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3.14 Evolution of Parietal Cortex in Mammals: From Manipulation to Tool Use

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Abstract

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 our limbs. This manual dexterity coevolved with an expansion of posterior parietal cortex (PPC), which contains areas involved in programming voluntary movements, coding reach targets in multiple reference frames, and decision-making. To enable our body to interact with our physical surroundings, these fields must also construct an internal model of the physical self: our body's configuration, the boundary between our body and external physical objects, and the temporary expansion of that self as we wield a tool that extends our reach and manual capabilities. Such comprehension of where and what the self is and even the ability to manipulate objects and use them as tools did not evolve de novo in humans, but rather emerged from simple networks present in early mammals. In this chapter, we consider not only the structure and function of PPC in primates, but also include data from nonprimate mammals in an effort to understand the basic processing networks that were present in our early ancestors, and how these networks evolved and expanded in primates.

3.14.1 Introduction

The extraordinary degree to which humans can interact with and physically change the world around them can be attributed, in large part, to the ability to use our hands in a sophisticated and coordinated fashion. This was achieved by the coevolution of the hand and motor and posterior parietal cortical areas that program and control reaching, grasping, and object exploration and acquisition (Fig. 1). Primate posterior parietal cortex (PPC) is comprised of a constellation of areas that differ in their function and connectivity, as well as the effectors, such as the eyes and the hands, which they help control. However, these areas are not strictly involved in motor control, but rather sit at the interface of perception and action, combining sensory information from several modalities with effector kinematics to compute various movements tailored to specific objects and contexts (see Andersen and Cui, 2009; Gottlieb and Snyder, 2010 for review). Together with motor cortices, several areas within the primate PPC form the frontoparietal reaching and grasping network that allows primates to so successfully interact with and manipulate their environment.

This ability to physically interact with our environment requires the PPC to construct an internal model of the physical self: our body's configuration, the boundary between our body and external objects, and the temporary expansion of that self as we wield a tool that extends our reach and manual capabilities. Yet comprehension of where the self is and even the ability to manipulate objects and use them as tools did not evolve de novo in humans, but emerged from simpler networks that were present in early primates (60 million years ago) and possibly even early mammals (over 200 million years ago). PPC networks in different mammals often evolved to solve very similar problems (eg, grasping food and bringing it to the mouth), but it is not clear if the solution to executing these fundamental manual behaviors is the same across species, especially when animals differ in body and forelimb morphology, use different major effectors to explore their environments, and have been independently evolving



Figure 1 Five different mammals shown grasping a food item, and corresponding hand morphology. Note the well-developed hand of the human and macaque monkey compared to the paw of the rat with a recessed digit 1 (D1). *p*, pads; *th*, thenar; *Hth*, hypothenar. Hands are not drawn to scale.

for millions of years (Figs. 1 and 2). The solution, computed in PPC, is the integration of sensory inputs providing information on the size, shape, texture, and location of objects in space (eg, food) with the internal representation of the body's current posture, dimensions, and physical capabilities. The ultimate behavioral outcome (eg, feeding) is similar, but it is not known how PPC networks in different mammals produce this behavior. One major problem when considering the evolution of frontoparietal networks in mammals, in addition to the species differences in morphology and effector use noted above, is determining the best criteria to define cortical areas in PPC in a wide range of mammals so that direct comparisons can be made, accurate inferences regarding the ancestral state can be articulated, and an appreciation of the evolution of this region of cortex can be fully understood.

Traditionally, sensory cortical areas, such as the primary and secondary somatosensory, visual areas, and auditory areas (Table 1) have been precisely defined using multiple criteria, including architectonic appearance, functional map organization, and



Expansion of PPC in primates

Figure 2 Cladogram showing the phylogenetic relationship of five different mammals with each branching point indicating the time of the last common ancestor. Brains are drawn to scale except the human brain, which is greatly expanded compared to the other mammals depicted. The location of the primary somatosensory area, S1 (*red*), the primary visual area, V1 (*blue*), and the posterior parietal cortex (PPC; *green*) are depicted. Note that the relative size of the PPC is greatly expanded in primates, particularly in humans.

Table 1	Common abbreviations of cortical fields, thalamic nuclei, body parts, and		
anatomical directions in different mammals			

Cortical fields	
1	Anterior parietal area 1
1+2	Anterior parietal areas 1 and 2
2	Anterior parietal area 2
3a	Anterior parietal area 3a
3b	Anterior parietal area 3b; primary somatosensory area
5	Brodmann area 5
5D	Area 5 (dorsal division)
5V	Area 5 (ventral division)
7	Brodmann area 7
A1	Primary auditory area
Α	Auditory cortex
AIP	Anterior intraparietal area
DG	Dysgranular zone
IPd	Intraparietal depth area (in depth of IPS, adjacent to POa and and PEa)
IPS	Intraparietal sulcus
LIPd	Lateral intraparietal area (dorsal division)
LIPv	Lateral intraparietal area (ventral division)
M1	Primary motor area
M1/PM	Primary motor area/premotor area
OPT	Area OPT, overlaps caudomedial 7a
OTr	Occipital temporal area (rostral division)

(Continued)

Table 1	Common abbreviations of cortical fields, thalamic nuclei, body parts, and	d			
anatomical directions in different mammals—cont'd					

PF	Superior parietal lobule
DEn	Superior parietal lobule (anterior division)
F Ed	
PEC	Superior parietal lobule (caudal division)
PF	Rostral inferior parietal lobule area
PFG	Rostral inferior parietal lobule area (transition area
	hetween PE and PG)
50	
PG	Rostral interior parietal lobule area
PGm	Rostral inferior parietal lobule area (medial division)
PM	Parietal medial area
PO	Parietal occipital area (V6 + V6a)
DO:	Derietal accipital area ($vo + voa$)
PUa	Parietal occipital area (anterior division)
PPC	Posterior parietal cortex
PPCc	Posterior parietal cortex (caudal division)
PPCr	Posterior narietal cortex (rostral division)
DV	Pariotal ventral area
F V	
S1	Primary somatosensory area
S2	Second somatosensory area
S2/PV	Second somatosensory area/parietal ventral area
63	Third sometosensory area
33	
IA	Temporal anterior area
TD	Temporal dorsal area
V1	Primary visual area
V2	Second visual area
	Vontral intronariatal area (lateral division)
VIPI	ventral intraparietal area (lateral division)
VIPm	Ventral intraparietal area (medial division)
Sulci	
CS	Central sulcus
	l ataral sulcus
LO	
IPS	intraparietai suicus
PCS	Precentral sulcus
Thalamic nuclei	
	lateral doreal nucleus
LD	
LP	Lateral posterior nucleus
Body parts	
cn	Chin
D1	Digit 1
dia	Digito
uly	Digits
fa	Forearm
fl	Forelimb
gen	Genitals
h to m	Hand to mouth
ni	Hindlimb
Hth	Hypothenar pad
11	Lower lip
nk	Neck
	Occinut
p1	Pad 1
p2	Pad 2
p3	Pad 3
n/	Pad 1
р л	r au T Choulder
SII	Shoulder
sn/j	Snout/jaw
T1	Toe 1
T1-2	Toes 1–2
T5_2	Toos 5-2
10-2	
th	Thenar pad
tr	Trunk
ul	Upper lip
Antaomical directions	
	Martial
IVI	Mediai
R	Rostral
Other	
mya	Millions of years and



Figure 3 Myeloarchitecture of parietal and motor cortex in rats, tree shrews, and galagos. In all three species, S1 is darkly stained, and its rostral and caudal boundaries are easily identified. In all three species, PPC has at least one medial moderately staining field and, in rats and tree shrews, lateral lightly staining field. We have tentatively termed these fields "PPCm" and "PPCI" in rats and tree shrews and have added the term "medial" to the PPCr subdivision in galagos. In galagos, PPCc is caudal to the divisions of PPCr and is not shown in this image. To determine homology of these fields across species, multiple criteria should be used including connections with motor cortex as well as the presence of motor maps generated using intracortical microstimulation. Abbreviations are in Table 1.

neuroanatomical connections. For example, the primary somatosensory area (S1) in all species examined has a distinct myeloarchitectonic and cytoarchitectonic appearance (Fig. 3). This architectonically defined field is coextensive with a complete map of cutaneous receptors of the contralateral body (Fig. 4), as well as a distinct set of thalamocortical, corticocortical, and interhemispheric connections. While these features clearly define S1 in all mammals tested, there are also derivations in S1 that are species specific. One such specialization is the cortical magnification of the representation of behaviorally relevant body parts such as the vibrissae of many rodents, the nose of star-nosed moles, the bill of platypuses, and the hand of primates (eg, Dooley et al., 2014; Fig. 5). Despite these specializations, S1 can still be defined across species and is considered homologous (inherited from a common ancestor).

Unfortunately, these same criteria are difficult to utilize when defining cortical fields in PPC. Cortical fields in PPC are not always distinct using traditional cytoarchitectonic methods. In addition, most often there is not a complete topographic representation of the sensory receptor array and a cortical magnification of behaviorally relevant body parts.

Other factors also make it difficult to clearly identify PPC. Neurons in PPC often do not respond in anesthetized animals. While a number of investigators have examined specific areas in PPC using single unit techniques in awake, behaving macaque monkeys (see later discussion), there is a paucity of similar data in other mammals. Further, even studies where such data do exist in other



Figure 4 Topographic maps of the body in four anterior parietal fields in macaque monkeys including areas 3a, 3b, 1, and 2. These maps were generated by recording from multiple sites in anterior parietal cortex (see *red box* in brain drawing at the top) and determining receptive fields on the body for neurons at each site. The body parts represented in the different maps are color coded and correspond to the body image to the left. Areas 3b and 1 contain maps of cutaneous receptors of the contralateral body, while areas 3a and 2 contain maps of deep receptors, muscle spindles, and Golgi tendon organs. Only area 3b corresponds to S1 in other mammals. Note that all body parts are represented, but more space is devoted to representing specific body parts (such as the hand and forelimb) compared to others (such as the trunk). Abbreviations are in **Table 1**. Combined maps have been adapted from Seelke, A.M., Padberg, J.J., Disbrow, E., Purnell, S.M., Recanzone, G., Krubitzer, L., 2012. Topographic Maps within Brodmann's Area 5 of macaque monkeys. Cereb. Cortex 22, 1834–1850.

mammals (eg, Marigold and Drew, 2011; Harvey et al., 2012; Whitlock et al., 2012; Whitlock, 2014), it is unclear if investigators are recording in homologous cortical areas. There are 5500 species of mammals distributed across 29 orders (Roskov, 2015). The order Rodentia alone is composed of 29 families. Despite the extraordinary diversity of extant mammals, most of what we know about PPC is from studies in primates, specifically macaque monkeys, and more recently, rats. Because of this, it is difficult to appreciate if there are homologous cortical areas in PPC across mammals and if there is a basic frontoparietal network that has evolved and been modified in different lineages. Importantly, because of the limited number of species examined, it is difficult, if not impossible, to directly relate data collected in rodents with data collected in primates.

