COMMENTARY

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# Human fronto-parietal and parieto-hippocampal pathways represent behavioral priorities in multiple spatial reference frames

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**Abbreviations:** PPC, posterior parietal cortex; fMRI, functional magnetic resonance imaging; dMRI, diffusion magnetic resonance imaging; FEF, frontal eye fields; SEF, supplementary eye field; IPS, intraparietal sulcus; SPL, superior parietal lobule; IPL, inferior parietal lobule; LIP, lateral intraparietal area; MIP, medial intraparietal area; AIP, anterior intraparietal area; VIP, ventral intraparietal area; PRR, parietal reach region; MTL, medial temporal lobe

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**We represent behaviorally relevant information in different spatial reference frames in order to interact effectively with our environment. For example, we need an egocentric (e.g., body-centered) reference frame to specify limb movements and an allocentric (e.g., world-centered) reference frame to navigate from one location to another. Posterior parietal cortex (PPC) is vital for performing transformations between these different coordinate systems. Here, we review evidence for multiple pathways in the human brain, from PPC to motor, premotor, and supplementary motor areas, as well as to structures in the medial temporal lobe. These connections are important for transformations between egocentric reference frames to facilitate sensory-guided action, or from egocentric to allocentric reference frames to facilitate spatial navigation.**

## Behavioral Priorities and Selective Attention

Visual scenes usually contain many different objects, which cannot all be processed simultaneously in detail due to the limited capacity of the visual system. Attentional mechanisms are therefore needed to select the most behaviorally relevant information for further processing. Converging evidence from electrophysiology and functional magnetic resonance imaging (fMRI) studies suggests that areas in frontal and posterior parietal cortex (PPC), often referred to collectively as the fronto-parietal attentional control network, are vital for controlling attentional selection in both the monkey and human brain.[1,2] These areas include the frontal eye field (FEF) and supplementary eye field (SEF) in frontal cortex and the intraparietal sulcus (IPS), superior parietal lobule (SPL) and inferior parietal lobule (IPL) in PPC. The macaque IPS has been further sub-divided into areas based upon their functional characteristics, including the lateral (LIP), medial (MIP), anterior (AIP), and ventral (VIP) intraparietal areas.[2] In the human brain, visuospatial topographic mapping has been used to identify several areas within and surrounding the IPS, including intraparietal areas 0–5 (IPS0-IPS5) as well as an area in the SPL, superior parietal lobule area 1 (SPL1).[3-6] While the functional characteristics of each of the macaque IPS areas are relatively well understood, studies have only just begun to identify how each human IPS area differs functionally and in anatomical connectivity.[5,7-11]

## Spatial Reference Frames

Because behaviorally relevant information selected by the fronto-parietal attention network will be used in parallel by different effector systems, the information needs to be represented in multiple spatial reference frames that are appropriate for the relevant effectors, e.g., eye-centered for saccades, body-centered for limb movements, object-centered for certain cognitive manipulations, and world-centered for navigation. Monkey studies have shown that the PPC performs transformations between different coordinate systems, allowing sensory and motor areas to effectively communicate in order to facilitate sensory-guided action.[12-18] Furthermore, computational studies have shown that it is possible to combine outputs from PPC neurons using egocentric, allocentric, or intermediate reference frames, to perform different spatial transformations.[19] This suggests that distinct pathways originating in parietal cortex and projecting to frontal or medial temporal cortex could give rise to spatial representations in different reference frames. However, how these transformations occur between reference frames and what areas mediate each transformation is poorly understood in the human brain.

All of the human IPS and SPL areas that have been topographically-defined to date contain a viewer-centered representation, since each area can be mapped using passive fixation[6] or memory-guided saccades.[3] Based upon evidence from recent neuroimaging studies as well as what is currently known about the functional characteristics of individual macaque PPC areas, here we will discuss the contribution of human fronto-parietal and parieto-hippocampal pathways to not only eye-centered spatial representations, but also to representations in body-centered, object-centered, or world-centered reference frames.

## IPS2-FEF Pathway

In a recent study,[20] we used fMRI and diffusion MRI (dMRI) to investigate the functional and structural connectivity, respectively, between frontal and parietal attention network areas in human subjects. We identified a dorsal pathway connecting FEF and IPS2, which represents space in viewer-centered coordinates. Several neuroimaging studies have provided evidence that human IPS1/2 shares similar response characteristics to macaque area LIP.[5,7-10,21-23] Neurophysiological studies have provided evidence that macaque FEF and LIP, which are directly connected,[24] contain salience maps in eye-centered coordinates to help guide exploration of the visual environment.[25,26] These data are consistent with the idea that the human FEF-IPS2 pathway supports spatial representations of attentional priorities and saccadic goals in an eye-centered reference frame.

