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Topographic maps in human frontal and parietal cortex

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Abstract

Retinotopic mapping of functional magnetic resonance (fMRI) responses evoked by visual stimuli has resulted in the identification of many areas in human visual cortex and a description of the organization of the visual field representation in each of these areas. These methods have recently been employed in conjunction with tasks that involve higher-order cognitive processes such as spatial attention, working memory, and planning and execution of saccadic eye movements. This approach has led to the discovery of multiple areas in human parietal and frontal areas, each containing a topographic map of visual space. In this review, we summarize the anatomical locations, visual field organization, and functional specialization of these new parietal and frontal topographic cortical areas. The study of higher-order topographic cortex promises to yield unprecedented insights into the neural mechanisms of cognitive processes and, in conjunction with parallel studies in non-human primates, into the evolution of cognition.

Topography: a fundamental organizing principle in cerebral cortex

Topographic representations are ubiquitous in cerebral cortical areas. For sensory cortex, these representations reflect the spatial layout of the sensory receptors: visual cortex contains retinotopic maps representing retinal locations, auditory cortex contains tonotopic maps reflecting the representation of temporal frequency in the cochlea, and somatosensory cortex contains maps corresponding to the surface of the body. Topographic maps have been postulated to be fundamental to the processing of sensory information, as neurons that are involved in the same sensory computations are in close spatial proximity, thereby minimizing connection distances [1].

In early visual cortical areas, topographic representations are maps of the contralateral visual field (Box 1). That is, a visual stimulus presented at a particular visual field location activates a corresponding location in the topographic visual field map in each of these cortical areas. The layout of the visual field in human primary visual cortex, or area V1, was first described by Inouye [2] in a study of soldiers who had suffered gunshot wounds to occipital cortex (translated into English in Ref [3]). In this study, a map of the visual field representation in area V1 was derived by correlating the location of the lesion was correlated with perceptual measures of visual field loss.

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Modern methods for determining visual field representations in human visual cortex often involve functional magnetic resonance imaging, or fMRI. A typical experiment involves the presentation of a high contrast stimulus that periodically traverses the visual field while the subject is fixating a central point, thereby evoking a traveling wave of activity in any brain area that contains a topographic visual field map (Box 1). This periodic mapping method, originally described by Engel et al. [4], has led to the discovery of many visual areas in human occipital and temporal cortex and to the characterization of the visual field layout in each of these areas (reviewed in Ref [5]). Cortical areas that can be defined with fMRI responses to visual periodic mapping stimuli include V1, V2, V3, and V4 (Ref [6]), V3A (Ref [7]), V3B (Ref [8]), V6 (Ref [9]), V7/IPS0 (Ref [10]), IPS1, IPS2, IPS3, and IPS4 (Ref [11]), LO1 and LO2 (Ref [12]), TO1 and TO2 (Ref [13]), VO1 and VO2 (Ref [14]), and PHC1 and PHC2 (Ref [15]) (see Figure 1A for example visual field maps in ventral visual cortex). In addition, visual field maps in subcortical structures such as the lateral geniculate nucleus (LGN) and the superior colliculus have been obtained with these methods [16,17] (see Figure 1B for examples of retinotopic LGN maps).

The existence of topographic representations in the brain has greatly facilitated the study of functional specialization of cortical areas (Box 2). Recently, the method of measuring cortical fMRI responses under passive viewing conditions in order to reveal topographic organization has been extended to a variety of more complex tasks and stimuli. Such ‘cognitive mapping’ approaches have revealed topographic organization in parietal and frontal cortex. Higher-order cortex has been implicated in the control of many cognitive processes, including attention, memory, and decision making. The systematic study of topographically-defined higher-order cortical areas in individual subjects promises to yield a mechanistic understanding of the neural underpinnings of these cognitive control processes.

Topographic organization in parietal cortex

The first evidence of topographic visual field organization within human parietal cortex was provided by Sereno and colleagues [18]. They employed a memory-guided saccade task in which the location of a target stimulus was remembered during the subsequent delay period, followed by a saccadic eye movement to the remembered location. The location of the target stimulus and saccade endpoint systematically traversed the visual field, and analysis of fMRI responses revealed a topographic map in posterior parietal cortex (PPC) that had not previously been detected in earlier experiments employing passive viewing of periodic visual stimuli.

