#### Chapter 7

# Multisensory and sensorimotor maps

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#### Abstract

The parietal lobe plays a major role in sensorimotor integration and action. Recent neuroimaging studies have revealed more than 40 retinotopic areas distributed across five visual streams in the human brain, two of which enter the parietal lobe. A series of retinotopic areas occupy the length of the intraparietal sulcus and continue into the postcentral sulcus. On the medial wall, retinotopy extends across the parieto-occipital sulcus into the precuneus and reaches the cingulate sulcus. Full-body tactile stimulation revealed a multisensory homunculus lying along the postcentral sulcus just posterior to primary somatosensory cortical areas and overlapping with the anteriormost retinotopic maps. These topologically organized higher-level maps lay the foundation for actions in peripersonal space (e.g., reaching and grasping) as well as navigation through space. A preliminary yet comprehensive multilayer functional atlas was constructed to specify the relative locations of cortical unisensory, multisensory, and action representations. We expect that those areal and functional definitions will be refined by future studies using more sophisticated stimuli and tasks tailored to regions with different specificity. The long-term goal is to construct an online surface-based atlas containing layered maps of multiple modalities that can be used as a reference to understand the functions and disorders of the parietal lobe.

## **INTRODUCTION**

Over the past two decades, noninvasive functional magnetic resonance imaging (fMRI) has made it easier to define the boundaries of topological maps in the human brain. Topological maps are neighbor-preserving maps, which means that nearby pairs of points in one area remain nearby when those pairs of points are mapped to another area; however, the relative distances of pairs of points extending in different directions are allowed to change, as in the well-known London Underground map. More formally, a topological map is a continuous function between two topological spaces (Trench, 2003).

Recent fMRI studies suggest that topological maps extend into higher-level regions of the parietal lobe important for integrating information across multiple sensory modalities. To illustrate map-based organization and functions of the parietal lobe, we construct a surfacebased atlas containing unisensory, multisensory, and sensorimotor maps based on fMRI data collected by us and others. Group-average maps are generated by averaging individual subject maps after spherical surface-based morphing, and then rendered on the cortical surface of a representative subject (Fischl et al., 1999; Hagler et al., 2007; Henriksson et al., 2012).

This chapter first delineates the overall extent of each modality on the cortical surface, and then summarizes the locations, topological organization, and functions of selected areas. Whenever possible, we have conservatively drawn on topological and functional maps previously established in nonhuman primates to name similar areas in humans (Lewis and Van Essen, 2000; Gattass et al., 2005; Rosa and Tweedale, 2005; Sereno and Tootell, 2005; Kaas et al., 2011; Seelke

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et al., 2012; Kaas and Stepniewska, 2016; see Chapters 2 and 4). From the occipital pole, dorsal visual areas extend anteriorly into the lateral, intraparietal, postcentral, parieto-occipital, and cingulate sulci on the posterior half of the cortical surface. Motor, somatosensory, and multisensory areas extend from the precentral and central sulci posteriorly, laterally, and medially to meet visual areas in lateral, postcentral, intraparietal, and cingulate sulci.

Multilayer maps rendered on the same cortical surface - a map overlay method typically used in geographic information systems like Google Earth - provide insight into understanding how cortical representations of different modalities (visual, somatosensory, and motor) partially overlap each other to support sensorimotor functions such as saccades, pointing, reaching, touching, grasping, eating, ducking, and walking in peripersonal space (Sereno and Huang, 2014). This atlas can be used as a general guide to locate topologically organized representations on the cortical surface. For most areas in this atlas, we point to key references with indepth descriptions and figures with more detailed maps (i.e., the beginnings of a Google Scholar and Google Images for functional brain areas) in an attempt to present an initial complete picture of the topological and functional organization of the parietal lobe.

# VISUAL MAPPING BEYOND THE OCCIPITAL LOBE

The visual system has long been divided into the dorsal and ventral streams, as initially suggested by monkey and human studies (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992). Recent models suggest that there is further branching in the dorsal visual stream of monkeys and humans (Rizzolatti and Matelli, 2003; Kravitz et al., 2011; Binkofski and Buxbaum, 2013). Mapping retinotopic areas is the first step toward understanding the extent and organization in each stream and its branches. Phase-encoded flickering checkerboard stimuli with central fixation were used in initial human fMRI studies to map early visual areas (Engel et al., 1994; Sereno et al., 1995), but they are less effective in mapping areas beyond the occipital lobe. More recent fMRI studies have used complex natural stimuli and visuospatial attention tasks to activate higher-level visual areas (Sereno et al., 2001; Hasson et al., 2004; Sereno and Huang, 2006). Furthermore, most retinotopic mapping experiments have used stimuli with a small visual angle (less than 15° eccentricity), which is not optimal for areas with a peripheral emphasis. Taken together, the use of wide-field natural stimuli and visuospatial attention tasks is essential for mapping higher-level areas, particularly in the dorsal visual stream.

### Five visual streams

The broadest extent of visual cortex has been outlined by natural viewing of movies (Hasson et al., 2004; Golland et al., 2007). In a block-design fMRI experiment, subjects watched videos (television shows) masked in a circular aperture ( $\sim$ 40° eccentricity) while fixating a central cross for 16 seconds, followed by central fixation against a black background for 16 seconds; the soundtrack was audible in both conditions (Sereno and Huang, 2006).

A group-average map shows that visually driven cortex extends from the occipital pole and branches out anteriorly into five streams on the posterior half of the cortical surface (Fig. 7.1): (1) the first extends through the middle temporal (MT) area into the superior temporal sulcus (STS), and reaches the parieto-insular vestibular cortex (PIVC) at the posterior lateral sulcus; (2) the second stretches along the intraparietal sulcus (IPS), and arrives at the superior postcentral sulcus (PoCS); (3) the third spreads across the parieto-occipital sulcus (POS) into the precuneus (PCu), and ends at the cingulate sulcus visual (CSv) area; (4) the fourth runs across POS into the retrosplenial cortex (RSC) at the isthmus of the cingulate gyrus, and reaches the lateral geniculate nucleus (LGN); and (5) the fifth follows the collateral sulcus and the fusiform gyrus into the ventral occipitotemporal lobe. Notably, there are regions ("holes") on the posterior superior surface not activated by videos: streams #1 and #2 are separated by the angular gyrus (AnG) while streams #3 and #4 are separated by the inferior posterior cingulate cortex (PCC). Both of those regions are part of the default-mode or intrinsic network (Raichle et al., 2001; Golland et al., 2007). Finally, the frontal lobe contains a separate stretch of visual areas, including the frontal eye fields (FEF), ventral premotor area (PMv), and dorsal lateral prefrontal cortex (DLPFC) (Figs 7.1 and 7.2; Hagler and Sereno, 2006; Silver and Kastner, 2009).