To understand how PPC and frontoparietal networks emerged in mammals, became expanded in primates, and ultimately became one of the hallmarks of human brain evolution, a comparative approach drawing on data from a variety of mammals is



Figure 5 Examples of magnification of behaviorally relevant body parts in sensory and motor cortex of different mammals. The duck-billed platypus has an enormous representation of the bill in S1 and two adjacent regions of somatosensory cortex (A). The representation of the nose of the starnosed mole is also magnified in S1 and surrounding sensory cortex (B) as is the whisker representation in the rat (C). Similar magnifications of behaviorally relevant body parts such as the superlaryngeal tract and oral structures are also observed in S1 of humans (D). Magnification of these body parts are also observed for movement representations in motor (M1) and premotor (PM) cortex, and together this region is often referred to as Broca's area. However, it should be noted that while Broca's area is a specialization of humans, the principle of cortical magnification is common to all mammals investigated. Abbreviations are in **Table 1**.

crucial. Making direct comparisons across a number of species, and ultimately linking these data to the disproportionally large data set in primates, will require the equal application of multiple techniques that can be used in animals that are less amenable to awake, behaving preparations.

In this chapter we will begin by outlining techniques that can be used effectively to explore PPC in primate and nonprimate mammals to help us define homologies across species. We will then briefly discuss what and where PPC is and examine the incomplete data sets for the existence of PPC in rodents and other nonprimate mammals. This chapter is not meant to be exhaustive, but aims to provide an understanding of the difficulty in determining homologies in PPC, and to explore the limited data that allow us to begin to construct a story on the evolution of PPC in mammals in general and primates in particular. Following this we will review both the classic and contemporary studies in primates that have allowed researchers to distinguish PPC from surrounding cortex based on anatomical and physiological criteria complemented by loss of function studies such as lesions and reversible deactivation. We focus mainly on areas in and adjacent to the intraparietal sulcus (IPS) in macaque monkeys, particularly in the context of manual behavior and tool use.

3.14.2 The Use of Long-Train Intracortical Microstimulation to Define Movement Representations in Motor Cortex and Posterior Parietal Cortex in Mammals

Over a decade ago it became clear that traditional views of motor cortex organization in macaque monkeys did not capture the complexity in organization that actually exists. Rather than a relatively simple map of movements of a selected portion of the body evoked with short-train intracortical microstimulation (ST-ICMS), the use of long-train intracortical microstimulation (LT-ICMS) revealed that in macaque monkeys there were domains of ethologically relevant movements overlaid upon this simple, grossly topographic motor map of the body (Graziano et al., 2005; Gharbawie et al., 2011b; Cooke and Graziano, 2004). Recently, using LT-ICMS, such domains have been demonstrated in squirrel monkeys, owl monkeys, and galagos, indicating that this type of organization of M1 is a general primate phenomenon (eg, Gharbawie et al., 2011a; Stepniewska et al., 2005, 2014). Similarly, this technique has been used recently to explore motor cortex in rats and tree shrews (Brown and Teskey, 2014; Baldwin et al., 2016; Cooke, 2016). As in primates, movement domains have been discovered, although they are

fewer in number. Despite these differences, these data in nonprimate mammals suggest that this type of organization of motor cortex evolved prior to the emergence of primates.

Important for our discussion, LT-ICMS has been used to subdivide divisions of PPC in New World monkeys (see Kaas et al., 2011, 2013 for review), galagos (Stepniewska et al., 2005, 2011; Cooke et al., 2015), and recently macaque monkeys (Baldwin, 2016). Recent work demonstrates that LT-ICMS can be used effectively in nonprimate mammals such as tree shrews and rats to appreciate the functional organization of PPC (Baldwin et al., 2016; Cooke, 2016). Thus, the use of LT-ICMS across cortical areas, especially within PPC, can provide insights into similar features of organization as well as the possible changes and specializations that have emerged across different cortical fields and mammalian orders. Indeed, with a lack of robust anatomical markers, and with the difficulty of obtaining and comparing neural responses to sensory stimulation within PPC of various species, LT-ICMS may be the best tool at this point in time for revealing homologies of this cortical region. However, we do not suggest that this is the only technique that can be used to help identify homologies in PPC. Rather, this technique promises to be an important first step in defining regions of PPC across primate and nonprimate mammals, and thus can guide future studies, using other techniques (eg, single unit recordings in awake animals), as to the location and size of possible homologous fields in PPC across mammals.

3.14.3 Where and What Is Posterior Parietal Cortex in Nonprimate Mammals?

To establish how the primate PPC may have evolved from the very small neocortex dominated by sensory areas in early mammals, one must have a definition of PPC that can span multiple species. As will be discussed later in the chapter, PPC in macaque monkeys is traditionally comprised of Brodmann architectonically defined areas 5 and 7. In nonprimate mammals, however, no easily identifiable homologues of these regions, distinguished using traditional architectonic methods, exist. While a number of studies of "PPC" have been conducted on rats, criteria for defining rodent PPC are not stated, are insufficient, or are omitted entirely. Indeed, making direct extrapolations from rats to monkeys is difficult if not impossible without examining the status of PPC in other mammals.

In this portion of the chapter we review data from a number of nonprimate mammals in which multiple criteria have been used, either in isolation or in combination, to define PPC. Probably the simplest definition of PPC is based on location. PPC can be defined as the region of cortex located between visual (V2) and somatosensory cortex (S1) (Fig. 6). However, this definition presents a problem in large-brained mammals in which there is a huge expanse of cortex between V2 and S1, and additional somatosensory fields (eg, areas 1 and 2) are present caudal to S1 proper (area 3b), and additional extrastriate fields are present rostral to V2. These additional fields are usually not considered part of PPC, but defining the exact boundaries between them and PPC can be difficult. Thus, even if a mammal (be it large or small brained) has an architectonically distinct region between \$1 and V2, one must first eliminate the possibility that it is an additional somatosensory or extrastriate visual field. PPC can also be defined by its connections, particularly direct and dense connections between motor cortex and rostral portions of PPC (PPCr), and direct inputs from visual cortex to caudal portions of PPC (PPCc). While some divisions of PPC are architectonically distinct in nonprimate mammals, there are little comparative data in which similar stains and techniques have been used across species and directly compared. However, our own laboratory has begun an architectonic analysis combined with LT-ICMS in several species of mammals including primates in an effort to make direct comparisons and establish homologous areas within PPC across species (eg, Fig. 3). Electrophysiological recordings have also been made in PPC in nonprimate mammals, but most of this work has been done in anesthetized preparations in which neurons in PPC often respond poorly (eg, squirrels, tree shrews, ferrets). As noted earlier, modern studies using LT-ICMS indicate that this technique in combination with others (eg, neuroanatomy, cortical architecture) may well be the best combination of current methods for use in a variety of primate and nonprimate mammals to determine homologous cortical areas within PPC as well as species-specific derivations.

3.14.3.1 Rodents

In rats, Krieg (1947) and later Kolb and Walkey (1987) identified a thin strip of cortex between "S1" and areas 18a and b as presumptive PPC, which corresponds to Krieg area 7. Several lines of evidence have been put forth to support the assertion that this region is homologous to primate PPC. This region in rats, called PM (parietal medial area) or Sc (somatosensory caudal area) by others (see Krubitzer et al., 2011; Ebner, 2015 for review), has been shown to have a pattern of thalamocortical connections that distinguish it from surrounding visual and somatosensory cortices (Chandler et al., 1992; Reep et al., 1994). Specifically, rat PM/PPC receives most of its input from thalamic nuclei LD and LP while receiving no input from the visual (dorsal lateral geniculate) or somatosensory [ventrobasal (VB) complex] nuclei that characterize V2 and S1, respectively. While this is indeed a compelling and distinctive feature of this region of rat cortex, the thalamocortical connections with PPC in other species have not been consistently documented and thalamocortical connections of PPC in primates have significant differences. Although both primate areas 5 and 7 receive a large amount of input from LD and LP as in rat PPC, they also receive input from several divisions of the VB complex (Padberg et al., 2009; Schmahmann and Pandya, 1990).

Perhaps the most compelling neuroanatomical evidence for rat PM/PPC being homologous to portions of primate PPC is the convergence of afferents from multiple sensory modalities. Miller and Vogt (1984) demonstrated that cortex immediately caudal to rat S1 (PM/Sc/PPC) receives dense projections from areas 18a/b as well as some sparse projections from area 17. Similarly, this region receives inputs from S1 (Fabri and Burton, 1991), particularly the dysgranular zone (Kim and Lee, 2013), and M1



Posterior parietal cortex in nonprimate mammals

Figure 6 Posterior parietal cortex in nonprimate mammals. Based on a number of different criteria including location relative to S1 and V2, connections with somatosensory and motor cortex versus visual cortex, and neural response properties (see text), this figure illustrates our hypothesis regarding the status of PPC in nonprimate mammals. Although the data are limited and not all criteria are used conjointly in the same animals, there is evidence for a rostral division (PPCr) and a caudal division (PPCc) in eutherian mammals and marsupials. There are limited data in monotremes, but a very small region of cortex in which neurons receive inputs from both visual and somatosensory cortex and in which neurons respond to visual and somatosensory stimulation is present. While these similarities suggest homologies with primates, they do not imply analogy (similar function), since primate PPC is greatly expanded and contains multiple divisions associated with the contextual use of major effectors (eg, hands and eyes). Rostral is left and medial is to the top. These figures are not drawn to scale. The scale bar = 2 mm. Cortical fields are color coded (see key). Abbreviations are in **Table 1**.

