Structural connectivity and functional properties of the macaque superior parietal lobule

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Title: **Structural connectivity and functional properties of the macaque superior parietal lobule**

Authors: Michela Gamberini, Lauretta Passarelli, Patrizia Fattori, Claudio Galletti

Affiliation: Department of Biomedical and Neuromotor Sciences, University of Bologna, 40126, Bologna, Italy

**Corresponding author:**

C. Galletti

Department of Biomedical and Neuromotor Sciences,

University of Bologna, 40126, Bologna, Italy

E-mail: claudio.galletti@unibo.it

Tel: +39 0512091741

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ORCID Michela Gamberini: 0000-0003-0945-9734
ORCID Lauretta Passarelli: 0000-0001-5009-2773
ORCID Patrizia Fattori: 0000-0002-0079-3755
ORCID Claudio Galletti: 0000-0001-8927-3408

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## *Abstract*

Despite the consolidated belief that the macaque superior parietal lobule (SPL) is **entirely** occupied by Brodmann's area 5, recent data show that macaque SPL also hosts a large cortical region with structural and functional features **similar to that** of Brodmann's area 7. According to these data, the anterior part of SPL **is occupied by a somatosensory-dominated cortical region that** hosts three architectural and functional distinct regions (PE, PEci, PEip), **and the caudal half of SPL by a bimodal somato-visual region** that hosts four areas: PEc, MIP, PGm, V6A.

**To date,** the most studied areas **of SPL** are PE, PEc, and V6A. PE is essentially a high-order somatomotor area, while PEc and V6A are bimodal somatomotor-visuomotor areas, the former with predominant somatosensory input, the latter with predominant visual input. The functional properties of these areas and their anatomical connectivity strongly suggest their involvement in the control of limb movements. PE is suggested to be involved in the preparation/execution of limb movements, in particular the movements of the upper limb; PEc in the control of movements of both upper and lower limbs, as well as in their interaction with the visual environment; V6A in the control of reach-to-grasp movements performed with the upper limb.

**In** human**s**, SPL **is traditionally** considered **to have a different organization** with respect to macaque**s**. **Here, we review several lines of evidence suggesting** that this is not the case, showing a similar structure for human and non-human primate SPLs.

## *Introduction*

The parietal **lobe of the Old World monkeys** can be **subdivided into** anterior and posterior **parts**. The anterior part occupies the postcentral cortex (yellow region in Fig. 1A), where the somatosensory Brodmann's areas 3, 1, 2 are located (Brodmann 1909). The posterior **part (posterior** parietal cortex; PPC) **can** in turn **be sub**divided into superior (SPL; green region in Fig. 1A) and inferior (IPL; red region in Fig. 1A) parietal lobules, separated by the intraparietal sulcus. According to Brodmann (1909), the SPL is almost entirely occupied by area 5 **(see blue region in the close-up of Fig. 1A)**, while area 7 occupies only a restricted **cortical** region in its caudalmost part (see **orange region in the** close-up **of** Fig. 1A). **Starting from Vogt and Vogt (1919), most** studies in the last century claimed that **although the architectural pattern changed moving rostro-caudally, the SPL** was entirely occupied by area 5 (Fig. 1B). In agreement with this view Pandya and Seltzer (1982), using the nomenclature previously proposed in humans by von Economo and Koskinas (1925), proposed the subdivision of macaque SPL in an area named PE, anteriorly, and another one named PEc, where 'c' stands for 'caudal', posteriorly (Fig. 1C), both described as **variants** of Brodmann's area 5. Other **variants** of area 5 adjoining PE laterally and medially were named by Pandya and Seltzer (1982) with the same prefix (areas PEa, PEci; Fig. 1C) to indicate a common structural organization. **The** thin stripe of area 7 that delimited the caudal **part** of area 5 in the original Brodmann's **description (orange region in the close-up of Fig. 1A)** was not reported by Pandya and Seltzer.

**Fig. 1 near here**

**Nowadays, it is evident that the SPL hosts a large number of cytoarchitectonic areas distributed along the exposed surface of SPL, the intraparietal and parieto-occipital sulci, and the precuneate cortex in the mesial surface of the hemisphere (see Fig. 2A). Moving in antero-posterior fashion across SPL, areas PE, PEip, PEci are located anteriorly and PEc, MIP, PGm, V6A posteriorly. The caudalmost part of SPL hosts, in the fundus of parieto-occipital sulcus, area V6. However, since V6 shows an occipital cytoarchitectural pattern (Fig. 2B; see details below), it is not considered as part of the parietal lobe, hence of SPL.**

The **presence in SPL** of different **cytoarchitectonic areas with** different functional properties **suggests that they have**

**somewhat** different functional roles. In the following sections we review the **anatomical** subdivisions of macaque SPL, together with **their cortical** connections and functional properties to **examine** their possible functional roles. **Finally, we present a brief** comparison with the human SPL.