#### Higher-level visual maps

Detailed retinotopic organization within each visual stream was mapped using wide-field phase-encoded natural-scene videos masked in a rotating wedge and in an expanding (or contracting) ring (Sereno and Huang, 2006; Huang and Sereno, 2013). The paradigms and stimuli were similar to those used in the early visual mapping studies (e.g., Sereno et al., 1995) except that the flickering checkerboards have been replaced by live-feed videos. The subject was instructed to continuously attend to the video while maintaining central fixation. The resulting group-average map of polar-angle representations is rendered on a flattened cortical surface of a representative subject (Fig. 7.2). Here, we briefly summarize the topographic relationships among areas in each stream, and then



**Fig. 7.1.** Five visual streams activated by wide-field videos. Group-average visual maps (n = 20; yellow regions) are rendered on cortical surfaces of a representative subject. Orange regions outline group-average maps (n = 11) of tactile face representations (Huang and Sereno, 2007). Visual streams are indicated by numbers in parentheses. *Cal. S*, calcarine sulcus; *Cing. S*, cingulate sulcus; *CS*, central sulcus; *Def*, default-mode network; *FFA*, fusiform face area; *LH and RH*, left and right hemispheres; *PPA*, parahippocampal place area; *PV*, parietal ventral area; *PZ*, polysensory zone; *SI* and *SII*, primary and secondary somatosensory cortex; *TOS*, transverse occipital sulcus; *VIP* +, human homolog of macaque ventral intraparietal. Other abbreviations as in text.

discuss retinotopic organization and functional roles of selected areas in dorsal streams in the following sections. Throughout the figures, we use green to indicate the lower visual field, blue to indicate the horizontal meridian, and red to indicate the upper visual field representations.

Anterior to dorsal early visual areas (V1d-V3d), stream #1 extends across the lateral occipitotemporal, middle temporal, and parieto-insular cortices. Two lateral occipital areas (LO-1 and LO-2) border the lower visual field representation of areas V3d and MT, respectively (Larsson and Heeger, 2006; Amano et al., 2009). The upper visual field representations of LO-1 and LO-2 border each other, as demonstrated in a few single-subject maps (Fig. 7.3); though the upper visual field representation is not clear in the group-average map (Fig. 7.2), and substantial intersubject variability in this area was reported earlier by Tootell and Hadjikhani (2001). Area MT is identified as a region with the upper visual field representation located anterior to the lower visual field representation (Amano et al., 2009; Kolster et al., 2010). The area anterior and superior to MT is labeled MSTd (dorsal part of the macaque medial superior temporal area) and the area anterior and inferior to MT is labeled FST (fundus of the STS area); both may contain multiple subdivisions (cf. Kaas and Morel, 1993). A recent model of retinotopic organization in the MT/V5

cluster and surrounding regions is shown in Figure 16 in Kolster et al. (2010). Further anterior along stream #1, retinotopy extends into areas STS and PIVC, as shown in the group-average map. Some single-subject maps show a partial (mainly lower visual field) to complete hemifield representation in both areas (Sereno and Huang, 2006; Huang and Sereno, 2013).

Stream #2 contains a series of retinotopic areas extending from the transverse occipital sulcus (TOS), along IPS, and into PoCS. Area V3A contains a complete map of the contralateral hemifield with its lower visual field representation bordering V3d and its upper visual field representation bordering V3B (Tootell et al., 1997; Smith et al., 1998). Area V3B contains a large upper visual field representation, as shown in the group-average map (Fig. 7.2), although a partial to complete hemifield representation is present in some singlesubject maps (Fig. 7.3). Beyond V3A, areas IPS-0 to IPS-5 lie along the posterior to anterior IPS (Sereno et al., 2001; Silver et al., 2005; Swisher et al., 2007; Konen and Kastner, 2008). In the group-average map, area IPS-0 is labeled V7 (Tootell et al., 1998), and areas IPS-1 to IPS-5 are indicated by numbers (Fig. 7.2). A region located medial and anterior to IPS-2 and IPS-3 is named superior parietal lobule 1 (SPL-1) (Konen and Kastner, 2008). Anterior to IPS-4 and



**Fig. 7.2.** A group-average retinotopic map rendered on a flattened left-hemisphere cortical surface (data were reanalyzed and averaged across 24 subjects from Huang and Sereno, 2013). Visual streams are indicated by corresponding numbers in Figure 7.1. Yellow dashed contours outline regions of tactile face representations outlined in Figure 7.1. *IFS* and *SFS*, inferior and superior frontal sulci; *LH*, left hemisphere; *LIP* +, human homolog of macaque lateral intraparietal area; *LoVF*, lower visual field; *OPA*, occipital place area; *UpVF*, upper visual field. Other abbreviations as in text.

IPS-5, the parietal face area (VIP+ cluster; probable human homolog of the macaque ventral intraparietal area (VIP)) extends between the superior PoCS and anterior IPS (Sereno and Huang, 2006). The parietal body area (PBA) and anterior intraparietal area (AIP) are located posterior medial and anterior lateral to VIP+, respectively (Huang et al., 2012, 2017; Sereno and Huang, 2014).

Beyond V3d on the medial wall, stream #3 contains retinotopic areas V6, V6A (V6Av, V6Ad), anterior PCu (aPCu), and CSv. Beyond the peripheral borders of areas V1 and V2, stream #4 contains two retinotopic regions, RSC and medial parieto-occipital area (POm), both with an emphasis on the far periphery and horizontal to upper visual field representations. The retinotopic organization and functions of areas in streams #3 and #4 are discussed later in this chapter. Beyond inferior early visual areas (V1v-V3v), stream #5 contains retinotopic areas hV4, ventral occipital areas VO-1 (V8) and VO-2, parahippocampal cortex (PHC-1, 2), and posterior inferotemporal area (PIT) on the ventral occipitotemporal cortex (for detailed ventral visual maps, see Wandell et al., 2007; Arcaro et al., 2009; Brewer and Barton, 2012).

## RETINOTOPIC MAPS IN POSTERIOR PARIETAL CORTEX

In monkey single-cell recording studies, it is challenging to map small higher-level areas with larger receptive fields (Sereno et al., 1994, 2015). For example, earlier studies in nonhuman primates did not show clear retinotopic maps in the macaque lateral intraparietal area (LIP) and VIP (Colby et al., 1993, 1996). In humans, the initial evidence for a retinotopic map in the posterior parietal cortex (PPC) was demonstrated using a phase-encoded delayed saccade task in an fMRI study (Sereno et al., 2001). Subsequent studies using eye movement and/or visuospatial attention tasks revealed a strip of retinotopic areas, IPS-0 to IPS-5, along the IPS (Schluppeck et al., 2005; Silver et al., 2005; Swisher et al., 2007; Konen and Kastner, 2008). The IPS-x strip, named using the anatomy-number scheme (Wandell et al., 2007), postulates a linear sequence of five reversals in the polar angle coordinate beyond V3A, implying six hemifield re-representations. The lower visual field representation of V7 (IPS-0) is located anterior to its upper visual field adjoining V3A. A polar angle reversal takes place at the border between V7 and IPS-1, and each subsequent



**Fig. 7.3.** Intersubject variability of retinotopic maps in the posterior parietal cortex (unpublished single-subject data from Sereno and Huang, 2006; Huang and Sereno, 2013). (A) Retinotopic areas are labeled according to the IPS-x model. (**B**–**H**) Retinotopic areas are indicated by arrows. Each arrow indicates a transition from lower to upper visual field. White arrows indicate a series of phase reversals forming an approximate linear path. Black arrows indicate additional phase transitions off the linear path. VIP+ (in yellow dashed contours) was activated by wide-field optic flow stimuli and/or air puffs to the face. Abbreviations as in Figure 7.2 and text.

reversal defines a new area along the strip (IPS-2 to IPS-5). However, the IPS-x strip only cuts a narrow path through a broader extent of retinotopic areas activated by wide-field phase-encoded video stimuli, as shown in the group-average map (Fig. 7.2).