(Mohammed and Jain, 2016) as well as from orbital and agranular frontal cortices (Kolb and Walkey, 1987; Reep et al., 1994). Unfortunately, since the rostrocaudal extent of PM/PPC is relatively thin (Fig. 6), it is quite difficult to inject neuroanatomical tracers into this area without contaminating adjacent somatosensory and visual cortices. This makes interpreting the results of neuroanatomical tracing studies of this area challenging. Similarly, although lesioning PM/PPC can evoke a suite of deficits that resemble those of primate PPC lesions, it is difficult to do so without encroaching on adjacent sensory cortices (Kolb and Walkey, 1987; Pinto-Hamuy et al., 1987).

Given the multimodal inputs to rat PM/PPC, one would expect to find an abundance of neurons responsive to multiple sensory modalities. Wallace et al. (2004) explored this by recording the proportion of neurons responsive to multimodal stimulation throughout sensory cortices in the anesthetized rat. While some of these neurons were found within PM/PPC, almost all were recorded at the border between this area and visual cortices. This phenomenon was also observed at the border between visual and auditory cortices as well as somatosensory and auditory cortices, something that has been observed by other groups exploring these border regions (Di et al., 1994). This suggests that these multimodal responses may represent a feature of cortical border regions rather than PM/PPC representing a site of multimodal convergence. Additionally, a much larger proportion of neurons that respond to multimodal stimulation was observed in anterior parietal (somatosensory) cortex compared with PM/PPC, a finding supported by connections between areas 18a/b and S1 (Miller and Vogt, 1984). Thus, neurons responding to multisensory stimulation are at the very least not a unique feature of PM/PPC when compared with adjacent cortices in rats. This raises the question of whether multisensory neurons are a defining feature of PPC in general, and if so, in what proportions must they be present. Interestingly, preliminary data from our laboratory indicate that movements can be evoked in rat PPC when LT-ICMS is used (Fig. 7). We find that PPC is dominated by representations of vibrissae movements, the major effector in the rat.

Data from other rodents such as squirrels indicate that cortex caudal to S1 and rostral to V2 has similar features as those described in the rat. Cortex just caudal to S1 has also been termed PM/PPC in squirrels (Krubitzer et al., 1995; Slutsky et al., 2000; see Krubitzer et al., 2011 for review), and neurons in this region are responsive to stimulation of deep receptors of the skin and joints. As in rats, squirrel PM/PPC has dense interconnections with M1 and area 3a (probably homologous to rat dysgranular zone in S1) and moderate connections with S1 (Krubitzer et al., 1986; Cooke et al., 2012), but these connections are with the more rostral portion of PPC. The caudolateral portion of this PPC region receives inputs from V1 and V2, although it was called OTr in an earlier study (Kaas et al., 1989). For consistency with the rat and other species, we refer to the rostromedial, somatomotor-receiving portion of PPC in rodents as PPCr and the caudolateral, visual portion of PPC as PPCc (Fig. 6). Obviously, more data on thalamocortical and corticocortical connections to these regions combined with architectonic analysis and LT-ICMS are needed in squirrels and other rodents to come to any firm conclusions about homology of PPC in different rodents and between rodents and primates.

Taken together, the data from rodents such as squirrels and rats indicate that there is a region of cortex between S1 and V2 that shares some of the features of some of the anterior portions of PPC in primates (PPCr). These include dense connections with motor and somatosensory cortex, some aspects of architecture, and the ability to evoke movements of major effectors when using LT-ICMS. While this region in some studies in rodents and other mammals was originally considered a somatosensory area (termed PM/Sc), we believe that the data indicate that this might be part of PPC. Further, a caudal portion of PPC (PPCc) appears to be more associated with the visual system, as evidenced by connections from V1 and V2. However, as noted later, PPC in primates, even those with a relatively small neocortex, is expansive and contains multiple cortical fields. Thus, without comparisons with other mammals, it is unclear if either part of PPC in rodents is homologous to any of the multiple PPC fields identified in primates.

The earlier section is a brief overview of the relative location and divisions of PPC in rodents, some of the neuroanatomical connections of PPCr and PPCc, and to a more limited extent, neural responses of the PPCr in anesthetized animals. There have been electrophysiological recording studies in awake rats and mice, and these studies indicate that cortex between S1 and V2 (although the actual location of recording is often times not demonstrated) is involved in a variety of functions, such as generating frames of reference for navigating the environment, spatial attention, perceptual decision-making (see Harvey et al., 2012; Krubitzer et al., 2011 for review; Wilber et al., 2014) as well as visual attention, working memory, and movement planning (see Whitlock, 2014 for review). Thus, PPC in rats computes navigational movement plans to generate meaningful interactions (eg, finding, acquiring, and eating food) within a spatial environment in an analogous manner to reaching and grasping movements that are computed in PPC in monkeys for acquiring target objects (Whitlock, 2014). Our recent preliminary data (Fig. 7) indicate that movements can be elicited in parietal and portions of PPC in rats and many of these evoked movements involve the vibrissae. These data suggest that comparisons between rats and monkeys may now be tractable if (1) standard, parallel techniques are utilized to define fields in PPC, and (2) species with intermediate types of organization and appropriate phylogenetic relationships are used as a link when making these comparisons.

3.14.3.2 Carnivores

Studies in both cats and ferrets in which neuroanatomical connections and neural response properties have been described indicate that cortex caudal to somatosensory cortex and rostral to visual cortex has some of the properties of PPC described in rodents, tree shrews (see later discussion), and primates. Immediately caudal to S1 in cats and ferrets is a field termed S3 (Garraghty et al., 1987; Foxworthy and Meredith, 2011). In cats a complete representation of the contralateral body has been described (somewhat similar to PM in squirrels), while in ferrets only representations of the face have been described in this same region. Just caudal to S3, cortex has been termed area 5 or 5a in cats (eg, Babb et al., 1984; Lajoie et al., 2010) and PPr in ferrets (Manger et al., 2002; Foxworthy et al., 2013a). Because we hypothesize that PPr in ferrets is homologous to PPCr in other species, we will term this field PPCr in ferrets for consistency and clarity. PPCr in ferrets contains neurons that respond to multimodal stimulation (Foxworthy et al., 2013b), and this region of cortex receives dense inputs from somatosensory cortex with moderate-to-small inputs from visual areas. Manger et al. (2002) report a gross retinotopy and somatotopy in PPCr, and this field appears to be dominated by the representation of the forelimb. Just caudal to PPCr in ferrets is a field termed PPc by Manger et al. (2002). Again, because of presumed homology with other species, we will term this field PPCc, which has also been explored by these same investigators and found to contain a gross retinotopic



Long-train ICMS in PPC

Figure 7 Motor maps of frontal and parietal cortex based on movements evoked by intracortical microstimulation (ICMS) at multiple sites in rats, tree shrews, and galagos. Different body part representations are color coded (see key at right); multiple body part movements are indicated by multicolor stripes. Note that rat PPC is dominated by vibrissae domain, the galago PPC is composed of multiple domains associated with movements of the hand and forelimb and represents ethologically relevant behaviors. Tree shrew PPC contains domains associated with the vibrissae and face, but also has domains associated with movements of the forelimb and hindlimb. See **Table 1** for abbreviations.

organization. Thus, PPCc appears to be more closely aligned with the visual system. This region of cortex in ferrets and cats receives inputs from V1 (Rockland, 1985; Han et al., 2008) and from extrastriate cortex in cats (eg, Olson and Lawler, 1987). While the overall organization has not been described for these fields in cats, lesion and single unit recording studies in the rostral portion of PPC (cat area 5) suggest that this region is involved in visually guided locomotion and computing the visuomotor transformations necessary for gait modification during locomotion (Lajoie and Drew, 2007; Lajoie et al., 2010;

Marigold and Drew, 2011). This rostral region of PPC in cats, as in ferrets, has interconnections with motor cortex (eg, Babb et al., 1984; Andujar and Drew, 2007). Taken together, the data in ferrets and cats indicate that PPC can be divided into two gross divisions, one rostral that has neurons with multimodal responses and interconnections with motor cortex, and a more caudal region, more closely aligned to the visual system. These may correspond to similar regions in rodents although the data are too sparse to support any firm conclusion. The status of S3 when compared to regions in rodent cortex is unclear. While it may resemble PM in squirrels and rats, it may also be a region unique to cats, since it appears to be much more like a somato-sensory field than a posterior parietal field.

3.14.3.3 Tree Shrews

Tree shrews are the closest living relative to primates and therefore represent an important animal model that can help link data from nonprimate mammals with that from primates. Early electrophysiological recording studies reported that immediately caudal to S1 lies a very narrow strip of cortex (less than 1 mm wide) that contains neurons responsive to somatic stimulation (Sur et al., 1980); these investigators termed this field Sc. However, no data were actually shown to support the existence of this field so its presence in tree shrews is questionable. Recent work in tree shrews in which neuroanatomical data were combined with ST-ICMS indicates that cortex caudomedial to S1 has dense interconnections with M1 (Remple et al., 2006). Based on location, this region includes Remple et al.'s (2006) Sc, as well as their areas PPd and TA (Remple et al., 2007). While the use of ST-ICMS failed to elicit movements in cortex caudal to S1 in tree shrews, recently our laboratory utilized LT-ICMS and found that movements can be evoked in a large swath of cortex in this region caudomedial to S1 which we term here PPCr (Fig. 7). Unlike movements evoked from a similar location in rat cortex, the suite of movements which can be evoked by LT-ICMS in tree shrew PPCr is not dominated by movements of the vibrissae, but has a more complete representation that includes not only portions of the face, but the forelimb and hindlimb as well. When compared with galagos, a prosimian primate, the organization of tree shrew PPC has a number of similarities (Fig. 7; see later discussion). However, additional work examining the connections of this field setween tree shrews and primates (if they are present).

