



## Review article

## Functional organization of the caudal part of the human superior parietal lobule

Valentina Sulpizio<sup>a,b,\*</sup>, Patrizia Fattori<sup>c</sup>, Sabrina Pitzalis<sup>b,d</sup>, Claudio Galletti<sup>c</sup><sup>a</sup> Department of Psychology, Sapienza University, Rome, Italy<sup>b</sup> Department of Cognitive and Motor Rehabilitation and Neuroimaging, Santa Lucia Foundation (IRCCS Fondazione Santa Lucia), Rome, Italy<sup>c</sup> Department of Biomedical and Neuromotor Sciences, University of Bologna, Bologna, Italy<sup>d</sup> Department of Movement, Human and Health Sciences, University of Rome "Foro Italico", Rome, Italy

## ARTICLE INFO

## Keywords:

Dorsal visual stream  
 Parieto-occipital cortex  
 Precuneus  
 Macaque monkey  
 Optic flow  
 Object- and self-motion  
 Reaching  
 Grasping  
 Arm movements  
 Leg movements  
 Locomotion  
 Navigation  
 Spatial attention  
 fMRI

## ABSTRACT

Like in macaque, the caudal portion of the human superior parietal lobule (SPL) plays a key role in a series of perceptive, visuomotor and somatosensory processes. Here, we review the functional properties of three separate portions of the caudal SPL, i.e., the posterior parieto-occipital sulcus (POs), the anterior POs, and the anterior part of the caudal SPL. We propose that the posterior POs is mainly dedicated to the analysis of visual motion cues useful for object motion detection during self-motion and for spatial navigation, while the more anterior parts are implicated in visuomotor control of limb actions. The anterior POs is mainly involved in using the spotlight of attention to guide reach-to-grasp hand movements, especially in dynamic environments. The anterior part of the caudal SPL plays a central role in visually guided locomotion, being implicated in controlling leg-related movements as well as the four limbs interaction with the environment, and in encoding egomotion-compatible optic flow. Together, these functions reveal how the caudal SPL is strongly implicated in skilled visually-guided behaviors.

## 1. Introduction

The parietal lobe is a structure that plays a key role in somatosensory and visuomotor integration as well as in cognitive processes (Vallar and Coslett, 2018). The posterior part of the parietal lobe, the so-called posterior parietal cortex (PPC), is divided by the intraparietal sulcus into superior and inferior parietal lobules in both human and non-human primates. Despite this similarity in gross anatomy, it has been thought for a long time that the superior parietal lobule (SPL) of the macaque had different architectural organization with respect to that of the human counterpart. Recent evidence, on the contrary, have suggested that macaque and human SPL are much more similar one another than previously thought (Gamberini et al., 2020). The present review will analyze in detail the functional properties of human SPL and draft a comparison between the SPL of the two species based on the most recent data available in literature. We will focus our attention on the caudal part of SPL, as it is the most studied in the two species. Since the SPL of

macaque has been the goal of recent reviews (Gamberini et al., 2020, 2021; Galletti et al., 2022), we here will only briefly summarize its structure and functional properties and then will describe in detail the structure and functional properties of the human SPL.

## 2. The caudal SPL in the macaque monkey

The macaque SPL is composed of a mosaic of areas with different architecture, functional properties, and patterns of anatomical connections (see Gamberini et al., 2020, 2021). As shown in Fig. 1A, the caudalmost part of SPL, i.e., the anterior bank of the parieto-occipital sulcus (POs), contains the visual motion area V6 (Galletti et al., 1996, 1999a) and the visuomotor area V6A (Galletti et al., 1996, 1999b). Area V6, located in the ventral part and fundus of the anterior bank of POs, shows an occipital cytoarchitectural pattern (Luppino et al., 2005). Area V6A, instead, that occupies most of the anterior bank of POs dorsally to V6, shows a parietal cytoarchitectural pattern (Luppino et al., 2005). It is

\* Correspondence to: Department of Psychology, "Sapienza" University of Rome, Via dei Marsi, 78, 00185 Rome, Italy.

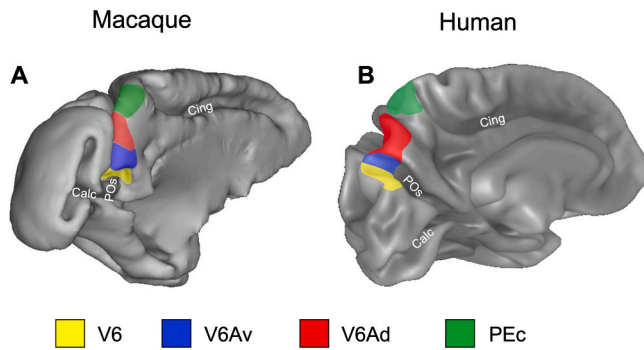
E-mail address: [valentina.sulpizio@uniroma1.it](mailto:valentina.sulpizio@uniroma1.it) (V. Sulpizio).

<https://doi.org/10.1016/j.neubiorev.2023.105357>

Received 16 March 2023; Received in revised form 31 July 2023; Accepted 9 August 2023

Available online 10 August 2023

0149-7634/© 2023 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).



**Fig. 1.** Brain location of areas V6, V6Av, V6Ad and PEc in macaque and human brains. The posteromedial view (left hemisphere) of the surface-based 3D reconstruction of macaque (A) and human (B) brains shows the extent of areas V6 (yellow), V6Av (blue), V6Ad (red) and PEc (green).

divided into a ventral (V6Av) and a dorsal (V6Ad) sector based on cytoarchitectonic (Luppino et al., 2005), connectional (Gamberini et al., 2009; Passarelli et al., 2011), and functional (Gamberini et al., 2011) criteria. Both sectors of V6A host visual and somatosensory cells, with the majority of visual cells in area V6Av. Area V6A represents the upper limb and most V6A cells respond to reach-to-grasp actions (Fattori et al., 2017; Galletti et al., 2022), with many cells selectively modulated by the direction of arm movement during reaching (Fattori et al., 2005) as well as by its amplitude in depth (Hadjidimitrakakis et al., 2014), and cells modulated by wrist orientation (Fattori et al., 2009) and the type of grip (Fattori et al., 2010) used during grasping. Several V6A cells are modulated by covert shifts of spatial attention (Galletti et al., 2010, 2022).

More anteriorly, in the dorsal exposed surface of the SPL, an additional cortical area, area PEc, has been defined both anatomically (Pandya and Seltzer, 1982) and functionally (Gamberini et al., 2020) (Fig. 1A). This area hosts visual and somatosensory cells like area V6A, but with a higher incidence of the latter with respect to V6A (Gamberini et al., 2018). Like V6A, most PEc cells respond to reach-to-grasp actions, but unlike V6A, PEc represents both lower and upper limbs (Breviglieri et al., 2006; Gamberini et al., 2018). Several cells in PEc are activated by optical flow stimulation (Battaglia-Mayer et al., 2001; Raffi et al., 2002, 2010, 2011, 2014). It has been suggested that PEc controls the interaction of the four limbs with the environment and the coordination of locomotion (Breviglieri et al., 2008; Bakola et al., 2010; Hadjidimitrakakis et al., 2015; Gamberini et al., 2018; Impieri et al., 2018).

### 3. The caudal SPL in human

In the last fifteen years, our group has described in humans the homologues of monkey areas V6 (Pitzalis et al., 2006, 2010), V6Av (Pitzalis et al., 2013a), V6Ad (Tosoni et al., 2015), and PEc (Pitzalis et al., 2019) by using a combination of fMRI brain mapping methods such as high-field functional magnetic resonance imaging, cortical surface-based analysis, wide-field video retinotopy, task-evoked activity and functional connectivity. In particular, to successfully map these regions, we used a mix of protocols consolidated through the years which include the use of different types of fMRI paradigms (i.e., phase-encoded, block-sequence, and event-related), dedicated functional localizer and the use of in-house MRI-compatible set-up for both visual stimulation (a wide-field stimulation, up to 110 deg in total visual extent; Pitzalis et al., 2006) and for the performance of long-range leg movements in the scanner (Pitzalis et al., 2019). As evident in Fig. 1B, these human counterparts of monkey areas are located in the caudal part of dorsomedial SPL cortex and occupy a similar position as the same areas in the macaque SPL. Table 1 provides the MNI coordinates of these regions. As we will review here below, all these areas have functional profiles, topographical organization, and connectivity patterns similar

**Table 1**

MNI coordinates of the human areas rV6, rV6Av, V6Ad, PEc. r stands for retinotopic. See below.

Human area	X	Y	Z
rV6	± 9	-82	36
rV6Av	± 15	-76	39
V6Ad	± 14	-72	51
PEc	± 12	-55	64

to those observed in the monkey counterparts.

A great deal of whole brain fMRI studies showed that the human caudal SPL is generally involved in visual motion perception and in the control of visuomotor and somatomotor activities, as well as in the guidance of visuospatial attention (Kalaska, 1996; Filimon, 2010; Sereno and Huang, 2014; Corbetta and Shulman, 2002; Corbetta et al., 1998, 2008). The complex mosaic of structurally distinct areas identified during the last years from our and other laboratories in the human caudal SPL reflects such a functional heterogeneity.

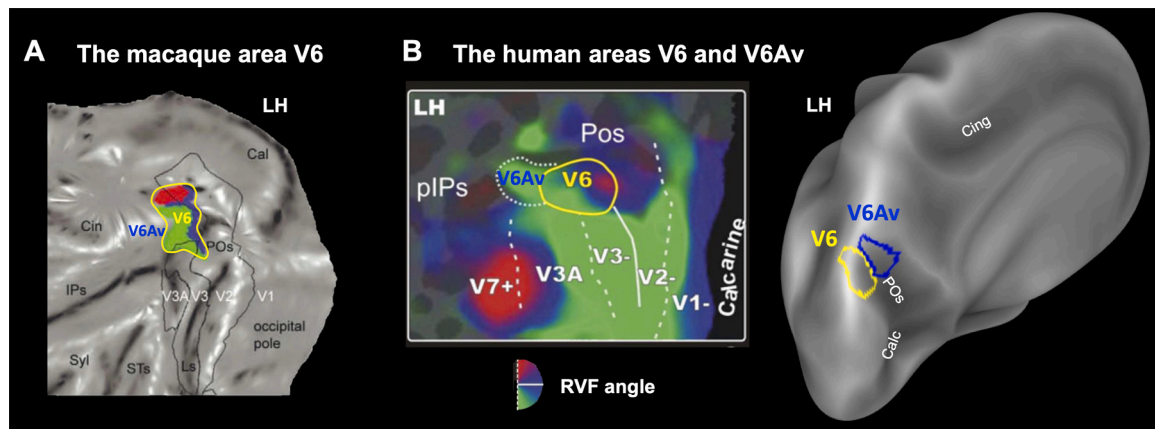
Consistent with recent models on visuo-spatial processing (Kravitz et al., 2011), a gradient of functional specialization and cortical connections along the caudal SPL has been proposed, with more posterior regions primarily dedicated to the analysis of many aspects of visual motion, including visual motion perception and object- and self-motion recognition, and the more anterior regions primarily dedicated to analysis of spatial information relevant for goal-directed action (Tosoni et al., 2015; Heed et al., 2011). Similarly, a posterior-to-anterior gradient within the PPC have been observed for eye vs limb processing (Heed et al., 2016; Bellagamba et al., 2022) as well as for visual vs somatic representations (Huang and Sereno, 2018). However, besides the above-described functional gradient along the caudal SPL, a clear idea on the specific functions of this part of the brain is still missing. Also, it is unknown if these functions are or not segregated within specific SPL areas. The following is an effort to check for this goal by systematically reviewing the data found in recent years on the functional properties of the caudal SPL in human.

For the sake of convenience, we will separately consider three separate portions of the caudal SPL (see Fig. 1B): 1) the posterior POs (that includes area V6), 2) the anterior POs, in correspondence of the dorsal-posterior precuneate cortex (that includes areas V6Av and V6Ad), and 3) the anterior part of the caudal SPL, in correspondence of the dorsal-anterior precuneate cortex (that includes area PEc).

#### 3.1. Functional properties of the posterior POs

One of the most studied areas in the caudal human SPL is area V6, located in the dorsal part of the parieto-occipital sulcus (Fig. 1B). Since its discovery in the macaque's brain (Galletti et al., 1999a), this area has attracted much attention in the neuroscience field given its quite unique emphasis in the representation of the far periphery of the visual field together with its high sensitivity to visual motion. After demanding research, our group succeeded in the identification of the human homologue of macaque area V6 by using widefield retinotopic mapping (Pitzalis et al., 2006), able to stimulate the entire visual field up to 110° in total visual extent (Pitzalis et al., 2006). The location and retinotopic organization of area V6 are shown in Fig. 2B where the position and borders of V6 are indicated by a yellow outline. Area V6 is located on the dorsalmost part of the posterior bank of the POs, with V3 and V3A located lateral to V6, and V2 posterior to it. It represents the entire contralateral hemifield, from the fovea to the far periphery, and it has an upper field representation located just anterior to peripheral V2/V3 lower representations. The study of the visual topography revealed as the retinotopic organization and neighbor relations of human V6 closely resemble those reported for macaque V6 (compare Fig. 2A with the left panel of Fig. 2B; Galletti et al., 1999; Fattori et al., 2009).

After having defined the V6, several fMRI experiments have been



**Fig. 2.** Retinotopy of polar angle representation in macaque and human areas V6 and V6Av. **A.** Location and extent of area V6, together with the location of area V6Av, are reported on close-up of the flattened map of the cortical surface reconstruction of the left hemisphere of macaque brain. **B.** Location and extent of areas V6 and V6Av are reported on both the close-up of the flattened map cortical surface reconstruction (left panel) and on the inflated reconstruction (right panel) of the left hemisphere of the human brain.

conducted by our and other research groups to further investigate its functional role (see for instance [Pitzalis et al., 2013d](#), [Arnoldussen et al., 2013](#); [Cardin and Smith, 2010](#); [Cardin et al., 2012](#); [Fischer et al., 2012](#)). Converging evidence suggests that the portion of cortex hosting area V6 is especially involved in 1) the analysis of coherent visual motion (and self-motion), 2) the detection of “real” motion of objects, and 3) the encoding of spatial information useful for navigation.

### 3.1.1. Analysis of coherent motion:

Since its discovery in the 2006 by retinotopic mapping ([Pitzalis et al., 2006](#)), our and other laboratories have tried to verify whether human V6 was a motion area like macaque V6 ([Galletti et al., 1996](#)). It's worth noting that during those years, before the human V6 definition, the majority of the fMRI studies on the neural correlates of visual motion perception in humans focused on the lateral walls of the brain, specifically on area MT and on the dorsal portion of area MST (MSTd) which were considered the two most prominent motion-sensitive regions in the human visual cortex (e.g., [de Jong et al., 1994](#); [Smith and Scott-Samuel, 1998](#); [Morrone et al., 2000](#); [Rutschmann et al., 2000](#); [Ptito et al., 2001](#); [Wunderlich et al., 2002](#); [Smith et al., 2006](#)). None of these cited studies looked at the medial cortex and figures often show only lateral views of the brain, thus making it difficult to assess whether the POs was also involved.

Results from several neuroimaging studies revealed that human V6, like macaque V6, is a motion area that responds to unidirectional motion ([Pitzalis et al., 2010](#)) and has a strong preference for coherent motion ([Cardin and Smith, 2010](#); [Helfrich et al., 2013](#); [Pitzalis et al., 2010](#); [von Pförtl et al., 2009](#)). A combined VEPs/fMRI work ([Pitzalis et al., 2013c](#)) has shown that V6 is one of the most precocious stations (together with MT) coding motion coherence (at about 100 msec after the onset of motion pattern). Notably, we found that one of the most effective visual motion stimuli used to activate human V6 is the flow field stimulus ([Pitzalis et al., 2010](#)), a complex pattern of coherent visual stimulation similar to the continuous changes of optic flow generated when we move through the environment ([Fig. 3A-B](#)).

Notably, the motion-related activation is not always restricted to the retinotopic V6 (see [Fig. 3B](#) for the topography of this motion-related region in some representative participants; [Pitzalis et al., 2010](#)), but it typically includes also adjoining voxels belonging to other areas, as for example the adjoining V6Av (which was found to respond to flowfields in [Tosoni et al., 2015](#), see below chapter 3.2 of this review). Thus, for sake of clarity, in the current review, we will refer to rV6 (retinotopic V6) to indicate the retinotopically defined area V6, while we will refer to V6+ to indicate the functionally defined area V6. In other words, we will use the term V6+ when we cannot disambiguate whether the functional

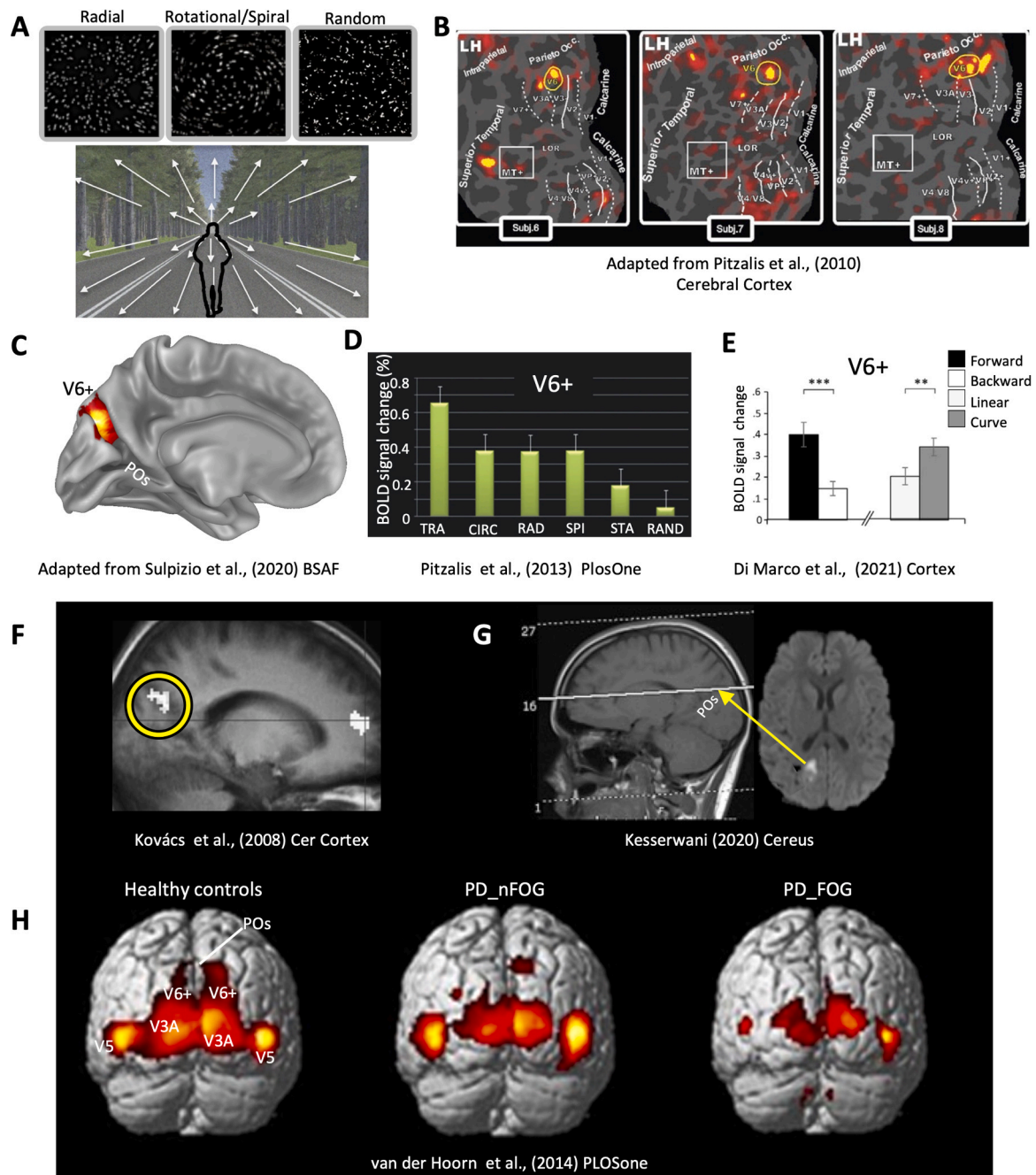
spot of motion-related fMRI activation includes only rV6 or also other possible neighboring motion areas.

