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The Evolution of Parietal Areas Associated with Visuomanual Behavior: From Grasping to Tool Use

DYLAN F. COOKE, ADAM GOLDRING, GREGG H. RECANZONE, AND LEAH KRUBITZER

One of the hallmarks of human evolution is the extraordinary degree to which we can manipulate the physical world with our hands or with tools that extend or amplify portions of our body. This manual dexterity coevolved with the expansion of areas of the brain associated with both visual processing and visuomanual coordination. Specifically, occipitotemporal cortex expanded and cortical areas emerged for the processing of motion, direction and heading (Britten, 2008), and the temporal lobe enlarged greatly to process information about object features such as faces. Cortical fields within posterior parietal cortex (PPC) also expanded and serve as an interface between perception and action. Areas in PPC combine the sensory information from multiple modalities with effector kinematics to compute and program visually guided reaching and grasping movements tailored to specific objects and contexts.

This link between manual dexterity and visual processing is best exemplified when one considers the importance of particular locations in extrapersonal space. Most manual activity takes place in front of the torso and face. This is the optimal space where the two hands meet, and from a visual and skeletal perspective, it is the most ergonomic bimanual work space. It is also a multimodal hot spot, the place where an object can easily be felt, seen, heard, smelled, and tasted. Perhaps unsurprisingly, monkeys' hands are found in this part of space more often than not, and nearly all grasping and manipulation occurs here (Graziano et al., 2004). In monkey motor cortex, electrical microstimulation causes arm movements that follow a similar pattern: overrepresentation of movements toward this central space, particularly when stimulation also evokes a grasp-like hand posture (Graziano et al., 2002, 2004), suggesting that object manipulation in this work space is a

fundamental feature of motor cortex organization. Human proprioceptive acuity for hand position in space is also nonuniform; that is, people have a more accurate kinesthetic sense of hand position at locations near the midline close to the body where this sense is continually being recalibrated with visual feedback (Rincon-Gonzalez, Buneo, & Helms Tillery, 2011; Tillery, Flanders, & Soechting, 1994). This space has been called a "motor fovea" (Tillery, Flanders, & Soechting, 1994) or "manual fovea" (Graziano et al., 2002). Like the overrepresentation of the fovea in the visual system, the brain regions contributing to this combination of manual behavior, sensory integration, and the representation of visual space may overrepresent this manual work space where food is prepared and eaten and tools are made and used.

This chapter focuses on some of the cortical areas that contribute to the visuomanual behaviors described above, which are located at the junction of sensory neocortex and PPC. These visuomotor behaviors are strongly dependent on tactile feedback, so we will begin with the anterior parietal area 2 and proceed to the more visually integrated regions in and around the banks of the intraparietal sulcus (IPS) such as area 5, the medial intraparietal area (MIP) and the anterior intraparietal area (AIP) (here and throughout, see table 73.1 for detailed explanations of abbreviations used), and lateral to this, 7b on the inferior parietal lobule. We discuss traditional views of these fields based on architectonic analysis and more modern concepts of how this region is subdivided based on multiple criteria including architecture, electrophysiological mapping data, and neuronal response properties. While most of our knowledge of these fields comes from studies in macaque monkeys, we broadly consider data from other nonhuman primates as well as humans to address

TABLE 73.1

Cortical areas, regions and somatosensory receptor locations

Abbreviation	Definition/description	Abbreviation	Definition/description
Parietal cortex (mostly figures 73.2, 73.3, 73.5)		IPS	Intraparietal sulcus
1	Area 1; cutaneous representation caudal to 3b	LIP	Lateral intraparietal area
		LIPd	LIP, dorsal division
1–2	Area 1–2 (galago and marmoset); of uncertain homology to areas 1 and 2 in other primates	LIPv	LIP, ventral division
		LS	Lateral sulcus
2	Area 2; representation of deep receptors caudal to area 1	MDP	Medial dorsal parietal area
		MIP	Medial intraparietal area
3a	Area 3a; somatosensory field rostral to 3b	Opt	Area Opt; overlaps caudomedial 7a
3b	Area 3b, primary somatosensory area, S1	PCS	Postcentral sulcus
5/BA5	Area 5/Brodmann's area 5; contemporary area 5 definitions encompass only part of BA5 which is used to refer only to Brodmann's original parcellation; on SPL	PE	Parietal area E; with other "PE" fields, mostly coextensive with BA5; on SPL of PPC
5D	5/BA5, dorsal division; on the rostral SPL	PEa	Parietal area E, anterior (not part of Seltzer and Pandya's (1986) PE); rostral/medial bank of IPS
5V	5/BA5, ventral division; in rostral bank of the IPS	PEc	Parietal area E, caudal (not part of Seltzer and Pandya's (1986) PE); between PE and PEa on the caudomedial SPL
5L	5/BA5, lateral division; from Seelke et al. (2012)	PEm	Parietal area Em, rostral division of PE from von Bonin and Bailey (1947)
7/BA7	Area 7/Brodmann's area 7; caudal bank of IPS and most or all of IPL	PEp	Parietal area Ep, posterior division of PE from von Bonin and Bailey (1947)
7a	Area 7a, caudal portion of 7; originally defined by Vogt and Vogt (1919) and subsequently further subdivided	PF	Parietal area F; rostral IPL; overlaps 7b
		PFG	Parietal area FG; rostral IPL (transitional area between PF and PG) from Seltzer and Pandya (1986); may straddle 7a/7b border
7a–l	Area 7a, lateral division		
7a–m	Area 7a, medial division		
7b	Area 7b, rostral portion of 7; originally defined by Vogt and Vogt (1919) and subsequently further subdivided	PG	Parietal area G; rostral IPL; overlaps 7a
		PGm	Parietal area Gm; on the medial wall portion of von Bonin's PE from Seltzer and Pandya (1986)
7op	Operculor area 7; lateral to 7b		
BA19	Area 19/Brodmann's area 19; overlaps several extrastriate visual areas	Pm	Parietal medial area (squirrel); may be homologous to primate PPC
aSMG	Anterior supramarginal gyrus (human); overlapping human PF	PO	Parietal occipital area (approximately V6 + V6a)
AIP	Anterior intraparietal area; overlaps BA7, Vogts' 7b (1919), POa	POa	Area POa (not part of PO); overlapping LIP and AIP; medial BA7
CIP	Caudal intraparietal area	PPc	Posterior parietal caudal area (galago, tree shrew)
CIP1	Caudal intralparietal 1, from Arcaro et al. (2011)		
CIP2	Caudal intralparietal 2, from Arcaro et al. (2011)	PPC	Posterior parietal cortex
		PPl	Posterior parietal lateral area (galago)
CS	Central sulcus	Pm	Parietal medial area (squirrel)
DZ	Dysgranular zone (rat); surrounded by S1	PPr	Posterior parietal rostral area (tree shrew)
Ig	Granular insular field; adjacent to S2 in LS, e.g., Friedman et al. (1986)	PR	Parietal rhinal area
		PRR	Parietal reach region
IPd	Intraparietal depth area (in depth of IPS, adjacent to POa and PEa)	PV	Parietal ventral area
		R	Rostral somatosensory area (striped possum, opossum)
IPL	Inferior parietal lobule		