Here, we discuss issues and limits of the IPS-x model and propose alternative views of retinotopic organization along IPS. First, there are often gaps between subdivisions or dropouts of activation (e.g., a missing partial or full quadrant) along the IPS-x strip (Schluppeck et al., 2005; Silver et al., 2005; Hagler et al., 2007; Swisher et al., 2007). This is likely because the stimulus size ( $\sim 10^\circ$  eccentricity) was insufficient to cover the maximum extent of visual field represented by these areas, and/or because there was a temporally uneven distribution of attention at different polar angles. Second, the contours outlining subdivisions along IPS are somewhat arbitrary across studies. Some large subdivisions appear to include more than one area (e.g., IPS-0 and IPS-1 extend areas on both banks of IPS), while some small subdivisions (e.g., IPS-4 and IPS-5) only include partial hemifield representations. Third, a large variation exists across subjects and the IPS-x model cannot fully account for the more complex formation observed in many single-subject maps in our and other studies (Fig. 7.3; Sereno and Huang, 2006; Hagler et al., 2007; Levy et al., 2007; Huang and Sereno, 2013; Sood and Sereno, 2016).

In a typical IPS-x strip, the first upper visual field representation beyond V7 (IPS-0) defines IPS-1 and IPS-2 while the second defines IPS-3 and IPS-4, as shown in subject 1 in Figure 7.3A. However, other subjects show one to three distinct or partially connected regions of upper visual field representation, and the IPS-x model does not straightforwardly apply to these maps (Fig. 7.3C–H). Such intersubject variation makes it difficult to match areas across studies. For example, the putative human LIP in Sereno et al. (2001) was placed

at a location further anterior and lateral to IPS-2 due to the use of different, somewhat incompatible, brain coordinate systems (see Figure 10 in Silver et al., 2005), and later assigned to IPS-3 (Hagler et al., 2007). To date, areas IPS-0 (V7), IPS-1, and IPS-2 have been consistently reported across studies (Levy et al., 2007; Swisher et al., 2007; Konen and Kastner, 2008; Saygin and Sereno, 2008; Helfrich et al., 2013; Sheremata and Silver, 2015). Beyond IPS-2, some subjects show a straight path with IPS-5 ending at the ridge of SPL, while others show a sharp bend with IPS-5 ending at the anterior IPS (Figure 4 in Konen and Kastner, 2008; Figure 1 in Helfrich et al., 2013; Figure 2 in Konen el al., 2013; Figure 2 in Mruczek et al., 2013; Figure 1 in Wang et al., 2015). Without further functional data, it is difficult to conclude that these anatomically separated areas are functionally equivalent or that they are organized consistently across all subjects.

The IPS-x model has helped to draw an initial picture of retinotopic organization along IPS. However, while convenient for subdividing areas in some single-subject maps, other individual subjects show a fan-shaped cluster (LIP+) rather than a linear formation (Fig. 7.3; see Hagler et al., 2007). For example, subject 4 in Figure 7.3E shows an LIP+ cluster with multiple lower visual field "blades" adjoining a confluent upper visual field "shaft." These "blades" were labeled with arrows instead of numbers to be conservative. Furthermore, retinotopy extends into the lateral bank of the caudal part of IPS, lateral to the IPS-x strip or LIP+, as shown in singlesubject and group-average maps and in other studies (Figs 7.2 and 7.3; Hagler et al., 2007; Levy et al., 2007; Swisher et al., 2007; Sheremata and Silver, 2015). We tentatively labeled the region anterior to V3B and lateral to V7 as cIPS, which contains a partial to full hemifield representation with the upper visual field adjoining V3B. Human fMRI studies show that this region is involved in the processing of surface orientation and depth, suggesting that it could be the human homolog of the macaque caudal intraparietal area (CIP; Tsao et al., 2003; Huang and Sereno, 2008; Shikata et al., 2008).

Retinotopic maps in the parietal lobe probably support higher-level functions such as visuospatial attention, short-term memory, numerosity, motion processing, visually guided actions, navigation, and language (Simon et al., 2002; Astafiev et al., 2003; Levy et al., 2007; Konen and Kastner, 2008; Silver and Kastner, 2009; Harvey et al., 2013; Helfrich et al., 2013; Huang and Sereno, 2013; Konen et al., 2013; Mruczek et al., 2014; Eger et al., 2015; Michalka et al., 2016; Sood and Sereno, 2016). Once a retinotopic basemap has been established for an individual subject, it can be overlaid with other maps activated by sensory, cognitive, or motor tasks within the same individual. The IPS-x model, where it applies, provides initial reference landmarks for interpreting these activation maps within each individual.

# MULTISENSORY PARIETAL FACE AND BODY AREAS

Parietal retinotopic maps extend beyond IPS and into PoCS, which contains multisensory parietal face and body areas immediately posterior to the primary somatosensory cortex (SI) (Sereno and Huang, 2006; Huang and Sereno, 2007; Huang et al., 2012, 2017). Macaque area VIP is located at the fundus of the IPS, and it contains neurons with aligned visual and tactile receptive fields anchored to the face and upper body (Colby et al., 1993; Duhamel et al., 1998; Avillac et al., 2005, 2007).

A probable human homolog of macaque VIP was originally identified as an area in the depth of IPS activated by visual, tactile, and auditory motion stimuli (Bremmer et al., 2001). At a slightly more medial and superior location, we later identified a parietal face area (VIP+) at the confluence of the superior PoCS and anterior IPS (Sereno and Huang, 2006), a region activated by wide-field videos, optic-flow stimuli, and air puffs on the face (Figs. 7.1–7.4). Subsequent studies using optic flow or vestibular stimuli have identified putative human VIP at a number of different locations in IPS, SPL, and PoCS (Figure 2 in Fasold et al., 2008; Figure 2 in Konen and Kastner, 2008; Figure 2 in Wall and Smith, 2008; Figure 1 in Cardin and Smith, 2010, which places VIP one sulcus posterior to the VIP in Wall and Smith, 2008; Figure 2 in Smith et al., 2012, which has VIP back in the PoCS; Figure 3 in Pitzalis et al., 2013a; Figure 2 in Furlan et al., 2014). For example, IPS-5 has been suggested to be identical to the parietal face area based on anatomic location and motion selectivity (Konen and Kastner, 2008); however, this could be true only if IPS-5 reaches the anterior IPS and adjoins or partially overlaps with the VIP+ cluster (Figs 7.2 and 7.3). As multiple areas along IPS are motion-sensitive, experiments using optic flow stimuli in conjunction with face tactile stimulation are critical to precisely define human VIP (Sereno and Huang, 2006; Eger et al., 2015).

Detailed somatotopic organization in VIP+ was mapped by phase-encoded air puffs slowly moving around the face (Huang et al., 2017; Sereno and Huang, 2006). Overlay of retinotopic maps obtained by wide-field phase-encoded videos revealed aligned tactile-visual representations of near-face space. A representative subject shows a multisensory map in which the forehead overlaps with the upper visual field representation and the chin overlaps with the lower visual field representation



**Fig. 7.4.** Aligned tactile-visual maps of the human parietal face area (VIP+) in a representative subject. *LH*, left hemisphere; *RH*, right hemisphere. (Reproduced from Sereno MI, Huang RS (2006) A human parietal face area contains aligned head-centered visual and tactile maps. Nat Neurosci 9: 1337–1343, Figure 3, with permission.)

(Fig. 7.4). Group-average and single-subject maps show an approximate upper to lower visual field progression extending from the superior PoCS into the anterior IPS (Figs 7.2–7.4). These aligned maps may help to efficiently detect impending objects (e.g., "Watch your head!") as well as to coordinate actions involving the face, such as avoiding obstacles, eating, or shaving (Graziano and Cooke, 2006). In addition to vision and touch, human VIP has been shown to be involved in vestibular, sensorimotor, and cognitive processing (Filimon et al., 2007, 2009; Fasold et al., 2008; Smith et al., 2012; Eger et al., 2015).

