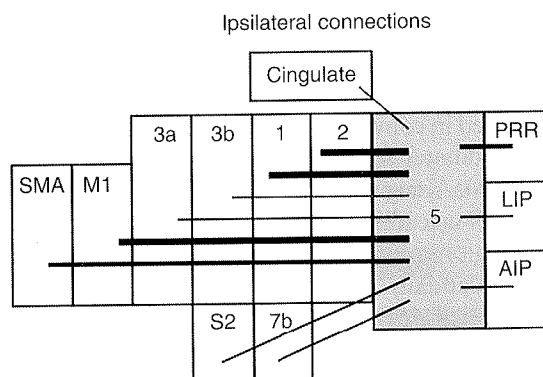
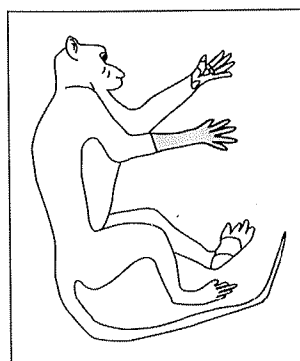
Based on these findings, we designed a simple functional magnetic resonance imaging (fMRI) experiment to identify area 5 in humans (Disbrow *et al.*, 2001). Stimuli were a moving tactile stimulus applied to the hand, foot, or face, and a visual flow field. Tactile and visual stimuli were presented both individually and simultaneously. When stimuli were presented individually, only primary fields were active; however, simultaneous presentation of visual and tactile stimulation resulted in activation of cortex caudal to anterior parietal somatosensory fields (Figure 4). This field, which we called area 5, was roughly somatotopically organized, and dominated by the hand representation as in the macaque monkey. We used this field as a landmark, and extended our examination of posterior parietal cortex to include more complex stimuli.



**Figure 2** Summary of an electrophysiological map. Area 2 was observed to contain neurons that responded to stimulation of deep receptors, and a zone of cortex containing neurons that responded to cutaneous somatosensory stimulation was observed within both areas 2 and 5. Neurons across a large extent of area 5 were observed to respond to stimulation of deep receptors of the hand and forelimb (FL). Additionally, many of the sites surveyed in area 5 were observed to contain neurons that responded to both deep somatosensory and visual stimulation. Adapted from 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. Abstr.* 511.26.

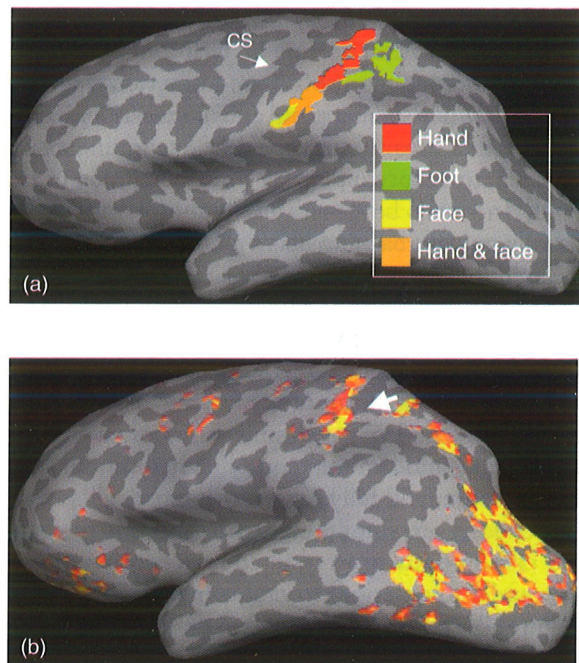
### 4.24.3 Effector Specific Network

In posterior parietal cortex cortical field organization based on somatotopy or retinotopy is inadequate. However, there is emerging evidence from studies of the macaque monkey that cortex is organized based on effector – the part of the body performing a movement (for review, see Andersen and Buneo, 2002). In order to identify areas of posterior parietal cortex selective for movements of the eyes, arms, and hands, the same group of subjects also performed a



**Figure 3** A summary of connections in case 01-45 resulting from injections in the distal forelimb representation in area 5. Labeled cells resulting from injections in area 5 were widespread and were found to be very dense in areas M1, 1, and 2. The PRR and SMA were observed to have dense label. Areas 3a, 3b, anterior cingulate cortex, S2, 7b, and extrastriate cortex, including LIP and AIP, were observed to have moderate label.