[Fig. 3C](#) shows the location and the extent of area V6+ mapped by the functional localizer coherent flow vs. randomly moving dots ([Sulpizio et al., 2020a](#)). The view that V6+ is involved in the estimation of self-motion (or “egomotion”; [Gibson, 1950](#)) has been confirmed also in other fMRI studies using similar optic flow stimuli (or egomotion compatible vs incompatible stimuli) ([Cardin and Smith, 2010](#); [Cardin et al., 2012a; b](#); [Cardin and Smith, 2011](#); [Huang et al., 2015](#); [Sherrill et al., 2015](#)). We also observed that this area is able to distinguish among different types of 3D egomotion (i.e., translational, circular, radial, and spiral motion; see [Fig. 3D](#)), with a preference for the translational egomotion ([Pitzalis et al., 2013d](#)). In line with this view, V6+ has been shown to have the highest response bias among motion-responsive regions toward stimuli simulating egomotion in depth (expansion flow) ([Pitzalis et al., 2010](#); [Cardin and Smith, 2010](#); [Serra et al., 2019](#)), and to achieve the highest integration between stereo-depth with 3D motion flow among flow-responsive regions ([Cardin and Smith, 2011](#)). Other studies showed that V6+ ([Furlan et al., 2014](#); [Field et al., 2007](#)) responds to changing heading directions, which is another important visual cue that contributes to the perception of self-motion. A recent fMRI study has also shown that V6+ shows a preference for optic flow stimulations that simulate locomotion-compatible curved paths, suggesting that this region is involved in encoding heading changes and in the estimation of path curvature ([Di Marco et al., 2021a](#); [Fig. 3E](#)). The same study also found that the area prefers forward visual motion (as compared to backward visual motion), suggesting its involvement in a fine visual analysis of the environment toward which one is moving during locomotion ([Di Marco et al., 2021a](#); [Fig. 3E](#)).

In the past, few previous neuroimaging studies have already reported the involvement of the POs or the posterior part of the precuneus in this kind of stimulation (e.g., [Cheng et al., 1995](#); [Brandt et al., 1998](#); [Galati et al., 1999](#); [Sereni et al., 2001](#); [Kleinschmidt et al., 2002](#); [Kovács et al., 2008](#)). An example is displayed in [Fig. 3F](#), that shows the POs region activated during optic flow stimulations that generate in the participant a vivid percept of three-dimensional motion ([Kovács et al., 2008](#)). A comparison with [Fig. 3C](#) shows that the optical flow stimulation activates a region of the POs along the sulcus, which is within the cortical territory of area V6+ ([Pitzalis et al., 2010](#); [Sulpizio et al., 2020a](#)). However, it is worth noting that none of these previous studies have directly related the observed activation to the still unknown area V6, but have referred it to a generic medial activation around the POs. Recently, we found that also macaque V6, like human V6, was strongly activated by flow field ([Pitzalis et al., 2021](#)).

The idea that human V6+ is an important cortical node specialized





**Fig. 3.** Involvement of the posterior POs in the analysis of coherent motion. **A.** Flow fields: the two frames of the ON phase show the two different types of coherent motion (radial and rotation/spiral motion) that switched almost every 500 ms; they were compared with random motion presented during the OFF phase (see [Pitzalis et al., 2010](#) for more details). The flow fields stimulus resembles the typical pattern of expanding retinal motion arising because of the observer's forward motion (see panel on the bottom of [Fig. 3A](#)). **B.** Brain location and extent of the motion selective activity arising from the flow field stimulus in some representative participants. **C.** Brain locations of V6+, defined by averaging individual V6+ from participants who underwent the flow field stimulus. Results are displayed on the medial folded representation of the left hemisphere of the template brain. **D.** The column plot represents the response profile of area V6+ to different types of 3D flow fields (Pitzalis et al., 2013). The averaged BOLD percent signal-change across subjects and hemispheres in the localizer-defined area V6 is shown for each experimental condition labelled as follows: TRA, translational; CIR, circular; RAD, radial; SPI, spiral; RAND, random; STA, static. **E.** The columns in the plot represent the averaged BOLD percent signal-change across subjects and hemispheres in the localizer-defined area V6 with respect to the four experimental conditions derived by the Direction (Forward, Backward) and Path (Linear, Curved) factorial design. \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ . **F.** Portion of POs activated during optic flow stimulations that generate in the participant a vivid percept of three-dimensional motion. **G.** Location of a brain lesion in a patient showing an optic flow motion deficit characterized by altered motion perception (courtesy of Hassan Kesserwani -[Kesserwani, 2020](#)). **H.** Activations related to wide-field radial optic flow in healthy controls (on the left) and in Parkinson patients (PD) without freezing of gait (PD\_nFOG; on the center) and with freezing of gait (PD\_FOG; on the right) are displayed. Note that V6+ (and other visual areas) was strongly activated in healthy control (on the left) while its activation was reduced in PD\_nFOG and was absent in PD\_FOG. (a-b) Modified from ([Pitzalis et al., 2010](#)). (c) Modified from [Sulpizio et al. \(2020a\)](#). (d) Modified from ([Pitzalis et al., 2013d](#)). (e) Modified from ([Di Marco et al., 2021a](#)). (f) Modified from ([Kovács et al., 2008](#)). (g) Modified from [Kesserwani, 2020](#). (h) Modified from [van der Hoorn et al. \(2014\)](#).



in the perception of self-motion (or “egomotion”; Gibson, 1950) is also supported by human clinical studies. For example, epileptic seizure localized in the paramedial part of the precuneus, very close to the parieto-occipital sulcus, evokes linear self-motion perception (Wiest et al., 2004). More recently, Kesserwani (2020) described a young patient who exhibited an optic flow motion deficit characterized by slow self-motion of the left half of his body and slow motion of the surroundings (so called Zeitraffer phenomenon) after an ischemic infarct of the banks of the right POs. Fig. 3G (Kesserwani, 2020) shows that the cortical lesion in this patient is similar in location and extent to the region activated by Kovács et al., (2008) (Fig. 3F), that is involved in generating a vivid percept of three-dimensional motion, and well corresponds to the motion area V6+ (see Fig. 3C).

Notably, the involvement of V6 in the analysis of the optic flow evoked by locomotion could explain the typical ‘freezing of gait’ observed in some Parkinson’s disease patients. In fMRI studies where healthy controls (HC) and patients with Parkinson’s disease (PD) watched radial expanding optic flow simulating the visual consequence of forward locomotion (van der Hoorn et al., 2014), the visual areas in the occipital pole, likely including the motion-specific areas V5 and V6+ besides other visual areas, were strongly activated in healthy control (HC; Fig. 3H, left panel) and reduced in PD patients (Fig. 3H, middle and right panels). Note that in the PD patients with freezing of gait (Fig. 3H, right panel), the activation of V5 and other visual areas was strongly reduced but still present, whereas that of V6+ completely disappeared. We suggest that in healthy subjects, V5 and V6+ analyze the visual stimulation evoked by locomotion, sending their output to cortical areas involved in the visuomotor control of locomotion, like area P<sub>Ec</sub> (see chapter 3.3 below). The reduction of activity of visual areas could be responsible for the difficulties and impairments in locomotion typical of PD, while the absence of activity in V6+ in PD patients with freezing of gait (Fig. 3H, right panel) suggests that the information sent by V6+ to the locomotor centers may be important to start locomotion in human, though causal evidence is still missing.

Beyond the sensitivity to coherent visual motion simulating self-motion, area V6+ is also responsive to coherent local motion compatible with object motion. In a recent study we have observed that V6+ responded to complex visual stimulation in which participants not only had the illusion to move through a realistic virtual environment, but also clearly perceived an object displacement within this environment (Pitzalis et al., 2020). Further neuroimaging studies have implicated V6+, or the cortical territory where the area is typically located, in a variety of aspects of object motion processing. For example, Calabro et al. (2019) have found activation in the posterior bank of the parieto-occipital sulcus during the estimate of time-to-arrival of objects moving along different trajectories. Huang et al. (2015) using a virtual reality environment simulating a daily scenario where doors randomly swing outward while walking in a hallway, observed that area rV6, together with other high-level areas belonging to the dorsal motion stream, was activated not only by passive observation of forward and translational egomotion, but also by observation of object motion (a swinging door).

Compatibly with this view, it has been demonstrated that patients with damage around the parieto-occipital sulcus showed deficits in a series of tasks including object motion perception. Vaina et al. (2014) tested two patients with occipital lobe lesion in a series of visual motion tasks. Although the perception of observer-scene motion seemed to be spared, the patients exhibited some deficits on motion processing, including detection of colliding object trajectory while they were stationary. Similar impairments were also observed in a group of stroke patients with occipito-parietal damage (Vaina et al., 2010). In addition, patients lesioned in the dorsal POs (that includes V6+) lose their ability to detect motion direction (Blanke et al., 2003), as predicted by the richness of direction selective cells shown in macaque area V6 (Galletti et al., 1996; see Fattori et al., 2009), and showed a complete loss of visual depth perception (Schaadt et al., 2015), likely because of a

magnocellular deficit (Castelo-Branco et al., 2006), because V6, at least in the macaque, receives direct input from the magnocellular cells of layer IVB of V1 (Galletti et al., 2001).

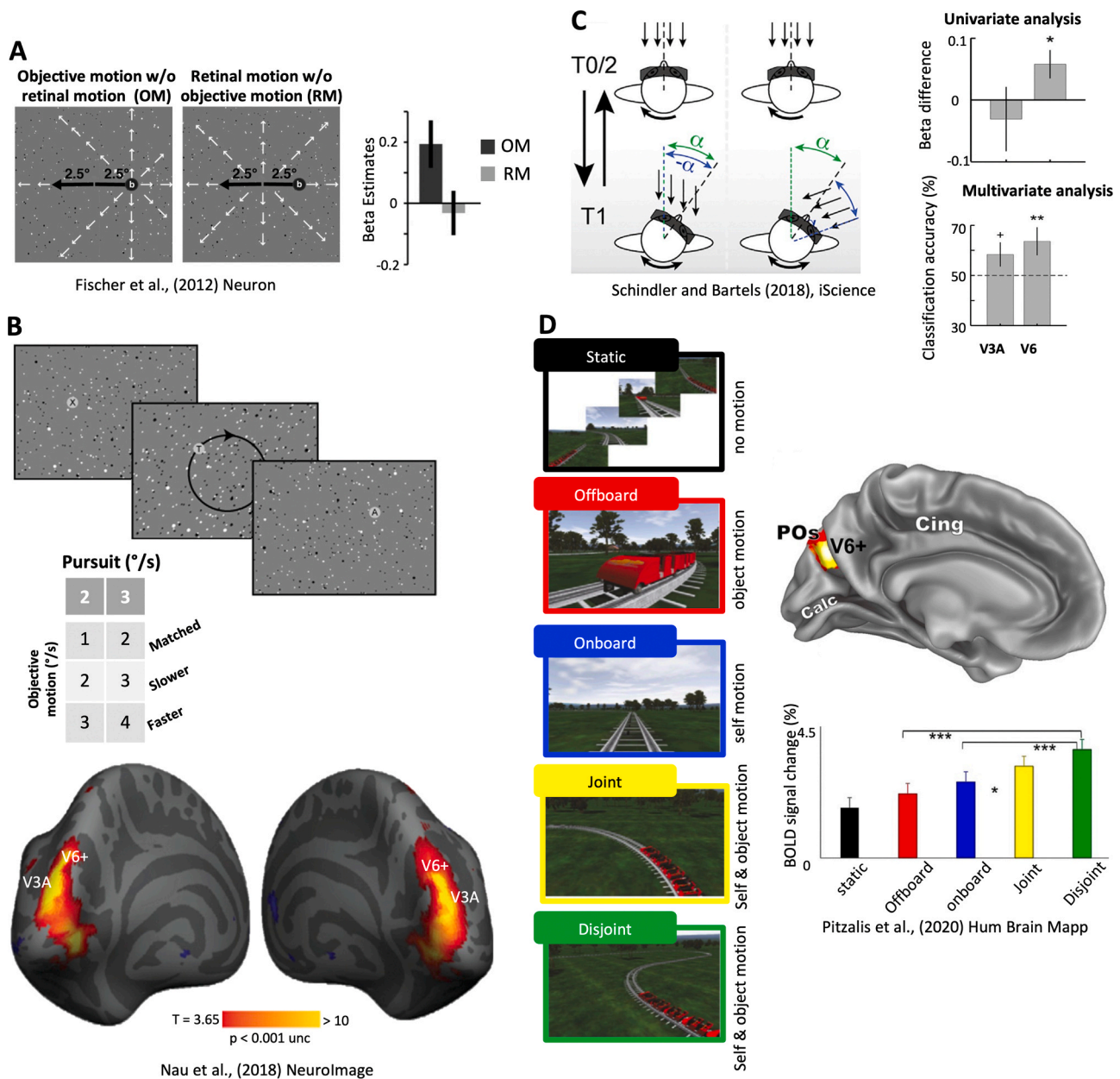
To sum up, brain imaging and lesions studies testing visual motion revealed that the posterior POs, including area V6+, is specialized in the analysis of visual cues coming from coherent motion and is involved in many aspects of visual motion processing, including perception of self- and object-motion.

### 3.1.2. “Real” motion detection:

Another important function ascribed to the dorsal part of the parieto-occipital cortex is the “real motion” detection. This function has been widely described in the monkey, where V6, V3A, and also earlier visual areas contain the “real-motion” cells, i.e., cells activated by the actual movement of an object in the visual field, but not by the movement of its retinal image self-induced by the eye movements (Galletti et al., 1984, 1988, 1990; see Galletti and Fattori, 2003 for a review). V6 and V3A are the areas that host the higher percentage of real-motion cells. Recent fMRI data suggest that also the human V6+ and V3A contain real-motion cells since they are involved in discarding self-induced retinal motion in order to infer the “real” motion. Specifically, Fischer and co-workers (2012; see Fig. 4A), by using fMRI paradigm combining physical planar motion with pursuit in a way that retinal motion could be either induced or cancelled by pursuit, demonstrated that V6+ (together with V3A) contributes to perceptual stability during pursuit eye movements, especially when a forward flow component simulating egomotion in depth was presented to participants. By using a similar task, Nau and co-workers (2018, see Fig. 4B) showed that areas V6+ and V3A are able to differentiate between distinct velocities of objective motion during pursuit, thus supporting the integration between the direction of retinal motion and that of eye movements. Nau and co-workers (2018) also demonstrated that not only higher-level motion regions such as V3A and V6+, but also early visual areas like V1, V2, and V3 signaled the velocity of objective motion, though with less efficacy. Interestingly, the efficiency in integrating retinal with non-retinal signals, higher in areas V3A and V6+ and weaker in early visual areas, mimicked the incidence of real-motion cells in the homologue macaque visual areas (Galletti and Fattori, 2003). More recently, an air pressure-based head-stabilization system (Fig. 4C), allowing subjects to move their head during fMRI scanning by exploiting the delay of several seconds between neural processing and blood oxygen level dependent (BOLD) signal, has been introduced to further explore the role of the visual system in compensating for self-induced head movements (Schindler and Bartels, 2018a). Thanks to this innovative setup, it was provided the first evidence for the integration of retinotopic representations and voluntary head-movement signals in the human homologue of area V6. This area, indeed, exhibited a significant difference between congruent and incongruent combinations of visual and extra-retinal signals in both univariate and multivariate analyses (Schindler and Bartels, 2018b, see Fig. 4C).

Taken together, these studies have provided evidence on the important role of V6+ (and V3A) in discounting extraretinal signals from retinal visual motion, and thus in the real motion perception, well in line with the high percentages of real-motion cells discovered in areas V6 and V3A in the macaque (Galletti and Fattori, 2003).

Further support to this view comes from lesion studies. A lesion of the human extrastriate cortex, likely including areas V3A, V6+, MT/V5, and MST, produced very selective impairment in motion detection (Haarmeier et al., 1997), with the patient unable to judge whether a retinal slip was self-induced by the eye movement or was caused by an actual movement of an object. Additionally, lesions or electrical stimulation of the POs produce motion-related visual disturbance (e.g., Heide et al., 1990; Richer et al., 1991; Blanke et al., 2003). Yet in agreement with this view, the lesion of patients exhibiting preserved awareness for moving but not stationary stimuli (Riddoch phenomenon) involves the occipitotemporal cortex, but spares the cortical territory likely including



**Fig. 4.** Involvement of the posterior POs in “real” motion detection. **A.** Illustration of the 3D expansion/contraction flow used in Fischer et al. (2012). The focus of expansion (FOE) of the flow corresponding to the fixation disc was both locked to objective planar motion (objective motion without retinal motion -OM-) or moving over the static background (retinal motion without objective motion -RM-). The plot shows the activation profile of area V6 (across subjects and hemispheres) to both objective and retinal motion conditions. **B.** Top: Illustration of visual stimuli used in Nau et al. (2018). At two different pursuit speeds ( $2^{\circ}/s$  and  $3^{\circ}/s$ ), objective motion could be  $1^{\circ}/s$  slower (slower condition), matched (matched condition) or  $1^{\circ}/s$  faster (faster condition) relative to pursuit (see table below). Bottom: Whole-brain activation map related to the faster > slower contrast reveals the involvement of area V6+ and other visual areas. **C.** Experimental procedure used by Schindler and Bartels (2018a); **b**: subjects performed voluntary head rotations while being approached by a simulated 3D dot cloud in both congruent and incongruent conditions. Head rotations in the congruent condition led to cloud rotation in opposite direction ( $-\alpha$ ) to the observer's head ( $\alpha$ ), as would be experienced when moving forward in a stable environment and looking around. In the incongruent condition, the cloud and head rotated in the same direction ( $\alpha$ ), resulting in perceptually arbitrary motion of the environment. Note that retinal flow as well as head motion were matched in both conditions. The plots show the response profile of areas V3A and V6 during the congruent vs. incongruent comparison as revealed by both univariate and multivariate analyses.  $^+ p < 0.05$ , uncorrected;  $* p < 0.05$ , FWE corrected;  $** p < 0.005$ ; FWE corrected. **D.** Motion conditions and results from Pitzalis et al. (2020). Left: Example of the 3 s movie types for the four motion conditions (Offboard-red, Onboard-blue, Joint-yellow, and Disjoint-green) and static frames (Black) are shown. Right: The overlap of all the individual V6+ ROIs, as defined by the flow field localizer, are displayed on the medial folded representation of the left hemisphere of the template brain. Plots represent the averaged BOLD percent signal changes in the localizer-defined area V6+ as a function of the experimental conditions. Notice that the area shows a preference for complex motion conditions, including both self- and object-motion, even when the images remain still (on the screen) because of self-movement. Significant comparisons are also reported.  $* p < 0.05$ ;  $** p < 0.01$ ;  $*** p < 0.001$ .