The full extent of multisensory areas in SPL was recently revealed by combining wearable full-body tactile stimulation and wide-field phase-encoded looming stimuli (Huang et al., 2012). Representations of fingers (hands), face (lips), shoulders (upper arms), legs, and toes are orderly arranged along the lateral (inferior) to medial (superior) PoCS and on to the midline, forming a rough nonprimary multisensory homunculus (Fig. 7.5; Figure 3C in Huang et al., 2012; Zlatkina et al., 2016). Notably, face (VIP+) and fingers (AIP) are arranged in an order (fingers inferior to face) opposite to that in SI (face inferior to fingers). Superimposing parietal face and body areas on retinotopic maps shows a lateral-to-medial progression of upper to lower visual field representations (Fig. 7.5; Figure 3 in Huang et al., 2012; Figure 1 in Sereno and Huang, 2014).

Medial and slightly posterior to the parietal face area, the parietal body area contains representations of the axial body, including shoulders, arms, legs, and toes overlapping with a region with primarily lower visual field representation extending into the superior anterior precuneus. The alignment between the lower limbs and lower visual field may facilitate the detection and



**Fig. 7.5.** A group-average map of somatotopic areas activated by passive tactile stimulation on six body parts. This map was constructed by merging body-part representations in group-average maps obtained by spherical averaging single-subject surface maps (n = 8-14) from Huang and Sereno (2007) and Huang et al. (2012), and then superimposed on a faded retinotopic map from Figure 7.2. Solid white contour indicates a region activated by brushing the toes. Abbreviations as in Figure 7.2 and text.

avoidance of obstacles in lower body space, e.g., "Watch your step!" (Marigold and Patla, 2008; Huang et al., 2012). Lateral and anterior to VIP+, a large region of finger (hand) representations extends from the postcentral gyrus (SI) into the inferior PoCS and anterior IPS (aIPS or AIP) (Ruben et al., 2001; Huang and Sereno, 2007; Cavina-Pratesi et al., 2010; Huang et al., 2012, 2017; Chen et al., 2017). In single-subject maps, AIP does not show consistent response to visual stimuli presented in eye-centered coordinates (Huang et al., 2012; Huang and Sereno, 2013), perhaps the result of inconsistent attention to peri-hand space.

Retinotopic and somatotopic maps in SPL are somewhat variable across subjects (Fig. 7.3; Sereno and Huang, 2006; Huang et al., 2012, 2017; Huang and Sereno, 2013). Some subjects show two complete visual hemifield representations in VIP+, and some show additional tactile representations of the face beyond VIP+ (see Figure S2 in Huang et al., 2012). In group-average maps, the most distinctive map structure around VIP+ is that it is adjoined by lower visual field representations laterally and medially (Figs 7.2 and 7.5; Sereno and Huang, 2014). Future studies using high-resolution fMRI will be required to refine the detailed organization in parietal face and body areas and validate each subdivision within and across subjects (Huang et al., 2017). In summary, topological maps extend throughout the entire parietal association cortex up to the highest level of the dorsal visual stream ("where/how" pathway). These multisensory maps may play important roles in supporting perception, action, and cognition in peripersonal space.

# PRIMARY AND NONPRIMARY SOMATOTOPIC MAPS

While an initial picture of retinotopic maps has been depicted, human somatotopic maps remain less complete. Compared with photoreceptors on the retina, somatosensory receptors are distributed across a much larger sheet over the entire body surface as well as in muscles and tendons. To construct a comprehensive sensory homuncular map, tactile stimuli must make physical contact with a wide range of complex-shaped body parts. This is challenging for fMRI experiments, as it is impractical to manually stimulate large portions of the body with precise timing, intensity, and localization. On the other hand, automatic stimulation devices face challenges of MRI compatibility, space and time constraints, and subject comfort.

To overcome these barriers, we previously developed an MRI-compatible system, Dodecapus, to deliver computer-controlled air puffs to the face, lips, and fingers (Huang and Sereno, 2007). More recently we developed a wearable technology for tactile stimulation from head to toe (Huang et al., 2012; Chen et al., 2017). In block-design fMRI experiments, randomized or sequential air puffs (tactile apparent motion) were delivered to



**Fig. 7.6.** A map of movement representations in a representative subject. Yellow contours outline the extent of retinotopic maps outlined from Figure 7.2. Abbreviations as in Figure 7.2 and text.

multiple sites on one body part bilaterally per block. An initial map of the greater sensorimotor cortex was constructed by merging multiple body-part representations in spherical group-average maps (Huang and Sereno, 2007; Huang et al., 2012), and then superimposing the results on retinotopic maps (Figs 7.2 and 7.5).

Passive tactile stimulation on the face, lips, and fingers activated the primary somatosensory cortex (SI), parietal operculum (secondary somatosensory area (SII), parietal ventral somatosensory area (PV), and area 7b), primary motor cortex (MI), dorsal and ventral premotor areas (PMd/PMv), and PPC. Finger (hand), face, and lip representations are arranged from superior to inferior, with partial overlap, along the postcentral gyrus (SI). Face and lip representations extend beyond the inferior part of the PoCS and divide into PV and SII branches on the upper bank of the lateral sulcus, roughly separated by the PV/SII representations of fingers (Disbrow et al., 2000; Eickhoff et al., 2007; Burton et al., 2008). The SII branch of the face/lips extends posteriorly into a putative area 7b overlapping with the visually driven PIVC. Across the central sulcus (CS), face and lip representations extend into MI and two multisensory areas in the frontal cortex, the polysensory zone (PZ) (Graziano and Gandhi, 2000) and PMv (Bremmer et al., 2001; Gentile et al., 2011). The dorsal region of finger representation includes MI and PMd (partially overlapping with FEF+), while the ventral region overlaps with PMv of face and lip representations (see PMd/PMv in Gentile et al., 2011; Brozzoli et al., 2014).

Air puffs moving across the arms, shoulders, legs, and toes only activated the parietal body area in superior

PoCS but apparently not SI. The coverage, density, intensity, and temporal patterns of air-puff stimuli need to be further improved to map body parts (e.g., legs) with a larger surface area, especially in cortical areas where their representations have small receptive fields. In a supplementary experiment in Huang et al. (2012), manual brushing across toes activated a wide range of areas, including MI (Fig. 7.5). Since it is difficult to completely inhibit passive toe movements during brushing, this may reflect a combination of somatosensory and motor activation (but note that there is direct ascending somatosensory input to MI via the ventrolateral thalamic nucleus). Currently, the region in primary somatosensory cortex between the fingers and toes was not reliably activated in our air-puff tactile maps. The expected locations of hand, arm, trunk, leg, and tongue representations in SI and MI are labeled in Figure 7.5.

Although voluntary (active) movements are more effective in mapping some of the larger body parts, it is challenging to restrict the joints and muscles involved in each type of movement. Here, we show an initial map of movement representations arranged in approximate homuncular organization in the primary and nonprimary sensorimotor cortex of a representative subject (Fig. 7.6). The subject made repeated minimal bilateral movements of body parts (tongue, lips, eyebrows, fingers, wrist, biceps, stomach, buttocks, quadriceps, ankle, and toes) in response to periodic auditory cues (Sood and Sereno, 2016).