**Figure 4** Human area 5. a, Area 5 was only active during a combination of visual and tactile stimulation. Activation from tactile stimulation alone was rostral to area 5 on the central sulcus (CS: arrow) and is not shown in this figure. Area 5 was roughly somatotopically organized, dominated by the representation of the hand (red and orange) as in other primates. b, Activation from a single subject performing a visually guided reaching and grasping task, contrasted with a motor control (eyes closed). Note the late activation in the hand representation of area 5 (arrow), as defined in (a). Visual cortex is active because subjects closed their eyes in the control but not the reaching condition. Adding a visual control reduced the volume of area 5 activation (not shown). Images are displayed on inflated brains (rostral is to the right). Dark gray indicates the location of sulci.

saccade task, a visually guided reaching task, and a haptic shape discrimination task (Disbrow *et al.*, 2001; Hinkley *et al.*, 2004). We hoped to identify a network involved in visually locating an object in space, reaching for and grasping that object, and manually exploring it.

First, we identified a group of cortical fields active during saccadic eye movements. The LIP region is believed to be involved in converting retinotopic visual information to coordinates for oculomotor intention (Mazzoni *et al.*, 1996). Along with LIP, areas of cortex more active during saccades in our subjects also included bilateral regions along the upper bank of the mid-IPS, extending caudally to the parieto-occipital sulcus (Figure 5). We believe that this pattern of activation corresponds to saccade-specific regions identified in monkeys (Duhamel *et al.*, 1992), and its location on a normalized Talairach atlas matches those identified in other human fMRI studies examining the preparation of saccadic eye movements (Connolly *et al.*, 2002; Sereno *et al.*, 2001) in retinotopic space.