TABLE 73.1

Abbreviation	Definition/description	Abbreviation	Definition/description
Ri	Retroinsular area; in the fundus of LS, adjacent to S2 and 7b, e.g., Friedman et al. (1986)	DP	Dorsal prelunate area
S1	Primary somatosensory area	MI	Primary motor cortex
S2	Second somatosensory area	MST	Medial superior temporal area; visual
SC	Somatosensory caudal area (tree shrew, striped possum, opossum); perhaps homologous to primate area 1 or areas 1+2.	MT	Middle temporal area; visual
		VI	Primary visual area
		V2	Second visual area
		V3	Third visual area
SPL	Superior parietal lobule	V3d	V3, dorsal division
VIP	Ventral intraparietal area	V3v	V3, ventral division
VIPl	VIP, lateral division	V3A	Visual area V3A; lateral to V3; also called DM
VIPm	VIP, medial division	V4	Fourth visual area; also called DL
V6	Visual area 6, medial to the caudal end of the IPS; with V6A, approximately overlapping PO	vis	Other visual areas
		Body parts and receptor types (figure 73.4)	
V6A	Visual area 6a, dorsal to (and not a division of) V6; with V6, approximately overlapping PO	cn	Chin
		cut	Cutaneous receptors on body part
		D1–5	Digits 1–5
VS	Ventral somatosensory area; part of the S2 complex from Krubitzer et al. (1995)	deep	Deep receptors on body part
		fa	Forearm
Other cortex (mostly figure 73.2)		gen	Genitals
A1	Primary auditory area	j	Jaw
aud	Other auditory areas	occ	Occiput
DL	Dorsolateral visual area; also called V4	sh	Shoulder
DLc	DL, caudal division	sn	Snout
DLr	DL, rostral division	tr	Trunk
DM	Dorsomedial visual area; visual; also called V3a	T1–5	Toes 1–5
		vis	Visual response

Note: All terms refer to macaque brains except where noted.

SENSORY VERSUS NONSENSORY "ASSOCIATION" CORTEX

The cortical sheet is divided into multiple cortical fields defined by their architecture, function, and connectivity. Several cortical areas including primary sensory areas (VI, S1, A1) and secondary areas (e.g., V2, S2/PV, A2) have been described in all mammals investigated (see figure 73.1). In these primary areas there is a relatively simple, first-order transformation or representation of the entire sensory epithelium or array. For example, in the visual system, retinotopic order is maintained in V1 and V2, with no or few splits in the representation of the visual hemifield. In mammals in which the relative size of the neocortex is larger, more cortical fields are observed (see figure 73.2). Neurons in this expanded cortex generally do not respond to the kind of simple sensory stimulation that easily activates neurons in primary and secondary areas nor do they respond under most anesthetic conditions. Traditionally considered "association" areas, these regions contain neurons with much more complex response properties (e.g., neurons in inferotemporal cortex respond to faces). Such higher-order, often multisensory areas are located between traditional unimodal sensory areas, and also vary greatly across primates and across mammals in general.

One such region is PPC, situated between somatosensory and visual cortex. Although PPC has been described in primates such as New World monkeys and prosimians

questions of how this boundary cortex evolved and how it covaries with sophisticated visuomanual behaviors that define primates.
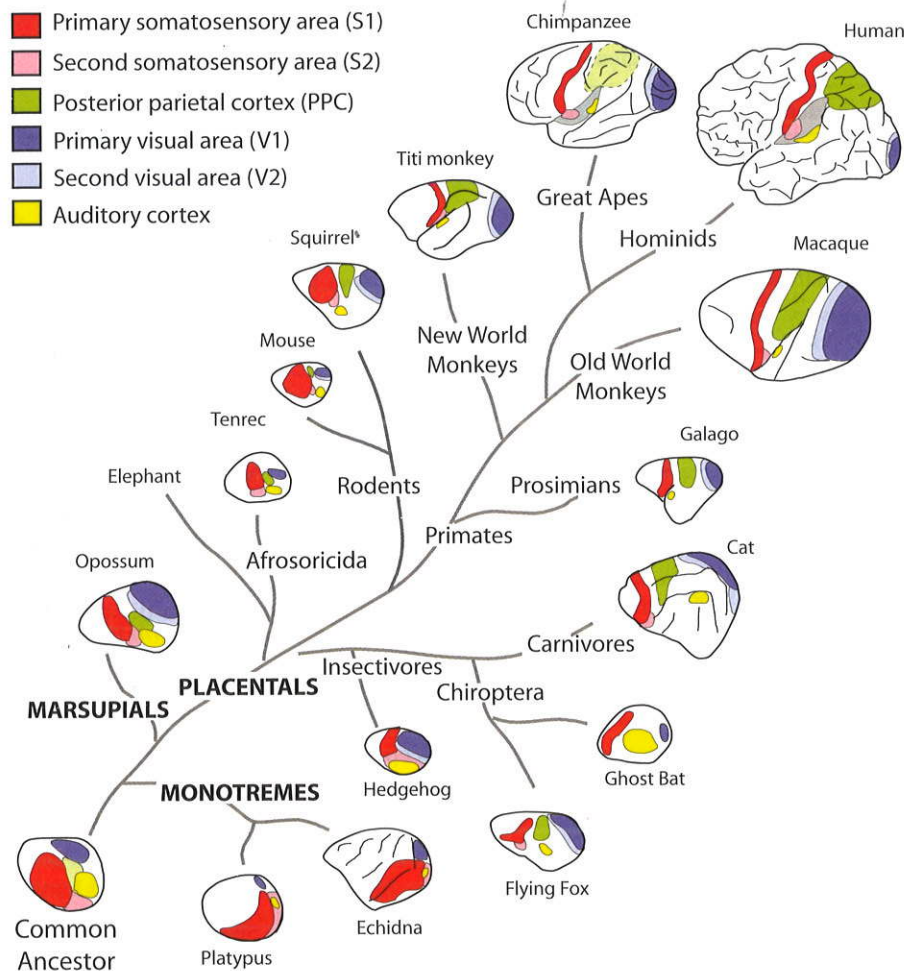
FIGURE 73.1   A cladogram illustrating the phylogenetic relationships for the major subclasses of mammals and some of the orders within each subclass. There is a constellation of cortical fields that is observed in all mammals. This constellation of fields is considered homologous and to have been present in the common ancestor. Posterior parietal cortex (green) or the presumptive posterior parietal cortex (light green) has also been described widely, but in species with small brains (e.g., mice and opossums), this generally encompasses a small zone of cortex between known visual (V1, dark blue; V2, light blue), somatosensory (S1, red; S2, pink), and auditory (yellow) fields in which neurons respond to stimulation of two or more modalities. See table 73.1 for abbreviations.