*Structural subdivision of macaque SPL*

**As mentioned above, the** macaque SPL is composed of a mosaic of areas (Fig. 2A) with different architecture, functional properties, and patterns of anatomical connections. The anterior bank of the parieto-occipital sulcus, which is the caudalmost part of the SPL, hosts two areas, V6 ventrally and V6A dorsally (Galletti et al. 1996, 1999a, b, 2005). **Area V6** shows a clear *occipital* cytoarchitectural pattern, **as shown in Fig. 2B (Luppino et al. 2005)**, with a homogeneous layer III, a compact layer **IV**, a light layer V, and a clear subdivision of layer VI into two sublayers. **Differently**, area V6A shows a typical *parietal* pattern with well developed layers III and V, a large, but relatively dense, layer IV, and a layer VI with a poorly evident subdivision into sublayers. Although Brodmann (**1909**) did not **examine** the cytoarchitectural pattern of the cortex buried in the parieto-occipital sulcus, the parietal pattern of V6A strongly suggests that **it** represents an extension of Brodmann's area 7, that from the exposed cortical surface of SPL (the thin stripe of area 7 originally reported by Brodmann; see close-up in Fig. 1A) extends into the dorsal two third of the anterior wall of the parieto-occipital sulcus. Since according to Brodmann (1909) the parietal area 7 abuts posteriorly the occipital area 19 (see Fig. 1A), it is logical to **assume** that area V6, **which abuts posteriorly area V6A** (Fig. 2A) and shows a clear occipital pattern (Fig. 2B; Luppino et al. 2005), is part of the Brodmann's area 19.

**The** mesial surface of the hemisphere at the level of SPL (the precuneate cortex) hosts the mesial **sectors** of areas V6A and PEc, as well as areas PGm and 31 **(Fig. 2A;** Pandya and Seltzer 1982; Cavada and Goldman-Rakic 1989; Morecraft et al. 2004; Passarelli et al. 2018). Anterior to the precuneate cortex, area PEci occupies the fundus of the caudal tip of the cingulate sulcus, while the mesial extension of area PE occupies the cortical region above and anterior to it (**Fig. 2A**; Pandya and Seltzer 1982; Morecraft et al. 2004). Notice that PGm shows a cytoarchitectural pattern similar to Brodmann's area 7, and in **line with this** Pandya and Seltzer (1982) maintained for this area the prefix 'PG' that they used **for** area 7 in IPL, and other authors called this region area '7m', where 'm' stands for medial (Cavada and Goldman-Rakic 1989). Area PEci, instead, shows a cytoarchitectural pattern similar to that of Brodmann's area 5 (Pandya and Seltzer 1982), and area 31 a pattern intermediate between those of PGm and 23c (Morecraft et al. 2004).

**Fig. 2 near here**

In the lateral part of SPL, the medial wall of intraparietal sulcus is occupied by two areas, PEip rostrally and MIP caudally (Fig. 2A; **Colby et al. 1988;** Colby and Duhamel 1991; Matelli et al. 1998; Lewis and Van Essen 2000b, a). PEip **occupies a** cortical region **similar to that** originally described by Pandya and Seltzer (1982) as area PEa (**compare Fig. 2A with** Fig. 1C**)**. **Since PEa is cytoarchitecturally similar to Brodmann's area 5 (Pandya and Seltzer, 1982) we suggest that PEip could be part of area 5.** Area MIP **was** originally defined on the basis of myeloarchitecture and cortical connections (Colby et al. 1988), **whereas it's cytoarchitectonic pattern has not been studied yet.** Interestingly, myeloarchitectonic studies showed that area MIP, **like V6A,** presents two clearly distinct bands of Baillarger, **whereas in** PEip the bands of Baillarger are barely visible (Fig. 2C; Bakola et al. 2017). **In short, MIP, like V6A, seems to be part of Brodmann's area 7.**

On the cortical convexity of SPL, two areas have been described: PE rostrally and PEc caudally (Fig. 2A; Pandya and Seltzer 1982). Both extend for several millimeters into the mesial surface of the hemisphere medially, and the medial wall of the intraparietal sulcus laterally. Both areas show a parietal cytoarchitectural pattern that Pandya and Seltzer (1982) described as **variants** of area 5. However, Luppino et al. (2005) **reported** that the cytoarchitecture of PEc **was**