As in rodents and carnivores, tree shrew PPC can be grossly divided into two regions based on inputs from different regions of cortex. The rostromedial region noted earlier (PPCr) contains movement domains identified using ICMS and has dense projections from M1 (and moderate projections from S1). A caudolateral region, referred to in previous studies as TD (Sesma et al., 1984) but here referred to as PPCc, receives input from both V1 and V2. Although sparse, these data appear similar to that described in rodents and carnivores.

3.14.3.4 Marsupials and Monotremes

Marsupials appear to have a PPC, or at least a small region of cortex between S1 and V2 that has several features of organization that are similar to rodents, carnivores, and tree shrews. Cortex immediately caudal to S1 has been demonstrated to contain neurons responsive to stimulation of deep receptors of the contralateral body in several marsupials (see Huffman et al., 1999; Elston and Manger, 1999). While receptive fields for neurons in this location have been defined for some of these species (eg, native cat, striped possum, brush-tailed opossum), in some species this region of cortex is extremely narrow in width and thus is difficult to record from. It has been termed C or Sc (Beck et al., 1996; Huffman et al., 1999), but like the data reviewed earlier, we believe that an alternate interpretation is that this cortex is part of the rostral division of PPC (termed PPCr). As in the species discussed earlier, in the marsupials that have been investigated PPCr receives input from S1 (Beck et al., 1996; Elston and Manger, 1999; Dooley et al., 2013) and from cortex just rostral to S1 [although it is not known if this frontal region is homologous with motor cortex in other mammals (Beck et al., 1996; Karlen and Krubitzer, 2007)]. Somewhat caudal to this, neurons are unresponsive or respond to multimodal stimulation including some combination of visual + somatosensory + auditory stimulation (Huffman et al., 1999). Further, the few studies of connections that have been done indicate that this caudal region (termed differently by different investigators) receives inputs from visual cortex (Crewther et al., 1984; Elston and Manger, 1999; Dooley et al., 2013; Martinich et al., 2000), much like PPCc in other species.

There is very little information available regarding PPC in monotremes. Extensive electrophysiological recording in these animals indicates that location is not a reliable criterion for defining PPC because the layout of the usual neighboring cortical fields in the two species that have been studied (duck-billed platypus and echidna) is remarkably different than in other mammals. Specifically, the monotreme primary visual cortex is located medial, rather than caudal to S1, and auditory cortex is embedded between S1 and S2/PV (Krubitzer et al., 1995). However, there is a small strip of cortex between V1 and S1 in which neurons respond to both somatosensory and visual stimulation (Fig. 6). There are no data on connections of this region in platypus and only limited data on connections of S1 and V1 in echidnas indicating that it receives inputs from both S1 and V1 (Krubitzer, 1998). Thus, we tentatively call this area PPC.

3.14.3.5 Conclusion

Taken together, the data reviewed here from rodents, tree shrews, carnivores, marsupials, and monotremes, as well as data from other nonprimate mammals such as flying foxes indicate that cortex that resides caudal to S1 and rostral to V2 has some of the

features of PPC described in primates. We tentatively term this region PPC and suggest that in all nonprimate mammals tested there is evidence that this region has at least two subdivisions. In species in which LT-ICMS has been used to delineate PPC, movements can be evoked in the rostromedial portion of PPC, in PPCr (eg, tree shrews). The comparative data in marsupials indicate that they appear to have two divisions of PPC with general characteristics of those of their eutherian counterparts, but the relative proportion of this cortex is much smaller. Thus, the presumptive PPCr and PPCc may have been present in the last common ancestor of marsupials and eutherians some 180 million years ago. The presence of a PPC-like region in monotremes seems unlikely since so little cortex exists between known sensory areas.

It is unclear if the rostral portion of PPC should be considered a caudal somatosensory area (terms PM, Sc, and analogous to primate area 1/2) that is situated between PPC and S1 in most of the species examined, or if this region of cortex should be included as part of PPC, specifically the rostral division of PPC termed PPCr, analogous to parts of primate area 5. This region of cortex is often characterized by neurons responsive to somatic stimulation (and in ferrets multimodal stimulation) and is interconnected with somatosensory cortex in all of the marsupials and eutherian mammals examined, and in eutherians with motor cortex as well. In the caudal portion of nonprimate PPC shares connections with visual cortex.

While this brief overview of the general organization of PPC in nonprimate mammals provides some insights into its evolution, it does not discuss how this cortex has coevolved with the unique behavioral repertoires that different animals possess. Importantly, we do not wish to imply that only two subdivisions of PPC exist in nonprimate mammals, but rather we tried to evaluate data in a way that would allow us to extract similarities between species. The methodological challenges we outlined earlier make defining homology in PPC incredibly difficult. Doing so will require multiple criteria and converging data from a variety of species. Even then, appreciating homologous divisions between species as disparate as mice and macaque monkeys may prove impossible. Perhaps the most critical element in this research program will be electrophysiological data in awake behaving animals from a few well-chosen species, which may reveal common features of the PPC cortex (if they exist), and how they evolved and expanded in primates.

3.14.4 Primates

The vast majority of what we know of PPC has come from studies in primates. Throughout the course of primate evolution, alterations in the morphology of the hand have allowed various species to exploit specific ecological niches and execute a variety of foraging and predation strategies (see Boyer et al., 2013; Almecija/Sherwood chapter 3.16, Hands, Brains, and Precision Grips: Origins of Tool Use Behaviors for review). Among these alterations, the evolution of an opposable thumb capable of performing a precision grip distinguishes catarrhines (humans, apes, and Old World monkeys) from most platyrrhines (New World monkeys), who primarily employ whole-hand power grasps to manipulate objects (see Napier and Tuttle, 1993). The exception to this is the New World tufted capuchin (also called cebus) monkey (Sapajus apella), which not only possesses an opposable thumb capable of performing a precision grip, but also uses these features to create and employ tools to perform various tasks (Christel and Fragaszy, 2000; Fragaszy et al., 2004; Spinozzi et al., 2004; Fig. 8). Perhaps unsurprisingly, these monkeys appear to have evolved a frontoparietal network that bears striking resemblance to that of Old World monkeys (Padberg et al., 2007). This remarkable example of homoplasy highlights the fact that the evolution of the hand and the brain areas supporting its movement are constrained, perhaps by the contingent nature of the genetic cascades involved in cortical development. This represents a compromise between contextual and experientially driven cortical plasticity and the homologous features of mammalian cortical organization that dictate the ways in which the cortical phenotype can be changed to solve a given problem (see Krubitzer, 2007 for review). In this case, this combination of form and function represents a common solution to a common evolutionary puzzle: how to analyze object affordances and compute movements that allow for interacting with that object in different ways depending on the current behavioral circumstances.

Direct measures and manipulations of the PPC have historically been performed in various species of macaque, which represent ideal animal models given the similarity in hand morphology to humans as well as the perceptual abilities critical to its use (ie, vision and somatosensation). Though it has been extensively subdivided in more contemporary investigations, the PPC is usually characterized as being comprised of Brodmann areas 5 and 7 (Fig. 9). Traditionally termed "association" cortex, most early investigations of these regions involved electrical stimulation in humans and other primates, with stimulation of area 7 generally eliciting arm, hand, and face movements laterally and eye movements medially. While stimulation of lateral portions of area 5 also elicited arm and face movements, more medial stimulation evoked trunk and hindlimb movements (eg, Fleming and Crosby, 1955). Early lesion and ablation experiments converged on several themes with regard to removal of various areas of the parietal lobe: unlike motor cortical lesions, parietal lesions did not cause paralysis of the contralateral body. Instead, subjects would display a reluctance to use the affected limb, hypotonia of that effector's muscle groups, weak or incomplete grasping, general ataxia, and erroneous limb trajectories which could be somewhat ameliorated by direct visual attention (see Peele, 1944 for review). Peele (1944) performed one of the first systematic, albeit qualitative, investigations of the effects of lesioning different areas of the parietal lobe alone or in combination. These results were generally congruent with electrical stimulation studies: lesions of areas 5 or 7 produced deficits which were less severe than ablation of anterior parietal cortex (APC; areas 3, 1, and 2) resulting in awkward movements and an ataxia that was ameliorated by visual attention or a heightened emotional state. Lesions to area 5 produced more severe deficits in movements of the hindlimbs while lesioning area 7 produced greater forelimb deficits. In addition, lesions to either area resulted in poor detection of various somatosensory stimuli and resulted in an inability to discriminate items by feel (such as food) without visual guidance.



Phylogeny of cortical areas and manual abilities in primates

Figure 8 A cladogram showing different primate taxa and characteristics of hand and hand use (eg, opposable thumb, complex manipulation, tool use) and cortical organization (eg, presence of an area 2, corticospinal terminals in the ventral horn of the spinal cord) that each species possess. Note that the only New World monkeys to possess features of the hand, uses of the hand, and cortical organization similar to that of many (but not all) Old World monkeys and humans are the cebus monkeys. Cebus monkeys possess additional somatosensory areas caudal to S1 (areas 1 and 2) while these areas are not apparent in other New World monkeys. Further, like anthropoid primates, cebus monkeys have a large expansion of posterior parietal cortex. Abbreviations are in **Table 1**. The cladogram was adapted from van Schaik, C.P., Deaner, R.O., Merrill, M.Y., 2003. The conditions for tool use in primates: implications for the evolution of material culture. J. Hum. Evol. 36, 719–741 and the illustration of the brain and hands is adapted from Padberg, J., Franca, J.G., Cooke, D.F., Soares, J.G., Rosa, M.G., Fiorani Jr., M., Gattass, R., Krubitzer, L., 2007. Parallel evolution of cortical areas involved in skilled hand use. J. Neurosci. 27, 10106–10115.

Though these early studies generated important hypotheses about the function of these "associative" cortical areas, elucidating the response properties of individual neurons remained difficult due to the lack of stimulus-driven activity that could be evoked under general anesthesia. However, with the advent of awake (Duffy and Burchfiel, 1971) and awake-behaving monkey preparations (eg. Sakata et al., 1973; Hyvarinen and Poranen, 1974; Mountcastle et al., 1975), researchers began to appreciate the complexity of the neural networks that comprise the PPC. This wealth of physiological data produced by awake preparations coincided with ever-increasing refinements in both connection tracing and architectonics, which allowed researchers to subdivide the two large fields in PPC initially described by Brodmann into multiple cortical areas (eg. Seltzer and Pandya, 1986, 1980; Pandya and Seltzer, 1982; Preuss and Goldman-Rakic, 1991; Lewis and Van Essen, 2000a,b; see Fig. 9).