(e.g., Padberg, Disbrow, & Krubitzer, 2005; Padberg et al., 2007; Stepniewska, Fang, & Kaas, 2009) and other mammals such as carnivores and rodents (Krubitzer, Campi, & Cooke, 2011), most studies of PPC have used the macaque monkey as an animal model for humans. Studies in macaques and humans indicate that PPC contains complex maps that are not obviously topographic or retinotopic, and are involved in complex, multidimensional computations such as calculating optic flow (Merchant, Battaglia-Mayer, & Georgopoulos, 2001; Siegel & Read, 1997), generating an internal coordinate reference of the body (see Chang & Snyder, 2010, for review ; Grefkes & Fink, 2005), and even tool action (Peeters et al., 2009). The cortical magnification commonly seen in primary sensory fields, such as the

fovea in primary visual cortex, is more extreme in PPC. Cortical fields in PPC often do not have a complete representation of the body surface or retina (Arcaro et al., 2011; Patel et al., 2010; Seelke et al., 2012), but rather represent or are associated with special effector organs such as the eye or hand, or they represent very specific aspects of visual processing. For example, caudal regions of macaque PPC, including the caudal intraparietal area, the ventral intraparietal area (VIP), and the lateral intraparietal area (LIP), are generally associated with aspects of visual processing such as extracting three-dimensional features of objects, generating head-centered coordinates, or programming saccade endpoints, respectively (Grefkes & Fink, 2005). Rostral posterior parietal fields in and around the banks
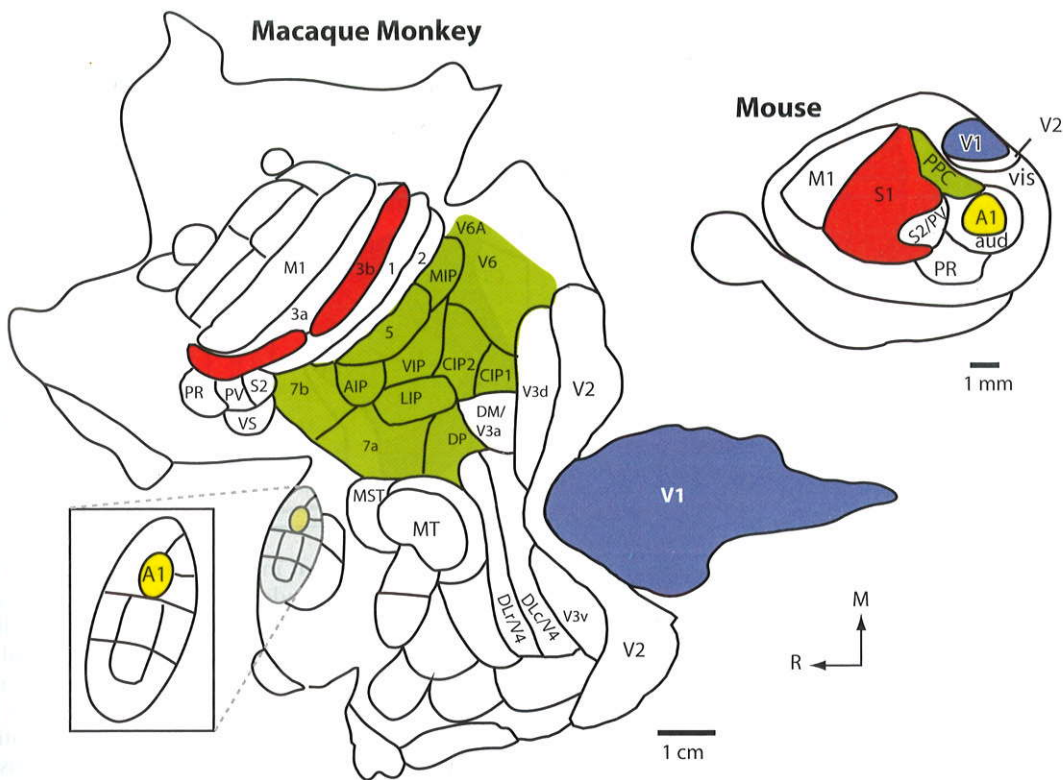
FIGURE 73.2   Drawings of a flattened cortex from macaque monkey and mouse illustrating the number and location of cortical fields. Some cortical fields such as the primary sensory areas (visual, blue; somatosensory, red; and auditory, yellow) have been described in all mammals investigated and are part of a homologous network. In animals with relatively large brains, such as macaque monkeys, the neocortex has greatly expanded and the number of visual and somatosensory areas has increased. Coincident with this increase in cortical sheet size and sensory cortical field number is also an increase in the relative size of posterior parietal cortex (PPC; green) and the number of subdivisions within this region. Divisions of PPC represent our interpretation of this region based on several studies including Stepniewska, Collins, and Kaas (2005), Orban (2008), Arcaro et al. (2011), and Seelke et al. (2012). See table 73.1 for abbreviations.