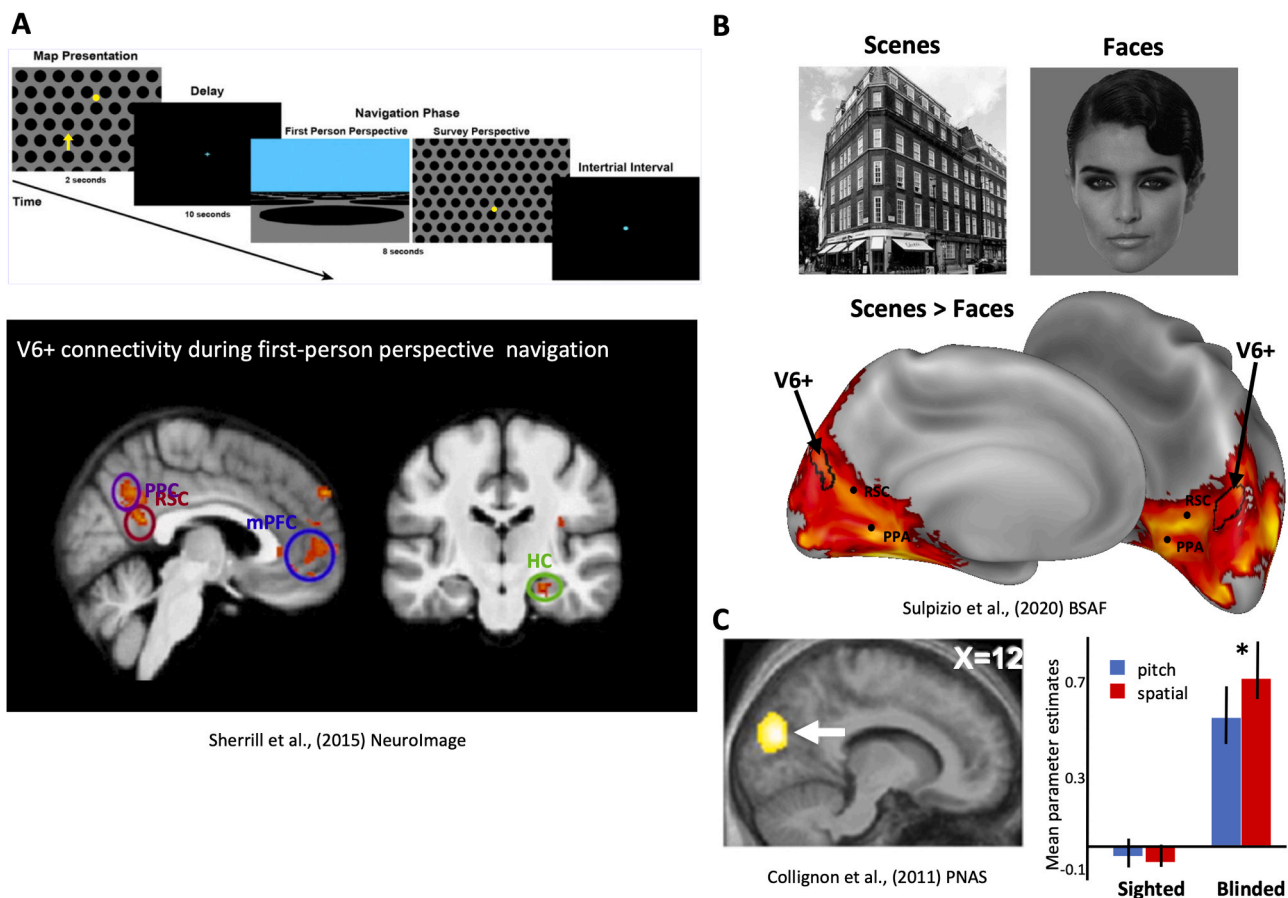
(a) Modified from Fischer et al. (2012). (b) Modified from Nau et al. (2018). (c) Modified from Schindler and Bartels (2018a). (d) Modified from Pitzalis et al. (2020).

areas V6+ and MT/V5 (Arcaro et al., 2019), the two ‘motion areas’ of the human brain (Pitzalis et al., 2010). Given that detecting object-motion can be accomplished also when the observer’s self-motion evokes plenty of confounding retinal image movements (optic flow), it has been proposed that area V6+ is involved in “subtracting out” self-motion signals across the whole visual field and in providing information about moving objects (Galletti et al., 2003; Galletti and Fat-tori, 2018). With this respect, a prominent hypothesis (flow parsing hypothesis) states that the brain identifies and subtracts the optic flow associated with the observer movement in order to isolate retinal motion arising from movement of objects within the scene (Warren and Rush-ton, 2008). Despite this account is largely accepted (see also Arnoldus-sen et al., 2013; Cardin et al., 2012a; Fischer et al., 2012), very few studies have focused on how the human brain accomplishes this mechanism using visual optic flow only. One recent study by our lab (Pitzalis et al., 2020; see Fig. 4D) took advantage of virtual reality and wide-field stimulation to compare visually induced self- and object-motion, in conditions of natural vision (free scanning). We observed that some motion-sensitive areas (including V6+) are able to extract object-motion information from the overall motion, recognizing

the real movement of a target object (i.e., a train) even when the images remain still (on the screen) because of self-movement. In other words, the sensitivity to self-motion compatible optic flow observed in these regions could be useful to ‘parsing’ the retinal motion information into self-motion and object-motion components. For this reason, we proposed V6+ as a good candidate for the “flow parsing” mechanism (Pit-zalis et al., 2020).

### 3.1.3. Visual control of navigation:

Recent pieces of evidence suggest that the caudalmost part of the medial parieto-occipital cortex (namely, areas V6+ and V3A) is also important for the analysis of visual motion cues useful for navigation. According to recent models of visuo-spatial processing, anatomical connectivity findings in primates suggest that the parieto-medial tem-poral pathway, known to be specialized in spatial navigation, originates from the caudal part of the inferior parietal lobule, which in turn receives a set of projections from temporal and parieto-occipital areas, including area V6+ (Kravitz et al., 2011). Beyond anatomical connec-tions, also functional connectivity findings in human support this view. For example, Tosoni and co-workers (2015) observed that area



**Fig. 5.** Involvement of the posterior POs in the visual control of navigation. **A.** Navigation task used by Sherrill et al. (2015). Participants were first presented a survey map of the environment with their start location and orientation (yellow arrow), and goal location (yellow dot) clearly marked. After a delay period, participants were required to actively navigate, both in first-person and in survey perspective, to the goal location (which was not present anymore). The whole-brain connectivity map, overlaid on the sagittal and coronal images of the brain, shown on the bottom revealed that area V6 is functionally connected with navigationally relevant regions as RSC and the hippocampus (HC) during the first-person navigational condition. **B.** Examples of stimuli used to localize scene-selective regions, inspired from the original paradigm by Epstein and Kanwisher (1998) and described in detail in Sulpizio et al. (2013). The whole-brain activation map shown on the bottom resulting from the scenes > faces contrast revealed that, beyond the typical scene-selective regions, also area V6+ shows a preference for navigationally relevant stimuli, being stronger activated by pictures of scenes than by pictures of faces. **C.** The whole-brain activation map (overlaid on the sagittal image of the brain) obtained from the study by Collignon et al. (2011). The specific contrast used to test the sensitivity to the spatial processing of sounds in blind subjects revealed an activation peak around a cortical region that likely included area V6+ . The plot shows the mean BOLD estimates associated with the processing of pitch (blue) or spatial (position in azimuth, red) attributes of sounds in both sighted and blind groups. \*p < 0.05.

(a) Modified from Sherrill et al. (2015). (b) Modified from Sulpizio et al. (2020a). (c) Modified from Collignon et al. (2011).



V6+ showed strong resting-state functional connectivity with the scene-selective regions parahippocampal place area (PPA, Epstein and Kanwisher, 1998) and retrosplenial complex (RSC, Epstein, 2008), which are known to be activated by navigationally-relevant stimuli. In a similar vein, both PPA and RSC showed strong resting-state functional connections with V6+ (Boccia et al., 2017). Notably, Sherrill et al. (2015) (see Fig. 5A) observed that the functional connectivity between V6+ and some navigationally relevant regions as RSC and the hippocampus (HC), increased during a first-person navigational task. The authors proposed that this functional link might reflect the ability to update representations of spatial positions based on self-motion cues inferred from first-person navigation perspective. By using a similar analysis, Schindler and Bartels (2016) showed an optic flow-dependent increase of functional connectivity between the early visual cortex and a network of motion areas including MT/V5, V3A, V6+, the cingulate sulcus visual area (CSv) and precuneus (Pc) and a decrease of functional connectivity between the early visual cortex and navigationally-relevant areas such as the entorhinal and the retrosplenial cortices.

Although the direct involvement of V6+ in spatial processing has not yet been established, several studies have found BOLD activation in correspondence of V6+ during spatial tasks such as first-person perspective visual virtual navigation (Ghaem et al., 1997; Grön et al., 2000; Spiers and Maguire, 2007; Vann et al., 2009; Boccia et al., 2014). It should be noticed that this area was typically broadly referred as “posterior-parietal”, “dorsal precuneus” and the “parieto-occipital sulcus” in the literature on spatial navigation. Only recently a direct involvement of both human areas V6+ and V3A in spatial processing has been demonstrated. In particular, we recently demonstrated that these egomotion-selective areas showed a stronger BOLD response to pictures of places (internal and external views of buildings) as compared to pictures of faces (Sulpizio et al., 2020a, see Fig. 5B), thus indicating that the mere exposure to static, but navigationally relevant, scenes is able to trigger the activity of these dorsal motion areas. The view of an involvement of V6+ in spatial navigation has been also supported by studies on congenitally blind participants. For example, Collignon et al. (2011) (see Fig. 5C) measured the BOLD responses of both congenitally blind and sighted participants while they processed either the identity (pitch) or the spatial (position in azimuth) attributes of exactly the same sounds. The authors found that some regions of the right dorsal occipital stream, likely including V6+ and V3A, are recruited during auditory-spatial navigation, but only in the congenitally blind group. Taken together, both connectivity data and navigationally-based functional data collected on both sighted and blind participants support the view that motion processing is important not only on its own, but also in support to other higher-level functions such as the control of spatial navigation in a structured environment (Cardin and Smith, 2011; Pitzalis et al., 2013b; Sulpizio et al., 2020a), likely performed by more anterior regions of the SPL (see below).

### 3.2. Functional properties of the anterior POs/dorsal-posterior precuneate cortex

In human, the anterior bank of the dorsal part of POs, and the corresponding part of the dorsal-posterior precuneate cortex, host the human homolog of monkey visuomotor areas V6Av and V6Ad (Fig. 1B).

After the retinotopic identification of the human area V6, we used the same wide-field retinotopic stimuli to reveal the presence of an additional area, V6Av, responding only to the lower visual field and separated from the lower field in V6 by a vertical meridian (Pitzalis et al., 2013a). The location and retinotopic organization of area V6Av are shown in Fig. 2B, where the position and borders of V6Av are indicated by a dotted white outline in the flat map in the left panel and by a blue outline in the three-dimensional reconstruction of the brain in the right panel. The lower field-only representation of V6Av is located on the dorsalmost part of the POs, anterior to the lower-field representation of V6 (yellow outline in Fig. 2B) and medial to the peripheral

lower field representation of area V3A. In contrast to human V6, human V6Av lacks a representation of the center of gaze and responds only to the very far periphery (starting from 30°). The retinotopic description of this new region is similar to that observed in the macaque V6Av, where Gamberini et al. (2011) described a clear overrepresentation of the periphery as well as of the lower visual field adjoining posteriorly the lower visual field of V6. Thus, although the anatomical position of V6Av across the two species is not exactly the same (i.e., ventral in macaque and posterior in human with respect to the other part of V6A) we maintained the same name ‘V6Av, ventral V6A’ for the human counterpart in respect of the analogies observed along the other main dimensions (i.e., retinotopy and neighboring relationships).

Anterior to V6Av, the visual topography becomes markedly inconsistent across subjects. Thus, in Tosoni et al. (2015) we identified the human homologue of macaque area V6Ad (the dorsal part of V6A) using not a retinotopic mapping but a combined approach of task-evoked activity and resting-state fMRI. Based on a combination of a visual motion task (the flowfields stimulus which we have previously proposed as a functional localizer for human V6, Pitzalis et al., 2010) and a visuomotor task (pointing vs. saccadic movements, Fig. 6A) we defined an area, V6Ad, immediately anterior to V6Av with different functional properties with respect to the neighboring retinotopic V6 and V6Av (Tosoni et al., 2015). Indeed, human V6Ad shows strong selectivity for the execution of pointing movements involving wrist rotation and significantly weaker responses to visual motion than rV6 and rV6Av (Fig. 6B), results that are consistent with monkey neurophysiological findings (Galletti et al., 2003; Fattori et al., 2005, 2009; Gamberini et al., 2011).

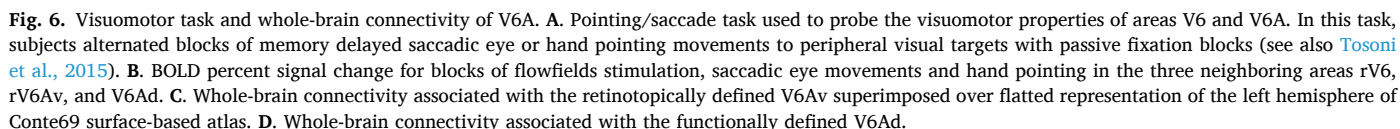
These findings demonstrate a gradient of functional specialization in the POs that follows a posterior-to-anterior axis, with V6, localized posteriorly, specialized for the visual analysis of coherent motion (Pitzalis et al., 2010; see also chapter 3.1); the putative V6Ad region, localized anteriorly (and dorsally), specialized in the execution of pointing movements (vs. saccadic eye movements) mirroring the functional profile of the macaque V6Ad (Fattori et al., 2017; Hadjidimitrakis et al., 2014, 2017; Bosco et al., 2019); and the rV6Av region, spatially interposed between the two regions, with both significant but not selective visual and motor responses. This topographical arrangement of functional specialization exactly mirrors that observed in the macaque (Gamberini et al., 2011).

A similar gradient of functional specialization was also found in the functional connectivity data (Fig. 6C, D; Tosoni et al., 2015). Indeed, while V6 is connected mainly posteriorly with early retinotopic visual and motion areas (data not shown), V6Av is connected with some higher order visual areas (V3A, V7, V6) and extends more anteriorly involving regions along the intraparietal sulcus (IPS1–4, VIP). In contrast, V6Ad has no connections with early retinotopic ventral and dorsal visual areas (with the only exception of V6 and V6Av). Laterally, it is more extensively connected to IPS regions including area LIP and it is the only POs region that shows connectivity with dorsal premotor and ventrolateral prefrontal cortex (areas 6 and 46, respectively). Overall, the functional connectivity data highlighted that these regions belonged to partially separate networks and that the differences in the pattern of connections observed between these regions mirror the differences observed in the task-evoked activity. The functional connectivity maps confirmed also that rV6Av behaves as a ‘middle-earth’ cortical region in between areas rV6 and V6Ad, which are instead dominated by visual and visuo-motor responses, respectively.

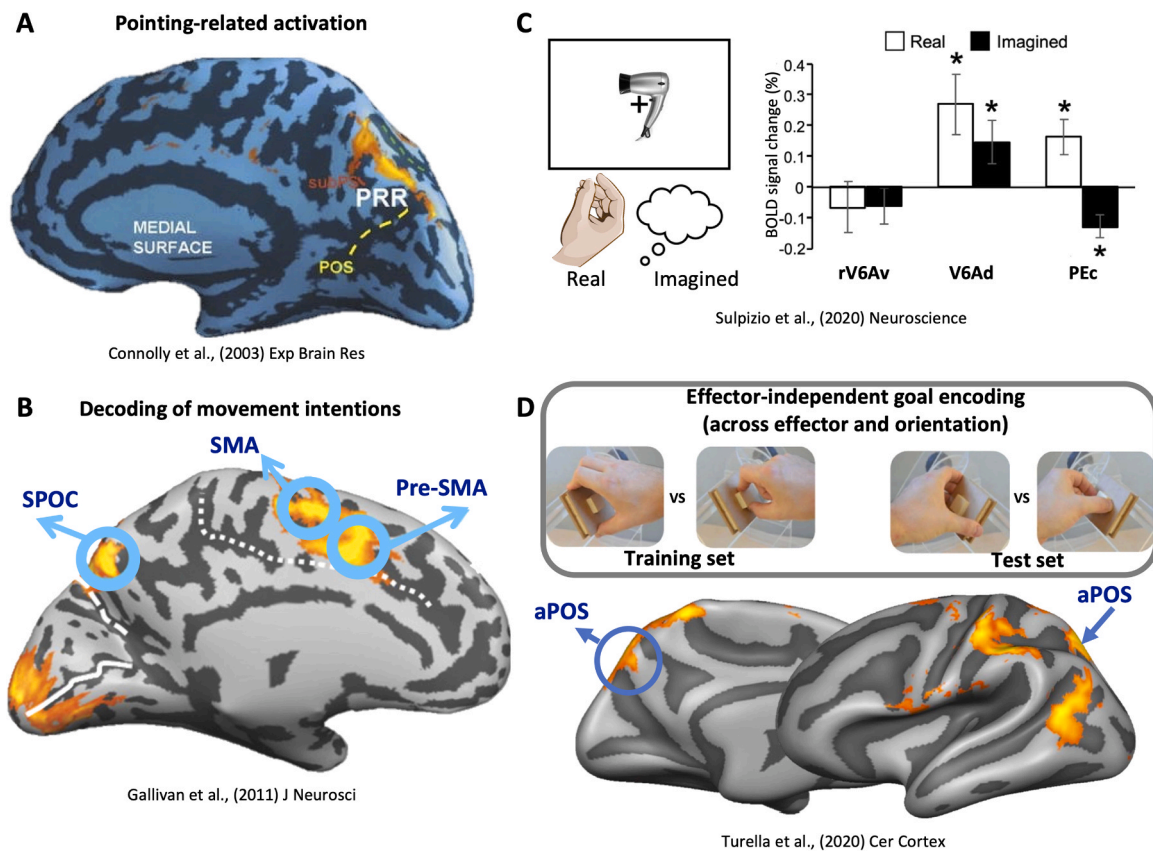
The portion of cortex hosting the visuomotor area V6A has received particular attention in many neuroimaging studies. These studies revealed that the region is especially involved in three related processes: 1) visuomotor control of hand-related movements, 2) visuomotor control of navigation, 3) shift of the focus of attention.