Subsequent investigations have used a variety of experimental paradigms including a visual spatial attention task [19], presentation of a colorful and dynamic periodic mapping stimulus [11], and a variation of the memory-guided saccade task originally used by Sereno and colleagues [20,21] to characterize topographic organization of responses in human PPC. To date, seven topographically organized parietal areas have been described: six of these areas form a contiguous band along the intraparietal sulcus (IPS), and one area branches off into the superior parietal lobule (SPL) (Figure 2A).

Each of these topographic areas contains a continuous representation of the contralateral visual field and is separated from neighboring areas by reversals in the orientation of the visual field representation. IPS0 is located at the intersection of the transverse occipital sulcus and the IPS, and IPS1 and IPS2 are in the posterior part of the IPS. Although the most posterior of these areas was originally named V7 [10], its anatomical location is within the IPS in some hemispheres, and it shares a foveal visual field representation with IPS1 [11]. This area has therefore been referred to as IPS0 (Refs [5,11]), and we have adopted this nomenclature. Anterior to IPS2, IPS3 and IPS4 are located in the anterior/lateral branch of the IPS, whereas the most anterior IPS area (IPS5) typically extends into the intersection between the IPS and the postcentral sulcus. Boundaries between these areas correspond to alternating representations of the upper (denoted in blue in Figure 2A) and lower (denoted in yellow) vertical meridian. Based on the location and organization of the visual field map in IPS3, it is likely that this area is identical to the topographic area initially identified in PPC by Sereno et al. [18]. An additional representation of the contralateral visual field, referred to as SPL1, typically branches off the most superior IPS areas and extends medially into the SPL. In most hemispheres IPS2 or IPS3 is the most superior area in the IPS, but there is some individual anatomical variability [21]. The lateral and medial borders of SPL1 represent lower and upper vertical meridian representations, respectively.

While most studies have used polar angle mapping (Box 1) to delineate area boundaries in human PPC, less is known about the representation of stimulus eccentricity in these areas. Swisher et al. [11] used expanding and contracting ring stimuli to characterize eccentricity representations in IPS1-4 and reported a lateral representation of the central visual field and a medial representation of the peripheral visual field in these areas. Further studies are necessary to gain a better understanding of eccentricity representation in human PPC.

In general, mapping of topographic PPC areas has been performed with tasks in which gaze is maintained at a central fixation point or with tasks involving saccadic eye movements to a peripheral target and then immediately back to fixation. For both of these tasks, a purely retinotopic coordinate frame cannot be differentiated from a head-centered coordinate frame (a topographic map that represents spatial locations relative to the head, independent of eye position). As a result, the spatial reference frames, or coordinate systems, are unclear for most of the topographic PPC areas. However, an area in human superior parietal cortex has been described that contains a topographic map of visual responses that is in spatial correspondence with a map of responses to tactile stimulation of near-face locations, indicating a head-centered coordinate frame [22].

Visualization of periodic mapping signals on computationally flattened patches of parietal cortex often reveals regions of the topographic maps which contain voxels that do not clearly exhibit spatial selectivity. These regions are evident as “dropout” of spatially-selective responses, or gaps in the measured topographic organization. The reasons for these apparent gaps in topography are not completely understood, but in some cases they may result from reduced signal due to errors in gray matter segmentation, the presence of large blood vessels, or other measurement artifacts. However, in topographic areas in the IPS, these regions have been reported to overlap with the spatial pattern of activation associated with performing a tactile discrimination while blindfolded [11]. That is, the tactile activations occupy portions of topographic areas in the IPS that are complementary to the regions exhibiting spatial selectivity of periodic mapping signals, apparently disrupting the continuous representation of the visual field on the cortical surface of topographic PPC areas. This suggests that within a topographically-defined area, there may be functionally heterogeneous subregions that are spatially distinct. An alternative possibility is that the tactile and visual activations represent different portions of space (e.g., central versus peripheral) that are mapped continuously with the IPS. Further investigation is needed to determine the functional significance of the parcellation of the representation of tactile and visual information in PPC.

Functional response characteristics of topographic parietal maps

A number of “classical” PPC functions that are well known from electrophysiological studies in macaque monkey [23,24] have recently been probed in topographic areas of human PPC (Table 1). These include responses related to eye movements [21], reaching movements [25, 26], stimulus motion [21], visual objects [27], and spatial attention [19,28,29]. Possible homologies between human and macaque PPC areas are discussed in Box 3.