of the IPS, such as area 5, MIP, and AIP, are associated with initiating a reach, preshaping the hand, and matching object shape with grasp configuration, tasks that utilize both somatosensory and visual information (Debowy et al., 2001; Eskandar & Assad, 2002; Gallese et al., 1994; Murata et al., 2000). Although the focus of this chapter is PPC, in macaque monkeys we will describe this region in the context of adjacent parietal fields in 3 regions: area 5, area 7, and area 2.
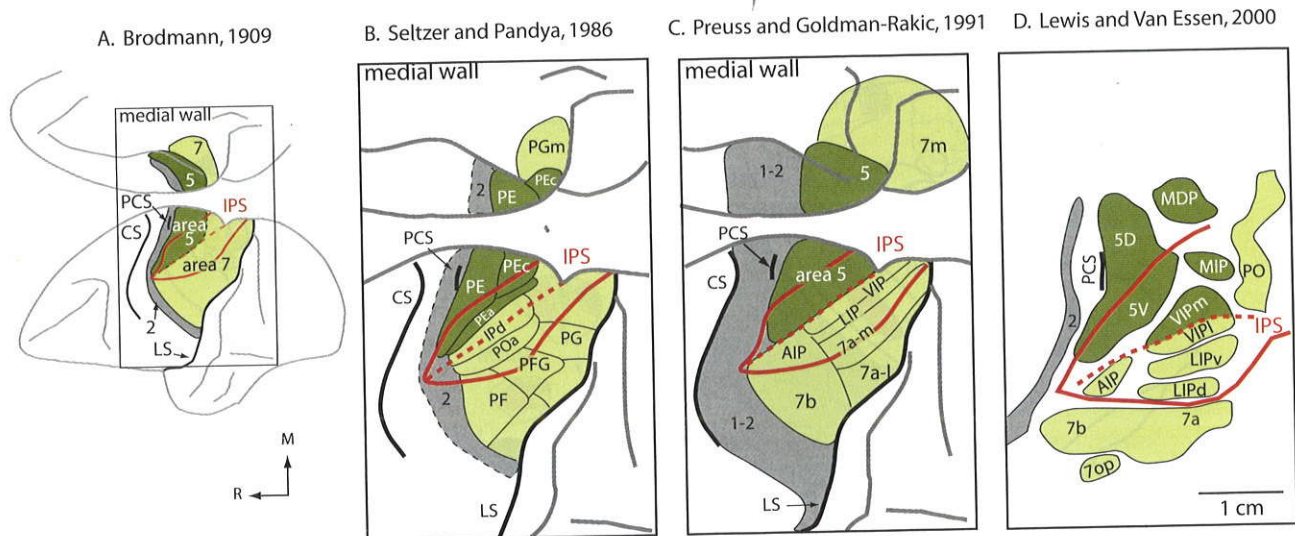
Areas on the Rostral Bank of IPS

In macaque monkeys, there are several fields at the junction of S1 and PPC. Posterior parietal area 5 is one of these "higher-order" cortical areas. Historically, there has been a great deal of contention over the status of Brodmann's area 5 (BA5) and how it should be subdivided. BA5 was described architectonically in Old World monkeys as a large triangular-shaped field caudal to

area 2 (Brodmann, 1909; figure 73.3). BA5 encompassed the rostral/medial bank of the IPS, meeting Brodmann's area 7 (BA7) in the IPS. BA5 extends onto much of the caudal portion of the postcentral gyrus, especially in the medial portion where BA5 is widest. Medially, it includes a section of the medial wall extending just across the cingulate sulcus. Henceforth we will use "BA5" to mean this large field and "area 5" to refer to the more recent and variable definitions of a smaller version of this field which along with MIP, the medial division of VIP (VIPm), and the medial dorsal parietal area, probably overlap at least in part with BA5 (figure 73.3).

An alternative nomenclature grew out of von Economo's (1929) parcellation of the human brain in which the location of BA5 was labeled the parietal area E, or "PE." Von Bonin and Bailey (1947) adapted this nomenclature for macaques, splitting the field into rostral PEm and caudal PE/PEp divisions and including the

A. Brodmann, 1909   B. Seltzer and Pandya, 1986   C. Preuss and Goldman-Rakic, 1991   D. Lewis and Van Essen, 2000

FIGURE 73.3   Architectonic parcellations of the posterior parietal cortex by different investigators. Brodmann (A) proposed the first comprehensive scheme of organization of posterior parietal cortex that included area 2 (gray), a large area 5 (dark green), and a large area 7 (light green). Subsequent schemes (B–D) have used different terminology and subdivided Brodmann's 5 and 7 divisions into multiple fields (B–D). Approximate correspondence between BA5 and BA7 and subsequent schemes are indicated by color (dark and light green, respectively). Note that as Brodmann (1909) generally did not illustrate cortical field boundaries within sulci, the borders of BA5 and BA7 (illustrated as a dashed line in panel A) as well as Brodmann's area 19 are not precisely known. In particular, correspondence of PO and adjacent fields to Brodmann's parcellation is uncertain. Intraparietal sulcus lips (solid line) and fundus (dashed line) are shown in red. Arrows next to A indicate rostral (R) and medial (M) anatomical directions. See table 73.1 for abbreviations.

entire portion of BA7 on the medial wall. Since these early publications, a number of histological techniques (e.g., Hof & Morrison, 1995) have been used to subdivide and refine the borders of area 5/PE. For example, Seltzer and Pandya (1980, 1986) subdivided PE into PE, PEc, and PEa (figure 73.3). More modern architectonic studies divided area 5 into two fields, dorsal area 5 (5D) and ventral area 5 (5V; Lewis & Van Essen, 2000b; figure 73.3B and D).

Functional studies of area 5 examining receptive field characteristics and neural response properties are variable in both their results and in the locations in which the recordings were made (Seelke et al., 2012). In early studies, most of the mediolateral extent of the rostral bank of the IPS and caudal portions of the postcentral gyrus was explored and considered to be "area 5" (e.g., Mountcastle et al., 1975; Sakata et al., 1973). The explored region did not include the lateral-most portion of the IPS or cortex on the medial wall. Subsequent studies of area 5 also differed greatly in the location of their recording sites (e.g., Gardner et al., 2007b; Iwamura, Iriki, & Tanaka, 1994; Kalaska, 1996; Taoka, Toda, & Iwamura, 1998; see Seelke et al., 2012, for review). Given these rather large differences in recording site location, it is not surprising that the results and interpretations regarding the function of area 5 varied as well.

That area 5 is unlike adjacent somatosensory fields on the postcentral gyrus first became apparent in early electrophysiological recording studies in awake monkeys by Duffy and Burchfiel (1971), Sakata and colleagues (1973), and Mountcastle and colleagues (1975; see figure 73.4). These investigators reported that receptive fields for neurons in area 5 are larger than in anterior parietal fields (3b, 1, and 2) and that neurons are most active during active arm movements. While individual neurons can be driven by a variety of stimuli, their optimal responses sometimes can involve highly specific and complex interactions of joint and skin stimulation (Sakata et al., 1973). Important for this review, a small proportion of neurons respond differentially during active reaching depending on the reward value of the reach target (Mountcastle et al., 1975).