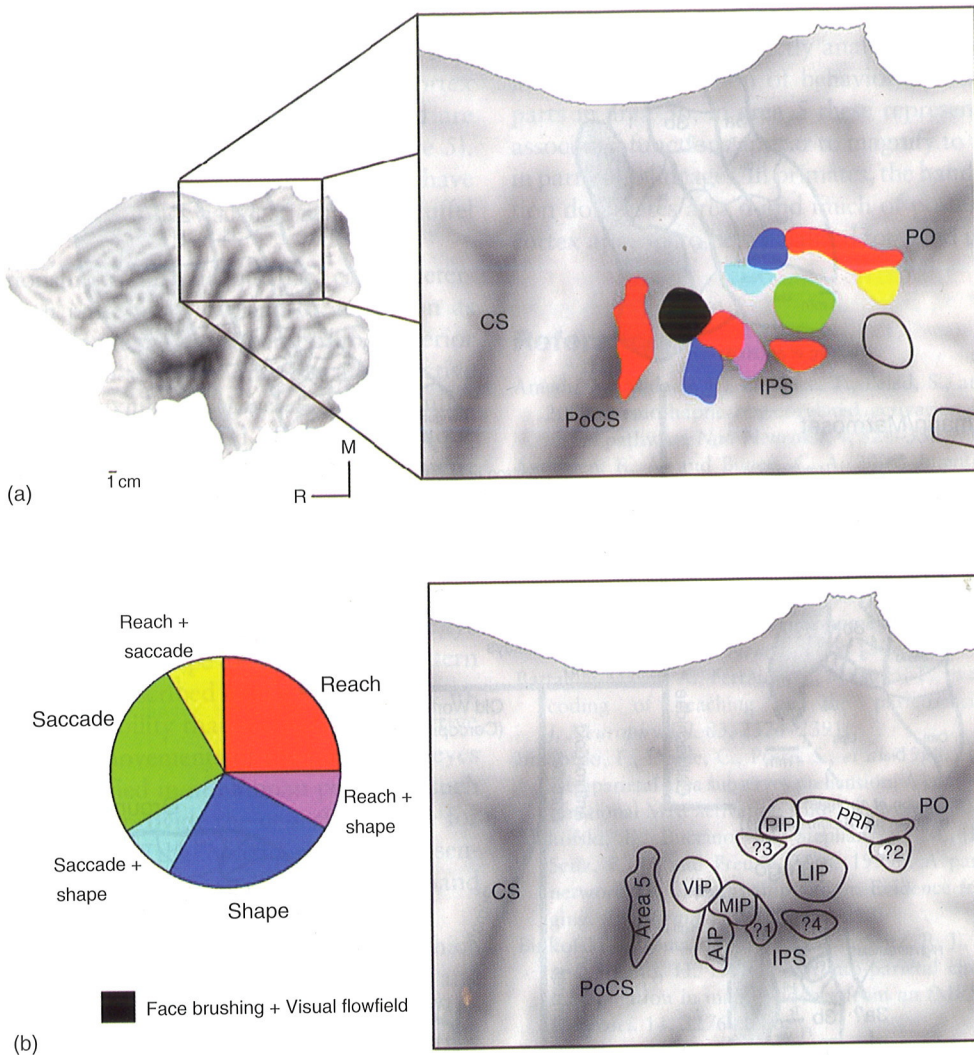
Next, we identified fields active during the guidance of a hand toward a visual target. In the macaque monkey the PRR consists of a number of different areas (Snyder *et al.*, 1997), including regions along the MIP portions of area 5 and cortex along the medial wall (7 m, Caminiti *et al.*, 1999). From our human fMRI study, areas more active when subjects are performing a visually-guided reach versus a motor control include cortex within the postcentral sulcus, and cortex along the upper bank of the IPS extending on to the superior parietal lobe at its junction with the parieto-occipital sulcus (Figure 5). Thus we saw unique activation within the PRR region, as well as overlap with activation observed during saccadic eye movements (Table 1).

During conditions where subjects were instructed to manipulate a plastic shape (haptic discrimination task) versus a nonshape (clay), the junction of the postcentral sulcus and lower bank of the IPS were bilaterally active, in a region of cortex other investigators have labeled as human AIP (Binkofski *et al.*, 1998; Culham *et al.*, 2003). In these human fMRI studies, this portion of posterior parietal cortex is more active during object exploration and identification. In macaque monkeys, neurons in the anterior regions of the IPS (AIP) are more active prior to the formation of the hand to interact with the shape of a given object (Sakata *et al.*, 1998) and are found to be selective for the visual and kinesthetic (motor) information from a specific shape (Murata *et al.*, 2000). In addition to AIP, the medial portion of the superior parietal lobe was also active bilaterally. This region of human cortex is also active during the discrimination of the three-dimensional features of an object based on both visual and somatosensory information (Shikata *et al.*, 2003). Similar areas in macaque monkey cortex caudal to AIP (a caudal intraparietal area; Shikata *et al.*, 1996 or posterior intraparietal area; Colby *et al.*, 1988) respond selectively to the orientation of a surface in three dimensions for visual stimuli (Taira *et al.*, 2000). This information is then transferred to anterior intraparietal fields, in order to guide the formation of the hand around an object, a process known as prehension (Gardner, 1998).