Responses to movements

Human PPC areas can be functionally differentiated based on their responses to saccadic or smooth pursuit eye movements (Table 1). Specifically, more posterior areas like IPS1, IPS2, and the medial SPL1 exhibit greater responses to saccadic compared to smooth pursuit eye movements, whereas more anterior areas like IPS3-5 show the opposite response pattern [21]. Additionally, both IPS1 and IPS2 respond robustly during saccades and arm reaches, with IPS1 showing equivalent responses for these two motor effectors and IPS2 exhibiting a preference for reaches [26]. Moreover, the topographic organization of responses associated with finger pointing and saccadic eye movements are quite similar in a number of human PPC maps [25].

Responses to motion and object stimuli

All topographically-organized areas of human PPC exhibit motion-selective responses evoked by radial, planar, and circular optic flow patterns (Table 1). Responses to radial motion are larger than those to planar or circular motion in IPS1-3, whereas the other areas do not discriminate among these different types of optic flow patterns [21]. In addition, object-selective responses have been documented in topographic PPC areas (Table 1). In particular, IPS1/2, but not IPS3/4, have been found to carry high-level object information, as indicated by object-selective responses that are independent of image transformations of viewpoint or size [27]. IPS1/2 exhibit object-selective responses to stimuli lacking semantic content (2D and 3D objects such as stars and spheres) as well as semantically meaningful stimuli (line drawings of common objects and tools) [27]. These object-selective responses in IPS1/2 (and their invariance to image transformations) are similar to those found in advanced processing stages within the ventral stream like the human lateral occipital complex. Invariant responses to image transformations indicate high-level representations of object information that are necessary to maintain the perceptual object constancy that is needed for efficient object recognition, as opposed to low-level representations of object features [30,31,32]. These findings suggest the existence of two hierarchical and parallel neural systems for representing object information in the human brain, one along the ventral and a second one along the dorsal visual pathway. The functional significance of high-level object information in the dorsal pathway is currently unknown (see Box 4).

Responses related to spatial attention

Human PPC is also part of a distributed network of areas that controls the allocation of spatial attention [33,34]. In the memory-guided saccade task that is often used to map topographic areas in human PPC, at least three factors could be contributing to the fMRI responses evoked during this task: a visual stimulus that is used to label the location to be encoded, spatial attention to the remembered location during the delay period, and a saccadic eye movement to the remembered location at the end of the trial. For the memory-guided saccade task, the relative contributions of these three factors cannot be determined. However, a study by Silver et al. [19] provides evidence for topographic maps of spatial attention signals in IPS1 and IPS2. Here, spatial attention was directed using an auditory numeric cue that indicated a particular visual field location within an annulus, and the locus of attention periodically traversed the visual field. Subjects performed a difficult contrast detection task at the cued location, but a grating was presented to each annulus location with a 50% probability on every trial. Thus, the pattern of visual stimulation was random and independent of the locus of attention. Recordings of eye position during performance of this task in the MR scanner demonstrated that the topographic signals in IPS1 and IPS2 were not due to systematic deviations from fixation. These results provide strong evidence for a topographic organization of spatial attention signals in IPS1 and IPS2. However, as in all covert spatial attention studies, a contribution from motor planning signals cannot be completely excluded. Topographic responses in IPS1 and IPS2 have also been described for a periodic mapping task involving spatial attention to stimuli comprised of point-light biological motion in the form of human figures [35].

The existence of topographic maps of spatial attention in IPS1 and IPS2 suggests that these areas could transmit spatially-specific top-down attention signals to early visual cortex. It is known that directing spatial attention to a particular visual field location increases fMRI responses in corresponding locations in early visual cortex, even in the absence of visual stimulation [36]. Furthermore, these fMRI responses are maintained for the full duration of periods of sustained attention [37]. The functional connectivity of attention signals in IPS1, IPS2, and several visual cortical areas has recently been characterized using fMRI coherency analysis [28]. Coherency analysis generates a magnitude value, describing the strength of the functional connectivity between two time series, and a phase value, indicating the temporal difference between the time series. Coherency values associated with sustained visual spatial attention were computed for all pairwise combinations of V1, V2d, V3d, V3A, V3B, IPS0, IPS1, and IPS2. Attention increased coherency magnitudes for many pairs of occipital and PPC areas, and analysis of coherency phase values showed that attention-specific activity in IPS1 and IPS2 precedes the activity obtained in visual cortex by a few hundred milliseconds, indicating a top-down flow of spatial attention signals from IPS1/2 to occipital cortex [28].