Subsequent studies suggest that portions of BA5 play an important role in sophisticated functions such as the programming of intended movements (Debowy et al., 2001; Snyder, Batista, & Andersen, 1997), the coding of reach targets in body- or shoulder-centered coordinates (Ferraina & Bianchi, 1994; Lacquaniti et al., 1995), and the kinematics of object acquisition (e.g., Kalaska, 1996; Wise et al., 1997). Recent studies demonstrate that neurons in area 5 fire maximally during a reaching task before the target object is contacted with the hand (Gardner et al., 2007a, 2007b), and that neurons
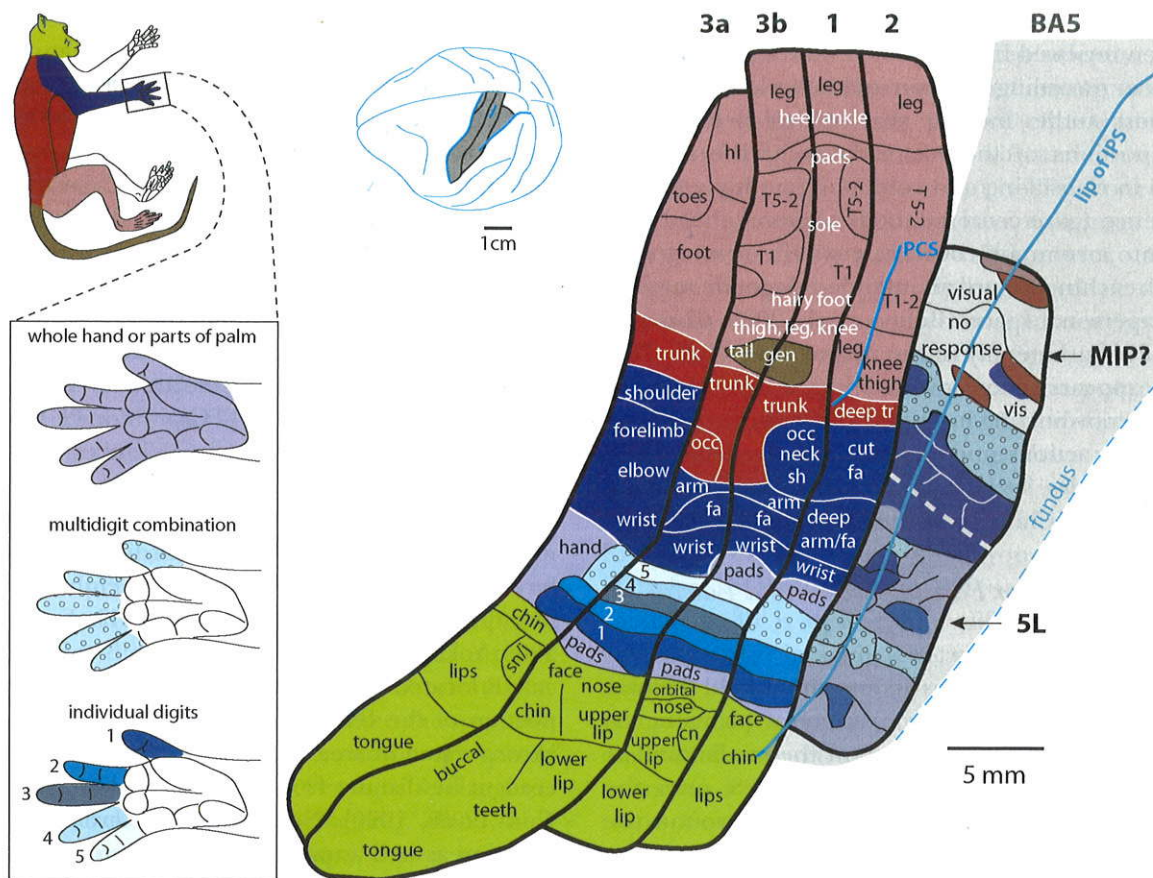
FIGURE 73.4   Summary of the functional subdivisions of anterior parietal areas 3a, 3b, 1, and 2 and posterior parietal areas 5L and the presumptive medial intraparietal area (MIP) from Seelke et al. (2012). Thick black lines are areal boundaries; sulci are shown in blue. Areas 3a, 3b, 1, and 2 have a clear parallel topographic organization not observed in posterior parietal areas. Areas 5L and the presumptive area MIP have fractured maps dominated by representations of the digits, hand and forelimb (thin black lines are body-part boundaries). Area 5L and MIP fall within Brodmann's area 5 (gray portion of enlarged view). In area 5L, digits are most often represented in various combinations (light blue stipple), or parts of the hand or the whole hand is represented (light purple). Schematic at top center shows location of these fields (gray) on the dorsolateral aspect of the brain. Schematic at left shows body-part color code: head, green; individual digits, various shades of blue; hand/forelimb, purple; trunk, red; hindlimb, pink; tail/genitals, brown. Topographic maps are redrawn from Krubitzer et al. (2004) (area 3a), Nelson et al. (1980) (areas 3b and 1), Pons et al. (1985) (area 2), and Rothemund et al. (2002) (genital/tail representation in areas 3b and 1). Conventions as in previous figures; see table 73.1 for abbreviations.

modulate their activity depending on how and when the hand is used in a grasp (Chen et al., 2009).

It is important to note that the architectonic divisions of area 5 do not correspond well to functional subdivisions, and some areas that may overlap BA5, such as the parietal reach region (PRR), have only been described using functional criteria. PRR has been proposed to overlap areas MIP and V6a (Snyder, Batista, & Andersen, 2000). While MIP is generally considered to be within BA5, V6a is probably not. Our own data and those of others indicate that BA5 contains a moderately sized functional area (5L) that is smaller than Brodmann's original architectonic description, and medial field (MIP). We use the term MIP because its location, architecture, and aspects of its organization are consistent with a previously explored area (termed MIP) defined using electrophysiological and/or architectonic criteria (Colby & Duhamel, 1991; Eskandar & Assad, 2002; Lewis & Van Essen, 2000b). Unlike anterior parietal areas, area 5L contains a fractured, nontopographically organized representation of muscles and joints of the hand and limb, and deep receptors of the skin (figure 73.4). This type of fractured representation is analogous to motor cortex and constitutes related groups of proprioceptors activated during behaviorally relevant movements.

Reports of neural response properties in this medial region vary greatly (Seelke et al., 2012); various

locations of recordings and descriptions of these data have been reviewed by Seelke et al. (2012). Despite differences in recording location and behavioral tasks utilized, most studies indicate that cortical fields in the medial portions of the rostral bank of the IPS are involved in translating and combining multiple frames of reference (gaze centered, body centered, head centered) into a common coordinate system or integrated plan for reaching toward an intended target in immediate extrapersonal space (Buneo et al., 2002; Chang & Snyder, 2010). Laterally in the rostral bank of the IPS, area 5L appears to be involved in the kinematics of reaching, coordinating multiple limb parts for reaching and grasping actions, and matching visually determined object properties, such as size and shape, with grasping configurations (Chen et al., 2009).