#### 3.2.1. Visuomotor control of hand-related movements:

Many studies have observed broad activations in response to arm



2011). This focus of activation likely corresponds to the superior parieto-occipital cortex (SPOC, as indicated by the Culham's group). SPOC is implicated in the guidance of arm movements (Cavina-Pratesi et al., 2010; Gallivan et al., 2011; Monaco et al., 2011), especially when these movements are directed towards targets located in the portion or near space rather than the far one (Quinlan and Culham, 2007; Rossit et al., 2013; Gallivan et al., 2009). This region showed adaptation for repeated hand orientation rather than for repeated object orientation (Monaco et al., 2010), and for repeated action-relevant features of the object (such as grasp-relevant dimension) rather than for repeated visual size during grasping (Monaco et al., 2014). All these pieces of evidence suggest that this portion of cortex is implicated in processing hand orientation and grip type during reach-to-grasp movements. Further evidence obtained by using decoding techniques from activation patterns (Gallivan et al., 2011; Fig. 7B) confirmed that this cortical region, likely including the human homolog of macaque area V6A, plays a role in processing wrist orientation and grip formation. Notably, however, all these studies described such dorsomedial activations elicited by reach-to-grasp movements in terms of whole-brain neural circuits, not ascribed to specific dorsomedial parietal areas. Only recently, a human fMRI study (see Fig. 7C) tested the sensitivity of both ventral and dorsal divisions of V6A, (i.e., V6Av and V6Ad) to both a pantomimed and an imagined grasping action (Sulpizio et al., 2020b). This study revealed



**Fig. 7.** Involvement of the anterior POs in the visuomotor control of hand-related movements. **A.** The whole-brain activation map (overlaid on the medial view of an inflated brain) shows a swath of activation along the anterior POs during memory-delay trials in which the subject planned to point to a specific location as compared to trials in which the subject planned to make a saccade to that same location (Connolly et al., 2003). **B.** Cortical areas that exhibited significant decoding accuracies for upcoming object-directed grasp and reach movements with respect to 50% chance. **C.** Schematic representation of the grasping task (real and imagined) used by Sulpizio et al. (2020b). The plot shows the average of BOLD signal change as a function of both real and imagined grasping in the cortical regions specialized in controlling limb movements (rV6Av, V6Ad, PEC). Only area V6Ad is activated by both real and imagined grasping movements, suggesting its role in creating a more abstract representation of object-directed actions. \* $p < 0.05$  FDR-corrected. **D.** Schematic representation of the decoding procedure used in Turella et al. (2020) to reveal the existence of an effector-independent (across effector and hand orientation) neural representation. The whole-brain map (overlaid on the medial and lateral views of an inflated brain) reveals that the portion of cortex near the anterior POs shows a significant effector-independent goal decoding. (a) Modified from (Connolly et al., 2003). (b) Modified from Gallivan et al. (2011). (c) Modified from Sulpizio et al. (2020b). (d) Modified from Turella et al. (2020).

that V6Ad is activated by both real and imagined grasping actions while the nearby V6Av is completely unresponsive to these conditions, thus suggesting that the dorsal but not the ventral portion of the area is involved in the control of grasping and in implementing all the visuomotor transformations needed to create an abstract representation of the object-directed action. This is in line with a recent report that used a multivariate pattern analysis approach of functional magnetic resonance imaging data (Turella et al., 2020). The authors asked participants to perform a grasping movement with different grip types (precision grip, whole hand grip), different wrist orientations (canonical, rotated), using either the left or right hand. This kind of paradigm was designed to disentangle three different levels of abstraction, i.e., concrete action, effector-dependent goal (invariant to wrist orientation), and effector-independent goal (invariant to effector and wrist orientation). Results from this study revealed the existence, in the cortical territory hosting V6Ad, of a convergence of action representations, ranging from the representation of hand-specific actions to the representation of effector-independent goals (Fig. 7D; Turella et al., 2020). These findings indicate that some visuomotor association areas are organized based on abstract action functions independent of specific sensorimotor parameters. The concept that the area V6Ad might represent not only concrete aspects of hand actions but also more abstract information is compatible with a recent human fMRI study exploring haptically guided grasping movements (Styrkowiec et al., 2019). The study revealed not only that

the portion of cortex including V6Ad is sensitive to a sensory modality different from the visual one, but also that the area is activated by both haptic exploration and planning of haptically guided grasp of both tools and no-tools, thus supporting its involvement in the most abstract levels of hand-based action planning. A convincing demonstration that human brain hosts a modality-independent representation also comes from experiments by Levy-Tzedek et al. (2012). In these experiments, visual sensory substitution devices use sound or touch to convey information that is normally perceived by vision. Participants were asked to make fast reaching movements to targets presented by this device. After only a short practice session, blindfolded sighted participants performed fast and accurate movements to presented targets, which did not differ significantly from movements performed with visual feedback in terms of movement time, peak speed, and path length.

Several studies have argued that the area within the dorsomedial stream roughly corresponding to the V6Ad plays a role in the planning phase of effector movements. For example, Vesia and co-workers (2017) used a dual-site, paired-pulse transcranial magnetic stimulation (TMS) paradigm to investigate functional connectivity between left SPOC and ipsilateral primary motor cortex (M1) during the planning of three different actions with the right hand, i.e., 1) a precision grip to grasp a small object, 2) a whole-hand grip to grasp a large object and, 3) a reach-to-touch movement with no hand shaping. The main finding of this study is that preparatory response amplitudes in the SPOC-M1



circuit of different hand muscles were selectively modulated early in the motor plan for different types of grasps, thus suggesting that SPOC specifies handgrip parameters in the early motor plan of an upcoming reach-to-grasp action. The involvement of human V6Ad in planning grasping movements is also confirmed by Breveglieri et al. (2022) who showed that TMS stimulations disrupted the re-programming of both grip aperture and wrist orientation, again documenting the causal role of V6Ad in the control of wrist orientation and grip formation during planning of grasping, paralleling monkey single cell recordings (Fattori et al., 2009, 2010).

Beyond grasping, converging evidence suggests the involvement of V6Ad also in the more proximal component of hand movements, such as reaching movements. Even in this case, the V6Ad activity seems to be more related with the planning phase of hand-related movements rather than with the execution phase. For example, Breveglieri et al. (2021) used a single-pulse TMS over a cortical territory that likely included V6Ad while participants were engaged in planning immediate, visually guided reaching movements by using different eye-hand configurations. The authors observed that when the TMS was delivered over V6Ad during reaction time (200 ms after the Go signal, before the movement onset), the accuracy of reaching movements decreased for targets located farther from the gazed location, but only if they were also located farther from the body. It should be noted that the coordinates of the stimulated area are similar to those used in other two TMS studies on V6Ad (Vesia et al., 2010; Ciavarro et al., 2013), both showing that a train of repetitive TMS applied over a cortical territory that likely included the V6Ad during reach planning causes a misreaching that resemble optic ataxia deficits, i.e., a deviation of memorized reaching endpoint toward the position of visual fixation. Notice that different from Ciavarro et al. (2013) and Vesia et al. (2010), Breveglieri and co-workers (2021) have tested reaching movements in depth and used a single pulse TMS, less efficient than a repetitive stimulation. Further support to the idea that the dorsomedial SPL is causally involved in the planning rather than in the execution of reaching movements comes from a recent TMS study, requiring participants to plan and execute reaching movements with both hand and foot effectors (Marigold et al., 2019). The authors observed the absence of a TMS modulation during action execution in IPS1 (likely including area V6Ad) when the visual target to be reached changed in position, likely indicating that the area is involved in planning, rather than execution and online control, of goal-directed limb movements.

Note that, although this corpus of TMS evidence suggests a causal role of V6A on the visuomotor control of hand-related movements, the limit in spatial location of such technique does not allow to attribute the observed dysfunctions specifically to V6Ad, but rather to a cortical territory around the stimulated region that likely included the V6Ad (see also the *General considerations* paragraph).

Taken together, both fMRI and TMS data on human demonstrate a causal role of dorsomedial SPL in the control of both grasping and reaching movements, well in agreement with the functional properties of the monkey V6A neurons (Gamberini et al., 2011; Fattori et al., 2017). Indeed, as reported above, the neural activity of V6A neurons is modulated by a number of factors all related to grasping and reaching movements: the orientation of the wrist/hand while grasping (Fattori et al., 2009), the grip used by the animal to grasp the object (Fattori et al., 2012; Fattori et al., 2010), the direction of arm movement (Fattori et al., 2005; Diomedes et al., 2020), and the distance reached by the hand (Hadjidimitrakakis et al., 2014; Hadjidimitrakakis et al., 2015). In addition, both imaging and TMS studies support the view that the cortical territory including area V6Ad plays a role in the planning rather than execution of arm movement, again a view well in agreement with the functional properties of the monkey V6Ad neurons (Santandrea et al., 2018).

### 3.2.2. Visuomotor control of navigation:

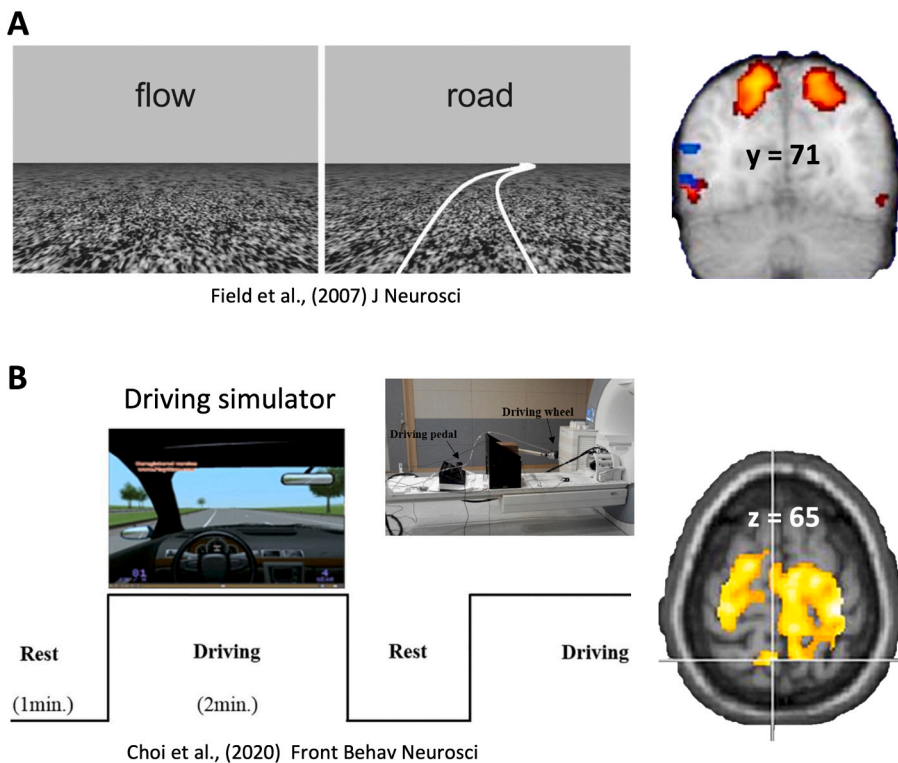
The V6Ad has been found to be activated in several neuroimaging

experiments where participants were engaged in tasks requiring a visuomotor control of hand actions aimed at guiding self-displacements (driving) through a patterned environment. In the fMRI study of Field et al. (2007), for instance, participants drove on a ground plane holding down left/right buttons to indicate the direction of their curved trajectories in two conditions: 'flow' and 'road' (Fig. 8A, left panels). In the flow condition, ground plane optic flow specified instantaneous curved heading, but future path information was not available. In the road condition, the same information was available, plus information about upcoming changes to heading from the road edges (future path). For effective steering, it is necessary to perceive an appropriate future path and then perform the required changes to heading to be rapid and efficient in changing the direction of movement. Field and co-workers (2007) found that a superior parietal region involving the posterior part of Brodmann area 7, likely including V6Ad, was activated by the perception of future path (Fig. 8A, right panel). Interestingly, the anterior part of this region proved to be critical for processing error signals during self-motion. In a more recent fMRI experiment (Choi et al., 2020) participants used a driving simulator (Fig. 8B, left panel). The subjects controlled a wheel with both hands and an accelerator and brake pedal with the right foot. Among the brain areas activated by driving, there was a precuneate region that likely included the human area V6Ad (Fig. 8B, right panel).

The above reported data suggest that V6A and neighboring areas of the dorsal stream host a spatial map of the environment used in navigation. There are data in literature showing that visual areas of the dorsal stream host spatial maps for navigation that are active even when no visual inputs are available. We have recalled above, in chapter 1.3, that Collignon and co-workers (2011) reported that V3A and V6 are recruited during auditory-spatial navigation in the congenitally blind group. More recent data have reported that blindfolded and congenitally blind individuals showed a strong brain activation in correspondence of areas V3A, V6 and V6A during a virtual maze navigation task performed with an auditory navigation aid (EyeCane) for non-visual navigation (Maidenbaum et al., 2018; Aggus-Vella et al., 2023). This evidence suggests that these important nodes of the dorsal visual stream are innately equipped for processing space independently of the type of sensory experience, and of the sensory developmental experience. In other words, they seem to host a spatial map of the environment to be used to interact with objects in the peripersonal space.

### 3.2.3. Shift of the focus of attention:

Goal-directed behaviors, such as grasping and reaching movements, but also any type of interaction with the external world, including visuomotor control of steering during navigation (driving), depend on the ability to flexibly adapt the motor plan in response to unexpected changes of target location. Such a flexible behavior depends on the ability to shift attention to a new location (attentional reorienting), with (overt) or without (covert) concomitant eye movements. It is well known that the allocation of spatial attention involves, among other different brain regions, the caudal part of the superior parietal lobule, anteriorly to the parieto-occipital sulcus (the so-called "dorsal" attention network; Corbetta and Shulman, 2002; Corbetta et al., 1998, 2008; Bisley and Goldberg, 2003, 2010; Petersen and Posner, 2012; Fiebelkorn et al., 2020). The involvement of single cells of the anterior POs in covert shifts of attention has been reported in area V6A of macaque monkeys (Galletti et al., 2010), where neurons discharged whenever the animal covertly directed its spotlight of attention towards particular parts of its field of view. Ciavarro and co-workers (2013) confirmed on humans the effect of V6A on covert attentional shifts in attentional reorienting (Fig. 9A). They used on-line rTMS over a cortical territory that likely includes the human V6Ad during a perceptive and reaching task requiring covert shifts of attention and planning of reaching movements, respectively, towards cued targets in space. The authors observed that in both tasks the TMS induced a significantly increase above the control level of response time when the cue did not correctly predict the target



**Fig. 8.** Involvement of the anterior POs in the visuo-motor control of navigation. **A.** Still frames from animated stimuli used by Field et al. (2007). In the flow condition, ground plane optic flow specified instantaneous curved heading, but future path information was not available. In the road condition, the same information was available, plus information about upcoming changes to heading from the road edges (future path). The whole-brain activation map (overlaid on the coronal image of the brain) resulting from the road > flow shows a spot of activation along the anterior POs. **B.** Examples of stimuli and experimental set-up (the MR-compatible driving simulator) used by Choi et al. (2020). Participants were instructed to actively drive by using wheel and pedals (accelerator and brake). Whole-brain activation map (overlaid on the axial image of the brain) revealed that a wide network of brain regions, including the anterior POs, is activated during driving.

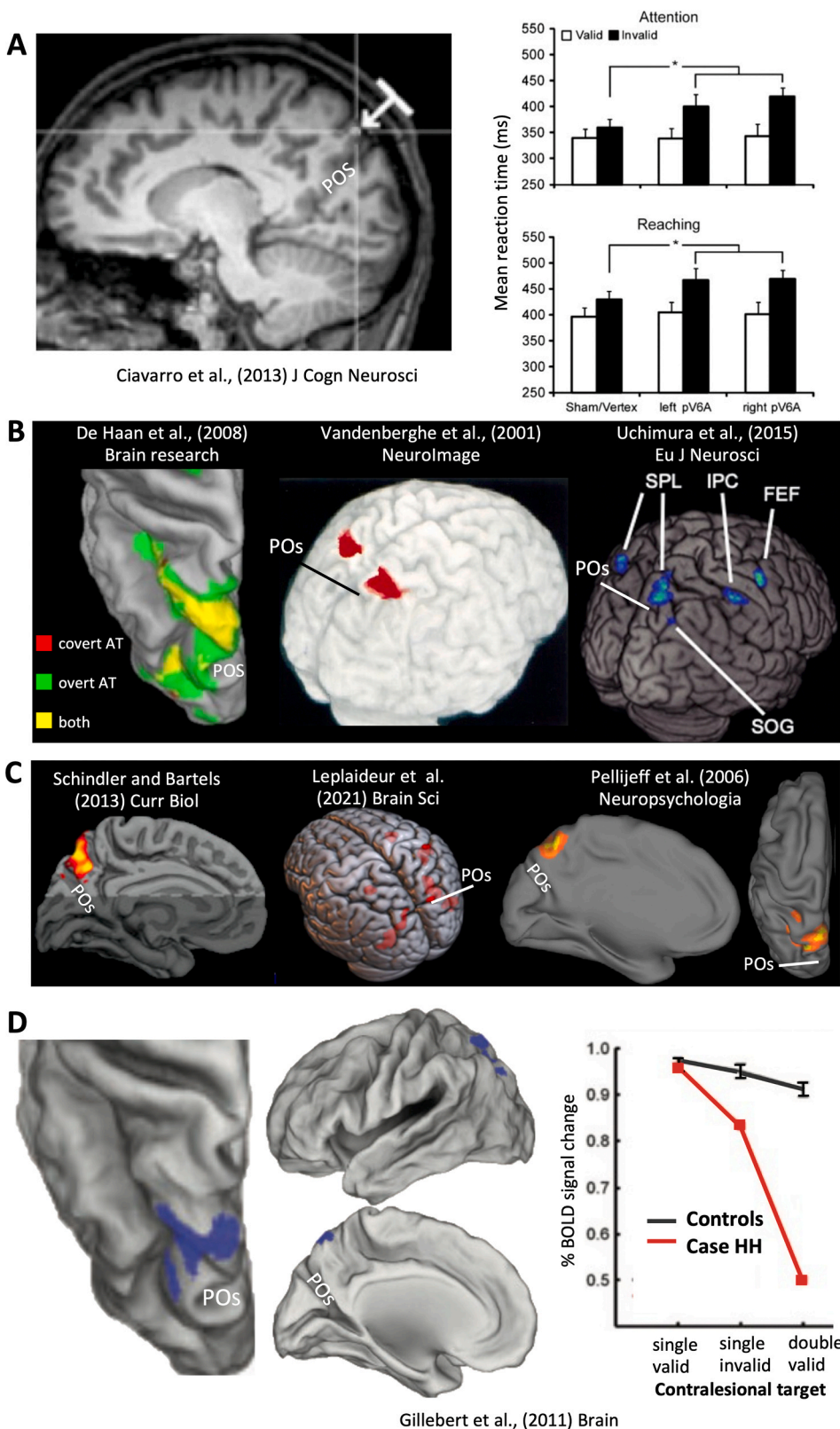
(a) Modified from Field et al. (2007). (b) Modified from Choi et al. (2020).

location (invalid trials), but not when the cue correctly predicted target location with 75% of probability (valid trials). This means that TMS was effective on both attentional and reaching reaction times, but only when it was concomitant with a shift of attentional spotlight. This points towards a causal role of V6Ad in attentional reorienting, i.e., when attention is disengaged from one peripheral location and redirected to another peripheral location. A similar pattern of results was observed in another TMS study targeting a portion of the medial SPL (mSPL) likely including V6Ad (Capotosto et al., 2013). This study, which implied a target discrimination task after a shift of attention, revealed selective impairments during covert spatial attention shifts, but not during simple contralateral orienting.