Other primary and nonprimary sensorimotor maps obtained by passive sensory stimulation, passive movements, and/or active movements are summarized as follows: (1) Figure 3 in Miyamoto et al. (2006): lips, tooth,



Fig. 7.7. Group-average maps of detailed somatotopic organization in face, lip, and finger representations. Data were reanalyzed and spherical-averaged across subjects (n = 4-9) from Huang and Sereno (2007). Each body part map is overlaid with somatotopic contours outlined from another body part map.

and tongue; (2) Figure 3 in Eickhoff et al. (2008): face, hand, and trunk; (3) Figures 3 and 4 in Meier et al. (2008): 10 body-part movements; (4) Figure 2 in Blatow et al. (2011): hand and foot (sensory stimulation and passive or active movements); (5) Figure 2 in Grabski et al. (2012): lips, jaw, larynx, and tongue; (6) Figure 5 in Cunningham et al. (2013): finger, elbow, and ankle; (7) Figure 5 in Weiss et al. (2013): thumb, foot, lips, and tongue; (8) Figure 1 in Makin et al. (2015): foot, arm, hand, and lips; (9) Figure 7 in Zeharia et al. (2015): somatotopic gradient maps of 20 body parts; (10) Figures 2, 5, and 7 in Zlatkina et al. (2016): foot, leg, arm, hand, mouth, and tongue; (11) Figures 1–3 in Carey et al. (2017): lip, tongue, throat, and larynx.

To map more detailed somatotopic organization while avoiding movements, air puffs were sequentially and periodically delivered to 12 sites on the face, or the lips, or the hands every 64 seconds in a phase-encoded experiment (Huang and Sereno, 2007). In the resulting groupaverage maps (Fig. 7.7), SI, MI, and VIP+ show approximate somatotopic organization, but other regions are less clear. The SI representation of thumb (D1) is located inferior to little finger (D5) on the postcentral gyrus as expected (for higher-resolution finger maps, see Mancini et al., 2012; Besle et al., 2013; Martuzzi et al., 2014). In the SI face representations, chin, cheek, and forehead extend from the inferior postcentral gyrus into the central sulcus. The SI lip representation largely overlaps with the face, and the lower-lip representation is inferior and posterior to the upper lip. To date, up to a dozen stimulation sites have been used to map the face and lip representations (Huang and Sereno, 2007; Kopietz et al., 2009; Moulton et al., 2009). These maps can be refined by using wearable two-dimensional (2D) grids (custom-molded face mask) with higher stimulation count and density in future studies (Huang et al., 2012, 2017; Chen et al., 2017).

While detailed mapping of somatotopic organization has long been carried out in nonhuman primates (e.g., Figure 1 in Kaas et al., 1979; Figure 9 in Seelke et al., 2012), existing human somatotopic maps can be refined in several ways. First, the number subdivisions of each body-part representation in both primary and nonprimary



**Fig. 7.8.** Group-average retinotopic maps and functional specialization on the medial wall. Polar angle and eccentricity maps were obtained by spherical averaging single-subject surface maps (n = 24), and then overlaid with spherical group-average activation maps (n = 10) of imagined navigation (magenta contours) and imagined rest (cyan contours) (data reanalyzed from Huang and Sereno, 2013). Yellow contours outline regions activated by passive dodges in spherical group-average maps (n = 10; data reanalyzed from Huang et al., 2015).

cortex need to be further delineated (Rizzolatti et al., 1998; Burton et al., 2008; Meier et al., 2008; Huang et al., 2012; Cunningham et al., 2013; Zlatkina et al., 2016). Second, the exact extent of each body-part representation and overlap among different representations need to be defined quantitatively (Meier et al., 2008). Third, the probability of ipsilateral, contralateral, and bilateral representations of each body part needs to be determined (Eickhoff et al., 2008). Fourth, fine-grained organization within each body-part representation can be mapped using 2D phase-encoded paradigms to distinguish mirror-image and nonmirror-image maps, originally developed for retinotopic mapping (Engel et al., 1994; Sereno et al., 1995; Servos et al., 1998; Huang and Sereno, 2007; Engel, 2012; Mancini et al., 2012; Besle et al., 2013).

## **MEDIAL PARIETAL MAPS**

On the medial wall, two visual streams extend into the precuneus and cingulate sulcus (visual stream #3) and into RSC (visual stream #4), separated by the inferiorly located PCC (Figs 7.1 and 7.2). Several multisensory and sensorimotor areas have recently been found partially overlapping with stream #3 (Figs 7.2 and 7.8). Anterior

to V3d, area V6 on the posterior bank of POS was activated by wide-field retinotopic and optic flow stimuli, and it contains a complete map of the contralateral peripheral hemifield (Pitzalis et al., 2006, 2013a). Area V6A adjoins V6 anteriorly and superiorly on the anterior bank of POS (Pitzalis et al., 2013b).

A number of fMRI studies have shown reachingrelated activation in regions roughly equivalent to V6A, including the parietal reach region (PRR; Connolly et al., 2003), superior POS (sPOS; Filimon et al., 2009), parieto-occipital junction (POJ; Bernier and Grafton, 2010), anterior superior parietal occipital sulcus (aSPOC; Cavina-Pratesi et al., 2010), superior parieto-occipital cortex (SPOC; Rossit et al., 2013); also see Filimon (2010), Konen et al. (2013), and Pitzalis et al. (2015).

V6A was later divided into V6Av (ventral) and V6Ad (dorsal) subdivisions (Pitzalis et al., 2015). V6Av contains a crude hemifield representation of the far periphery, adjoining a confluent lower visual field representation with V7 (IPS-0) and IPS-1 (Fig. 7.2). Initial evidence suggests the posterior precuneus region overlapping with V6Ad contains horizontal to lower visual field representations (Huang et al., 2012; Huang and Sereno, 2013; Sereno et al., 2013), but further

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studies are required to refine retinotopic organization in the region between V6 and aPCu (Figs 7.2 and 7.8; Pitzalis et al., 2015).

Retinotopy extends beyond V6A into the precuneus, which is known to be involved in higher-level cognitive functions and mental imagery (Cavanna and Trimble, 2006; Margulies et al., 2009). Part of the anterior precuneus was also activated by reaching movements with or without visual feedback (i.e., proprioception) (Filimon et al., 2007, 2009; Rossit et al., 2013) and egomotioncompatible stimuli (Cardin and Smith, 2010; Huang et al., 2015; Uesaki and Ashida, 2015). Several studies have shown retinotopic activation in the precuneus (Jack et al., 2007; Levy et al., 2007; Saygin and Sereno, 2008; Huang et al., 2012; Sereno et al., 2013; Sood and Sereno, 2016). Posterior to the marginal sulcus (the ascending ramus of the cingulate sulcus) and medial inferior to PBA, area aPCu contains a complete map of the contralateral hemifield, with the upper visual field representation located inferior to the lower visual field representation (Figs 7.2 and 7.8; Huang and Sereno, 2013). The subdivisions and functions in the PCu remain unclear, and they need to be refined by integrating retinotopic mapping, visuomotor tasks, functional connectivity, and cytoarchitectonic analysis in future studies (Scheperjans et al., 2008; Margulies et al., 2009; Filimon, 2010; see Chapter 3).

Anterior to the precuneus, area CSv is found to be activated by optic flow stimuli (Wall and Smith, 2008; Cardin and Smith, 2010) at the anteriormost end of visual stream #3. Wide-field phase-encoded videos further showed that CSv contains predominantly peripheral and lower visual field representation (Figs 7.2 and 7.8; Huang and Sereno, 2013). Furthermore, CSv also responds to galvanic vestibular stimulation (Smith et al., 2012), and it may overlap with Brodmann area 5Ci (Scheperjans et al., 2008). Adjoining V6, V2d, and V1d is an area containing upper to horizontal visual field representation, which extends anteriorly and inferiorly along the POS (Figs 7.2 and 7.8). We tentatively consider this area the human homolog of the macaque POm area (Galletti et al., 1999). Anterior to POm, retinotopy extends across POS into RSC at the anteriormost end of visual stream #4 (Fig. 7.8), a region found to be activated by real or imagined scenes (Nasr et al., 2011; Huang and Sereno, 2013).