Areas on the Inferior Parietal Lobule and Lateral Bank of the IPS

Brodmann's area 7 (BA7) is an enormous field that was architectonically defined in a variety of primates. As defined by Brodmann, it begins on the medial wall, it wraps around the caudal bank of the IPS, onto the inferior parietal lobule, and it continues around the upper bank of the lateral sulcus laterally (see figure 73.3). Subsequent studies have divided this region into 7a and 7b (Vogt & Vogt, 1919) or multiple cortical areas using various terminologies (see figure 73.3). More recently, using a combination of architecture, neuroanatomical data, and neurophysiological recording studies, Lewis and Van Essen (2000a, 2000b) divided BA7 into multiple regions, including 7b, 7op, 7a, AIP, divisions of LIP and VIP, MIP, and PO (figure 73.3D). As with BA5, architectonic divisions of area BA7 are often inconsistent with the location of functionally defined divisions of this region. We are most interested in the portions of area 7 that border known somatosensory fields, areas 7b and AIP as defined by Preuss and Goldman-Rakic (1991) and Lewis and Van Essen (2000b). These nomenclatures and divisions appear to be the most widely used in studies of this region of cortex.

Early electrophysiological investigations indicated that neurons in classically defined areas 7a and 7b of Vogt and Vogt (1919) responded primarily to visual fixation and eye movements (7a), or to somatosensory stimulation and passive movements of the arms and hands (7b) (Hyvarinen & Poranen, 1974; Leinonen et al., 1979; Mountcastle et al., 1975). Importantly, cells in both 7a and 7b were most active in awake animals when the monkey reached, grasped, and manipulated various visually targeted objects (Hyvarinen & Poranen, 1974).

Recent studies indicate that areas 7a and 7b overlap four architectonically distinct zones (Gregoriou et al., 2006; Pandya & Seltzer, 1982; Rozzi et al., 2006, 2008) that have distinct neuroanatomical connections: PG and Opt largely overlap 7a, PFG probably straddles the 7b/7a border, and PF lies within 7b. Collectively, these fields form a gradient of sensory and motor function that progresses from vision- and eye-related functions to somatosensation- and hand/face-related functions as one moves rostrolaterally along the IPS. Thus, PG contains visual fixation neurons and neurons responsive to eye and arm movements related to reaching and grasping while neurons in PFG and/or PF have visual responses to objects presented within manual space, are involved in goal-directed reaching, and appear to code motor acts predominantly related to hand use, orofacial movements, and hand–mouth coordination but are differentially active when these acts are embedded in different actions (e.g., Bonini et al., 2011; Fogassi et al., 2005; Yokochi et al., 2003).

AIP, located on the caudal (lateral) bank of the lateral portion of the IPS (figure 73.3C–D), was traditionally incorporated in area 7, and then 7b, but is now considered to be distinct from 7b (e.g., Gallese et al., 1994; Taira et al., 1990). Neurons in AIP are active during grasping as well as passive viewing of an object shaped to require the same grasp (Murata et al., 2000; Sakata et al., 1995) and code three-dimensional features of an object with shorter latency and less sensitivity to curves and edges than temporal cortical areas (Srivastava et al., 2009). AIP neurons also preferentially respond to visually targeted objects within reach (Srivastava et al., 2009), but many respond equally well to memory-guided object manipulations made in darkness (Murata et al., 1996). Importantly, neurons in AIP respond maximally during the early stages of prehension, increasing their firing just prior to contacting an object (Gardner et al., 2007b), consistent with AIP's role in preshaping the hand prior to a grasp (Debowy et al., 2001; Gallese et al., 1994).

Areas on the Postcentral Gyrus

Although area 2 is considered to be a proprioceptive area associated with somatosensory processing, it is important to establish its spatial relationship to area 5, as well as its contribution to reaching, grasping, bilateral coordination, and dexterity. Using multiunit electrophysiological recording techniques, Pons and colleagues (Pons & Kaas, 1985; Pons et al., 1985) determined that the organization of area 2 is parallel to that of 3b and 1 and contains an inverted representation of the body from medial (feet) to lateral (head; figure

73.4). While some neurons in area 2 respond to stimulation of cutaneous receptors, the majority of neurons respond to stimulation of deep tissue (Taoka, Toda, & Iwamura, 1998) or noncutaneous stimulation of varying types (Hyvärinen & Poranen, 1978). When the area 2 representation of digits 1 and 2 are electrically stimulated using "long" duration pulse trains, the evoked grasp-like movement is the opposition of these digits. Interestingly, this area 2 "grasp zone" appears not to share direct connections with similar motor and premotor grasp zones, suggesting parallel pathways with slightly different functions (Gharbawie et al., 2011).

Recent studies indicate that neurons in the monkey S1 complex (including areas 3b and 1 as well as area 2) show changes in baseline firing rate when visual attention is directed to the tactile stimuli on specific digits of the hand (Meftah, Shenasa, & Chapman, 2002). This modulation is proposed to enhance salient features of the stimulus, such as texture, rather than simply improve overall tactile discrimination. In humans, studies using noninvasive imaging techniques demonstrate that viewing a stimulated body part modulated the response evoked by a tactile stimulus in somatosensory cortex (Forster & Eimer, 2005; Longo, Pernigo, & Haggard, 2011; Taylor-Clarke, Kennett, & Haggard, 2002), and these visual effects in somatosensory cortex improve tactile detection, tactile discrimination, and tactile acuity (Heller, 1982; Kennett, Taylor-Clarke, & Haggard, 2001; Ladavas et al., 1998). These data indicate that our concepts regarding unimodal sensory areas, their function, and their evolution should be reconsidered.

EVOLUTION OF PARIETAL CORTEX AND COEVOLUTION OF THE HAND IN PRIMATES

Thus far we have focused on the organization of portions of PPC in nonhuman primates, particularly macaque monkeys. However, because expansions of PPC are accompanied by expansions of sensory neocortex, it is important to discuss the relationship between sensory fields and the posterior parietal fields to which they provide inputs. The Kaas chapter in this volume provides an excellent overview on the evolution of the visual system of primates. Especially interesting is the expansion of the temporal lobe and the addition of new cortical fields associated with object and face identification and recognition. Areas at the boundary of occipital cortex and PPC have also expanded to include fields such as the middle temporal and medial superior temporal areas that are involved in object motion and self-motion (Britten, 2008). These additional areas in the temporal lobe do not appear to be present in nonprimate mammals, and if there are analogous areas, such

as those that process motion, comparative studies suggest that they have evolved independently.