Although the activation of the mSPL during shifts of covert attention in humans is well established (Vandenberghe et al., 2001; Tosoni et al., 2013; de Haan et al., 2008; Vossel et al., 2009; Kelley et al., 2008; Molenberghs et al., 2007; Serences and Yantis, 2006; Yantis et al., 2002; Wojciulik and Kanwisher, 1999), it is unclear whether the human shift-selective mSPL corresponds to the monkey area V6A. Caspari et al. (2018) in a comparative fMRI study on humans and monkeys used an interspecies beta-correlation method whereby task-related beta-values obtained from the shift-selective attention region in human mSPL were correlated to the corresponding beta-values of each voxel in monkeys. The main finding of this study was that the shift-selective human mSPL mainly correlated with monkey area V6A, thus indicating a good correspondence between the shift-selective regions of the two species.

Interestingly, de Haan et al. (2008) observed that within the post-eromedial portion of the human SPL, a small region just anterior to the POs, likely including area V6Ad, is activated by both covert and overt shift of spatial attention (yellow area in Fig. 9B, left panel). This region is involved in attentional shifts rather than in sustained attention, with no difference between covert and overt shifting (Fig. 9B, middle panel; Vandenberghe et al., 2001). More specifically, it seems clear that what really matters to this cortical region is shifting attention towards a spatial location, regardless of what triggers the spatial shift. Molenberghs and co-workers (2007) observed that mSPL is preferentially activated in all conditions requiring a spatial displacement towards the

location of the target (or distractor), independently of the origin of the spatial shift (exogenous or endogenous). Fig. 9B shows that the small cortical region specifically activated by covert shifts of attention (colored in yellow in the left panel and in red in the middle panel), located just anterior to the POs, is the same cortical region implicated in coding target and background information in terms of spatial (egocentric) coordinates (see SPL activation in the right panel of Fig. 9B; Uchimura et al., 2015), that is the same coordinates used to direct the spotlight of attention. In support to this view, Schindler and Bartels (2013) found prominent evidence for egocentric space encoding in a posterior precuneate region that likely encompasses V6Ad (see Fig. 9C, left panel), and Leplaideur et al. (2021) found that the evaluation of egocentric space activates, among others, a region of the anterior POs where V6d is typically located (see Fig. 9C, central panel). We suggest that this cortical region hosts an egocentric spatial map of the environment that receives spatial information useful for navigation from areas V3A and V6, as described in the above chapter 3.1.3, and for directing the limbs in reach-to-grasp movements, as suggested in the above chapter 3.2.1, particularly towards moving objects and during self-motion (see Pitzalis et al., 2015; Galletti and Fattori, 2018; Galletti et al., 2022). Notably, Schindler and Bartels (2013) highlighted that the posterior precuneate region they found activated (Fig. 9C, left panel) showed a decoding performance strongly associated with visual covert attention and reaching. Pellijeff et al. (2006) found that a similar precuneate region (Fig. 9C, right panels) was activated when participants executed a reaching movement so as to bring their index finger to contact the point of the chin, varying the hand starting position at each movement across trials. The same activation was observed when instead of reaching a fixed target position (the chin) from a variable starting position, participants were required to reach from a fixed starting position to a target position that was defined posturally, and which varied across trials. It is clear that the activation of the cortical area depended on the actions performed by participants but did not depend on the direction of these actions, nor on the posture of the arm. Since reaching movements were performed without vision, we can postulate that the focus of attention of participants guided the limb movements across



**Fig. 9.** Involvement of the anterior POs in shifting the focus of attention. **A.** Stimulation site on a sagittal T1-weighted MRI (left panel) and the rTMS effects (right panel) during an attention and a reaching task requiring covert shifts of attention and planning of reaching movements toward cued targets in space. The plots show that rTMS on a cortical region likely including area V6Ad increased RTs to invalidly cued but not to validly cued targets during both the attention and reaching task. \* $p < 0.05$ ; (Ciavarro et al., 2013). **B.** Activation maps showing that the anterior POs is involved in several attentional tasks: it responds to both covert and overt shift of spatial attention (de Haan et al., 2008), during shifting of attention rather than during sustaining attention (Vandenberghe et al., 2001), and it shows an adaptation effect for repeated presentations of a frame in terms of the egocentric coordinates (corresponding to the endogenous attentional coordinates; Uchimura et al., 2015). **C.** Activation maps showing how the anterior POs is associated with the representation of the egocentric unseen space (left panel, Schindler and Bartels, 2013), egocentric demands toward the extracorporeal space (central panel, Leplaideur et al., 2021) and egocentric reaching movements regardless the direction of the movement (right panel, Pellijeff et al., 2006), all activities requiring a shift of the attentional focus. **D.** Left: Lesion of patient H.H. described by Gillebert et al. (2011) overlaid on the folded surface-based reconstruction of the brain (dorsal, medial and lateral views). Right: The plot shows the patient's performance (as compared to that of healthy controls) reflecting the pathological increase of the invalidity effect when invalid/single trials were compared with valid/single trials for contralateral targets, and the increase of impairment when multiple shifts of the spotlight of attention were required (valid/double). (a) Modified from Ciavarro et al. (2013). (b) Modified from de Haan et al. (2008), Vandenberghe et al. (2001), Uchimura et al. (2015). (c) Modified from Schindler and Bartels, (2013), Leplaideur et al. (2021), Pellijeff et al. (2006). (d) Modified from Gillebert et al. (2011).

trials by shifting from the starting to the final positions of them, and as we have seen above, this is a strong way to activate the V6Ad.

The causal role of mSPL/V6A in shifting attention is also confirmed by lesion studies. In particular, Gillebert et al. (2011) (see Fig. 9D) observed that a lesion of the exposed surface of the caudal SPL, likely including area V6Ad, resulted in a shifting attention deficit since the

patient (HH) was impaired in discriminating invalidly (compared with validly) cued trials for both left- and right-sided target (see also Vandenberghe et al., 2012 for a review). It is worth noting that the patient HH in Gillebert et al. (2011) had a small lesion in the caudal SPL just anterior to the POs (Fig. 9D, left panel) that almost matched the region activated by both the covert and the overt shifts of spatial attention in de



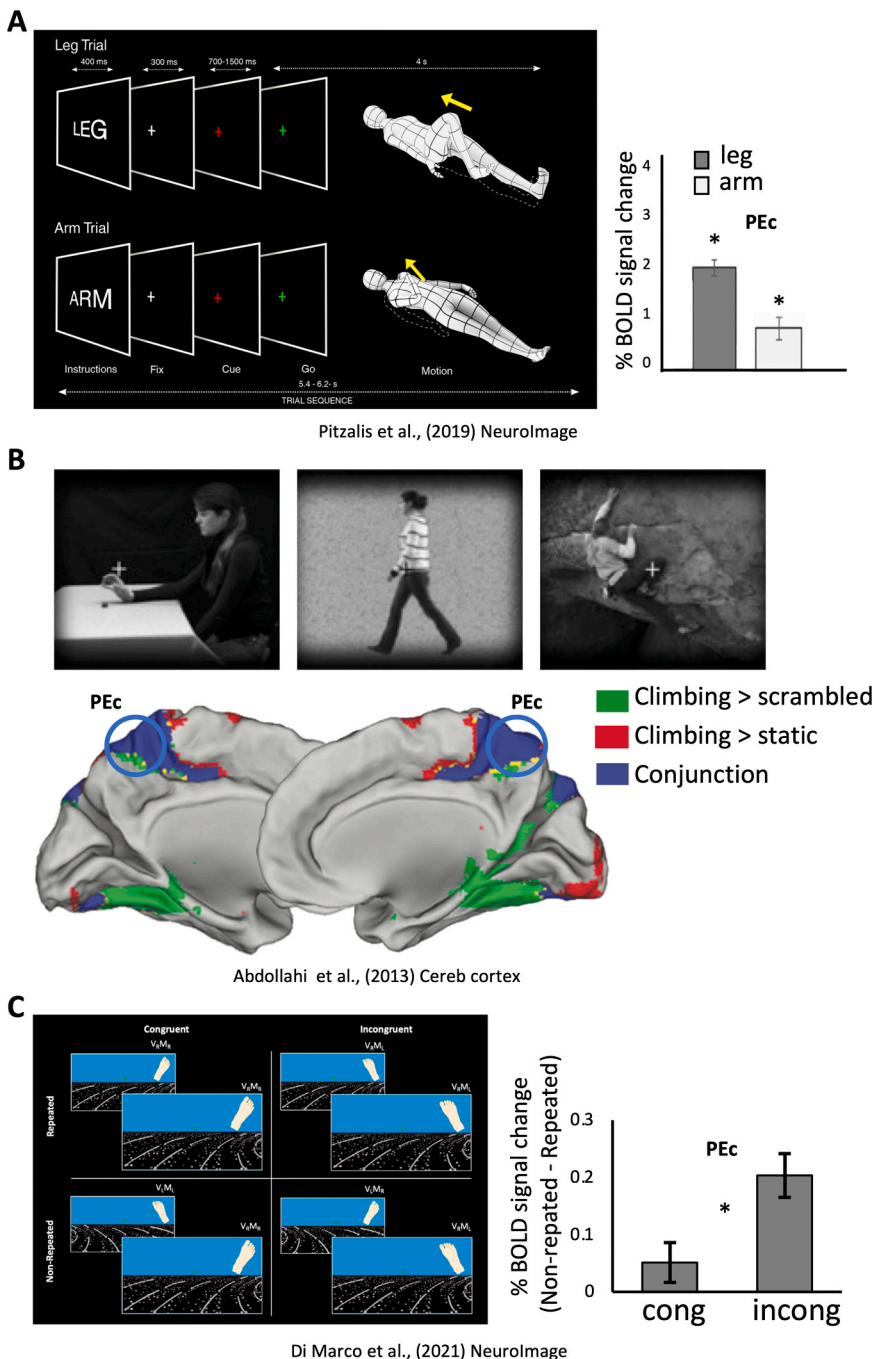
Haan et al. (2008) experiments (the yellow area in Fig. 9B, left panel), which in turn matches the area V6Ad. Patient HH was particularly impaired in the presence of distractors (double valid trials; Fig. 9D, right panel), that is when repeated shifts of spatial attention were required. As a further support to this view, the Balint's syndrome (Balint, 1909), that is typically associated with bilateral damage of the mSPL extending into the occipito-parietal cortex (Karnath and Perenin, 2005), is characterized by ocular apraxia, i.e., a deficit in the control of voluntary, purposeful eye movements, and by simultagnosia, the inability to perceive more than one object at a time (Ptak and Muri, 2013). Both these deficits have been interpreted as reflecting a breakdown of the attentional shift mechanisms (Vandenberghe et al., 2012).

To sum up, shifts of spatial attention typically activate a portion of the cortex of the caudal SPL which involves the cortex anterior to the POs, where the human homolog of area V6Ad is located. As previously

hypothesized in monkeys (Galletti et al., 2010, 2022), such attentional modulation is helpful in guiding the hand during reach-to-grasp movements, especially when acting in motion and in a dynamic environment.

### 3.3. Functional properties of the anterior part of the caudal SPL

The rostralmost part of the caudal SPL, which includes the dorsal-anterior precuneate cortex, hosts the newly defined multisensory area P<sub>Ec</sub> (Fig. 1B; Pitzalis et al., 2019). Although only a few studies have been conducted to specifically investigate the functional role of this region in humans, there is strong evidence in literature for an important role of this region, and more specifically of the region likely hosting area P<sub>Ec</sub>, in a set of multisensory processes. Beyond sharing some properties with the nearby area V6Ad, such as response to hand-related movements (i.e., pointing: Pitzalis et al., 2019; grasping: Sulpizio et al., 2020b), and to



**Fig. 10.** Involvement of the dorsal-anterior precuneate cortex in leg-related responses. **A.** Schematic representation of the somatomotor task used by Pitzalis et al. (2019) to elicit leg-related activation in the dorsal portion of the anterior precuneate cortex. Subjects alternated blocks of leg or arm movements with passive fixation blocks. 3D manikins indicate the kinematic of up and down limb movements. The plot shows the BOLD response of area P<sub>Ec</sub> to both arm and leg movements. **B.** Top: Frames taken from videos of the 3 action types (hand actions, locomotion, climbing) used by Abdollahi et al. (2013). Bottom: Whole-brain activation map overlaid on the folded surface-based reconstruction of the brain (medial view of both hemispheres) as resulted by the observation of climbing actions. The dorsal-anterior precuneate cortex, which includes area P<sub>Ec</sub>, is clearly activated during observation of climbing. **C.** Schematic representation of the experimental paradigm used by Di Marco et al., (2021b). Participants performed a long-range movement using their right leg while observing an optic flow visual stimulus simulating a direction of self-motion that could be either congruent or incongruent with that of leg movement. A repetition suppression paradigm was used to probe the neural sensitivity to the repeated presentation of these bimodal trials. The plot shows that the adaptation effect (stronger BOLD activation for non-repeated as compared to repeated trials) in area P<sub>Ec</sub> was significantly different for congruent and incongruent trials, suggesting the role of the area in integrating visual and motor signals coming from locomotion.

(a) Modified from Sulpizio et al. (2022). \* $p < 0.05$ ; Modified from Pitzalis et al. (2019). (b) Modified from Abdollahi et al. (2013). (c) \* $p < 0.05$ ; modified from Marco et al. (2021b).

shifts of focus of attention (Simon et al., 2002; Molenberghs et al., 2007; Spreng et al., 2013; Caspari et al., 2018), PEC seems to be particularly sensitive to two sources of somatomotor and visual stimulations tightly intertwined with the visually-guided locomotion: 1) leg-related movements and 2) egomotion-compatible optic flow.

### 3.3.1. Leg-related response:

In macaque, area PEC shows functional properties very similar to those of area V6Ad (Gamberini et al., 2018) but, differently from V6Ad, the PEC also represents the legs, besides the arms. We reasoned that the leg representation could be the signature of area PEC also in humans. In the attempt to identify a possible human homolog of macaque area PEC, we have used an innovative set-up allowing participants to perform a pure motor task requiring controlled leg movements during fMRI scanning (Pitzalis et al., 2019; Sulpizio et al., 2022; see Fig. 10A). In this way we identified the caudalmost station for leg representation in the dorsal precuneate cortex and proposed this region as the human homolog of macaque area PEC (Pitzalis et al., 2019). Notice that human PEC is activated by both arm and leg movements (Fig. 10A), well in line with the somatomotor properties observed in the macaque PEC (Breveglieri et al., 2006, 2008; Gamberini et al., 2018, 2020).

Additional evidence indicating a lower limb preference in the dorsal-anterior precuneate cortex comes from a series of fMRI studies of other laboratories testing memory guided eye, hand, and foot movements towards peripheral visual targets (Heed et al., 2011, 2016; Leone et al., 2014; Pitzalis et al., 2019; Medendorp and Heed, 2019; Maltempo et al., 2021). These studies revealed distributed networks of activations following a lateral-to-medial hand-to-foot gradient, with overlapping activations mainly located along the IPS and in the medial aspects of the dorsal SPL (Heed et al., 2011; Huang et al., 2012; Leone et al., 2014; Pitzalis et al., 2019). By using a regional approach, we specifically found that area PEC showed reliable responses to both hand and foot pointing, with a preference for the latter (Pitzalis et al., 2019; see Fig. 10A). Such a visuomotor property suggests a role in the control of limb interaction with the environment, likely with the aim of guiding locomotion. Compatibly with this view, Maltempo et al. (2021) observed that PEC is strongly activated by limb movements directed towards visual targets located in the lower compared to the upper VF, well in line with the higher distribution of receptive fields in the lower VF observed in the macaque PEC (Gamberini et al., 2018, 2020). The involvement of area PEC in a range of body-to-environment interactions, including locomotion, is further supported by an fMRI study by Abdollahi et al. (2013) in which different movies reproducing human actions implying limb interaction with the environment were presented during fMRI scanning (Fig. 10B). The authors reported that the observation of locomotion and climbing evoked activity in dorsal SPL, in a region clearly including the PEC (Fig. 10B, bottom).

A recent TMS study (Altomare et al., 2021) has demonstrated that the stimulation of the dorsal portion of the anterior precuneus produced a significant reduction of a previously described behavioral advantage for footstep execution (vs. simple release) in response to stimuli located in the far vs. near extrapersonal space (Di Marco et al., 2019). This result emphasizes the role of this portion of cortex in processing spatial features (i.e., distance) for the purpose of walking-related locomotion (Altomare et al., 2021). A more direct link between foot/leg related actions and locomotion can be established based on results by Di Marco et al. (2021b); (see Fig. 10C). In this study, somatomotor inputs from lower limbs were combined with egomotion-compatible visual stimulations in a way that the direction of leg movements could be either compatible (congruent trials) or not (incongruent trials) with that of visual self-motion. One of the main findings of the study is that PEC showed the capability to integrate between these two inputs, with a preference for incongruent combinations of them (see plots in Fig. 10C) likely to signal a mismatch between these multisensory signals with the aim of promoting adjustments in lower limb movements during locomotion (Di Marco et al., 2021b).