#### 4.24.4 The Evolution of Posterior Parietal Cortex

Primates are unique in that they have an expanded posterior parietal cortex compared to other mammals, and our data support the contention that primate brain size and complexity increase in proportion to the ratio of brain to body size, for example, from Old World monkeys to humans (Kaas, 2004). Although the



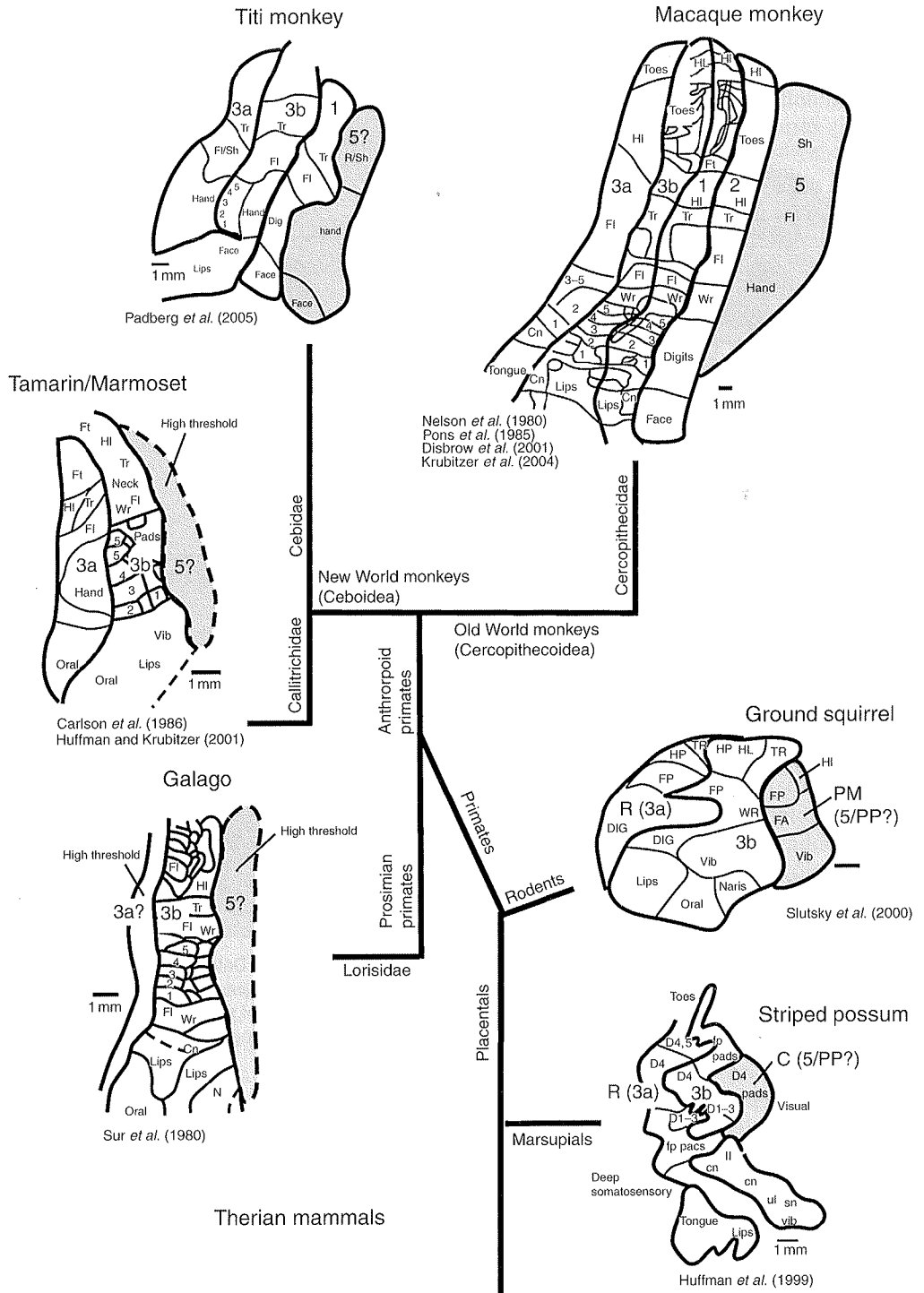


**Figure 5** a, Schematic of a group analysis of data from 12 subjects on a flattened brain. Data from three stimulus conditions are overlaid (inset): (1) saccadic eye movements vs. fixation; (2) visually guided reaching and grasping vs. motor control; and (3) haptic exploration of object shape vs. manipulation of clay. b, Location of putative homologues of several cortical fields described in the macaque monkey. Note that there are four areas of activation that do not correspond in location or activation pattern to any field described in the macaque.