Similar expansions have occurred among somatosensory fields of the anterior parietal cortex and lateral sulcus and are clearly associated with and contribute to the unique processing that occurs in PPC. For example, while all mammals examined have a primary somatosensory area (S1, also termed 3b), cortex caudal to S1 appears to be differently organized in different mammals and even in different primates (see figure 73.5). Further, a region termed PPC, situated between S1 and V1, has been described in a variety of mammals including marsupials, rodents, and tree shrews (figure 73.5). While all primates examined have areas 3b/S1, S2, PV, and at least one other lateral sulcus area (Coq et al., 2004; Hinkley et al., 2007; Krubitzer & Kaas, 1990; Krubitzer et al., 1995; Qi, Lyon, & Kaas, 2002; Stepniewska, Preuss, & Kaas, 2006), cortex immediately caudal to 3b is different in different suborders. In galagos, cortex immediately caudal to area 3b contains neurons that are responsive to stimulation of deep receptors, muscles and joints or high-threshold cutaneous stimulation. This region is termed 1–2 because of uncertain homology with areas 1 and 2 in other primates. Cortex between area 1–2 and known extrastriate visual areas such as the dorsomedial visual area is termed PPC and is clearly a sensorimotor area like that described for subdivisions of PPC in macaque monkeys. Intracortical microstimulation of PPC in galagos reveals very gross topographic organization in which movements can be evoked from hind limb, then forelimb, then face in a mediolateral progression. Importantly, the evoked movements resemble ethologically relevant behaviors, and sites that evoke identifiable behavioral categories such as reaching, hand-to-mouth movements resembling feeding, and apparent defensive or aggressive movements are clustered (Stepniewska, Fang, & Kaas, 2005, 2009).

The organization of posterior portions of anterior parietal cortex and PPC itself is highly variable in New World monkeys. In the miniature marmoset monkey, cortex caudal to 3b is much like that in galagos and is also termed area 1–2 (Huffman & Krubitzer, 2001). However, there is a greater expansion of known visual cortex in marmosets (particularly in regions of the temporal lobe) and an accompanying increase in PPC. There has been some attempt to subdivide this rather large region of cortex to include areas VIP, LIP, and MIP based on connections, but no data on functional mapping or electrophysiological recordings in awake behaving marmosets have been published. Cortex just caudal to 3b in other New World Monkeys such as owl monkeys, titi monkeys, and squirrel monkeys have a
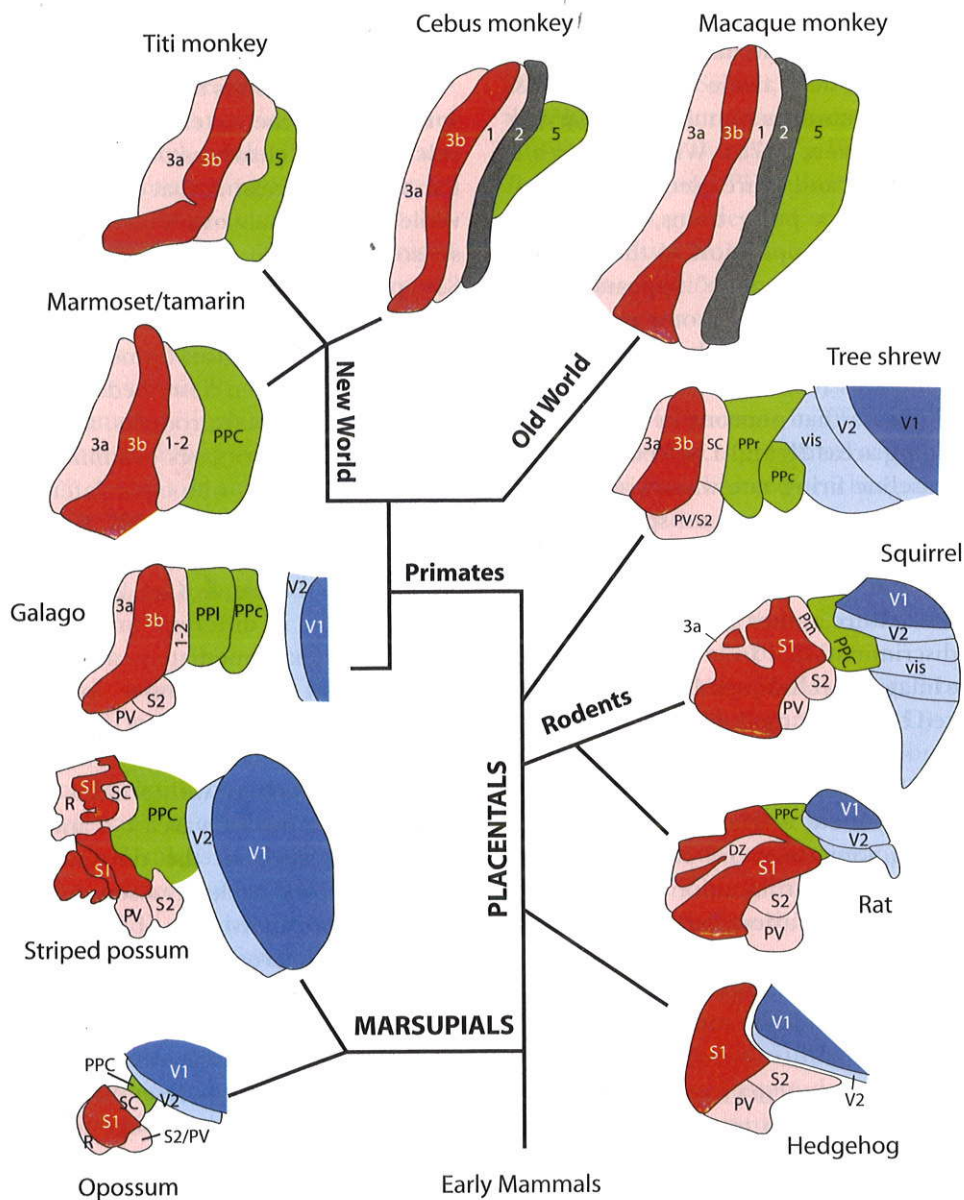
FIGURE 73.5 Cladogram showing the relationships of major mammalian lineages and changes that have taken place in the relationship between rostral somatosensory areas and posterior parietal cortex (PPC). In mammals whose ancestors branched off early from the primate lineage (e.g., opossums and hedgehogs) the amount of cortex considered PPC is small or nonexistent (hedgehogs) although in some marsupials such as striped possum there was an independent expansion of PPC. Rodents have a small PPC, but squirrels appear to have an expanded visual and somatosensory cortex and a relatively larger PPC than rats. PPC began to expand in the mammalian ancestor of tree shrews and primates and then greatly expanded in the primate lineage. For New and Old World monkeys, visual cortex and the caudal portion of PPC is not shown. However, these species illustrate the relationships between the expanding somatosensory cortex and PPC. Illustrations are modified from Huffman et al. (1999) (opossum, striped possum), Catania, Collins, and Kaas (2000) (hedgehog), Padberg, Disbrow, and Krubitzer (2005) and Padberg et al. (2007) (summary of titi, galago, macaque, and cebus monkey), Krubitzer, Campi, and Cooke (2011) (squirrel, rat), and Wong and Kaas (2009, 2010) (tree shrews, galagos). Conventions as in previous figures; see table 73.1 for abbreviations.