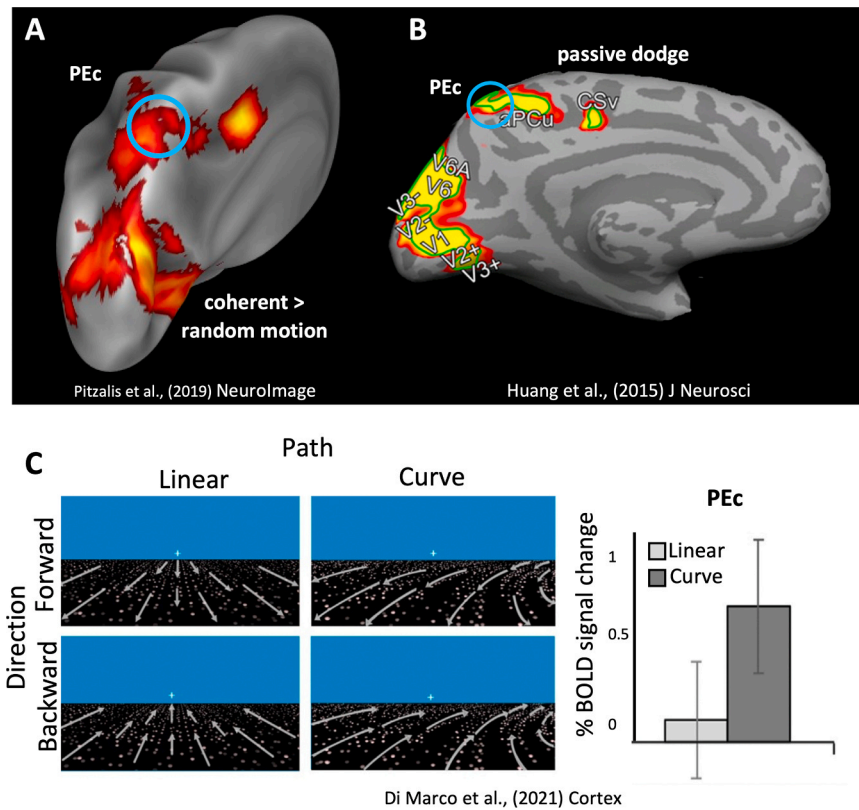
### 3.3.2. Sensitivity to egomotion-compatible optic flow:

Similarly to what observed in the macaque area PEC (Battaglia-Mayer et al., 2001; Raffi et al., 2002, 2010, 2011, 2014), also the human counterpart is involved in visual motion and optic flow processing (Pitzalis et al., 2019; Pitzalis et al., 2020; Di Marco et al., 2021a). Besides responding to an abstract pattern of coherent optic flow, such as the flow field stimulus (Fig. 11A; Pitzalis et al., 2019), PEC has a reliable preference for simulated self-motion through a virtual environment (Pitzalis et al., 2020), indicating a more strictly sensitivity to visual stimulation reproducing self-displacements in ecologic environments. Although many previous studies on humans did not specifically refer to PEC as a motion sensitive area, several pieces of evidence support the idea that the dorsalmost portion of the anterior precuneate cortex (or aPCu), that likely includes the PEC, responds to egomotion-compatible stimuli. For example, Huang et al. (2015) (see Fig. 11B) observed a wide strip of activation, extending along the dorsal portion of the anterior precuneate cortex so that to likely include area PEC, during passive observation of both forward and translation egomotion within a virtual environment simulating daily life experiences such as avoiding obstacles while walking. Similarly, part of the dorsal-anterior precuneus was activated by more abstract egomotion-compatible stimuli, such as clouds of moving dots (Cardin and Smith, 2010; Uesaki and Ashida, 2015; Pitzalis et al., 2019). Compatibly with this view, this portion of the precuneus has been implicated in a variety of processes such as proprioception, imagined egomotion and vestibular processing (Filimon et al., 2009; Cardin and Smith, 2010; Huang et al., 2012; Huang and Sereno, 2013). In a recent study (Di Marco et al., 2021a; see Fig. 11C) we observed that, when the visual motion stimulus simulated a change in the self-motion direction, area PEC showed stronger activation as compared to visual stimulus simulating linear path (see plots in Fig. 11C), thus indicating a more advanced role of the area in monitoring heading changes. It should be noted that such ability to monitor continuous changes in heading direction is an essential requisite to permit an accurate control of locomotion.

## 4. General considerations

A potential limitation of the current review is that evidence from humans cannot be compared to the level of precision and cytoarchitectonic specificity characterizing the primate research. A large corpus of imaging evidence reviewed here has used a combination of advanced brain mapping procedures (i.e., retinotopy, surface-based mapping, resting-state functional connectivity) to identify, at the individual level, the human homologues of a series of macaque areas (V6: Pitzalis et al., 2006, 2010; V6Av: Pitzalis et al., 2013a; V6Ad: Tosoni et al., 2015; PEC: Pitzalis et al., 2019). However, some of the human imaging studies reviewed here did not directly assess the role of SPL and its functional subdivisions, since they generally rely on methods that have limited spatio-temporal resolution, and anatomical precision is often severely reduced by spatial smoothing, inter-subject spatial normalization, and reliance on group analysis, all of which could obscure the anatomical localization of functional responses of subregions discussed here. Thus, rather than attributing isolated functions to strictly segregated subregions of the SPL, in the current review we mainly tried to better characterize the functional properties of the caudal SPL in humans, based on the most recent evidence available in literature.

A second limitation concerns the contribution of lesion studies we reviewed here. Most of these studies (Kesserwani, 2020; Vaina et al., 2014; Blanke et al., 2003; Haarmeier et al., 1997; Gillebert et al., 2011) described focal brain damage after stroke affecting the caudal portion of the SPL. However, the causal effect of these lesions on the specific function we described cannot be attributed to the isolated region since brain damages often include several cortical neighboring regions. In a similar vein, TMS studies, that cause temporary “virtual lesion” of a cortical target do not affect a specific (cytoarchitectonic) region, but rather a wider cortical territory likely including that specific region.

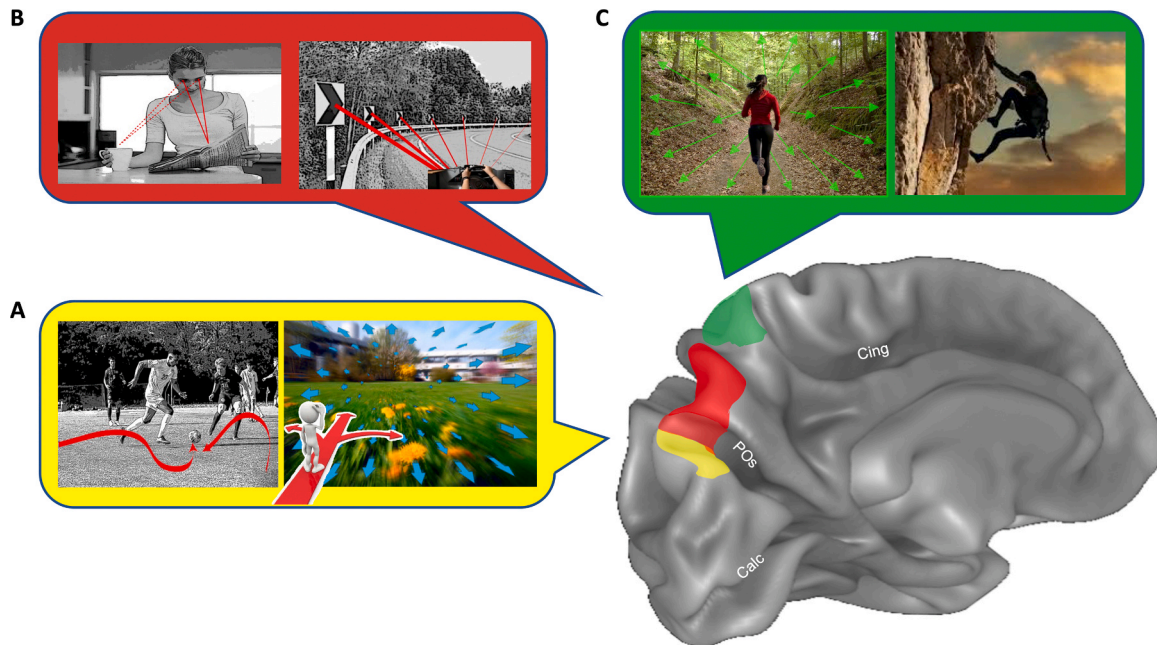


**Fig. 11.** Involvement of the dorsal-anterior precuneate cortex in the analysis of egomotion-compatible optic flow. **A.** Whole-brain activation map overlaid on the folded surface-based reconstruction of the left hemisphere (post-eromedial view) resulting from the coherent > random motion contrast of the flow field stimulus. Beyond the well-known high-level egomotion regions, the flow field-related activation map includes the dorsalmost portion of the anterior precuneate cortex, where the PEC is located. **B.** The whole-brain activation map as resulting from the observation of passive dodges during egomotion is shown overlaid on the medial view of the folded surface-based reconstruction of the left hemisphere (Huang et al., 2015). The map shows the involvement, among others, of the anterior portion of the dorsal precuneate cortex, in correspondence and around area PEC. **C.** Schematic representation of the four coherent motion conditions organized according to a  $2 \times 2$  factorial design (Direction -forward, backward- by Path -linear, curved-) used in Di Marco et al. (2021a). The plot shows the BOLD response estimated in area PEC revealing the main effect of Path (curved > linear). (a) Modified from Pitzalis et al. (2019). (b) Modified from Huang et al. (2015). (c) Modified from Di Marco et al. (2021a).

Thus, the contribution of these studies in characterizing the functional properties of different portions of human SPL should be interpreted with caution, considering the limits of such approaches in targeting delimited brain regions.

## 5. Conclusions

Research in the last decades have demonstrated that the caudal portion of the human SPL includes several areas with different



**Fig. 12.** Schematic representation of the functional specialization along the posterior POs (A), the anterior POs and the corresponding part of the dorsal-posterior precuneate cortex (B), and the dorsal-anterior precuneate cortex (C). **A.** The posterior POs, including area V6+, is mainly involved in the analysis of visual motion cues with the aim of promoting self- and object-motion recognition and visual control of navigation. **B.** The anterior POs, and area V6A in particular, is mainly devoted to the visuomotor control of hand actions directed towards the external world (including navigation) and in using the spotlight of attention to guide these goal-directed arm/hand actions. **C.** The dorsal-anterior precuneate cortex, and area PEC in particular, is mainly dedicated to the analysis of visual and somatomotor signals related to egomotion, with the aim of visually guiding leg-related actions as locomotion.



anatomical structure and functional properties. Although human research on SPL lacks the anatomical accuracy characterizing the decennial animal research in this brain region, in this review we have highlighted different pieces of evidence showing a functional and anatomical organization of human caudal SPL that somehow resembles that observed in the macaque caudal SPL. For instance, the more posterior part of human caudal SPL (posterior POs) is mainly dedicated to the analysis of visual motion suitable for real motion detection and spatial navigation, while the more anterior parts, i.e., the anterior POs and the posterior and anterior portions of the dorsal precuneate cortex, are more concerned with planning and execution of limb interaction with the environment (reach-to-grasp movements, climbing, locomotion), with the analysis of visual signals related to egomotion, and with the control/detection of shift of the focus of attention, as schematically represented in Fig. 12. We suggest that the analysis of visual motion information performed by the posterior part of SPL allows to infer self- and object motion in dynamic contexts and is a prerequisite for the skilled visually guided behaviors supported by more anterior parts of the SPL.

For the scientific community, the current review might provide a significant value by furthering the knowledge of the functional organization of the human caudal SPL and it might provide a solid basis for future investigations. Challenges for the future include investigating how these regions might interact during such visually guided complex actions, like locomotion, and cooperate in the context of larger brain networks. At a more applicative level, one relevant future direction would be to take advantage of the available evidence on neural signals from human SPL with the aim of using neural interfacing techniques, i. e., brain-machine interface, to guide neural prosthetics in tetraplegic patients during such as skilled actions. In addition, all the findings reviewed here might be relevant for expanding the current application of virtual reality tool for gait rehabilitation. A novel therapeutic strategy may approach gait impairment from a perceptual point of view by employing locomotion-compatible optic flow stimuli by means of immersive virtual reality. This could be relevant in Parkinson's disease (Canning et al., 2020), which also manifests deficits in optic flow perception that can affect locomotion control (Halperin et al., 2020). The findings summarized here might be relevant also for the assessment of rehabilitation protocols, identifying the neurobiological correlates of the therapeutic actions (i.e., significant clinical improvements). This makes recommendations for future research using a virtual-reality fMRI task on locomotion in such clinical populations with the aim of testing how gait/balance rehabilitation is able to evoke brain function changes.

## Funding

This work was supported by grants from Ministero dell'Università e della Ricerca (20208RB4N9); European Commission funded project H2020-EIC-FETPROACT-2019-951910-MAIA.

## References

- Abdollahi, R.O., Jastorff, J., Orban, G.A., 2013. Common and segregated processing of observed actions in human SPL. *Cereb. Cortex* 23, 2734–2753.
- Aggius-Vella, E., Chebat, D.R., Maidenbaum, S., Amedi, A., 2023. Activation of human visual area V6 during egocentric navigation with and without visual experience, 27, S0960-9822(23)00165-3 *Curr. Biol.* <https://doi.org/10.1016/j.cub.2023.02.025>.
- Altomare, E.C., Comitteri, G., Di Matteo, R., Capotosto, P., Tosoni, A., 2021. Automatic coding of environmental distance for walking-related locomotion in the foot-related sensory-motor system: a TMS study on macro-affordances. *Neuropsychologia* 150, 107696. <https://doi.org/10.1016/j.neuropsychologia.2020.107696>.
- Andersen, R.A., Snyder, L.H., Bradley, D.C., Xing, J., 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu. Rev. Neurosci.* 20, 303–330. <https://doi.org/10.1146/annurev.neuro.20.1.303>.
- Arcaro, M.J., Thaler, L., Quinlan, D.J., Monaco, S., Khan, S., Valyear, K.F., Goebel, R., Dutton, G.N., Goodale, M.A., Kastner, S., Culham, J.C., 2019. Psychophysical and neuroimaging responses to moving stimuli in a patient with the Riddoch phenomenon due to bilateral visual cortex lesions. *Neuropsychologia* 128, 150–165. <https://doi.org/10.1016/j.neuropsychologia.2018.05.008>.
- Arnoldussen, D.M., Goossens, J., van den Ber, A.V., 2013. Differential responses in dorsal visual cortex to motion and disparity depth cues. *Front. Hum. Neurosci.* 7, 815. <http://doi.org/10.3389/fnhum.2013.00815>.
- Astafiev, S.V., Shulman, G.L., Stanley, C.M., Snyder, A.Z., Van Essen, D.C., Corbetta, M., 2003. Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *J. Neurosci.* 23, 4689–4699.
- Bakola, S., Gamberini, M., Passarelli, L., Fattori, P., Galletti, C., 2010. Cortical connections of parietal field PEc in the macaque: linking vision and somatic sensation for the control of limb action. *Cereb. Cortex* 20, 2592–2604. <https://doi.org/10.1093/cercor/bhq007>.
- Balint, R., 1909. Seelenlähmung des “Schauens” optische Ataxia, räumliche Störung des Aufmerksamkeits. *Monatsschrift für Psychiatrie und Neurologie* 25, 51–81.
- Battaglia-Mayer, A., Ferraina, S., Genovesio, A., Marconi, B., Squatrito, S., Molinari, M., Lacquaniti, F., Caminiti, R., 2001. Eye-hand coordination during reaching. II. An analysis of the relationships between visuomotor signals in parietal cortex and parieto-frontal association projections. *Cereb. Cortex* 11, 528–544.
- Bellagamba, M., Sulpizio, V., Fattori, P., Galati, G., Galletti, C., Maltempo, T., Pitzalis, S., 2022. Egomotion-related visual areas respond to goal-directed movements brain structure and function. *Press. Brain Struct. Funct.* 227, 2313–2328. <https://doi.org/10.1007/s00429-022-02523-9>.
- Bernier, P.M., Grafton, S.T., 2010. Human posterior parietal cortex flexibly determines reference frames for reaching based on sensory context. *Neuron* 68, 776–788. <https://doi.org/10.1016/j.neuron.2010.11.002>.
- Beurze, S.M., de Lange, F.P., Toni, I., Medendorp, W.P., 2007. Integration of target and effector information in the human brain during reach planning. *J. Neurophysiol.* 97, 188–199.
- Beurze, S.M., de Lange, F.P., Toni, I., Medendorp, W.P., 2009. Spatial and effector processing in the human parietofrontal network for reaches and saccades. *J. Neurophysiol.* 101, 3053–3062.
- Bisley, J.W., Goldberg, M.E., 2003. Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299, 81–86. <https://doi.org/10.1126/science.1077395>.
- Bisley, J.W., Goldberg, M.E., 2010. Attention, intention, and priority in the parietal lobe. *Annu. Rev. Neurosci.* 33, 1–21.
- Blanke, O., Landis, T., Mermoud, C., Spinelli, L., Safran, A.B., 2003. Direction-selective motion blindness after unilateral posterior brain damage. *Eur. J. Neurosci.* 18, 709–722.
- Boccia, M., Nemmi, F., Guariglia, C., 2014. Neuropsychology of environmental navigation in humans: review and meta-analysis of fMRI studies in healthy participants. *Neuropsychol. Rev.* 24, 236–251. <https://doi.org/10.1007/s11065-014-9247-8>.
- Boccia, M., Sulpizio, V., Nemmi, F., Guariglia, C., Galati, G., 2017. Direct and indirect parieto-medial temporal pathways for spatial navigation in humans: evidence from resting state functional connectivity. *Brain Struct. Funct.* 222, 1945–1957. <https://doi.org/10.1007/s00429-016-1318-6>.
- Bosco, A., Breveglieri, R., Filippini, M., Galletti, C., Fattori, P., 2019. Reduced neural representation of arm/hand actions in the medial posterior parietal cortex. *Sci. Rep.* 9, 936. <https://doi.org/10.1038/s41598-018-37302-2>.
- Brandt, T., Bucher, S.F., Seelos, K.C., Dieterich, M., 1998. Bilateral functional MRI activation of the basal ganglia and middle temporal/medial superior temporal motion-sensitive areas: optokinetic stimulation in homonymous hemianopia. *Arch. Neurol.* 55, 1126–1131.
- Breviglieri, R., Galletti, C., Gamberini, M., Passarelli, L., Patrizia, F., 2006. Somatosensory cells in area PEc of macaque posterior parietal cortex. *J. Neurosci.* 26, 3679–3684.
- Breviglieri, R., Galletti, C., Monaco, S., Fattori, P., 2008. Visual, somatosensory, and bimodal activities in the macaque parietal area PEc. *Cereb. Cortex* 18, 806–816.
- Breviglieri, R., Bosco, A., Borgomaneri, S., Tessari, A., Galletti, C., Avenanti, A., Fattori, P., 2021. Transcranial magnetic stimulation over the human medial posterior parietal cortex disrupts depth encoding during reach planning. *Cereb. Cortex* 31, 267–280. <https://doi.org/10.1093/cercor/bhaa224>.
- Breviglieri, R., Borgomaneri, S., Filippini, M., Tessari, A., Galletti, C., Davare, M., Fattori, P., 2022. Complementary contribution of the medial and lateral human parietal cortex to grasping: a repetitive TMS study. *Cereb. Cortex*. <https://doi.org/10.1093/cercor/bhac404>.
- Calabro, F.J., Beardsley, S.A., Vaina, L.M., 2019. Differential cortical activation during the perception of moving objects along different trajectories. *Exp. Brain Res.* 237, 2665–2673. <https://doi.org/10.1007/s00221-019-05613-z>.
- Canning, C.G., Allen, N.E., Nackaerts, E., et al., 2020. Virtual reality in research and rehabilitation of gait and balance in Parkinson disease. *Nat. Rev. Neurol.* 16, 409–425.
- Capotosto, P., Tosoni, A., Spadone, S., Sestieri, C., Perrucci, M.G., Romani, G.L., Della Penna, S., Corbetta, M., 2013. Anatomical segregation of visual selection mechanisms in human parietal cortex. *J. Neurosci.* 33, 6225–6229.
- Cardin, V., Smith, A.T., 2010. Sensitivity of human visual and vestibular cortical regions to egomotion-compatible visual stimulation. *Cereb. Cortex* 20, 1964–1973.
- Cardin, V., Smith, A.T., 2011. Sensitivity of human visual cortical area V6 to stereoscopic depth gradients associated with self-motion. *J. Neurophysiol.* 106, 1240–1249. <https://doi.org/10.1152/jn.01120.2010>.
- Cardin, V., Sherrington, R., Hemsworth, L., Smith, A.T., 2012a. Human V6: functional characterisation and localization. *PLoS One* 7 (10), e47685. <https://doi.org/10.1371/journal.pone.0047685>.
- Cardin, V., Hemsworth, L., Smith, A.T., 2012b. Adaptation to heading direction dissociates the roles of human MST and V6 in the processing of optic flow. *J. Neurophysiol.* 108, 794–801. <https://doi.org/10.1152/jn.00002.2012>.