## SPL1-SEF Pathway

Functional and anatomical connectivity data suggest a pathway between SEF and SPL1,[20] medial to the FEF-IPS2 pathway. The evidence is consistent with the SEF-SPL1 pathway flexibly supporting spatial representations in object- or viewer-centered coordinates, depending on behavioral demands. Previous studies have shown overlapping activations for egocentric and allocentric processing in superior and medial parietal cortex,[27,28] at least partly including SPL1. In macaques, SEF and PPC represent attentional priorities in multiple reference frames, including eye- and object-centered representations.[29,30] Furthermore, there are anatomical connections between medial PPC and SEF in macaques.[31] Taken together, the SPL1-SEF pathway enables flexible spatial representations, suitable for condition-action associations, a feature of SEF and the supplementary motor cortex more broadly,[32] as well as task-switching, in which the SEF and SPL play important roles.[33,34]

## Parietal Grasp Area and Ventral Premotor Cortical Connections

Anterior portions of the human IPS are activated while subjects make grasping movements.[10,35,36] These grasp-related activations partially overlap with IPS5 and extend beyond the IPS to the junction of the postcentral sulcus. However, most of the grasp-related activity is located outside of the topographically mapped areas of human IPS.[10] In macaques, area AIP contains neurons that are sensitive to the shape and orientation of objects[37] and inactivation of AIP interferes with a monkey's ability to shape its hand in order to grasp an object.[38] AIP is anatomically connected to ventral premotor area F5.[39] A proportion of F5 neurons have similar functional properties to neurons in AIP[40] and inactivation of F5 produces grasping impairments that are similar to those observed following AIP inactivation.[41] This suggests that the pathway between AIP and F5 is important for the generation of object-oriented hand actions. In humans, dMRI evidence suggests anatomical connections between anterior IPS and ventral premotor cortex.[42] Because the anterior portions of human IPS share functional similarities with macaque area AIP, a human fronto-parietal pathway from anterior IPS to ventral premotor cortex may also be important for spatial transformations into hand-centered representations for grasping.

## IPS5 and Premotor Cortical Connections

Previous studies have suggested that human IPS5 shares functional similarities with macaque area VIP. For example, both IPS5 and VIP contain a co-registered, bimodal representation of tactile and visual space[43,44] and both respond preferentially to smooth-pursuit (vs. saccadic) eye movements and motion-induced optic flow patterns.[7] It has been suggested that VIP is important for the construction of multisensory representations of peripersonal space, for heading perception for instance,[45] with VIP neurons representing space not only in head-centered coordinates,[46,47] but also in eye-[47] and body- (and possibly world-) centered[12] coordinates as well as intermediate[13] reference frames. VIP shares connections with area F4 of premotor cortex in the macaque,[39] which contains neurons that represent face, neck, and proximal arm movements and most likely codes peripersonal space in body- or head-centered reference frames.[48,49] In humans, resting-state functional connectivity and dMRI studies suggest a pathway between anterior IPS, likely including IPS5, and premotor cortex.[50] Because of the number of shared response characteristics between human IPS5 and macaque VIP, a human IPS5-premotor cortical pathway may also support multisensory integration and a peripersonal spatial representation.