**Table 1** Pattern of activation for saccade reach and shape tasks in various human cortical fields and their putative homologues

Task	Caudal ISPL	Medial ubIPS	AIPS+ PoCS	Caudal PoCS	Caudal mSPL	Anterior ubIPS	PO + SPL	Lateral SPL	Medial SPL	Fundal IPS
Saccade										
Reach										
Shape										
Flowfield + face										
Putative homologue	LIP	?1	AIP	VIP	PRR	MIP	?2	?3	PIP	?4

AIPS, anterior intraparietal sulcus; mSPL, medial superior parietal lobule; PO, parietal occipital; PoCS, posterior central sulcus; ubIPS, upper bank, Intraparietal sulcus.



**Figure 6** 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), a rostral field (3a or R), and a caudal area (5 or PP, gray). Some species such as simian primates have evolved a low-threshold cutaneous (or deep) representation just caudal to 3b, termed area 1. 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 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 fields, such as area 5, were modified both functionally and connectionally for sophisticated hand use. Phylogenetic relationships come from Murphy *et al.* (2001) and Eisenberg (1981). Cortical organization of different species depicted here is modified from studies listed for each species. Adapted from Padberg, J., 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(12): 1938–1963.

relative locations of the functionally defined areas on the human cortical sheet are similar to the patterns seen in the macaque, additional regions in parietal cortex are active outside our putative homologues and are likely specializations of human neocortex (Figure 5). Unique areas of human posterior parietal cortex have also been described using visual stimuli (Vanduffel *et al.*, 2002).

The relationship to the macaque data can be determined through patterns of overlap of activation as well. For example, at the caudal end of the superior parietal lobe, reach-selective and saccade-selective areas of activation exhibit a degree of overlap similar to the border between PRR and LIP in the macaque monkey (Calton *et al.*, 2002). Conversely, unique patterns of overlap in our data set which do not fit existing macaque literature might represent regions of cortex independently derived in humans. For example, a region of the lateral portion of the superior parietal lobe was active during both saccadic eye movements and haptic shape exploration – a pattern which has not been described in macaques. While we leave open the possibility that such an area selective for both complex movements of the hands and eyes has yet to be identified in nonhuman primates, such novel regions might provide the neural substrate for higher-order functions that would require fast sensorimotor transforms, such as eye–hand coordination.

In contrast, a region resembling area 5, in which neurons respond to deep somatic stimulation and often visual stimulation, has been identified in a variety of mammals (Figure 6), such as squirrels (Slutskey *et al.*, 2000), insectivores (Krubitzer *et al.*, 1997), and marsupials such as the striped possum (Huffman *et al.*, 1999) and the flying fox (Krubitzer and Calford, 1992), as well as New and Old World monkeys and humans. Thus, area 5 appears to be part of a common plan of organization in all primates, and in all mammals, and were interleaved between area 5 and V3a in the human. These new areas may be related to the evolution of the hand and complex cortical processing networks associated with hand use.

While area 5 may be a retained or homologous field in mammals, the addition of new areas and new connections likely promotes new functions of retained cortical fields. Our work in the macaque and titi monkey indicates that area 5 has a unique pattern of connections providing the anatomical substrate for its role in the motor aspects of visually guided reaching, the motivational state of reaching, as well as its role in intermanual transfer of information across hemispheres necessary for bilateral coordination of the hands (Padberg *et al.*, 2004, 2005). Thus, area 5 in

squirrels and flying foxes may be homologous to area 5 in primates, but not strictly analogous. Indeed, much like the magnification of behaviorally relevant body parts in area 3b, in area 5 these representations and associated functions appear to magnify to the extreme in particular lineages. In primates, the hand representation dominates area 5 and much of posterior parietal cortex appears to be specialized for hand use.

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