- Caspari, N., Arsenault, J.T., Vandenberghe, R., Vanduffel, W., 2018. Functional similarity of medial superior parietal areas for shift-selective attention signals in humans and monkeys. *Cereb. Cortex*. <https://doi.org/10.1093/cercor/bhx114>.
- Castelo-Branco, M., Mendes, M., Silva, M.F., et al., 2006. Specific retinotopically based magnocellular impairment in a patient with medial visual dorsal stream damage. *Neuropsychologia* 44, 238–253.
- Cavina-Pratesi, C., Monaco, S., Fattori, P., Galletti, C., McAdam, T.D., Quinlan, D.J., Goodale, M.A., Culham, J.C., 2010. Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *J. Neurosci.* 30, 10306–10323.
- Cheng, K., Fujita, H., Kanno, I., Miura, S., Tanaka, K., 1995. Human cortical regions activated by wide-field visual motion: an H2 150 PET study. *J. Neurophysiol.* 74, 413–427.
- Choi, M.H., Kim, H.S., Chung, S.C., 2020. Evaluation of effective connectivity between brain areas activated during simulated driving using dynamic causal modeling. *Front. Behav. Neurosci.* 23, 14–158. <https://doi.org/10.3389/fnbeh.2020.00158>.
- Ciavarro, M., Ambrosini, E., Tosoni, A., et al., 2013. rTMS of medial parieto-occipital cortex interferes with attentional reorienting during attention and reaching tasks. *J. Cogn. Neurosci.* 25, 1453–1462. <https://doi.org/10.1162/jocn.2013.00409>.
- Colby, C.L., Duhamel, J.R., 1997. Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia* 29, 517–537. [https://doi.org/10.1016/0028-3932\(91\)90008-v](https://doi.org/10.1016/0028-3932(91)90008-v).
- Colby, C.L., Gattass, R., Olson, C.R., Gross, C.G., 1988. Topographic organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. *J. Comp. Neurol.* 269, 392–413.
- Collignon, O., Vandewalle, G., Voss, P., Albouy, G., Charbonneau, G., Lassonde, M., Lepore, F., 2011. Functional specialization for auditory-spatial processing in the cortex of congenitally blind humans. *Proc. Natl. Acad. Sci. USA* 108, 4435–4440. <https://doi.org/10.1073/pnas.1013928108>.
- Connolly, J.D., Andersen, R.A., Goodale, M.A., 2003. fMRI evidence for a “parietal reach region” in the human brain. *Exp. Brain Res.* 153, 140–145.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215.
- Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., Shulman, G.L., 1998. A common network of functional areas for attention and eye movements. *Neuron* 21, 761–773. [https://doi.org/10.1016/S0896-6273\(00\)80593-0](https://doi.org/10.1016/S0896-6273(00)80593-0).
- Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324.
- Di Marco, S., Tosoni, A., Altomare, E.C., Ferretti, G., Perrucci, M.G., Committeri, G., 2019. Walking-related locomotion is facilitated by the perception of distant targets in the extrapersonal space. *Sci. Rep.* 9, 9884 <https://doi.org/10.1038/s41598-019-46384-5>.
- Di Marco, S., Fattori, P., Galati, G., Galletti, C., Lappe, M., Maltempo, T., Pitzalis, S., 2021a. Preference for locomotion-compatible curved paths and forward direction of self-motion in somatomotor and visual areas. *Cortex* 137, 74–92.
- Di Marco, S., Sulpizio, V., Bellagamba, M., Fattori, P., Galati, G., Galletti, C., Pitzalis, S., 2021b. Multisensory integration in cortical regions responding to locomotion-related visual and somato-motor signals. *Neuroimage*. <https://doi.org/10.1016/j.neuroimage.2021.118581>.
- Diomedes, S., Vaccari, F.E., Filippini, M., et al., 2020. Mixed selectivity in macaque medial parietal cortex during eye-hand reaching. *iScience* 23, 101616. <https://doi.org/10.1016/j.isci.2020.101616>.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. *Nature* 392, 598–601. <https://doi.org/10.1038/33402>.
- Epstein, R.A., 2008. Parahippocampal and retrosplenial contributions to human spatial navigation. *Trends Cogn. Sci.* 12, 388–396. <https://doi.org/10.1016/j.tics.2008.07.004>.
- Fattori, P., Kutz, D.F., Breveglieri, R., et al., 2005. Spatial tuning of reaching activity in the medial parieto-occipital cortex (area V6A) of macaque monkey. *Eur. J. Neurosci.* 22, 956–972. <https://doi.org/10.1111/j.1460-9568.2005.04288.x>.
- Fattori, P., Breveglieri, R., Marzocchi, N., et al., 2009. Hand orientation during reach-to-grasp movements modulates neuronal activity in the medial posterior parietal area V6A. *J. Neurosci.* 29, 1928–1936. <https://doi.org/10.1523/JNEUROSCI.4998-08.2009>.
- Fattori, P., Raos, V., Breveglieri, R., et al., 2010. The dorsomedial pathway is not just for reaching: grasping neurons in the medial parieto-occipital cortex of the macaque monkey. *J. Neurosci.* 30, 342–349. <https://doi.org/10.1523/JNEUROSCI.3800-09.2010>.
- Fattori, P., Breveglieri, R., Raos, V., Bosco, A., Galletti, C., 2012. Vision for action in the macaque medial posterior parietal cortex. *J. Neurosci.* 32, 3221–3234. <https://doi.org/10.1523/JNEUROSCI.5358-11.2012>.
- Fattori, P., Breveglieri, R., Bosco, A., et al., 2017. Vision for prehension in the medial parietal cortex. *Cereb. Cortex* 27, 1149–1163. <https://doi.org/10.1093/cercor/bhv302>.
- Fiebelkorn, I.C., Kastner, S., 2020. Functional specialization in the attention network. *Annu. Rev. Psychol.* 71, 221–249. <https://doi.org/10.1146/annurev-psych-010418-103429>.
- Field, D.T., Wilkie, R.M., Wann, J.P., 2007. Neural systems in the visual control of steering. *J. Neurosci.: Off. J. Soc. Neurosci.* 27 (30), 8002e8010.
- Filimon, F., 2010. Human cortical control of hand movements: parieto-frontal networks for reaching, grasping, and pointing. *Neuroscientist* 16, 388–407.
- Filimon, F., Nelson, J.D., Hagler, D.J., Sereno, M.I., 2007. Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *Neuroimage* 37, 1315–1328.
- Filimon, F., Nelson, J.D., Huang, R.-S., Sereno, M.I., 2009. Multiple parietal reach regions in humans: cortical representations for visual and proprioceptive feedback during on-line reaching. *J. Neurosci.* 29, 2961–2971.
- Fischer, E., Bülthoff, H.H., Logothetis, N.K., Bartels, A., 2012. Human areas V3A and V6 compensate for self-induced planar visual motion. *Neuron* 73, 1228–1240.
- Furlan, M., Wann, J.P., Smith, A.T., 2014. A representation of changing heading direction in human cortical areas VIP and CSv. *Cereb. Cortex* 24, 2848e2858 <https://doi.org/10.1093/cercor/bht132>.
- Galati, G., Pappata, S., Pantano, P., Lenzi, G.L., Samson, Y., Pizzamiglio, L., 1999. Cortical control of optokinetic nystagmus in humans: a positron emission tomography study. *Exp. Brain Res.* 126, 149–159.
- Galati, G., Committeri, G., Pitzalis, S., Pelle, G., Patria, F., Fattori, P., Galletti, C., 2011. Intentional signals during saccadic and reaching delays in the human posterior parietal cortex. *Eur. J. Neurosci.* 34, 1871–1885.
- Galletti, C., Fattori, P., 2003. Neuronal mechanisms for detection of motion in the field of view. *Neuropsychologia* 41, 1717–1727.
- Galletti, C., Fattori, P., 2018. The dorsal visual stream revisited: stable circuits or dynamic pathways? *Cortex* 98, 203–217.
- Galletti, C., Squatrito, S., Battaglini, P.P., Grazia Maioli, M., 1984. “Real-motion” cells in the primary visual cortex of macaque monkeys. *Brain Res.* 301, 95e110.
- Galletti, C., Battaglini, P.P., Aicardi, G., 1988. “Real-motion” cells in visual area V2 of behaving macaque monkeys. *Exp. Brain Res.* 69, 279e288.
- Galletti, C., Battaglini, P.P., Fattori, P., 1990. “Real-motion” cells in area V3A of macaque visual cortex. *Exp. Brain Res.* 82, 67–76.
- Galletti, C., Fattori, P., Battaglini, P.P., Shipp, S., Zeki, S., 1996. Functional demarcation of a border between areas V6 and V6A in the superior parietal gyrus of the macaque monkey. *Eur. J. Neurosci.* 8, 30–52.
- Galletti, C., Fattori, P., Gamberini, M., Kutz, D.F., 1999a. The cortical visual area V6: brain location and visual topography. *Eur. J. Neurosci.* 11, 3922–3936.
- Galletti, C., Fattori, P., Kutz, D.F., Gamberini, M., 1999b. Brain location and visual topography of cortical area V6A in the macaque monkey. *Eur. J. Neurosci.* 11, 575–582.
- Galletti, C., Gamberini, M., Kutz, D.F., et al., 2001. The cortical connections of area V6: an occipito-parietal network processing visual information. *Eur. J. Neurosci.* 13, 1572–1588. <https://doi.org/10.1046/j.0953-816x.2001.01538.x>.
- Galletti, C., Breveglieri, R., Lappe, M., et al., 2010. Covert shift of attention modulates the ongoing neural activity in a reaching area of the macaque dorsomedial visual stream. *PLoS One* 5, e15078. <https://doi.org/10.1371/journal.pone.0015078>.
- Galletti, C., Gamberini, M., Fattori, P., 2022. The posterior parietal area V6A: An attentionally-modulated visuomotor region involved in the control of reach-to-grasp action. *Neurosci. Biobehav. Rev.* 141 (2022 Oct), 104823 <https://doi.org/10.1016/j.neubiorev.2022.104823>.
- Gallivan, J.P., Cavina-Pratesi, C., Culham, J.C., 2009. Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *J. Neurosci.* 29, 4381–4391.
- Gallivan, J.P., McLean, D.A., Valyear, K.F., Pettypiece, C.E., Culham, J.C., 2011. Decoding action intentions from preparatory brain activity in human parieto-frontal networks. *J. Neurosci.* 31, 9599–9610.
- Gamberini, M., Passarelli, L., Fattori, P., et al., 2009. Cortical connections of the visuomotor parietooccipital area V6Ad of the macaque monkey. *J. Comp. Neurol.* 513, 622–642. <https://doi.org/10.1002/cne.21980>.
- Gamberini, M., Galletti, C., Bosco, A., et al., 2011. Is the medial posterior parietal area V6A a single functional area. *J. Neurosci.* 31, 5145–5157. <https://doi.org/10.1523/JNEUROSCI.5489-10.2011>.
- Gamberini, M., Dal Bò, G., Breveglieri, R., Briganti, S., Passarelli, L., Fattori, P., Galletti, C., 2018. Sensory properties of the caudal aspect of the macaque’s superior parietal lobule. *Brain Struct. Funct.* <https://doi.org/10.1007/s00429-017-1593-x>.
- Gamberini, M., Passarelli, L., Fattori, P., Galletti, C., 2020. Structural connectivity and functional properties of the macaque superior parietal lobule. *Brain Struct. Funct.* 225, 1349–1367. <https://doi.org/10.1007/s00429-019-01976-9>.
- Gamberini, M., Passarelli, L., Filippini, M., et al., 2021. Vision for action: thalamic and cortical inputs to the macaque superior parietal lobule. *Brain Struct. Funct.* 226, 2951–2966. <https://doi.org/10.1007/s00429-021-02377-7>.
- Ghaem, O., Mellet, E., Crivello, F., Tzourio, N., Mazoyer, B., Berthoz, A., Denis, M., 1997. Mental navigation along memorized routes activates the hippocampus, precuneus, and insula. *Neuroreport* 8, 739–744. <https://doi.org/10.1097/00001756-199702100-00032>.
- Gibson, J.J., 1950. *The perception of the visual world*. Houghton Mifflin, Boston.
- Gillebert, C.R., Mantini, D., Thijs, V., Snaert, S., Dupont, P., Vandenberghe, R., 2011. Lesion evidence for the critical role of the intraparietal sulcus in spatial attention. *Brain* 134, 1694–1709. <https://doi.org/10.1093/brain/awr085>.
- Grön, G., Wunderlich, A.P., Spitzer, M., Tomczak, R., Riepe, M.W., 2000. Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nat. Neurosci.* <https://doi.org/10.1038/10338>.
- Guttenberg, T.P., Petridou, N., Dumoulin, S.O., Harvey, B.M., Aarmoutse, E.J., Kenemans, J.L., Neggers, S.F., 2015. Action preparation shapes processing in early visual cortex. *J. Neurosci.* 35, 6472–6480.
- de Haan, B., Morgan, P.S., Rorden, C., 2008. Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Res* 1204, 102–111. <https://doi.org/10.1016/j.brainres.2008.01.105>.
- Haarmeier, T., Thier, P., Repnow, M., Petersen, D., 1997. False perception of motion in a patient who cannot compensate for eye movements. *Nature* 389, 849–852.
- Hadjidimitrakaki, K., Bertozzi, F., Breveglieri, R., et al., 2014. Common neural substrate for processing depth and direction signals for reaching in the monkey medial posterior parietal cortex. *Cerebr. Cortex* 24, 1645–1657.