The role of PPC areas in spatial attention has been further corroborated in a study in which subjects were instructed to covertly direct attention to a peripheral location in either the left or right visual hemifield and to detect targets embedded in a stream of visual stimuli [29]. Activity in most of the topographic PPC areas was found to be spatially-specific, with stronger responses associated with directing attention to the contralateral as compared to the ipsilateral visual field (Table 1). Importantly, two hemispheric asymmetries were noted [29]. First, right, but not left SPL1 carries spatial attention signals, as measured with fMRI. Second, left FEF and left IPS1/2 generate stronger contralateral biasing signals than their counterparts in the right hemisphere. These asymmetries may be related to the right hemispheric dominance in visual attentional deficits observed in neuropsychological patients.

Non-spatial PPC functions

A wide variety of other processes that are not obviously directly related to the representation of space have also been localized to human PPC using fMRI. These include visual short-term memory [38–40], episodic memory retrieval [41,42], tool use [43,44], numerosity [45,46], and perceptual decision variables [47,48]. A critical goal of research on human PPC function is to determine the relationships between the brain regions associated with these diverse functions and the topographic visual field maps described in this paper (see Box 4).

Topographic organization and functional specialization in frontal cortex

Topographic maps have also been discovered in frontal cortex using memory-guided saccade [49], spatial working memory [49], finger pointing [25], and face working memory [50] tasks. In studies employing memory-guided saccade and spatial working memory tasks, two topographic maps were found in frontal cortex, one in the superior branch of precentral cortex (PreCC), in the approximate location of the human frontal eye field (FEF), and a second one in the inferior branch of PreCC (Figure 2B).

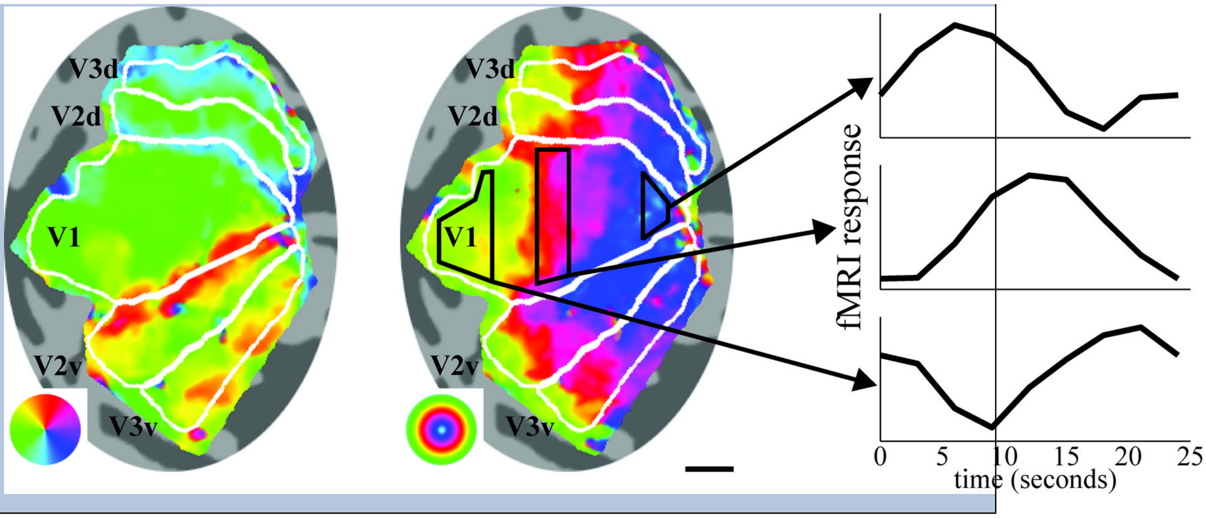
Both of these areas were also activated by visually-guided saccadic eye movements ([49]; see yellow outlines in Figure 2B), and their topographic representations had several characteristic features. First, there was a bias towards a contralateral representation of both saccade directions and memorized locations in each area. Second, similar saccade directions were commonly represented in neighboring locations of each topographic map, and this was also true for the representation of memorized locations in these areas. Finally, for each area, particular saccade directions or memorized locations were represented redundantly in several parts of the topographic map. Thus, the representation of visual space in these frontal maps appears to be different from the organization of occipital and parietal maps, which typically exhibit a one-to-one mapping between locations in visual space and locations on the cortical surface. In contrast, in the frontal maps, particular saccade directions and memorized locations were sometimes represented in multiple locations in each topographic area. Together, these organizational characteristics are compatible with a columnar organization of saccade direction and memorized locations in human frontal cortex. Such an organization has been reported in monkey FEF for saccade direction [51–53] and in monkey dorsolateral PFC for memory fields [54–56]. Remarkably, topographic representations in frontal cortex showed significant variability across subjects but were highly reproducible within subjects. Multiple brain regions showing topographically-organized maps of responses during performance of a face working memory task, including regions in the superior precentral sulcus and inferior frontal sulcus, have also been reported [50].