## Parietal Reaching Areas and Dorsal Premotor Cortical Connections

Responses to visually-guided reaching in the human brain have been reported in posterior-medial PPC, including the SPL,[51,52] parietal-occipital cortex,[51-53] and medial IPS[54,55] extending into the precuneus.[56] A recent study has suggested that some of this reaching-related activity overlaps with SPL1,[10] although a majority of studies have found activations outside of topographically-mapped cortex and outside of the human IPS. In the macaque brain, neurons that respond to the planning and execution of reaching movements are found in the medial bank of the IPS and the anterior wall of the parieto-occipital sulcus, constituting the functionally-defined parietal reach region (PRR).[14,57] These parietal areas use eye-[15,16] and body-centered[51] as well as intermediate[17,18] reference frames. The macaque PRR is connected to dorsal premotor cortex,[58,59] and dorsal premotor cortex represents space in a variety of reference frames, including eye-,[60] limb-,[61] and intermediate reference frames.[62,63] In humans, dMRI evidence suggests anatomical connectivity between medial parietal cortex (likely including SPL1) and dorsal premotor cortex.[64] A recent fMRI study also found that both medial PPC and dorsal premotor cortex respond strongly during reaching in human subjects.[51] This suggests that there is a human fronto-parietal pathway between medial parietal and dorsal premotor cortex for visually-guided reaching. Because SPL1 also contributes to object-based processing,[20] it may be a suitable site for combining eye- and body-centered information with object information, during reaches for objects. This is supported by evidence that SPL lesions give rise to optic ataxia, characterized by difficulty with reaching and prehension.[65,66] These deficits do not appear to affect the retinotopic representation of the visual field itself, but rather the location of relevant objects.[66]

## IPS3 and IPS4

The functional specializations of IPS3 and IPS4 are currently unclear. IPS3 and IPS4 are strongly activated during allocation of spatial attention,[9] but are not selective for saccadic eye movements,[7] visual working memory,[8] reaching and grasping,[10] or episodic memory retrieval[11] and have not been reported to demonstrate object selectivity.[21] It is possible that these areas emerged with the expansion of human PPC relative to the macaque brain,[67] in which case IPS3/4 may serve functions more prominent in humans. Human (and macaque) IPS is activated during numerical processing,[68] and these activations appear to at least partially overlap with IPS3 and IPS4.[69,70] Evidence suggests there is a close link between numerical and spatial representations,[71] and it is possible that parietal cortex not only represents behavioral priorities in external space, but also in more abstract spaces, such as numerical space. Interestingly, numerical representations have also been reported in dorsolateral and inferior prefrontal cortex,[72] raising the possibility of a fronto-parietal link. Alternatively, IPS3/4 could be involved in representing spatial coordinate systems that have not yet been directly tested in visuospatial topographically-organized human PPC, such as body-centered reference frames. Further research is needed to determine the underlying functions of IPS3/4 and their connection patterns with frontal cortex.

## IPL-Medial Temporal Interactions

Numerous studies have demonstrated that medial temporal lobe (MTL) structures, including the hippocampal formation, parahippocampal gyrus, and subiculum, are important for spatial navigation.[73] The rodent hippocampus contains place cells, which fire when the animal is at particular locations in its environment.[74] This led to the idea that the hippocampus supports a cognitive map, where groups of cells represent space in an allocentric reference frame.[75] Similar cells have been found in the human hippocampus and to a lesser degree in the parahippocampal region during virtual navigation.[76] Damage to the parahippocampal cortex, for example, leads to anterograde topographic disorientation, where patients are unable to learn new routes through unfamiliar settings.[77] This suggests that the human MTL (and not only rodent MTL) is important for allocentric processing. It has been proposed that the neural mechanisms supporting spatial navigation may also support episodic memory.[73]

In the macaque brain, multiple direct and indirect connections exist between the caudal IPL and MTL structures.[78-80] Caudal IPL, area 7a in particular, contains neurons with eye-centered,[81] object-centered,[30] and world-centered[82] reference frames. This region is therefore well positioned to mediate spatial transformations between the egocentric (eye- or body-centered) reference frames that are commonly represented in PPC and the allocentric (object- or world-centered) reference frames that are commonly represented in the MTL. In humans, pathways from the IPL (angular gyrus) to the hippocampus and parahippocampal gyrus have been identified using dMRI.[42,83] These pathways between PPC and MTL structures could be used for spatial transformations between egocentric and allocentric coordinate systems during navigation. For example, PPC may provide information to the MTL to integrate egocentric information with the existing allocentric representations in the hippocampal formation, and PPC may transform the output of the hippocampal formation (via entorhinal cortex) into egocentric coordinates to support appropriate movements through the environment.[78,84]

## Conclusion

We suggest that multiple pathways exist in the human brain, each of which connects areas in PPC to either motor, premotor and supplementary motor areas in frontal cortex to facilitate sensory-guided action, or to MTL structures to facilitate spatial navigation. PPC, premotor cortex, and the MTL contain populations of neurons that represent space in multiple, and sometimes intermediate, reference frames. This flexibility allows the fronto-parietal and parieto-hippocampal pathways to support spatial transformations between multiple reference frames, depending on behavioral demands.

### Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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