In the following sections we describe both early and more contemporary investigations of the neuronal response properties of primate areas 5 and 7, focusing mainly on the rostrolateral portions that have been studied in the context of complex manual dexterity. Compared to other mammals, we devote more space to what is known about these areas in primates (specifically rhesus macaques). The reason for this is that these studies represent the largest and most detailed set information about the functional properties of PPC neurons in any mammal. This is largely due to the fact that, given the current state of technology, macaques represent the animal model most amenable to the types of awake-behaving electrophysiology necessary to reveal the unique sensorimotor responses of PPC neurons. As such, almost any investigation of PPC in other mammals must be considered in the context of monkey data to determine not only what might constitute PPC, but also whether a given PPC region is homologous.



Different schemes for organization of PPC in macaque monkeys

Figure 9 Architectonic maps of posterior parietal cortex described in different studies. One of the first architectonic studies of this region of cortex was by Brodmann (1909). In this early study (A), two large divisions of cortex were described, area 5 (*light green*) and area 7 (*dark green*). Subsequently, different schemes of how this cortex was organized in macaque monkeys were proposed by different investigators (B–D). While different investigators have proposed different schemes of organization, all agree that multiple cortical fields exist within this large expanse of cortex. Abbreviations are in **Table 1**. This figure was adapted from Seelke, A.M., Padberg, J.J., Disbrow, E., Purnell, S.M., Recanzone, G., Krubitzer, L., 2012. Topographic Maps within Brodmann's Area 5 of macaque monkeys. Cereb. Cortex 22, 1834–1850.

3.14.4.1 Brodmann Area 5: Early Studies

Brodmann area 5 in monkeys occupies a large section of cortex caudal to area 2 on the postcentral gyrus and extending into the IPS where it abuts a portion of area 7. Its share of the postcentral gyrus is widest medially where at the midline it wraps onto the medial wall where it extends just beyond the cingulate sulcus (Brodmann, 1909). Subsequent to these early descriptions of area 5, modern anatomical techniques have parcellated this rather large cortical field into several overlapping subfields with differing nomenclature (Fig. 9; Seltzer and Pandya, 1986; Pandya and Seltzer, 1982; Lewis and Van Essen, 2000b).

The earliest studies of area 5 in awake macaques noted that, although neurons within this field responded primarily to tactile and proprioceptive stimuli, their receptive fields were larger and more complex than neurons in APC and often responded to the movement of multiple joints (Duffy and Burchfiel, 1971). Sakata et al. (1973) noted that neurons in this area sometimes possessed ipsilateral or bilateral receptive fields and were often highly selective to certain stimulus parameters. Arguably the most seminal electrophysiological study of this area was performed by Mountcastle et al. (1975) in which the monkeys experienced both active and passive stimulation of their extremities in various behavioral contexts. Mountcastle and his colleagues found that in comparison with APC neurons, neurons in area 5 were less active when the monkey was in a resting state, and were driven less directly by sensory input. For instance, when the monkey was falling asleep it was difficult to evoke responses from these neurons. While many of the neurons which responded to manipulations of the joints had receptive fields which resembled those of area 2 neurons, they were often more responsive during active movements. Conversely, neurons that responded to cutaneous stimulation displayed receptive fields that were much larger than those found in APC neurons and often spanned the entire palm or volar surface of the arm. Many of these neurons responded more vigorously to moving stimuli and were often directionally selective. Perhaps most significantly, a group of neurons dubbed "projection" and "hand manipulation" neurons were strongly modulated by the behavioral context of a given movement. These neurons tended to be most active when reaching for food or something that would dispense a reward and were silent when the same movements were made in a nonrewarding context.

From these early studies it became clear that, to appreciate the unique response properties of area 5 (and other PPC) neurons, awake-behaving electrophysiology in carefully controlled conditions is essential. Advances in technology have allowed for more refined behavioral measures that have provided more detailed and precise accounts of these response properties. However, as described in the next section, the precise function and organization of area 5 and the subfields within it is still contentious.

3.14.4.1.1 Brodmann Area 5: Contemporary Studies

Given the size of Brodmann area 5 and the complex stimuli that seem to drive neurons within it, it is not surprising that subsequent investigations attempting to characterize its function have produced a myriad of different results. One reason for this is that the portion of area 5 from which recordings were made varied between laboratories (see Figure 2 of Seelke et al., 2012). This, combined with the variability in the behavioral tasks employed by different investigators, has implicated Brodmann area 5 in such diverse processes as coding of reach intention (Snyder et al., 1997; Debowy et al., 2001; Calton et al., 2002), reach and grasp kinematics (Kalaska, 1996; Wise et al., 1997), online monitoring of different reach styles during object approach (Gardner et al., 2007a,b; Chen et al., 2009), and the coordinate transformation of reach targets into body- and shoulder-centered coordinates (Lacquaniti et al., 1995; Ferraina and Bianchi, 1994) or eye-centered coordinates modulated by limb position (Pesaran et al., 2006). Complicating matters further, some investigations of area 5 describe subfields in purely functional terms without reference to architectonics of the cortical tissue. The most well-studied example of this is the parietal reach region (PRR), originally proposed by Snyder et al. (1997). This is defined as the region within the superior parietal lobule that predominantly contains neurons that are more responsive to reaches than to saccades (Batista and Andersen, 2001). While numerous subsequent studies have implicated this region in effector-specific movement intention (as opposed to attention, see Andersen and Cui, 2009 for review), it appears to overlap several architectonically distinct regions such as the medial intraparietal area (MIP), the medial dorsal parietal area (MDP), and V6a (Snyder et al., 2000). In light of the diverse stimuli and effector movements to which neurons in Brodmann area 5 respond, it is very likely composed of several distinct cortical areas. Recent efforts by our laboratory have characterized one such subfield, area 5L, which has a distinct electrophysiological, architectonic (Seelke et al., 2012), and connectional (Cooke, 2013) profile, setting it apart from adjacent fields such as area 2 and MIP. Unlike anterior parietal fields, the functional topography of this region is fractured and contains an incomplete representation of the body notable for its extreme magnification of the hand and forelimb (Seelke et al., 2012). Similarly, MIP is characterized by a unique set of architectonic (Seelke et al., 2012; Lewis and Van Essen, 2000b), functional (Colby and Duhamel, 1991; Eskandar and Assad, 2002), and connectional (Lewis and Van Essen, 2000a) characteristics that, when considered together, make a compelling case for it being another distinct region within area 5.

Recently, PPC has been explored using long-train intracortical stimulation, and ethologically relevant movement domains have been demonstrated in squirrel monkeys, owl monkeys (see Kaas et al., 2011, 2013 for review), and galagos (Fig. 7; Stepniewska et al., 2005, 2011; Cooke et al., 2015; see Kaas Chapters 2.04, The Early Mammalian Brain, 3.11, Evolution of Visual Cortex in Primates, and 3.15, Evolution of Parietal-Frontal Networks in Primates for review). These studies demonstrate that the rostral portion of PPC (galago PPCr/monkey area 5) contains domains of ethologically relevant movements such as reach, grasp, and hand-to-mouth. Importantly, this rostral portion of PPC has dense interconnections with motor cortex. In macaques the rostral portion of area 5, particularly area 5L, is interconnected with motor, premotor, and supplementary motor cortex (Jones et al., 1978; Deacon, 1992; Darian-Smith et al., 1993; Luppino et al., 1993; Ghosh and Gattera, 1995; Tanne-Gariepy et al., 2002; Gharbawie et al., 2011b; Cooke, 2013). While the rostral portion of PPC is connected to both motor, premotor, and to a lesser extent supplementary motor cortices in squirrel monkeys (Gharbawie et al., 2011a), galagos (Fang et al., 2005; Stepniewska et al., 2009), and marmosets (Burman et al., 2014a,b); this portion of PPC seems to have few connections to primary motor cortex in owl monkeys (Stepniewska et al., 1993), although premotor connections are still present (Gharbawie et al., 2011a). While movement domains in macaque monkeys are found in multiple noncontiguous areas of parietal cortex [area 2, ventral (VIP) and lateral (LIP) intraparietal areas; Thier and Andersen, 1996, 1998; Cooke et al., 2003; Gharbawie et al., 2011b], their PPC has not been thoroughly explored using LT-ICMS, as in smaller-brained primates. Preliminary data from our own laboratory indicate that a larger amount of cortex on the postcentral gyrus, within the IPS and on the marginal gyrus (caudal to IPS), contains these movement domains, underscoring the need for a systematic study of movement domains in macaque PPC (Baldwin, 2016). Thus, even in primates, it is unclear which areas of PPC are homologous in Old and New World monkeys and prosimian galagos. This is further complicated by the fact that connections with motor cortices are a common but not unique feature of rostral PPC, as all of these species show varying degrees of connectivity between APC and motor cortical regions (see earlier discussion; Burton and Fabri, 1995). As noted in the previous section, the use of LT-ICMS combined with architectonics and studies of connections may be the best way in which to make comparisons across PPC in primates and other mammals.