Conclusions

The studies reviewed in this article demonstrate that topographic areas can be defined for many cortical locations outside of primary sensory or motor cortex. For other cortical regions involved in higher-order cognition, the relevant dimensions of the topographic maps may not yet be known. However, recent investigations of human prefrontal cortex have revealed a hierarchical organization of cognitive control functions along a rostro-caudal axis [57], providing a framework for future research in defining possible topographic representations of these functions. Given the prevalence of topographically-organized areas in parietal and frontal cortex, it seems likely that a better understanding of functional specialization in higher levels of cortex will lead to the discovery of additional ‘cognitive’ maps. This, in turn, will allow exploration of more specific hypotheses regarding the computations associated with each of these areas, leading to functional parcellation of the cerebral cortex based on objective, task-independent topographic criteria.

Box 1 - Measuring topographic organization in the cerebral cortex

In visual cortex, the technique of phase-encoded mapping [4] has been used to identify more than fifteen areas. This method employs periodic stimuli that traverse the visual field while the subject is maintaining fixation at a central point. These stimuli elicit waves of activity that travel across the surface of any cortical area that has a topographic representation of responses to the stimulus. The spatial distribution of responses to rotating wedge (left panel) and expanding ring (middle panel) stimuli is displayed on flattened representations of cortical areas V1, V2, and V3 in the right hemisphere. The right panel contains average fMRI responses for a single cycle of expanding ring stimuli for portions of V1 representing central, middle, and peripheral eccentricities. The temporal delay of the fMRI response of each voxel relative to the stimulus cycle was computed and expressed as a temporal phase value. A color map of these phase values is shown in the insets, and these maps relate location in the visual field to location on the cortical surface for each topographic area. Specifically, area V1 contains a full contralateral hemifield representation of the left visual field, dorsal V2 and V3 represent the lower left quadrant, and ventral V2 and V3 represent the upper left quadrant (left panel). All of these early visual cortical areas share a common foveal representation on the right side of the flattened cortical patch, and isoeccentricity lines cross all of these areas (right panel). Scale bar, 1 cm.



Box 2 - Utility of topographic mapping for studying functional specialization

The ability to define the boundaries and spatial representations of topographically-organized cortical areas provides significant advantages for investigating the computations performed by these areas. In fMRI experiments, the location and spatial extent of a given topographic area can be objectively identified in each subject. The sizes of topographic areas and their locations relative to gross anatomical features vary greatly from subject to subject. For example, the sizes of V1, V2, and V3 on the cortical surface vary by a factor of about 2.5 across individuals [58], and IPS1 and IPS2 [19], LO1, LO2, TO1, and TO2 [13], and V4, VO1, VO2, PHC1, and PHC2 [15] all exhibit similar variability in surface area. Given this variability, fMRI studies that employ spatial normalization of each subject's brain to a standardized template followed by group averaging will necessarily generate activations that contain signals representing contributions from multiple functional areas. This imposes severe limitations on the information that can be obtained regarding functional specialization of individual cortical areas. In contrast, the identification of topographic areas in individual subjects allows group-level analyses to be performed on sets of fMRI responses that represent the same functional area in each subject.

Box 3 - Homologies with primate areas?

Evidence from fMRI studies suggests that human IPS1/2, SPL1, and IPS5 serve similar functions as macaque lateral intraparietal area (LIP), area 7a, and the ventral intraparietal area (VIP), respectively (for a more general review of functional macaque/human PPC homologies, see Ref [75]). Like human IPS1/2 and SPL1, both LIP and 7a have been shown to respond more strongly to saccadic than to smooth pursuit eye movements [59–62] and are involved in spatial attention and working memory [61,63–65]. LIP, but not 7a, exhibits reach-related activity [66] and carries shape-related object information [67], properties also exhibited by human IPS1/2 (but not SPL1).

