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

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Glossary

3h Brodmann's area 3h, synonymous with S1.
AIP Anterior intraparietal area.
area 5 Brodmann's area 5.
area 7 Brodmann's area 7.
aptic shape perception Tactile sampling of a shape.
LIP Lateral intraparietal area.
MIP Medial intraparietal area.
multimodal Neurons that respond to more than one type of sensory stimulus.
PRR Parietal reach region.
PV Parietal ventral area.
reomotory An ordered representation of the visual field in areas of the visual cortex.
SI Primary somatosensory area.
S2 Secondary somatosensory area.
saccade Rapid eye movements resulting in fixation from one point in the visual field to another.
somatotopy An ordered representation of the skin surface in areas of the somatosensory cortex.
VIP 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; Andersen et al., 1997; Andersen and Barone, 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 movement during visually guided reaching (Mountcastle et al., 1975; Lacquaniti et al., 1985; Johnson et al., 1996; Gregoriou and Savaki, 2001; Barone 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; Tsumura 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 (Fiallenot 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 (SI) 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 visuospatial 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 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; Debowy 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 (Dishbrow 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

![Figure 1](image.png)

*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.
Motor Systems in Primates). There is also evidence that human posterior parietal cortex plays a role in shape perception (Faillence et al., 1997; Binkofski et al., 1999a, 1999b; Kourtzi and Kanwisher, 2000; Amor et al., 2001; Bodgard et al., 2001; Greffels 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.

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Similarly, in preliminary studies of macaque monkeys, we examined responses to somatosensory and visual stimulation in the hand representation. As in the previous experiments, 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 connectional data indicate that area 5 is involved in integrating visual and somatosensory inputs specifically related 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 study area 5 in humans (Diibrow et al., 2001). Stimuli were moving tactile stimuli applied to the hand, foot, or face, and a visual flow field. Tactile and visual stimuli were both individually and simultaneously. While 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.

4.2.4.3 Effector Specific Network

In posterior parietal 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 Bunes, 2000). 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
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 the 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.

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
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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 (Bikson et al., 1998; Calhoun 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 bilaterally active. 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 (Sakata et al., 2003). Similar in macaque monkey cortex caudal to AIP (a caudal intraparietal area; Shikata et al., 1996 or posterior intraparietal area; Colby et al., 1998) 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 asprehension (Gardner, 1998).

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

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<th>Caudal IPS</th>
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<th>AIP</th>
<th>Caudal PoCS</th>
<th>Caudal SPL</th>
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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 27? 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 primate 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 lobes, reach-selective and saccade-selective areas of activation exhibit a degree of overlap similar to the border between PPR and LIP in the macaque monkey (Calnon 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 have open the possibility that such a region might be for both complex movements of the hands and eyes has yet to be identified in nonhuman primates, such move regions might provide the neural substrate for higher-order functions that would require fast sensorimotor transformations, such as eye-hand coordination.

In contrast, a region resembling area 5, in which neurons respond to both somatic stimulation and often visual stimulation, has been identified in a variety of mammals (Figure 6), such as squirrels (Monsky 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 Callard, 1992), as well as New and Old World monkey species and humans. Thus, area 5 appears to be a part of a common plan of organization in all primates, and in all mammals, and was intercleaved between area 5 and 6 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 higher mammals, the addition of new areas and new connections likely promotes new functions of retained cortical fields. Our work in the macaque and human 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 the internal transfer of information across hemispheres necessary for bilateral coordination of the hands (Pandberg 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 the extent in particular lineages. In primates, the hand representation dominates area 5 and much of posterior parietal cortex appears to be specialized for hand use.

References