# PERIPERSONAL SPACE AND ACTIONS

Recent electrophysiologic studies in nonhuman primates have suggested that motor, premotor, and posterior parietal cortices are organized into overlapping action zones, rather than distinct body-part or muscle representations, for generating complex movements near the body (Stepniewska et al., 2005; Graziano and Aflalo, 2007; Kaas et al., 2011; Kaas and Stepniewska, 2016). Human neuroimaging studies have also revealed cortical specializations underlying visually guided actions such as saccades, pointing, reaching, and grasping in peripersonal space (Culham and Valyear, 2006; Filimon, 2010; Vesia and Crawford, 2012; Sereno and Huang, 2014). To illustrate cortical representations of peripersonal space and actions, we construct a functional model (Fig. 7.9) by combining retinotopic, somatotopic, and movement maps on the same cortical surface (Figs 7.2, 7.5, 7.6, and 7.8). Areas in this model are labeled according to anatomic locations, retinotopic and somatotopic areas, effectors, and actions. In the following section, we discuss areas involved in different actions in space near the face (head), hand, and body (including upper and lower limbs).

The human parietal face area (VIP+) at the superior PoCS contains aligned visual-tactile maps representing near-face space. In macaque monkeys, electrical stimulation of areas VIP and PZ or air puffs delivered to the face evoked defensive behaviors, e.g., as if blocking an object approaching the face (Graziano and Cooke, 2006). Macaque area VIP also responds to visual, auditory, or tactile motion (externally induced), self-motion, eye movements, and vestibular stimulation (Bremmer, 2011). Here, we tentatively consider defense ("D" in Fig. 7.9) as one of the foremost functions of human VIP, which needs to be confirmed by performing minimal defensive movements in the MRI scanner.

Recent fMRI studies have also demonstrated other functions of human VIP, including motion processing, vestibular and proprioceptive sensation (Fasold et al., 2008; Smith et al., 2012; Billington and Smith, 2015), and visual and nonvisual reaching beside the face (Filimon et al., 2007, 2009). Furthermore, part of VIP responds to tactile stimulation on the lips and fingers (Figs 7.5 and 7.7; Huang and Sereno, 2007; Huang et al., 2012). Arranged in close proximity along the PoCS, the parietal face, lip, and hand (AIP) areas may help to coordinate hand-to-mouth (self-feeding) movements ("F" in Fig. 7.9; Stepniewska et al., 2005; Graziano and Aflalo, 2007; Kaas et al., 2011; Sereno and Huang, 2014; Kaas and Stepniewska, 2016).

Multiple subdivisions of hand and arm representations have been revealed in the PPC of nonhuman primates (Rizzolatti et al., 1998; Breveglieri et al., 2008; Kaas et al., 2011; Seelke et al., 2012; Kaas and Stepniewska, 2016). Similarly, the human parietal lobe contains multiple representations of manual actions in peripersonal space (Culham and Valyear, 2006; Blangero et al., 2009; Filimon, 2010; Vesia and Crawford, 2012; Zlatkina et al., 2016). Passive stimulation on the fingers (hands) activated a region extending from the inferior PoCS into



**Fig. 7.9.** A model of action representations in parietal and frontal cortices. Areas IPS-1 to IPS-5 are indicated by white dashed contours beyond V7 (IPS-0). *D*, defense; *E*, eye movements; *F*, feeding; *G*, grasping; *P*, pointing; *R*, reaching; *T*, touching; *W*, walking.

aIPS (Ruben et al., 2001; Huang and Sereno, 2007; Huang et al., 2012), which is considered the human homolog of macaque AIP (Binkofski et al., 1998).

The human AIP (aIPS) was activated by grasping movements in a large number of fMRI studies (see Figure 2 in Vesia and Crawford, 2012; Figure 6 in Konen et al., 2013). Phase-encoded videos or looming objects presented directly in front of the face (i.e., with aligned eye-centered and head-centered coordinates) activated an anterior IPS region with an emphasis on the lower visual field representation adjoining AIP, as outlined by passive tactile stimulation (Figs 7.2 and 7.5). Although AIP did not show consistent retinotopic activation, it was activated by real objects presented near the hand (i.e., in hand-centered coordinates), and it showed stronger response to visuotactile stimulation than to unisensory stimulation (Makin et al., 2007; Gentile et al., 2011; Brozzoli et al., 2014). Furthermore, AIP is also found to be involved in visuohaptic processing of grating orientation and shape selectivity (Kitada et al., 2006; Stilla and Sathian, 2008; Hinkley et al., 2009; Kim and James, 2010).

Reaching (arm transport) movements activated two major clusters in medial and superior PPC (Fig. 7.9). The first cluster is located anterior superior to POS on the medial wall, partially overlapping with the posterior medial part of the IPS-x strip (Figure 2 in Konen et al., 2013). This cluster overlaps with human V6A, as defined in the retinotopic map (Fig. 7.2), and it may correspond to PRR (Connolly et al., 2003), sPOS (Filimon et al., 2009), POJ (Bernier and Grafton, 2010), aSPOC (Cavina-Pratesi et al., 2010), or SPOC (Rossit et al., 2013). The second cluster extends from anterior IPS into the SPL (partially overlapping with VIP+ and PBA) and into the anterior superior precuneus (Filimon et al., 2007, 2009; Hinkley et al., 2009; Bernier and Grafton, 2010; Cavina-Pratesi et al., 2010; Vesia and Crawford, 2012).

Finger pointing with minor wrist or forearm movements activated parietal regions that overlap with grasping- and reaching-related regions anteriorly, and to a lesser degree with saccade-related regions posteriorly ("E" in Fig. 7.9) (Simon et al., 2002; Hagler et al., 2007: Levy et al., 2007: Heed et al., 2011: Leone et al., 2014). In most pointing-related and some reaching-related experiments, visual targets were presented in eye-centered coordinates via mirrors, where hand movements were not directly visible to the subject. Further studies are required to delineate visual, motor, and proprioceptive representations of direct-view eyehand coordination in eye-, hand-, head-, or bodycentered reference frames (Avillac et al., 2005; Sereno and Huang, 2006; Filimon et al., 2009; Bernier and Grafton, 2010; Brozzoli et al., 2014).

Medial to human VIP+, PBA contains overlapping representations of the shoulders, arms, legs, and toes. In nonhuman primates, a region medial to a VIP-like, "head defense" region in rostral PPC is also found to contain hindlimb and forelimb representations (see Figure 5 in Kaas and Stepniewska, 2016). Electrical stimulation of this region evoked locomotory movements such as climbing (Kaas et al., 2011). Here, we tentatively consider walking as one of the foremost functions of PBA because its lower-body representations overlap with a large region of lower visual field representation (Figs 7.2, 7.5, and 7.9). Two higher-level motionsensitive areas, CSv and superior frontal sulcus (SFS), also contain primarily lower visual field representation adjoining foot motor and premotor areas (Figs 7.5 and 7.6). These aligned visuomotor representations may help to coordinate lower-limb movements in the lower-body space, e. g., when watching one's steps. The anterior SPL region was also activated in a number of fMRI experiments, including voluntary leg or foot (ankle) movements (Cunningham et al., 2013; Zlatkina et al., 2016), imagery or observation of foot movements (Lorey et al., 2014), planning of foot-pointing movements (Heed et al., 2011; Leone et al., 2014), selfgenerated foot movements with visual feedback (Christensen et al., 2007), execution and observation of walking (Dalla Volta et al., 2015), and heading judgment and obstacle avoidance (Billington et al., 2010, 2013; Huang et al., 2015).