3.14.4.2 Brodmann Area 7: Early Studies

As is the case with area 5, monkey area 7 occupies a large section of cortex within and caudal to the IPS. By Brodmann's original definitions, it occupies the entirety of the inferior parietal lobule, the caudal bank of the IPS, the upper bank of the lateral sulcus, and portions of the medial wall (Fig. 9; Brodmann, 1909). In 1919, Vogt and Vogt used additional architectonic criteria to divide this





Figure 10 Examples of some of the characteristics of stimuli that proved to be effective for driving neurons in area 7 of macaque monkeys. All neurons responded to visual stimuli that were moving in a given direction (see *arrows* above monkey illustrations). Some cells responded to stimuli approaching the hands (right figure). All neurons had receptive fields in which neurons responded to cutaneous stimulation (*light gray* shading), and all neurons were activated by palpation of the muscles (see *circle* in right figure) or rotation of the joints (*curved arrows* in left figure). This figure was redrawn from Leinonen, L., Hyvarinen, J., Nyman, G., Linnankoski, I., 1979. I. Functional properties of neurons in lateral part of associative area 7 in awake monkeys. Exp. Brain Res. 34, 299–320.

region into areas 7a and 7b. Much like area 5, more contemporary anatomical investigations have divided these areas further into overlapping regions with various naming schemes (Seltzer and Pandya, 1980, 1986; Pandya and Seltzer, 1982; Preuss and Goldman-Rakic, 1991; Lewis and Van Essen, 2000a,b; Gregoriou et al., 2006). The earliest electrophysiological investigations of these areas demonstrated that, while neurons within 7a primarily responded to movements of the eyes and visual fixation, neurons within 7b primarily responded to somatosensory stimulation as well as passive movements of the arms and hand (Hyvarinen and Poranen, 1974; Mountcastle et al., 1975; Leinonen and Nyman, 1979; Leinonen et al., 1979). Like area 5, cells in both 7a and 7b were most active in awake animals when the monkey reached, grasped, and manipulated various visually targeted objects, although it was noted that area 7 contained more neurons that responded to stimulation of the ipsilateral and bilateral body compared to area 5 (Hyvarinen and Poranen, 1974; Mountcastle et al., 1975). The receptive fields of area 7 neurons were generally large, with complex response properties. For instance, cells responding to cutaneous stimulation were often directionally selective. Additionally, some cells responded to both visual and somatosensory stimuli focused on the same region of the body (Fig. 10; ie, a cell with a cutaneous receptive field on the arm also responded to objects approaching that arm).

3.14.4.2.1 Brodmann Area 7: Contemporary Studies

Contemporary architectonic investigations of the inferior parietal lobule have subdivided monkey 7a and 7b into four distinct zones, PF, PFG, PG, and OPT (Fig. 9; Pandya and Seltzer, 1982; Gregoriou et al., 2006). In addition to architectonic differences, investigators have recently found that each zone possesses distinct connection patterns and that these regions form a functional gradient of neurons responsive to certain sensory stimuli and movements as one proceeds from caudal to rostral. Area 7a is comprised of areas OPT and PG, fields dominated by neurons responsive to visual stimuli, eye movements, and arm movements related to reaching and grasping. Area 7b is comprised of areas PFG and PF and is dominated by neurons responsive to somatosensory stimulation of the arm, hand, and mouth. Within PFG/PF, neurons which respond to motor actions are predominantly related to hand use, orofacial movements, and hand-mouth coordination (Yokochi et al., 2003; Rozzi et al., 2008; Fogassi et al., 2005; Bonini et al., 2011). Recently, long-train microstimulation of 7b and the rostrolateral portion of 7a has revealed that, much like areas 1 and 2, movement representations are dominated by flexion and extension of the wrist and digits. Interestingly, stimulation of these regions reveals a greater representation of digit 1 and 2 (d1 and d2) movements compared with APC. Specifically, within these domains, stimulation elicits a d1-d2 precision grip rather than a whole-hand power grasp (Baldwin et al., 2016).

Much like area 5, several regions within monkey area 7 are located in the IPS, including the anterior intraparietal area (AIP) and LIP (Lewis and Van Essen, 2000b). Of particular interest to prehension, neurons within AIP are active during grasping, with different neurons tuned to certain objects that require a particular grasp type. A subpopulation of AIP neurons tuned to a certain grasp type will respond during passive viewing of an object that requires use of that same grasp type (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000). The visual receptive fields of many AIP neurons have been found to be nonuniform with multiple maxima and minima in both visual hemifields and the highest firing rate usually found foveally or parafoveally in a retinotopic reference frame (Romero and Janssen, 2016). These receptive fields can vary dramatically in size and are significantly modulated by stimulus type, with preferred and nonpreferred stimuli evoking differently shaped receptive fields. Although visual stimulation modulates the response of most AIP neurons, many respond equally well to memory-guided

object manipulations made in darkness (Murata et al., 1996). Recently, it was found that this subpopulation of AIP neurons was also active when the monkey passively viewed a video of the same grasping action, even when the object itself was occluded (Pani et al., 2014). Other groups have also found mirrorlike neurons in AIP, though not as frequently as in the subdivisions of area 7b (Maeda et al., 2015). Neurons in AIP also appear capable of representing grasp types independent of object features, a property that would allow for the manipulation of the same object in different ways (Baumann et al., 2009). While it is still an open question whether AIP neurons primarily represent grasps or objects that require a grasp, it is clear that at some point the visual properties of an object must be extracted to determine what type of grasp is most appropriate. How AIP neurons accomplish this is an active area of research.

While many AIP neurons respond robustly to two-dimensional visual representations of small objects (Durand et al., 2007; Romero et al., 2012), a large portion also appear capable of extracting three-dimensional features of objects, although in a coarser and faster manner than neurons located in inferotemporal (IT) cortex (Srivastava et al., 2009). For many AIP neurons, this responsiveness to 3D objects seems to arise from a selectivity for particular binocular disparities (Verhoef et al., 2010; Romero et al., 2012, 2013). When examined in the context of decision-making (ie, discriminating a concave vs. convex surface), AIP neuronal activity correlates with a perceptual choice more slowly than IT neurons unless the monkey is required to make the decision quickly, in which case this correlation arises much earlier (Verhoef et al., 2010, 2015). This suggests that the sensitivity to curvature and depth found in these neurons serves to make rapid perceptual decisions based on an object's properties rather than categorizing that object. Presumably, these neurons serve to match the 3D features of an object to specific grasp postures, depending on the object's affordances. Indeed, when examined during actual acts of prehension, most AIP neurons that show disparity-driven 3D object selectivity are active during object grasping (Theys et al., 2013). It should be noted, however, that while many AIP neurons exhibit this disparity-driven selectivity, many of those same neurons retain their object selectivity when 3D stimuli are reduced to two-dimensional silhouettes and outlines (Romero et al., 2012, 2013) and even retain their selectivity when image outlines are broken into elementary fragments (Romero et al., 2014). These responses to elementary spatial features combined with the fact that object selectivity is highly dependent on the stimulus' position in space (Romero et al., 2012, 2014) further highlights the differences in how neurons in AIP and IT represent the shape of objects.

Studies comparing the activity of monkey AIP neurons to other parietal and motor neurons during reaching and grasping behavior have found that AIP neurons respond maximally during the early stages of prehension, increasing their firing prior to contacting an object (Gardner et al., 2007a), consistent with AIP's role in preshaping the hand prior to a grasp (Gallese et al., 1994; Debowy et al., 2001). More recent studies have found that at a population level, object orientation (Townsend et al., 2011), grasp types, and movement kinematics can be reliably decoded from groups of AIP neurons with the most reliable decoding occurring during the movement planning epoch (Lehmann and Scherberger, 2013; Menz et al., 2015; Schaffelhofer et al., 2015). When considered at the level of local field potentials (LFPs), however, grasp type can be decoded across all task epochs (not just during movement planning) in all frequency bands analyzed (Lehmann and Scherberger, 2015). Interestingly, whether decoded from multiunits or LFPs, both gaze direction and target position can be extracted from the activity of AIP neurons. Like the AIP receptive fields themselves, these position signals seem to be coded in retinotopic coordinates. What role these signals play in the planning of reaching and grasping movements has yet to be elucidated. However, given that chemical inactivation of AIP produces deficits in grasping but not reaching (Gallese et al., 1994; Fig. 11), this spatial information may serve to provide further context for the selection of appropriate grasp types.



Figure 11 Drawings of video frames of an animal preshaping the hand prior to the use of a precision grip under normal conditions (A) and following an injection of Muscimol into anterior intraparietal area (AIP) of macaque monkeys (B). A precision grip used to grasp a small target (*red*) between two plates in a normal macaque monkey (C) and in a monkey following injections of Muscimol into AIP (D). Note that not only is the actual grasp abnormal, but also the animal is unable to match hand grasping posture with the target prior to the grasp. Redrawn from Gallese, V., Murata, A., Kaseda, M., Niki, N., Sakata, H., 1994. Deficit of hand preshaping after muscimol injection in monkey parietal cortex. NeuroReport 5, 1525–1529.

Though not directly related to the act of grasping, in one view LIP neurons are thought to create priority maps of space, directing visual attention and therefore saccades to important objects and locations that the animal can subsequently evaluate and/or act upon (see Bisley and Goldberg, 2003; Bisley and Goldberg, 2010 for review). However, Andersen and colleagues have emphasized the intentional component of neuronal responses in LIP and the PPC in general (see Snyder et al., 2000; Andersen and Cui, 2009 for review). For instance, Quian Quiroga et al. (2006) have shown that in a reach versus saccade task, trial by trial decoding predicts effector choice (ie, reach vs. saccade) far better than target location. However, given that intention and attention are inextricably linked during normal behavior, the distinction is only useful insofar as it demonstrates that elements of each can be found depending on what one is looking for.

Another well-studied area within the IPS is the monkey VIP, which straddles the area 5/7. Originally defined based on projections from the medial temporal area (Maunsell and van Essen, 1983; Colby et al., 1993), investigators distinguished this region from surrounding cortex based both on myelination patterns and the response properties of neurons within these borders. Neurons within this region were noted for having large visual receptive fields sensitive to moving stimuli, with a large proportion displaying directional selectivity. Some of these neurons were highly selective for the distance at which the visual stimuli were presented, especially for locations very close to the monkey's head. That same study found that many neurons fired in response to somatosensory stimuli with many responding to bimodal visual and somatosensory stimulation with an overlapping receptive field. Interestingly, some bimodal neurons tuned to objects moving toward the monkey had receptive fields that corresponded to a point of impact on the monkey's face rather than some sort of retinal vector. This study and later investigations examining eye movement during microstimulation of VIP suggested that VIP neurons code visual stimuli in a head-centered reference frame for the monitoring of objects in immediate peripersonal space (Thier and Andersen, 1996, 1998), a perspective supported by data showing that motion detection in these neurons is modulated by attention (Cook and Maunsell, 2002).