Like human IPS5, macaque VIP responds to smooth pursuit eye movements [68] and optic flow patterns [69], and the majority of VIP neurons respond both to tactile and visual stimulation [70,71]. In addition, tactile and visual receptive fields close to the face are often aligned, suggesting a broader sensory-motor function in defensive behavior [72]. The coregistration of tactile and visual spatial maps has also been reported for an area in human superior parietal cortex [22], and based on topographic organization and anatomical location, this superior parietal area may correspond to IPS5 [21]. Together, these response characteristics suggest that the macaque brain may contain functional homologues of human IPS1/2, SPL1 and IPS5.

In contrast, functional homologies for human IPS3 and IPS4 remain puzzling. Since LIP, 7a, and VIP are adjacent areas in macaque IPS, it is interesting to note that IPS3 and IPS4 break the contiguity between IPS1, IPS2, and IPS5 in the human brain. Thus, it is possible that IPS3 and IPS4 are human-specific areas related to the disproportional enlargement of PPC and resulting in a wider distribution of functions in human as compared to monkey PPC [73,74]. Further comparative studies of perceptual and cognitive functions of the PPC areas in the human and macaque brain may ultimately lead to a more profound understanding of the evolution of cognition.

Box 4 - Questions for future research

- Why are there so many topographic cortical areas, each having its own representation of the same visual field locations? What are the functional differences in the neural computations performed by these areas?
- How many of these topographic areas are present in non-human animals, and how many are uniquely human?
- Do areas that are homologous across species maintain similar functional specialization in these species, or do they acquire additional high-level cognitive functions during evolution?
- To what extent do the neural representations of non-spatial functions (episodic retrieval, numerosity, etc.) spatially overlap with the topographic maps of space that comprise much of PPC?
- Can theories of the function of higher-order areas such as prefrontal cortex be used to develop tasks that reveal additional topographic representations in these brain regions?
- What is the relationship between the high-level object information encoded in topographic PPC areas and the proficiency of humans in the use of tools?
- How are object and spatial information in the dorsal pathway organized in patients with ventral pathway lesions suffering from visual agnosia?

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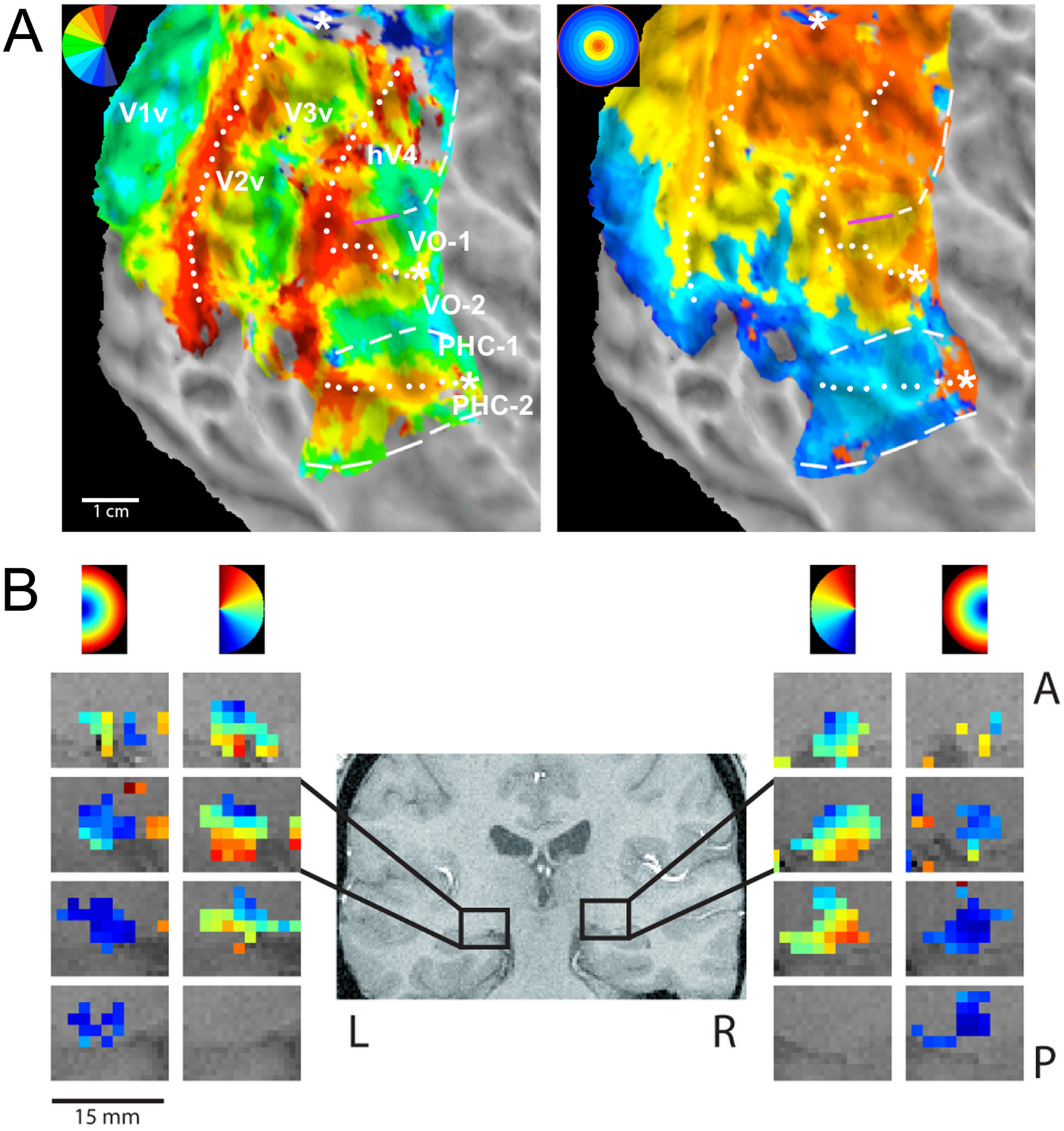