Taken together, human PPC contains modules specialized for different actions that form a nonprimary homunculus with the hand (fingers), face (lips), and legs (toes) arranged along the PoCS, the eyes located along the IPS, and multiple arms distributed in the anterior IPS, posterior medial IPS into anterior superior POS, and SPL into anterior superior precuneus (Fig. 7.9). The parietal face area contains aligned visual-tactile maps representing the contralateral visual hemifield and hemiface. The parietal arm and hand areas adjoin or overlap with lower visual field representations at aIPS, SPL, and anterior superior POS. The parietal leg and toe areas (part of PBA) overlap with a region with primarily lower visual field representation at SPL. These multisensory alignments may facilitate actions within different subspaces (action zones) near the body (Graziano and Aflalo, 2007; Rossit et al., 2013). The spatial relationship among face, hand, and eye representations is largely consistent with the arrangement of areas VIP, AIP, and LIP in macaque PPC (Figure 2B in Rizzolatti et al., 1998; Figure 1 in Gattass et al., 2005; Figure 1 in Culham and Valyear, 2006; Figure 5 in Kaas et al., 2011). While macaque LIP is located at the lateral bank of IPS (Colby et al., 1996), human LIP+ has been displaced onto the medial bank of IPS by the enlarged human angular gyrus (Figure 3 in Sereno and Huang, 2014). Medial to VIP+ and anterior to LIP+, human PBA contains both lower- and upper-limb representations, which may be equivalent to macaque areas MIP or 5 (PE/PEc) (Breveglieri et al., 2008; Seelke et al., 2012).

The proposed multisensory homuncular model aims to illustrate the relative locations among different

body-part and action representations in human parietal lobe. It is important to note that each type of action may be represented by multiple detached brain regions, and each region may contain overlapping representations of different body parts and actions (Graziano and Aflalo, 2007; Meier et al., 2008). Future studies, using smooth gradient changes in multi-dimensional representations of multisensory stimuli as well as movements of different body parts, might be able to better model the distribution of body-part and action representations over the cortical surface (Op de Beeck et al., 2008; Heed et al., 2011; Leone et al., 2014; Zeharia et al., 2015).

## HIGHER-LEVEL MOTION AREAS AND NAVIGATION

Each of the three dorsal visual streams contains higherlevel motion areas playing important roles in navigation through space (Bremmer, 2011). Here, we construct a map with multilayer contours outlining regions activated by motion stimuli and/or navigation tasks in our studies (Fig. 7.10) in order to show their relation to unisensory and multisensory maps. The first stream includes areas MT+ (MT, MSTd, and FST), STS, and PIVC, which are distributed across the middle temporal and parietoinsular cortices. The second stream includes areas V3A, V3B, V7, part of the IPS-x strip, SPL-1, PBA, and VIP+, which extend from TOS, along IPS, and into the superior PoCS. The third stream includes areas POm, V6, V6Av, aPCu, and CSv, which extend from POS into the cingulate sulcus. Notably, each stream ends with a multisensory area (PIVC, VIP, or CSv) sensitive to egomotion-compatible stimuli.

Using a wide-field version of low-contrast concentric ring patterns (Tootell et al., 1995), a block design experiment comparing moving and stationary stimuli activated peripheral V1-V3 (both dorsal and ventral), V6, V6Av, V7, V3A, V3B, LO-1, LO-2, MT+, and a region adjoining IPS-3 and IPS-4 (Fig. 7.10). In another block design experiment, areas V6, V6Av, POm, VIP+, CSv, PIVC, PZ, and part of FEF+ were more strongly activated by wide-field optic flow patterns (dilations, contractions, spirals, and rotations) than by random-dot local motion (Fig. 7.10; Sereno et al., 2001; Sereno and Huang, 2006). Among these areas, V6, VIP+, MT+, CSv, and PIVC have also been activated by optic flow patterns in other studies (Wall and Smith, 2008; Cardin and Smith, 2010; Pitzalis et al., 2013a; Furlan et al., 2014; Uesaki and Ashida, 2015; Wada et al., 2016).

In a recent fMRI study, a virtual-reality scene was constructed to simulate a daily scenario where doors randomly swing outward while walking in a hallway (Huang et al., 2015). Subjects passively observed computer-simulated dodges (translational egomotion)



**Fig. 7.10.** A group-average map of motion and navigation-related regions. Regions of active and passive dodges were from spherical group-average maps (n = 10) in Huang et al. (2015). Regions of imagined navigation (red) and imagined rest (green) were from spherical group-average maps (n = 10) in Huang and Sereno (2013). Black contours ("Optic Flow vs. Random") outline spherical group-average (n = 21) regions activated by contrasting optic flow patterns and random-dot local motion. Darkened regions enclosed in white contours ("Low-contrast Motion") outline spherical group-average (n = 19) regions activated by contrasting moving and stationary low-contrast concentric ring patterns.

in one experiment, and actively dodged swinging doors in the other experiment. In addition to areas activated by low-contrast motion and optic flow patterns (Fig. 7.10), passive dodges also activated areas IPS-1, IPS-2, SPL-1 (Konen and Kastner, 2008), PBA (anterior superior to SPL-1), aPCu (see Figs 7.2 and 7.8; also known as the precuneus motion area, PcM, in Cardin and Smith, 2010; Uesaki and Ashida, 2015; Wada et al., 2016), part of FEF+, and a motion area at the superior frontal sulcus (SFS; Sunaert et al., 1999). Passive dodges more strongly activated PBA than VIP+, suggesting that whole-body translational egomotion engages more than just the head (face) representations. The SPL region spanning between the dorsal medial bank of IPS and superior end of PoCS (overlapping with areas IPS-2, IPS-3, SPL-1, and PBA in Fig. 7.10) has been shown to be involved in heading judgment and obstacle avoidance during simulated egomotion (Field et al., 2007; Billington et al., 2010, 2013).

Active dodges most strongly activated MSTd, STS, and PIVC in the temporal - vestibular stream (#1), with the strongest activation located in the right PIVC (Huang et al., 2015). The main difference from previous optic flow studies is that subjects actively controlled their

horizontal movements and received real-time visual optic-flow feedback in the virtual-reality environment, similar to what they would perceive while moving their body or head in the real world. However, it is arguable whether active control of "virtual" egomotion indeed involves vestibular processing, or whether the PIVC activated in this study is only visual processing. Recent studies have shown overlapping visual and vestibular subdivisions in the region commonly labeled PIVC (Brandt and Dieterich, 1999; Cardin and Smith, 2010; Smith et al., 2012; Frank et al., 2014; Billington and Smith, 2015; see Chapter 6). In future studies, multisensory subdivisions (including PV, SII, 7b, PIC, and PIVC) and their mutual overlap at the posterior lateral sulcus need to be refined using a combination of visual, somatosensory, and vestibular stimuli within the same fMRI session.