- Hadjidimitrakakis, K., Dal, B.G., Breveglieri, R., Galletti, C., Fattori, P., 2015. Overlapping representations for reach depth and direction in caudal superior parietal lobule of macaques. *J. Neurophysiol.* 114, 2340–2352.
- Hadjidimitrakakis, K., Bertozzi, F., Breveglieri, R., et al., 2017. Temporal stability of reference frames in monkey area V6A during a reaching task in 3D space. *Brain Struct. Funct.* 222, 1959–1970. <https://doi.org/10.1007/s00429-016-1319-5>.
- Halperin, O., Israeli-Korn, S., Yakubovich, S., Hassin-Baer, S., Zaidel, A., 2020. Self-motion perception in Parkinson's disease. *Eur. J. Neurosci.* <https://doi.org/10.1111/ejn.14716>.
- Heed, T., Beurze, S.M., Toni, I., Rofder, B., Medendorp, W.P., 2011. Functional rather than effector-specific organization of human posterior parietal cortex. *J. Neurosci.* 31, 3066–3076.
- Heed, T., Leone, F.T.M., Toni, I., Medendorp, W.P., 2016. Functional versus effector-specific organization of the human posterior parietal cortex: revisited. *J. Neurophysiol.* 116, 1885–1899.
- Heide, W., Koenig, E., Dichgans, J., 1990. Optokinetic nystagmus, selfmotion sensation and their after-effects in patients with occipitoparietal lesions. *Clin. Vis. Sci.* 5, 145–156.
- Helfrich, R.F., Becker, H.G., Haarmeier, T., 2013. Processing of coherent visual motion in topographically organized visual areas in human cerebral cortex. *Brain Topogr.* 26, 247–263. <https://doi.org/10.1007/s10548-012-0226-1>.
- Huang, R., Sereno, M.I., 2018. Multisensory and Sensorimotor Maps, first ed. The Parietal Lobe. Elsevier B.V.
- Huang, R.S., Sereno, M.I., 2013. Bottom-up Retinotopic Organization Supports Top-down Mental Imagery. *Open Neuroimag.* J. 7 (30), 58–67. <https://doi.org/10.2174/187444001307010058>.
- Huang, R.S., Chen, C., Tran, A.T., Holstein, K.L., Sereno, M.I., 2012. Mapping multisensory parietal face and body areas in humans. *Proc. Natl. Acad. Sci. USA* 109, 18114–18119.
- Huang, R.S., Chen, C.F., Sereno, M.I., 2015. Neural substrates underlying the passive observation and active control of translational egomotion. *J. Neurosci.* 35, 4258–4267. <https://doi.org/10.1523/JNEUROSCI.2647-14.2015>.
- Impieri, D., Gamberini, M., Passarelli, L., Rosa, M.G.P., Galletti, C., 2018. Thalamo-cortical projections to the macaque superior parietal lobule areas Péc and PE. *J. Comp. Neurol.* 526, 1041–1056.
- de Jong, B.M., Shipp, S., Skidmore, B., Frackowiak, R.S., Zeki, S., 1994. The cerebral activity related to the visual perception of forward motion in depth. *Brain* 117, 1039–1054. <https://doi.org/10.1093/brain/117.5.1039>.
- Kalaska, J.F., 1996. Parietal cortex area 5 and visuomotor behavior. *Can. J. Physiol. Pharmacol.* 74, 483–498.
- Karnath, H.O., Perenin, M.T., 2005. Cortical control of visually guided reaching: evidence from patients with optic ataxia. *Cereb. Cortex* 15, 1561–1569. <https://doi.org/10.1093/cercor/bhi034>.
- Kelley, T.A., Serences, J.T., Giesbrecht, B., Yantis, S., 2008. Cortical mechanisms for shifting and holding visuospatial attention. *Cereb. Cortex* 18, 114–125. <https://doi.org/10.1093/cercor/bhm036>.
- Kessserwani, H., 2020. The zeitraffer phenomenon: a strategic ischemic infarct of the banks of the parieto-occipital sulcus - a unique case report and a side note on the neuroanatomy of visual perception. *Cureus* 12 (7), e9443. <https://doi.org/10.7759/cureus.9443>.
- Kleinschmidt, A., Thilo, K.V., Buchel, C., Greysty, M.A., Bronstein, A.M., Frackowiak, R.S., 2002. Neural correlates of visual-motion perception as object- or self-motion. *Neuroimage* 16, 873–882.
- Kovács, G., Raabe, M., Greenlee, M.W., 2008. Neural correlates of visually induced self-motion illusion in depth. *Cereb. Cortex* 18, 1779–1787. <https://doi.org/10.1093/cercor/bhm203>.
- Kravitz, D.J., Saleem, K.S., Baker, C.I., Mishkin, M., 2011. A new neural framework for visuospatial processing. *Nat. Rev. Neurosci.* 12, 217–230. <https://doi.org/10.1167/11.11.923>.
- Leone, F.T.M., Heed, T., Toni, I., Medendorp, W.P., 2014. Understanding effector selectivity in human posterior parietal cortex by combining information patterns and activation measures. *J. Neurosci.* 34, 7102–7112. <https://doi.org/10.1523/JNEUROSCI.5242-13.2014>. PMID: 24849346.
- Leplaideur, S., Moulinet-Raillon, A., Duché, Q., Chochina, L., Jamal, K., Ferré, J.C., Bannier, E., Bonan, I., 2021. The Neural Bases of Egocentric Spatial Representation for Extracorporeal and Corporeal Tasks: An fMRI Study. *Brain Sci.* 11, 963. <https://doi.org/10.3390/brainsci11080963>.
- Levy-Tzedek, S., Hanassy, S., Abboud, S., Maidenbaum, S., Amedi, A., 2012. Fast, accurate reaching movements with a visual-to-auditory sensory substitution device. *Restor. Neurol. Neurosci.* 30, 313–323. <https://doi.org/10.3233/RNN-2012-110219>.
- Luppino, G., Ben Hamed, S., Gamberini, M., et al., 2005. Occipital (V6) and parietal (V6A) areas in the anterior wall of the parieto-occipital sulcus of the macaque: a cytoarchitectonic study. *Eur. J. Neurosci.* 21, 3056–3076. <https://doi.org/10.1111/j.1460-9568.2005.04149.x>.
- Maidenbaum, S., Chebat, D. and Amedi, A. 2018. Human Navigation Without and With Vision - the Role of Visual Experience and Visual Regions. *bioRxiv*. <https://doi.org/10.1101/480558>.
- Maltempo, T., Pitzalis, S., Bellagamba, M., Di Marco, S., Fattori, P., Galati, G., Galletti, C., Sulpizio, V., 2021. Lower visual field preference for the visuomotor control of limb movements in the human dorsomedial parietal cortex. *Brain Struct. Funct.* <https://doi.org/10.1007/s00429-021-02254-3>.
- Marigold, D.S., Lajoie, K., Heed, T., 2019. No effect of triple-pulse TMS medial to intraparietal sulcus on online correction for target perturbations during goal-directed hand and foot reaches. *PLoS One* 14 (10), e0223986. <https://doi.org/10.1371/journal.pone.0223986>.
- Medendorp, W.P., Heed, T., 2019. State estimation in posterior parietal cortex: distinct poles of environmental and bodily states. *Prog. Neurobiol.* 183, 101691. <https://doi.org/10.1016/j.pneurobio.2019.101691>.
- Molenberghs, P., Mesulam, M.M., Peeters, R., Vandenberghe, R.R.C., 2007. Remapping attentional priorities: differential contribution of superior parietal lobule and intraparietal sulcus. *Cereb. Cortex* 17, 2703–2712. <https://doi.org/10.1093/cercor/bhl179>.
- Monaco, S., Krolczak, G., Quinlan, D.J., et al., 2010. Contribution of visual and proprioceptive information to the precision of reaching movements. *Exp. Brain Res.* 202, 15–32. <https://doi.org/10.1007/s00221-009-2106-9>.
- Monaco, S., Cavina-Pratesi, C., Sedda, A., Fattori, P., Galletti, C., Culham, J.C., 2011. Functional magnetic resonance adaptation reveals the involvement of the dorsomedial stream in hand orientation for grasping. *J. Neurophysiol.* 106, 2248–2263.
- Monaco, S., Chen, Y., Medendorp, W.P., et al., 2014. Functional magnetic resonance imaging adaptation reveals the cortical networks for processing grasp-relevant object properties. *Cereb. Cortex* 24, 1540–1554. <https://doi.org/10.1093/cercor/bht006>.
- Morrone, M.C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., Burr, D.C., 2000. A cortical area that responds specifically to optic flow, revealed by fMRI. *Nat. Neurosci.* 3, 1322–1328.
- Nau, M., Schindler, A., Bartels, A., 2018. Real-motion signals in human early visual cortex. *Neuroimage* 175, 379–387. <https://doi.org/10.1016/j.neuroimage.2018.04.012>.
- Pandya, D.N., Seltzer, B., 1982. Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. *J. Comp. Neurol.* 204, 196–210.
- Passarelli, L., Rosa, M.G.P., Gamberini, M., et al., 2011. Cortical connections of area V6Av in the Macaque: a visual-input node to the eye/hand coordination system. *J. Neurosci.* 31, 1790–1801. <https://doi.org/10.1523/JNEUROSCI.4784-10.2011>.
- Pellieff, A., Bonilha, L., Morgan, P.S., McKenzie, K., Jackson, S.R., 2006. Parietal updating of limb posture: an event-related fMRI study. *Neuropsychologia* 44, 2685–2690.
- Petersen, S.E., Posner, M.I., 2012. The attention system of the human brain: 20 years after. *Annu. Rev. Neurosci.* 35, 73–89. <https://doi.org/10.1146/annurev-neuro-062111-150525>.
- von Pfölst, V., Stenbacka, L., Vanni, S., Parkkonen, L., Galletti, C., Fattori, P., 2009. Motion sensitivity of human V6: a magnetoecephalography study. *NeuroImage* 4, 1253–1263. <https://doi.org/10.1016/j.neuroimage.2008.12.058>.
- Pitzalis, S., Galletti, C., Huang, R.S., Patria, F., Committeri, G., Galati, G., Sereno, M.I., 2006. Wide-field retinotopy defines human cortical visual area V6. *J. Neurosci.* 26, 7962–7973. <https://doi.org/10.1523/JNEUROSCI.0178-06.2006>.
- Pitzalis, S., Sereno, M.I., Committeri, G., Fattori, P., Galati, G., Patria, F., Galletti, C., 2010. Human V6: the medial motion area. *Cereb. Cortex* 20, 411–424.
- Pitzalis, S., Sereno, M.I., Committeri, G., Fattori, P., Galati, G., Tosoni, A., Galletti, C., 2013a. The human homologue of macaque area V6A. *Neuroimage* 82, 517–530. <https://doi.org/10.1016/j.neuroimage.2013.06.026>.
- Pitzalis, S., Fattori, P., Galletti, C., 2013b. The functional role of the medial motion area V6. *Front. Behav. Neurosci.* 6, 91.
- Pitzalis, S., Bozzacchi, C., Bultrini, A., Fattori, P., Galletti, C., Di Russo, F., 2013c. Parallel motion signals to the medial and lateral motion areas V6 and MT+. *NeuroImage* 67, 89–100. <https://doi.org/10.1016/j.neuroimage.2012.11.022>.
- Pitzalis, S., Sdoia, S., Bultrini, A., Committeri, G., Di Russo, F., Fattori, P., Galati, G., 2013d. Selectivity to translational egomotion in human brain motion areas. *PLoS One* 8 (4), e60241.
- Pitzalis, S., Fattori, P., Galletti, C., 2015. The human cortical areas V6 and V6A. *Vis. Neurosci.* 32, E007. <https://doi.org/10.1017/S0952523815000048>.
- Pitzalis, S., Serra, C., Sulpizio, V., Di Marco, S., Fattori, P., Galati, G., Galletti, C., 2019. A putative human homologue of the macaque area Péc. *Neuroimage* 202, 116092.
- Pitzalis, S., Serra, C., Sulpizio, V., Committeri, G., de Pasquale, F., Fattori, P., Galletti, C., Sepe, R., Galati, G., 2020. Neural bases of self- and object-motion in a naturalistic vision. *Hum. Brain Mapp.* 41, 1084–1111. <https://doi.org/10.1002/hbm.24862>.
- Pitzalis, S., Hadj-Bouziane, F., Dal Bò, G., Guedj, C., Strappini, F., Meunier, M., Galletti, C., 2021. Optic flow selectivity in the macaque parieto-occipital sulcus. *Brain Struct. Funct.* <https://doi.org/10.1007/s00429-021-02293-w>.
- Ptak, R., Muri, R.M., 2013. The parietal cortex and saccade planning: lessons from human lesion studies. *Front. Hum. Neurosci.* 7, 254. <https://doi.org/10.3389/fnhum.2013.00254>.
- Ptito, M., Kupers, R., Faubert, J., Gjedde, A., 2001. Cortical representation of inward and outward radial motion in man. *Neuroimage* 14, 1409–1415.
- Quinlan, D.J., Culham, J.C., 2007. fMRI reveals a preference for near viewing in the human parieto-occipital cortex. *NeuroImage* 36, 167–187. <https://doi.org/10.1016/j.neuroimage.2007.02.029>.
- Raffi, M., Squatrito, S., Maioli, M.G., 2002. Neuronal responses to optic flow in the monkey parietal area Péc. *Cereb. Cortex* 12, 639–646.
- Raffi, M., Carrozzini, C., Maioli, M.G., Squatrito, S., 2010. Multimodal representation of optic flow in area Péc of macaque monkey. *Neuroscience* 171, 1241–1255. <https://doi.org/10.1016/j.neuroscience.2010.09.026>.
- Raffi, M., Maioli, M.G., Squatrito, S., 2011. Optic flow direction coding in area Péc of the behaving monkey. *Neuroscience* 194, 136–149. <https://doi.org/10.1016/j.neuroscience.2011.07.036>.
- Raffi, M., Persiani, M., Piras, A., Squatrito, S., 2014. Optic flow neurons in area Péc integrate eye and head position signals. *Neurosci. Lett.* 568, 23–28. <https://doi.org/10.1016/j.neulet.2014.03.042>.
- Richer, F., Martinez, M., Cohen, H., Saint-Hilaire, J.M., 1991. Visual motion perception from stimulation of the human medial parieto-occipital cortex. *Exp. Brain Res.* 87, 649–652.



- Rossit, S., McAdam, T., McLean, D.A., Goodale, M.A., Culham, J.C., 2013. fMRI reveals a lower visual field preference for hand actions in human superior parieto-occipital cortex (SPOC) and precuneus. *Cortex* 49, 2525–2541. <https://doi.org/10.1016/j.cortex.2012.12.014>.
- Rutschmann, R.M., Schrauf, M., Greenlee, M.W., 2000. Brain activation during dichoptic presentation of optic flow stimuli. *Exp. Brain Res.* 134, 533–537.
- Santandrea, E., Breveglieri, R., Bosco, A., et al., 2018. Preparatory activity for purposeful arm movements in the dorsomedial parietal area V6A: beyond the online guidance of movement. *Sci. Rep.* 8, 6926 <https://doi.org/10.1038/s41598-018-25117-0>.
- Schaadt, A.K., Brandt, S.A., Kraft, A., Kerkhoff, G., 2015. Holmes and Horrax (1919) revisited: impaired binocular fusion as a cause of "flat vision" after right parietal brain damage - a case study. *Neuropsychologia* 69, 31–38. <https://doi.org/10.1016/j.neuropsychologia.2015.01.029>.
- Schindler, A., Bartels, A., 2013. Parietal cortex codes for egocentric space beyond the field of view. *Curr. Biol.* 23, 177–182.
- Schindler, A., Bartels, A., 2016. Motion parallax links visual motion areas and scene regions. *NeuroImage* 125, 803–812. <https://doi.org/10.1016/j.neuroimage.2015.10.066>.
- Schindler, A., Bartels, A., 2018a. Integration of visual and non-visual self-motion cues during voluntary head movements in the human brain. *NeuroImage* 172, 597–607. <https://doi.org/10.1016/j.neuroimage.2018.02.006>.
- Schindler, A., Bartels, A., 2018b. Human V6 integrates visual and extra-retinal cues during head-induced gaze shifts. *iScience* 7, 191–197. <https://doi.org/10.1016/j.isci.2018.09.004>.
- Serences, J.T., Yantis, S., 2006. Selective visual attention and perceptual coherence. *Trends Cogn. Sci.* 10, 38–45. <https://doi.org/10.1016/j.tics.2005.11.008>.
- Sereno, M.I., Huang, R.S., 2014. Multisensory maps in parietal cortex. *Curr. Opin. Neurobiol.* 24, 39–46.
- Sereno, M.I., Pitzalis, S., Martinez, A., 2001. Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science* 294, 1350–1354.
- Serra, C., Galletti, C., Di Marco, S., Fattori, P., Galati, G., Sulpizio, V., Pitzalis, S., 2019. Egomotion-related visual areas respond to active leg movements. *Hum. Brain Mapp.* 40, 3174–3191. <https://doi.org/10.1002/hbm.24589>.
- Sherrill, K.R., Chrastil, E.R., Ross, R.S., Erdem, U.M., Hasselmo, M.E., Stern, C.E., 2015. Functional connections between optic flow areas and navigationally responsive brain regions during goal-directed navigation. *NeuroImage* 118, 386–396. <https://doi.org/10.1016/j.neuroimage.2015.06.009>.
- Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33, 475–487.
- Smith, A.T., Scott-Samuel, N.E., 1998. Stereoscopic and contrast-defined motion in human vision. *Proc. Biol. Sci.* 265, 1573–1581.
- Smith, T., Wall, M.B., Williams, A.L., Singh, K.D., 2006. Sensitivity to optic flow in human cortical areas MT and MST. *Eur. J. Neurosci.* 23, 561–569.
- Snyder, L.H., Batista, A.P., Andersen, R.A., 1997. Coding of intention in the posterior parietal cortex. *Nature* 386, 167–170.
- Spiers, H.J., Maguire, E.A., 2007. Decoding human brain activity during real-world experiences. *Trends Cogn. Sci.* 11, 356–365. <https://doi.org/10.1016/j.tics.2007.06.002>.
- Spreng, R.N., Sepulcre, J., Turner, G.R., Stevens, W.D., Schacter, D.L., 2013. Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. *J. Cogn. Neurosci.* 25, 74–86. <https://doi.org/10.1162/jocn.2012.00281>.
- Styrkowiec, P.P., Nowik, A.M., Krolczak, G., 2019. The neural underpinnings of haptically guided functional grasping of tools: an fMRI study. *NeuroImage* 194, 149–162. <https://doi.org/10.1016/j.neuroimage.2019.03.043>.
- Sulpizio, V., Committeri, G., Lambrey, S., Berthoz, A., Galati, G., 2013. Selective role of lingual/parahippocampal gyrus and retrosplenial complex in spatial memory across viewpoint changes relative to the environmental reference frame. *Behav. Brain Res.* 242, 62–75. <https://doi.org/10.1016/j.bbr.2012.12.031>.
- Sulpizio, V., Galati, G., Fattori, P., Galletti, C., Pitzalis, S., 2020a. A common neural substrate for processing scenes and egomotion-compatible visual motion. *Brain Struct. Funct.* 225, 2091–2110.
- Sulpizio, V., Neri, A., Fattori, P., Galletti, C., Pitzalis, S., Galati, G., 2020b. Real and imagined grasping movements differently activate the human dorsomedial parietal cortex. *Neuroscience* 434, 22–34. <https://doi.org/10.1016/j.neuroscience.2020.03.019>.
- Sulpizio, V., Strappini, F., Fattori, P., Galati, G., Galletti, C., Pecchinenda, A., Pitzalis, S., 2022. The human middle temporal cortex responds to both active leg movements and egomotion-compatible visual motion. *Brain Struct. Funct.* 227, 2573–2592. <https://doi.org/10.1007/s00429-022-02549-z>.
- Tosoni, A., Galati, G., Romani, G.L., Corbetta, M., 2008. Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nat. Neurosci.* 11, 1446–1453.
- Tosoni, A., Shulman, G.L., Pope, A.L.W., et al., 2013. Distinct representations for shifts of spatial attention and changes of reward contingencies in the human brain. *Cortex* 49, 1733–1749. <https://doi.org/10.1016/j.cortex.2012.03.022>.
- Tosoni, A., Pitzalis, S., Committeri, G., Fattori, P., Galletti, C., Galati, G., 2015. Resting-state connectivity and functional specialization in human medial parieto-occipital cortex. *Brain Struct. Funct.* 220, 3307–3321.
- Turella, L., Rumiati, R., Lingnau, A., 2020. Hierarchical action encoding within the human brain. *Cereb. Cortex* 30, 2924–2938. <https://doi.org/10.1093/cercor/bhz284>.
- Uchimura, M., Nakano, T., Morito, Y., Ando, H., Kitazawa, S., 2015. Automatic representation of a visual stimulus relative to a background in the right precuneus. *Eur. J. Neurosci.* 42, 1651–1659. <https://doi.org/10.1111/ejn.12935>.
- Uesaki, M., Ashida, H., 2015. Optic-flow selective cortical sensory regions associated with self-reported states ofvection. *Front. Psychol.* 6, 1–9. <https://doi.org/10.3389/fpsyg.2015.00775>.
- Vaina, L.M., Sikoglu, E.M., Soloviev, S., LeMay, M., Squatrito, S., Pandiani, G., Cowey, A., 2010. Functional and anatomical profile of visual motion impairments in stroke patients correlate with fMRI in normal subjects. *J. Neuropsychol.* 4, 121–145. <https://doi.org/10.1348/174866409x471760>.
- Vaina, L.M., Buonanno, F., Rushton, S.K., 2014. Spared ability to perceive direction of locomotor heading and scene-relative object movement despite inability to perceive relative motion. *Med. Sci. Monit.* 20, 1563–1571. <https://doi.org/10.12659/MSM.892199>.
- Vallar, G., Coslett, H.B., 2018. The Parietal Lobe. Academic Press. <https://doi.org/10.1016/B978-0-444-63622-5.09990-3>.
- van der Hoorn, A., Renken, R.J., Leenders, K.L., de Jong, B.M., 2014. Parkinson-related changes of activation in visuomotor brain regions during perceived forward self-motion. *9 (4)*, e95861. <https://doi.org/10.1371/journal.pone.0095861>.
- Vandenbergh, R., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2001. Location-or feature-based targeting of peripheral attention. *Neuroimage* 14, 37–47. <https://doi.org/10.1006/nimg.2001.0790>.
- Vandenbergh, R., Molenberghs, P., Gillebert, C.R., 2012. Spatial attention deficits in humans: the critical role of superior compared to inferior parietal lesions. *Neuropsychologia* 50, 1092–1103. <https://doi.org/10.1016/j.neuropsychologia.2012.03.002>.
- Vann, S.D., Aggleton, J.P., Maguire, E.A., 2009. What does the retrosplenial cortex do? *Nat. Rev. Neurosci.* 10, 792–802.
- Vesia, M., Prime, S.L., Yan, X., Sergio, L.E., Crawford, J.D., 2010. Specificity of human parietal saccade and reach regions during transcranial magnetic stimulation. *J. Neurosci.* 30, 13053–13065.
- Vesia, M., Barnett-Cowan, M., Elahi, B., Jegatheeswaran, G., Isayama, R., Neva, J.L., Davare, M., Staines, W.R., Culham, J.C., Chen, R., 2017. Human dorsomedial parieto-motor circuit specifies grasp during the planning of goal-directed hand actions. *Cortex* 92, 175–186. <https://doi.org/10.1016/j.cortex.2017.04.007>.
- Vossel, S., Weidner, R., Thiel, C.M., Fink, G.R., 2009. What is "odd" in Posner's location-cueing paradigm? Neural responses to unexpected location and feature changes compared. *J. Cogn. Neurosci.* 21, 30–41.
- Warren, P.A., Rushton, S.K., 2008. Evidence for flow-parsing in classic 2D optic flow displays. *Vis. Res.* 48, 655–663.
- Wiest, G., Zimprich, F., Prayer, D., Czech, T., Serles, W., Baumgartner, C., 2004. Vestibular processing in human paramedian precuneus as shown by electrical cortical stimulation. *Neurology* 62, 473–475.
- Wojcik, E., Kanwisher, N., 1999. The generality of parietal involvement in visual attention. *Neuron* 23, 747–764. [https://doi.org/10.1016/S0896-6273\(01\)80033-7](https://doi.org/10.1016/S0896-6273(01)80033-7).
- Wunderlich, G., Marshall, J.C., Amunts, K., Weiss, P.H., Mohlberg, H., Zafiris, O., Zilles, K., Fink, G.R., 2002. The importance of seeing it coming: a functional magnetic resonance imaging study of motion- in-depth towards the human observer. *Neuroscience* 112 (3), 535–540.
- Yantis, S., Schwarzbach, J., Serences, J.T., et al., 2002. Transient neural activity in human parietal cortex during spatial attention shifts. *Nat. Neurosci.* 5, 995–1002. <https://doi.org/10.1038/nn921>.