Figure 1. Topographic maps in ventral visual cortex (A) and the lateral geniculate nucleus (B)

A: Flattened surface reconstructions of early and ventral visual cortical areas in the right hemisphere of a single subject. The left panel shows the polar angle maps; the right panel shows the eccentricity maps. White lines denote area boundaries, which are formed by phase angles at or close to the upper (dotted) or lower (dashed) vertical meridian. Pink lines denote the reversal in eccentricity between V4 and VO-1. Asterisks indicate foveal representations. Adapted with modification from Ref [15]. B: Polar angle and eccentricity maps in the LGN are shown for both hemispheres of a single subject. The central panel shows an anatomical image in the coronal plane through the posterior thalamus. The black boxes indicate the anatomical locations of the panels to the left and right. Details of the polar angle maps in the left (L) and right (R) LGNs are shown in the near left and right columns, arranged in several consecutive slices from anterior (A) to posterior (P). The eccentricity maps are shown in the far left and right columns and are spatially coregistered with the polar angle maps. Adapted from Ref [16], in modified form. The color code indicates the phase of the fMRI response and labels the portion of the visual field to which the voxel is most responsive, as depicted in the visual field color legends in panels A and B.

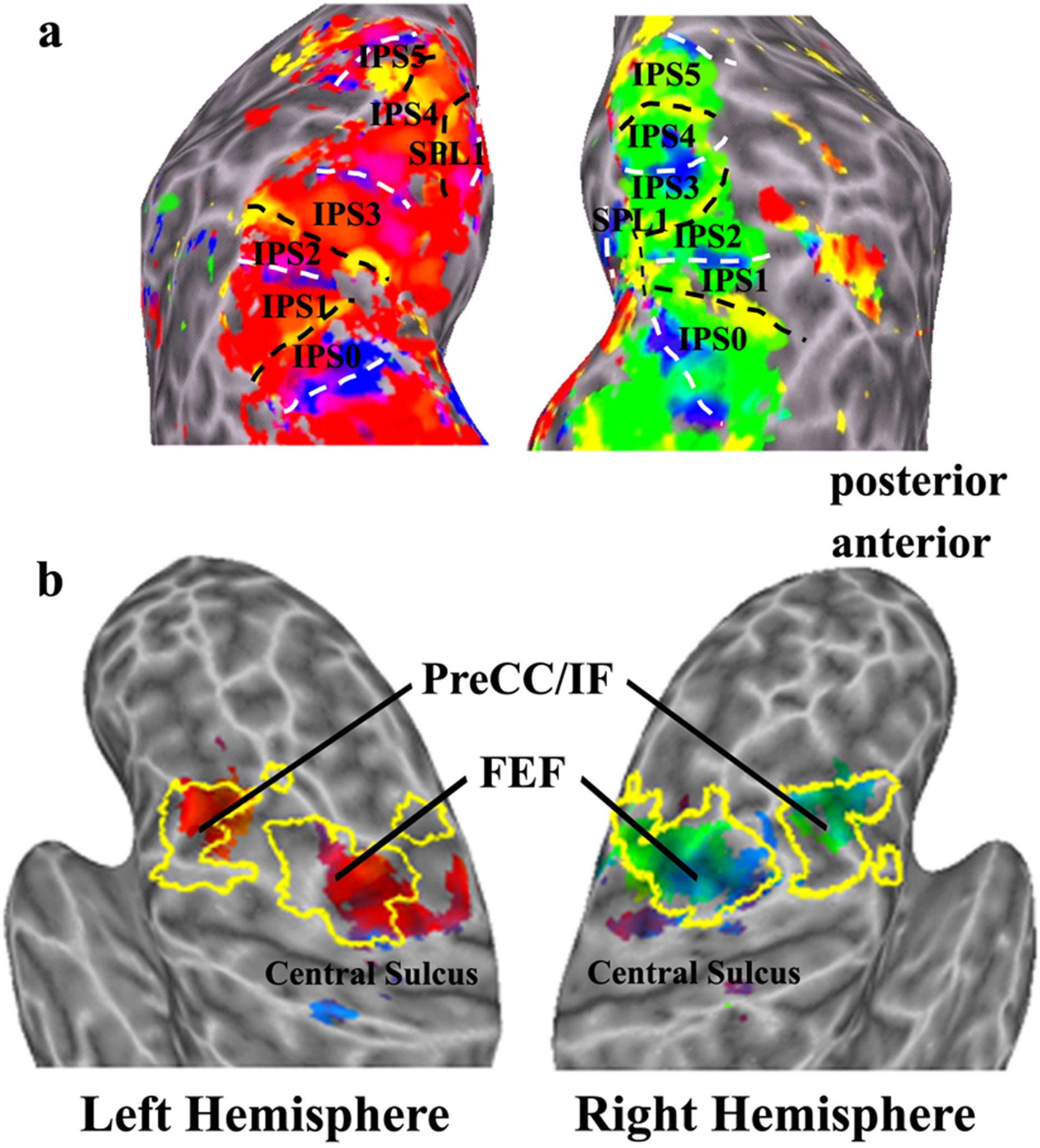

Figure 2. Topographic areas in human parietal (A) and frontal (B) cortex