Since then numerous studies have been conducted to try and elucidate the function of this region, especially with regards to the vestibular and multimodal stimuli. The use of three-dimensional motion platforms has greatly expanded the types of simulated movements that researchers can use to stimulate the vestibular system beyond isolated translations and rotations (Chen et al., 2011a,b, 2013a,c). These studies have demonstrated that VIP occupies an intermediate level in the processing hierarchy for vestibular stimuli, with neurons exhibiting peak directional tuning more quickly than the dorsal aspect of the medial superior temporal area (MSTd) but more slowly than parietoinsular vestibular cortex (Chen et al., 2011a). The tuning curves of VIP neurons are invariant to both head and eye movements, indicating a body (or world)-centered reference frame for vestibular stimuli (Chen et al., 2013c). Neurons tuned to different types of vestibular motion (ie, rotation and translation) can be found throughout VIP in addition to neurons that are optimally tuned to a combination of these movements (ie, curvilinear motion; Chen et al., 2016).

Many monkey VIP neurons are tuned to optic flow stimuli, have a preference for expanding flow patterns, and process optic flow stimuli in discrete clusters tuned to similar headings (Bremmer et al., 2002a; Zhang et al., 2004; Chen et al., 2011b). The heading tuning curves of most VIP neurons have been shown to remain largely unaltered during eye movements (Zhang et al., 2004; Kaminiarz et al., 2014) but generally shift with eye position, indicating an eye-centered reference frame for optic flow stimuli (Chen et al., 2013b). While previous studies using moving bar stimuli have reported head-centered reference frames for VIP neurons (Duhamel et al., 1997; Avillac et al., 2005), those using large-field stimuli generally support an eye-centered reference frame (Chen et al., 2013b, 2014). This highlights the fact that the coordinate system a PPC neuron employs can be dependent on both the sensory modality (ie, vestibular vs. visual) as well as the quality of the stimulus itself (small shapes vs. full-field stimuli). The invariance of heading tuning curves in the face of eye movements suggests that reafferent signals of eye movement may play a role in compensating for this distortion of the visual field (Kaminiarz et al., 2014). Indeed, neurons have been found within VIP that carry a fast and accurate eye position signal that when modeled at the population level can mimic the spatiotemporal dynamics of the eye during saccades (Morris et al., 2012, 2013, 2016). However, recent studies have found that VIP neurons can achieve invariant heading tuning using purely visual cues, such as motion parallax and global perspective cues, and have identified a population of neurons capable of jointly representing visual translation and rotation (Sunkara et al., 2015, 2016). Neurons that respond to combined visual-vestibular information have been well documented in VIP (Bremmer et al., 2002b; Chen et al., 2011b, 2013a; Yang et al., 2011), lending weight to the idea that VIP may represent a site of multimodal convergence for the purpose of spatial navigation (Bremmer et al., 2002a,b). Cells that respond to the same direction of visual and vestibular stimuli (ie, congruent stimuli) have been found to have lower heading discrimination thresholds compared to those neurons that have incongruent visual and vestibular tuning (Chen et al., 2013a). While it has been shown that the response properties of incongruent cells are not an artifact of head-fixation and viewing geometry (Yang et al., 2011), their exact function remains unclear. Despite the fact that these neurons are relatively rare within populations tuned for behaviorally relevant headings (Chen et al., 2013a), the presence of incongruent visual-vestibular direction preferences in this region suggests that it may also function to distinguish self-motion from object motion (Schlack et al., 2002). This possibility is bolstered by the fact that bilateral deactivation of VIP seems to have no effect on heading discrimination ability (Chen et al., 2016), although this may be an artifact of fixation as previous work by Zhang and Britten (2011) demonstrated that short-train microstimulation of VIP neuronal clusters can bias heading judgments during smooth-pursuit eye movements.

Interestingly, studies employing high-amplitude long-train microstimulation have provided a slightly different perspective. Cooke et al. (2003) found that stimulation of different sites in VIP evoked a relatively small set of movements seemingly related to defensive behavior. These movements included blinking, folding the pinnae against the head, contraction of facial muscles, shrugging of the shoulders, and a lateral movement of the arm which resembled a blocking posture. These movements often occurred in combination and were nearly identical to a set of movements evoked by puffing air at the monkey's face (Cooke et al., 2003). This has led to the idea that this region may serve, at least in part, to maintain a margin of safety around the animal's head and face in response to violation of peripersonal space or during natural navigation behaviors as the animal passes by obstacles in its environment (Graziano and Cooke, 2006). Likely VIP serves multiple functions related to the monitoring of peripersonal space and relating the movement of the head, eyes, and arms to the movement of nearby objects in terms of a range of reference frames (Duhamel et al., 1997, 1998; Avillac et al., 2005; Chen et al., 2013b,c) and sensory modalities (Duhamel et al., 1998; Schlack et al., 2002). Indeed, whether measured using optic flow (Yang et al., 2011) or two-dimensional motion stimuli (Bremmer et al., 2013), the majority of VIP neurons prefer binocular disparities which correspond to near stimuli. Interestingly, this monitoring of peripersonal space may extend to the monitoring of other individuals as mirror neurons have recently been found in this region (Ishida et al., 2010).

Much like AIP, VIP is reciprocally connected with both subdivisions of 7b, another region in which mirror neurons can be found (Rozzi et al., 2006). In addition to defense and spatial navigation, it may be the case that neurons in VIP are tuned to other instances of self versus object motion such as hand-mouth coordination and feeding behavior. However, motion perception may not be the only function subserved by the region. Neurons have been found in VIP that appear to be tuned to different elements of numerosity, a quality also observed in different portions of area 5 (see Nieder, 2013 for review) and a subject which will be discussed in further detail in Canlon chapter.

3.14.4.3 Somatosensory Input to the Posterior Parietal Cortex in Primates

The preponderance of PPC neurons sensitive to tactile and proprioceptive stimulation likely reflects their role in monitoring the position of the limbs during reaching as well as the haptics (ie, active sensory exploration) of object manipulation. While neurons within these regions receive their own input from somatosensory regions of the thalamus (eg, Padberg et al., 2009; Schmahmann and Pandya, 1990), the majority of the somatosensory input to these regions ascends from the thalamus and through areas within APC before converging on these higher-order neurons (Burton et al., 1995; Burton and Fabri, 1995; Cusick et al., 1985; Darian-Smith et al., 1993; Gharbawie et al., 2010,b; Lewis and Van Essen, 2000a; Pons and Kaas, 1986; Rozzi et al., 2006). Classical models of somatosensory processing liken these pathways to the visual system, where information is processed in a serial, hierarchical manner (see Iwamura, 1998; Dijkerman and de Haan, 2007 for review). Support for this model comes not just from the increasing size and complexity of somatosensory receptive fields as one proceeds from rostral to caudal in the parietal lobe (Hyvarinen and Poranen, 1978a,b; Costanzo and Gardner, 1980; Iwamura et al., 1985a,b, 1980, 1993, 1994; Nelson et al., 1980; Sur, 1980; Iwamura, 1983a,b; Gardner, 1988; Pei et al., 2010; Papadelis et al., 2011; Wacker et al., 2011; Sanchez-Panchuelo et al., 2012; Yau et al., 2013; Ashaber et al., 2014) but also from the fact that ablation of "lower-order" regions in this hierarchy can abolish neural responses in "higher-order" areas (Garraghty et al., 1990). Similarly, the degree of qualitative behavioral deficits observed after lesioning APC are not exacerbated by later lesioning PPC (Peele, 1944), suggesting that input from APC is critical for PPC function as it pertains to movement and prehension. Indeed, even within APC it seems as though areas become more "PPC-like" the further caudal one goes, with receptive fields not only becoming larger, but also being more strongly modulated by attention (Hyvarinen et al., 1980; Hsiao et al., 1993; Burton et al., 1997, 1999; Burton and Sinclair, 2000; Meftah el et al., 2002; Spingath et al., 2011, 2013; Wang et al., 2012).



Figure 12 Different types of receptive field changes following deactivation of areas in posterior parietal cortex (area 7b) and motor cortex (M1 and PM) in macaque monkeys. Reversible deactivation was accomplished via cooling, and neurons were recorded in areas 1 and 2 during cooling. Both expansions and contractions of receptive fields for neurons in areas 1 and 2 were seen following deactivation of area 7b (and M1/PM), but the most common type of alterations to receptive fields when area 7b was cooled were expansions. Adapted from Cooke, D.F., Goldring, A.B., Baldwin, M.K., Recanzone, G.H., Chen, A., Pan, T., Simon, S.I., Krubitzer, L., 2014. Reversible deactivation of higher-order posterior parietal areas. I. Alterations of receptive field characteristics in early stages of neocortical processing. J. Neurophysiol. 112, 2529–2544.

Despite this apparent hierarchy, the connections between APC and PPC are reciprocal, with portions of both areas 5 and 7 sending feedback to APC either directly through corticocortical connections (Pons and Kaas, 1986; Cavada and Goldman-Rakic, 1989a,b; Felleman and Van Essen, 1991; Burton and Fabri, 1995; Rozzi et al., 2006) or indirectly through the thalamus (Weber and Yin, 1984; Yeterian and Pandya, 1985; Padberg et al., 2009). While the exact function of these feedback connections is still being investigated, our laboratory has demonstrated that the shape and size of receptive fields of anterior parietal neurons can be altered by reversibly deactivating portions of area 5L and 7b (Fig. 12; Goldring et al., 2014; Cooke et al., 2014). Thus neurons within the PPC have the potential to gate and refine incoming somatosensory information from APC neurons, possibly via selective attention in a manner analogous to the visual system.

3.14.5 Posterior Parietal Cortex and Tool Use

One of the most complex and cognitively advanced examples of manual dexterity is the temporary extension and specialization of peripheral morphology via the use of tools. Tool use as defined by Shumaker et al. (2011) is "the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool." Although this category of manual ability was originally thought to be an exclusive and defining feature of human behavior, researchers now appreciate that New World monkeys, Old World monkeys, and great apes also use tools in the wild to varying degrees, a subject explored in Dorothy Fragazy chapter 3.17, Tool Use in Nonhuman Primates: Natural History, Ontogenetic Development and Social Supports for Learning. Given the multisensory integration and contextual deployment that tool use requires, it is perhaps not surprising that these behaviors are likely correlated with an expansion and specialization of posterior parietal cortical areas. As discussed in Almecija/Sherwood chapter 3.16, Hands, Brains, and Precision Grips: Origins of Tool Use Behaviors, humans have evolved specialized portions of the PPC not seen in macaques that have been implicated in complex tool use that goes beyond simple object grasping and manipulation. Namely, activity in the anterior portion of Brodmann area 40 on the supramarginal gyrus of the left hemisphere is correlated with the execution and observation of tool use behavior, while damage to this general region is associated with apraxias characterized by deficits in tool use ability (see Goldenberg and Spatt, 2009; Orban and Caruana, 2014 for review).