**different from that of PE and** similar to that of V6A, hence to that of Brodmann's area 7: **both PEc and V6A showed well developed layers III and V, a bi-laminated layer IV and a layer VI with a relatively blurred border against the white matter.** A very recent study supports this view reporting that **also** the chemoarchitecture of area PEc is more similar to that of area 7 than that of area 5 (Impieri et al. **2019**). On the other hand, it is worthwhile to remind that the caudalmost part of SPL dorsal convexity was originally reported as area 7 by Brodmann himself (**see orange region** in close-up **of** Fig. 1A; Brodmann 1909). Overall, these data suggest that PEc is indeed part of area 7, instead of area 5 as **previously** suggested by Pandya and Seltzer (1982).

The above reviewed data support the view that area 7 **is** *wider* than originally reported by Brodmann, **encompassing** a large part of the anterior wall of parieto-occipital sulcus (area V6A), the caudal **half** of the dorsal surface of SPL (area PEc), area PGm in the precuneate cortex, and the caudal half of the medial wall of the intraparietal sulcus (area MIP). Notice that all these areas are bimodal in nature, being activated by both visual and somatosensory stimulations, **a property that** is typical of Brodmann's area 7, but not of area 5 (see below **for details**).

***Cortical** connections of macaque SPL*

Each area of SPL is connected to a set of parietal and premotor areas involved in specific functional roles. Fig. 3 illustrates the cortical connections of the five SPL areas studied by our laboratory, namely PE, PEc, V6A, PGm, MIP. The cortical connections of the other areas **of the SPL**, taken from literature, will be described only in the text.

The major cortical afferents of PE (Fig. 3A; Bakola et al. 2013) are the primary somatosensory and motor cortices, in particular Brodmann's areas 2 and 4 (or F1, according to Matelli and coworkers nomenclature; Matelli et al. 1991). As shown in detail in Fig. 4, PE receives inputs from motor and premotor cortical regions representing upper and lower limbs, particularly from the region of the primary motor area F1 that represents the arm (compare labelling distribution in Fig. 4C with the leg and arm representations in F1 and F2 as shown in Fig. 4D). PE also receives somatosensory/somatomotor inputs from parietal (areas PEc, PEci, MIP, PEip, PGop, PFop, Ri) and cingulate (areas 23, 24) cortices, and premotor inputs from the supplementary motor area (SMA according to Penfield and Welch 1951 or F3 according to Matelli et al. 1991). Area PEc (Fig. 3B; Bakola et al. 2010) shares **several** cortical connections with PE, but also shows important differences. **Regarding** somatosensory and motor inputs, PEc receives a weak input from area 2 (but not at all from area 3) and a very week input from F1. PEc also receives a strong input from premotor area F2 and very week input from F3, **which is the opposite with respect to PE**. Also, PEc receives afferents from somatosensory-related areas of parietal (areas PE, MIP, PG, PGop) and mesial (areas PEci, 23, 24, 31) cortices that are quite different from those of area PE. Finally, PEc receives an input from the visuomotor area V6A which is not connected with PE. Interestingly, **while** both PE and PEc receive motor signals related to limb movements, PEc is more strongly connected with the **sectors of motor and premotor cortex representing** the lower limb than with those representing the upper limb, as shown in Fig. 4 (compare labelling distribution in Fig. 4C with leg and arm representations in F1 and F2 as shown in Fig. 4D). **The** overrepresentation of lower limb input to PEc is not the result of a bias in injection site **as the whole extent of the area was injected** (Fig. 4A). It is also worthwhile to notice that PE receives only somatic information while PEc receives both somatic and visual information (from V6A), in agreement with the somatic and bimodal nature, respectively, of the two areas, and with the functional roles suggested for these two areas by the properties of their neurons (see below).