Lastly, we discuss higher-level areas involved in mental navigation. In a block design fMRI experiment, eyeclosed subjects imagined walking between two locations in a familiar building for 16 seconds, and then imagined resting at the intermediate goal location for 16 seconds (Huang and Sereno, 2013). Imagined navigation activated a network including RSC, part of POm, parahippocampal place area (partially overlapping with PHC), occipital place area (OPA; partially overlapping with V3B and cIPS at the posterior IPS), PMv, a dorsal premotor region overlapping with FEF+ and SFS, supplementary motor area (SMA), posterior to anterior IPS, and medial IPS into PCu precuneus (Figs 7.2, 7.8, and 7.10). Several regions were activated during imagined rest or deactivated during imagined navigation. These regions include PCC, AnG, and medial prefrontal cortex (mPFC), which are part of the default-mode network ("Def" in Fig. 7.10). Imagined navigation did not activate motion-sensitive areas, but instead deactivated areas MT and V3A. The map overlay shows that retinotopy extends into scene-selective regions, RSC, PPA, and OPA, which have an emphasis on the periphery and horizontal to upper visual field representations (Figs 7.2 and 7.8; Huang and Sereno, 2013). Further studies are needed to determine the exact location, extent, and retinotopic organization of each scene-selective region (Arcaro et al., 2009; Nasr et al., 2011; Silson et al., 2015). The precuneus and RSC are known to be involved in higher-level cognitive functions, such as mental imagery, episodic memory, scene perception, and navigation (Cavanna and Trimble, 2006; Nasr et al., 2011). Bottom-up retinotopic organization in these higher-level regions may help to efficiently process scene and route information in eye-centered coordinates for top-down, internally generated mental navigation (Huang and Sereno, 2013). Lastly, mental navigation regions minimally overlap with motion and vestibular areas across the three dorsal visual streams. Together, they may serve complementary roles in supporting real and imagined egomotion in daily life.

# MAKING AND USING THE ATLAS

Understanding the topological and functional organization of the parietal lobe involves the integration of retinotopic, motion, somatotopic, vestibular, proprioceptive, action, and cognitive representations in the same map. Recent studies have demonstrated a combined bottom-up and top-down approach to interpret functional activation in relation to topologically organized areas in the same subject (Konen and Kastner, 2008; Nasr et al., 2011; Helfrich et al., 2013; Huang and Sereno, 2013; Konen et al., 2013; Mruczek et al., 2013; Somers and Sheremata, 2013; Hutchinson et al., 2014; Silson et al., 2015; Michalka et al., 2016; Sood and Sereno, 2016).

Here, we construct a rough but comprehensive atlas with layers of unisensory and multisensory maps. We did our best to label brain areas and subdivisions consistent with findings in other studies. Although various naming conventions are used by different research groups, we have tried to use existing names established in nonhuman primates. In each map, labels indicate the central locations of areas while contours outline the approximate extent of selected areas. When reading these maps, the first goal is to identify the location of each area relative to nearby sulci, gyri, and neighboring areas. For example, VIP+ is located between the superior PoCS and anterior IPS, adjoined by SI (fingers/hand), AIP, PBA, IPS-4, and IPS-5 (Figs 7.2 and 7.5).

The initial atlas discussed here will eventually be refined and revised in several ways. First, optimal stimuli and tasks can be selected for activating areas serving different functional roles. For example, the rotating wedge in a retinotopic mapping experiment can be filled with more homogeneous but still interesting contents, such as optic flow patterns or looming objects, to maximally activate VIP+ (Huang et al., 2012, 2017). Second, highlyaccelerated imaging protocols and high-count multielement coils can be used to delineate topological subdivisions and their exact extent at a higher spatial resolution. Third, probabilistic or high-dimensional gradient maps can be constructed to test the reproducibility of each area within and across subjects (Op de Beeck et al., 2008; Heed et al., 2011; Leone et al., 2014; Wang et al., 2015; Chen et al., 2017). These maps will further refine the influence of each modality (visual, tactile, or motor) in each area. Fourth, most stimuli are currently presented in eye-centered coordinates. Further studies are required to determine stimulus selectivity in different body-part centered reference frames (Avillac et al., 2005; Sereno and Huang, 2006; Filimon et al., 2009; Bernier and Grafton, 2010; Brozzoli et al., 2014).

To date, a tremendous amount of neuroimaging data has been accumulated around the world. Due to constraints on publication space and formats (e.g., non-interactive 2D figures), each article typically shows functional activation overlaid on a few anatomic images or 3D cortical surfaces of representative subjects along with tables of peak activation coordinates. It is difficult to match corresponding areas (e.g., subdivisions of the IPS-x strip) on various forms of cortical surfaces (partially or fully inflated) reconstructed by different software packages. A convenient approach is to display Talairach or Montreal Neurological Institute coordinates of activation foci from different studies on the same cortical surface (e.g., Figure 2 in Vesia and Crawford, 2012; Figure 6 in Konen et al., 2013). However, these volumebased coordinates are only very crude estimates generated by 3D registration with standard brain datasets, and it is easy to confuse locations without considering their sulcal/gyral contexts.

An alternative approach is to morph individual cortical surfaces and register them in a spherical

surface-based coordinate system (Fischl et al., 1999; Van Essen and Dierker, 2007; Henriksson et al., 2012). Recently, several groups have started to build surfacebased population-average functional atlases such as SumsDB (http://sumsdb.wustl.edu; Van Essen and Dierker, 2007). Freesurfer label and annotation files for the spherical average subject, fsaverage, similarly provide a method of distributing more detailed, higher-resolution specifications of cortical areal boundaries. In the near future, one might hope to create more comprehensive online atlases for searching and browsing functional brain areas, with interactive multilayer features similar to Google Earth (www.google.com/ earth/), such as central locations and contours of topological areas (cf. GPS coordinates and county lines), and links to related publications and figures (cf. Google Scholar and Google Images) on the same interface.

# CONCLUSION

The parietal lobe plays a major role in sensorimotor integration and transformation for supporting actions in peripersonal space. Recent human neuroimaging studies have revealed topologically organized maps in higherlevel cortical regions that were not thought to be organized this way. To date, more than 40 retinotopic areas have been mapped in the human brain, including those distributed in dorsal streams encompassing the parietal lobe. Beyond areas V3A and V3B, a series of retinotopic areas extend from the medial posterior to anterior IPS and into the superior PoCS. On the medial wall, retinotopy extends across the POS into the precuneus and reaches the cingulate sulcus. Full-body tactile stimulation revealed a multisensory homunculus lying along the PoCS, bordering unisensory maps anteriorly (somatosensory) and posteriorly (visual). These topologically organized areas lay the foundation for supporting sensorimotor actions such as reaching and grasping in, and defending peripersonal space. Additionally, some of these areas play important roles in motion perception, vestibular processing, and navigation.

The multisensory parietal atlas in this chapter aims to provide a guide map to investigate the neural substrates of "How do we perceive and interact with the world around us?" This initial atlas helps to specify the relative locations of unisensory, multisensory, and action representations; but their exact names, locations, and contours remain tentative. We expect that those areal and functional definitions will be refined by future studies using more sophisticated stimuli and tasks tailored to regions with different specificity. The subdivisions in each area also need to be further refined with high-resolution neuroimaging techniques. The long-term goal of these endeavors is to construct an online surface-based atlas containing multilayer maps of all modalities that can be used as a reference to understand the functions and disorders of the parietal lobe.

#### ACKNOWLEDGMENTS

This work was supported by US National Institutes of Health Grant R01 MH081990 to M.I.S. and R.-S.H., a Royal Society Wolfson Research Merit Award to M.I. S, and by Wellcome Trust 091593/Z/10/Z for development of pulse sequences.

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