Of the species amendable to direct electrophysiological recording and experimental manipulation of function, cebus monkeys (Sapajus sp.) represent ideal model organisms for studying the neurological basis of tool use behavior. Unlike rhesus macaques, which only use tools under experimental conditions (eg, Iriki et al., 1996; Quallo et al., 2012; Umilta et al., 2008), these monkeys use tools in the wild and appear capable of extracting the affordances of different tools based on their physical properties and select the appropriate tool for the appropriate action or action sequence (see Fragazy chapter 3.17, Tool Use in Nonhuman Primates: Natural History, Ontogenetic Development and Social Supports for Learning). Like humans, they possess an opposable thumb capable of executing a thumb and forefinger precision grip that allows for the kind of fine object manipulation that just is not possible using a power grasp. Interestingly, they seemed to have independently evolved a proprioceptive cortical area 2 and an architectonically distinct area 5 that contains neurons which exhibit a similar response profile to those of macaque monkeys when measured in an anesthetized preparation (Padberg et al., 2007; Seelke et al., 2012). Recently, Mayer et al. (2016) conducted a detailed architectonic survey of the cebus monkey parietal lobe using a combination of stains (SMI-32, nissl, and myelin) that have been used successfully to anatomically parcellate PPC in rhesus macaques. Using these techniques, they identified a suite of anterior and posterior parietal subdivisions of the postcentral gyrus and anterior IPS that seem to mirror the architectonic schema of macaques. This is striking because all other New World monkeys tested lack most if not all of these divisions and therefore they appear to have arisen independently of their analogues in Old World monkeys. Future studies paralleling those in macaques (ie, anatomical connections, LT-ICMS, and awake-behaving electrophysiology) will be necessary to determine which aspects of PPC organization and function have independently arisen in these species. In addition, these types of studies will allow researchers to determine if nodes specialized for tool use exist in the cebus frontoparietal reaching and grasping network. These data would not only reveal potential mechanisms for how human tool use regions evolved but also shed light on the basic organizational principles of how the cortex can change to accommodate this kind of complex sensorimotor behavior.

3.14.6 Posterior Parietal Cortex in Humans

Some of the earliest knowledge regarding the function of the PPC arose from case studies of humans who sustained damage to different parts of the parietal lobe (see Fleming and Crosby, 1955 for review). Advances in functional imaging and the advent of transcranial magnetic stimulation have allowed researchers to characterize the organization of the human frontoparietal reaching and grasping network. Establishing homologies between human and monkey PPC areas, however, must be undertaken with caution as a number of factors differ in the methodologies of each type of investigation including: temporal and spatial resolution of neuroimaging versus neurophysiology, the dynamics of excitation versus inhibition in the BOLD (blood oxygenation level dependent) response underlying fMRI, and the criteria used to define what constitutes an area (Culham et al., 2006). Even with the aid of architectonics, individual differences in the location of cortical regions complicate matters when mapping onto a normalized brain (eg, Caspers et al., 2006; Krubitzer et al., 2004). That is, if an fMRI signal is mapped onto

a standard "reference" brain, this does not take into account that the exact location and extent of a brain area in one subject may not match that of another subject in the study. Nevertheless some general patterns have emerged that allow one to draw parallels between functionally similar areas in monkeys and humans.

One method of parcellating the human parietal lobe is by examining topographic maps (ie. representations of adjacent regions of sensory space in adjacent parts of cortex) during the presentation of different visual stimuli or the performance of saccades to different regions of space. Borders can then be drawn based on the locations of reversals in the orientation of the visual field (Silver and Kastner, 2009). Using this methodology, at least seven different regions can be identified along the human IPS and superior parietal lobule in which grasping-related activation transitions to reaching-related as one proceeds anterolaterally to posteromedially through these regions (Konen et al., 2013). Similar trends can be seen when one relates the loci of activation for a given task to the location of sulci and gyri located in approximately the same areas in humans and macaques: as one proceeds from the anterior end of the IPS in a posteromedial direction, activation foci respond to grasps, then reaches, and then saccades (eg, Hinkley et al., 2009). The anterior end of the human IPS is often equated with macaque AIP, and like monkey AIP has been shown to be active during both passive viewing and active nonvisual manipulation of different objects (eg, Grefkes et al., 2002). A human area dubbed the "posterior eye field" (see Grefkes and Fink, 2005) has been shown to exhibit similar saccade-related activity to monkey LIP when comparing both species in an identical fMRI saccade paradigm (Koyama et al., 2004). Interestingly, in humans this posterior eye field is actually located medial to the IPS, on the superior parietal lobule, rather than within it. This highlights the fact that homologous areas may be located in different regions in different species. A region near the medial portion of the IPS in humans, roughly analogous in location to monkey MIP and PRR, has been shown to display reaching-related BOLD responses (Prado et al., 2005) and is purported to perform coordinate transformations (Grefkes et al., 2004) when employing a joystick paradigm similar to that employed by Eskandar and Assad (2002) to study such phenomena in macaque MIP. Similarly, a region in the ventral portion of the human IPS has been shown to respond to combined visual, tactile, and auditory stimuli in a manner analogous to monkey VIP (Bremmer et al., 2001). In addition, like language, there are myriad behavioral and cognitive functions that have been specialized and lateralized to one hemisphere or the other in human PPC in ways not seen in other primates. However, a full discussion of this is beyond the scope of this chapter (see Rosati chapter 3.23, The Evolution of Primate Executive Function: From Response Control to Strategic Decision-Making).

3.14.7 Conclusion

When considering the organization of the neocortex, establishing homologies across species can be difficult. This is particularly true for PPC. One reason for this difficulty is that we currently do not have a species-agnostic definition of PPC nor do we use a robust set of criteria for identifying PPC across primate and nonprimate mammals. In addition, species differ in body morphology, sensory effector specialization, and ethologically relevant behavior, and these differences are reflected in sensory cortex, such as somatosensory cortex, and amplified in PPC. However, recent studies utilizing LT-ICMS combined with studies of connections from motor cortex and architectonic analysis have allowed us to begin to establish PPC homologues between primates. These techniques have also allowed us to examine cortex in the relative location of PPC in nonprimate mammals and make comparisons of this region with primates. However, data of this sort have only been gathered from a few species so that establishing homologies across groups is possible, but more data are needed to determine if this cortex is in any way analogous to PPC regions in primates. Further, while these techniques have proved useful for establishing a basic framework for PPC organization in all mammals, they do not speak to how PPC generates behavior.

While rats have proven to be a tractable nonprimate model in the context of awake-behaving electrophysiology, contemporary studies of rat "PPC" indicate that it is involved in navigation, spatial attention, and decision-making: all complex behaviors that make parsing the specific functional organization of the presumptive rodent PPC difficult, especially since a species-agnostic definition of PPC has largely been overlooked.

By far most work on PPC has been done in nonhuman primates, particularly the macaque monkey. The macaque PPC is comprised of subdivisions whose function and connectivity distinguish them from adjacent visual and somatosensory cortical areas. While those adjacent "early" sensory processing areas are characterized by features such as a complete topographic representation of the sensory epithelium and mirror reversals at areal borders (eg, Kaas et al., 1979), regions within the PPC contain fractured and sparse representations of somatosensory (eg, area 5L; Seelke et al., 2012) and visual (eg, LIP; Gottlieb et al., 1998) space, as well as magnified representations of ethologically relevant effectors (Seelke et al., 2012). PPC is the ultimate destination of what Mishkin and Ungerleider (1982) described as the "where" pathway, noting that the destruction of this dorsal stream of visual processing severely impaired a monkey's ability to localize objects in space (as opposed to the ventral, "what" stream responsible for object identification). Later work by Goodale and Milner (1992) modified this dichotomy by suggesting that the "what" and "where" streams would be better thought of as the ventral "perception" and the dorsal "action" streams. Indeed, since then the view of the dorsal stream as an "action" pathway has dominated theories regarding the function of PPC, which is now recognized as the cortical hub of attention, intention, and reference-frame transformation. Recently, this schema has been further elaborated into an "action affordances" model (Cisek, 2007), which seeks to supplant the information processing perspective that segregates perception, cognition, and action into separate domains that operate in a serial manner to analyze sensory data and make a single decision. Instead, as reviewed by Cisek and Kalaska (2010), the experimental data argue for a more distributed set of processes which operate throughout sensorimotor cortex and an organizational schema that is optimized for a continuous and dynamic interaction with the environment. From this perspective, a number of different actions compete for execution as sensory data accumulate, and are biased by contextual signals from prefrontal cortices and the basal ganglia.

Finally there is a recent plethora of studies of PPC in humans. While some homologies have been established between humans and monkeys (eg, AIP and VIP), the overall number of cortical fields, their connectivity, and their integrated function are not well understood. What is clear is that this region of the neocortex has been greatly enlarged in primates, especially humans, and has coevolved with the elaboration of the hand and sophisticated manual behaviors that define the human condition. To answer ultimate questions about how PPC has evolved, parallel studies employing the same methodology (ie, anatomy, LT-ICMS, reversible inactivation) in multiple mammalian species are essential. Similarly, to answer proximate questions about the treatment of PPC damage or the use of PPC in brain–machine interfaces in humans, an understanding of PPC organization in intermediate species will allow researchers to more easily extrapolate results from rodent models in which more precise methods of neuronal manipulation (ie, optogenetics) are readily available. As we enter a new era where our ability to process information and interact with our surroundings is inextricably linked with technology dependent on skilled movements of the hands and eyes, an understanding of the brain networks guiding those actions is imperative to understanding ourselves and how will we adapt to the future that we construct.

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