Activations from a single subject overlaid on inflated left and right cortical hemispheres. The color code is shown only for those voxels whose responses were correlated with the fundamental frequency of saccade direction in a memory-guided saccade task ($p < 0.001$). The responses are lateralized such that the right visual field is represented in the left hemisphere, whereas the left visual field is represented in the right hemisphere. In parietal cortex (A), area boundaries correspond to the alternating representation of either the upper or lower vertical meridian. In frontal cortex (B), the extent of the activations evoked by saccadic eye movements is outlined in yellow, indicating that the topographic areas fall within the regions of the superior and inferior frontal eye fields. Adapted with modifications from Refs [21,49].

Table 1

Functional specialization in human posterior parietal cortex

All areas respond to planar, circular, and radial motion, with IPS1-3 preferring radial motion over the other motion types. IPS1/2 and SPL1 respond preferentially to saccadic eye movements, while IPS3-5 respond more strongly to smooth pursuit eye movements. All areas except for left SPL1 carry spatial attention signals. IPS1/2 encode high-level object information, whereas the other areas do not exhibit object-specific responses.

	IPS1	**IPS2**	**IPS3**	**IPS4**	**IPS5**	**SPL1**
Responses to optic flow motion stimuli	radial > (planar = circular)	radial > (planar = circular)	radial > (planar = circular)	radial = planar = circular	radial = planar = circular	radial = planar = circular
Responses to eye movements	saccade > smooth pursuit	saccade > smooth pursuit	smooth pursuit > saccade	smooth pursuit> saccade	smooth pursuit > saccade	saccade > smooth pursuit
Spatial attention signals	left and right hemisphere	left and right hemisphere	left and right hemisphere	left and right hemisphere	left and right hemisphere	only left hemisphere
Object-specific responses	yes	yes	no	no	no	no