clearly defined area 1 that contains a complete representation of skin receptors of the contralateral body that mirrors that of area 3b (Padberg, Disbrow, & Krubitzer, 2005; Padberg et al., 2007). However, area 2 appears to be absent. Electrophysiological exploration

of cortex caudal to area 1 in titi monkeys revealed a field that had many of the properties of area 5 in macaque monkeys, specifically an extreme magnification of the forelimb and hand and a fractured map. These studies indicate that although posterior parietal

area 5 abuts area 2 in Old World monkeys, its relative position to somatosensory areas in most New World monkeys is different in that it is immediately adjacent to area 1 (or area 1–2). Based on its appearance in all monkeys that have been studied, the only certainty is that this posterior parietal region had already begun to expand in the common ancestor of New and Old World monkeys and likely contained multiple subdivisions.

New World cebus monkeys deviate from this general New World monkey plan of organization in which area 2 may be absent or combined with area 1. Rather, in cebus monkeys, a clear proprioceptive area 2 has emerged, and area 5L is a well-defined field with a distinct architecture and fractured topography (Padberg et al., 2007). We proposed that the emergence of area 2 in cebus monkeys coevolved with the large expansion of the neocortex, the evolution of the hand, and the emergence of opposable thumbs that allows for a precision grip. These differences also coevolved with changes in the corticospinal system in that there are direct and rich projections from motor cortex to alpha motor neurons of the ventral horn that control the muscles of the digits (Bortoff & Strick, 1993; Heffner & Masterton, 1983; Lemon & Griffiths, 2005). These alterations in both motor cortex and PPC are proposed to subserve the increased dexterity observed in cebus monkeys compared to their New World cousins and may form the basis for even greater cognitive, visuomanual abilities such as tool use.

Cebus monkeys selectively utilize tools under experimental conditions, and unlike macaques, also regularly use tools in the wild (e.g., Ferreira, Emidio, & Jerusalinsky, 2010; Schrauf, Huber, & Visalberghi, 2008; Visalberghi et al., 2007, 2009). They are arguably the best primate model for the study of tool use in humans. Cebus can also utilize the same tool for different tasks, they can use one tool to make another (Mannu & Ottoni, 2009), and they can learn to use a novel tool by observation (Fredman & Whiten, 2008). Thus, the implicit knowledge of object features and how they can be used to manipulate or transform other objects, once considered to be a unique feature of human brains, appears to be present to some degree in cebus monkeys as well.

Like cebus monkeys, these same abilities coevolved in humans with an expansion of the cortical sheet, an increase in the number of cortical areas, alterations in the connections within the brain, and changes in the morphology and use of the hand. The human hand–wrist consists of 27 bones and 39 intrinsic and extrinsic muscles (Hepp-Reymond, Huesler, & Maier, 1996) and has evolved a number of important changes including alterations in the size of the distal, middle, and proximal phalanges. The carpal and metacarpal joints—particularly the trapezium in the wrist, the articulation between the first and second carpals, and the metacarpophalangeal joints—have undergone significant alterations as did the size and position of associated ligaments (Lewis, 1977). The skin of the distal digit tips has evolved epidermal ridges and a high concentration of mechanosensory receptors such as Merkel disks and Meissner's corpuscles (Pare, Smith, & Rice, 2002). These transformations of the hand allow for an expanded repertoire of grips, including a precision grip in which the thumb can be opposed to digit 2 or other digits and independent use of individual digits. Many of these adaptations are proposed to have evolved for tool use (Marzke, 1997). Of course, in modern humans these adaptations of the hand and associated brain areas have been co-opted for tasks removed from those that would have exerted selective pressure on our hominid ancestors such as using a computer keyboard and intricate independent use of the fingers for playing a piano or violin. Interestingly, these are often learned as visuomanual skills but can progress to a stage (e.g., touch-typing) where vision is not necessary. This, in turn, allows for indirect but arguably more complex visuomotor integration such as sight-reading music. Thus, the most significant human adaptation for tool use may have been manual and cognitive flexibility.

While investigators have begun to explore the cortical areas associated with tool use in humans, the use of the traditionally used macaque model may not be appropriate for this specialization since they seldom use tools in the wild. Because of this dramatic ethological difference it is not surprising that although macaques and humans share homologous networks for hand use, including areas in PPC (e.g., 5 and AIP), ventral premotor cortex, and areas in temporal cortex (Gardner et al., 2007a, 2007b; Hinkley et al., 2009; Peeters et al., 2009; Valyear et al., 2007; Vingerhoets et al., 2009; Yalachkov, Kaiser, & Naumer, 2009), there are areas on the inferior parietal lobule associated with tool action that are unique to humans. Cebus monkeys, however, have independently evolved an opposable thumb, a precision grip, and tool selectivity, in addition to changes in motor cortex and PPC, so it is likely that they have evolved areas of the cortex analogous to those in humans (anterior supramarginal gyrus and superior parietal lobule) that represent tool action.

CONCLUSIONS

Our sense of three-dimensional space and our ability to move within and to physically manipulate objects in the world are, in addition to language, essential elements

of human experience and culture. When considering how and why PPC evolved in humans, a broader perspective is needed regarding the array of changes that have necessarily coevolved with this region. For example, changes in effectors of the body, such as the frontal placement of the eyes and the ability to rapidly and accurately place the retinal fovea in a region of interest, arose along with a ballooning set of specialized visual cortical areas involved in perceiving complex motion and honing in specifically on faces and hands. Changes to the morphology of that other main effector, the hand, expanded the ability to generate grip types from forceful to fine. These too occurred in tandem with elaboration of somatosensory areas of the post central gyrus and lateral sulcus. These effectors, eyes and hands, meet in an optimal ergonomic extrapersonal work space that is constrained by the geometry of the skeletal system and the acuity of the visual system. PPC appears to have expanded in concert with the new visual and somatosensory areas of the neocortex, and these inputs generate networks in PPC devoted to the coordination of the hands and eyes through the transformation of sensory information into a coordinate system in which actions can be initiated. The further expansion of areas on the inferior parietal lobule in the human brain where tool action is encoded is a significant departure from the effector-based computations of other posterior parietal areas. These unique human cortical areas represent the ultimate, often indirect goals that tools can achieve.

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