**Fig. 3 near here**

**Fig. 4 near here**

The caudalmost part of SPL is occupied by the visuomotor area V6A (Fig. 2A). V6A is a relatively wide parietal area that extends medially into the mesial surface of the hemisphere, where it abuts area PGm, and laterally into the most lateral end of parieto-occipital sulcus, where it abuts area MIP at the limit of the caudalmost part of intraparietal sulcus (Fig. 2A). Area V6A (Fig. 3C; Gamberini et al. 2009; Passarelli et al. 2011) (see also Shipp et al. 1998; Matelli et al. 1998) shows reciprocal connections with the dorsal premotor areas F2 and F7, as well as with several visual and parietal visuomotor areas. V6A receives visual information from the extrastriate areas of the occipital lobe (V2, V3, V4, MST, V6) and from the visual **and visuomotor** areas of posterior parietal cortex (including AIP and LIP), and could receive somatosensory and somatomotor inputs from PEc and MIP (Bakola et al. 2010, 2017). **While both V6A and PEc receive projections from premotor area F2, the rest of their connections shows a clear complementary pattern:** PEc is mainly connected with somatically-dominated cortical areas, **whereas** V6A is mainly connected with visually-dominated areas (see Fig. 3B, C). Finally, in agreement with the reaching/grasping activity and **the primarily** upper-limb representation in V6A (see below), this area is strongly connected with the **sectors of premotor area F2 representing the upper limb, but not with those representing the lower limb** (compare labelling distribution in Fig. 4C with leg and arm representations in F2 as shown in Fig. 4D).

Area PGm, located on the mesial surface of the hemisphere (Fig. 2A), shows a pattern of cortical connections similar to that of V6A, with which it is reciprocally connected, but with some quantitative and qualitative differences (Fig. 3D; Passarelli et al. 2018) (see also Morecraft et al. 2004). In fact, PGm receives afferents from the lateral intraparietal cortex (area LIP) and inferior parietal lobule (**areas** Opt and PG) that are similar to those of V6A, **whereas the visual input from the extrastriate areas to PGm** is much weaker. The major difference **between the two areas regards the connections of PGm** with the visual areas of the ventral part of the precuneus (VIS, RSC), the cingulate cortex (area 23), and the prefrontal cortex (PFC, that includes the 'frontal eye fields'), **which are absent in V6A**.

Besides PGm, the mesial surface of SPL also hosts areas PEci and 31 (Fig. 2A). According to Pandya and Seltzer (1982) and Morecraft et al. (2004), area PEci (also called SSA - supplementary somatosensory area - by Murray and Coulter 1981a) is connected with the supplementary motor area F3, cingulate areas 23 and 24, **the** transitional sensory area, **the** medial portion of the primary motor (F1) and of somatosensory (areas 3, 1, 2) **cortex, and with** superior parietal areas PE, PEc, 31 and PGm. On the lateral surface of the brain, PEci is directly connected with SII, insula, areas PGop, PG **and** MST. Finally, the frontal lobe connections of PEci, besides with the medial part of F1, are with the premotor cortices F2 and F7. Interestingly, PEci shares many connections with PE, **but not with PEc. Like PE,** PEci is strongly connected with motor and premotor cortical regions and does not receive visual inputs, whereas PEc receives somatomotor *and* visual inputs, as reported above. PEci and PE are directly connected with the spinal cord, while PEc does not (Murray and Coulter 1981b). These sets of connections are in line with the view that PEci **could be part of** Brodmann's area 5, **whereas areas** PEc, V6A and PGm **could be classified as sectors of Brodmann's area 7**. Area 31, located anterior to PGm on the mesial surface of the brain (Fig. 2A), is strongly connected with premotor (F2) and parietal sensorimotor (V6A, PEci, PE) **areas**, and with cingulate cortex (areas 23 and 24). The connections of area 31 are quite similar to those of PGm, but the analysis of the laminar patterns of these connections suggests that area PGm represents a higher level of processing in comparison with area 31 (see Passarelli et al. 2018).

As far as the SPL areas buried within the intraparietal sulcus are concerned, area PEip **is** located in the anterior part of the medial wall of intraparietal sulcus (Fig. 2A) and **was** identified on the basis of cortico-spinal projections (Matelli et al. 1998). **PEip** is target of motor and premotor areas, including the PMd, PMv, **the** mesial motor areas **like** SMA, CMAd and CMAv (Matelli et al. 1998; Riehle and Vaadia 2004), and of parietal areas PE, MIP, and VIP (Bakola et al. 2013, 2017). Area MIP, located posterior to PEip in the **caudal** part of the medial wall of intraparietal sulcus (Fig. 2A), is strongly connected with dorsal premotor area F2 and less with the primary motor area F1 **(Fig. 3E)**. MIP is also strongly connected with visual areas VIP and V6A, with PEc and PE, and with PEip and PEci (Bakola et al. 2017). The stronger connections of PEip with F1 **compared to** F2 and the reverse behaviour of MIP, **combined** with **the direct connection of PEip (but not of MIP) with the spinal cord and the** much weaker visual **afferents to PEip relative** to MIP, are in line with the view that PEip is **part of the somatosensory** Brodmann's area 5 and MIP **of the** bimodal visual/somatosensory area 7.

*Functional properties of macaque SPL*

In the past, the PPC was classically defined an 'association cortex' and viewed as a structure mainly dedicated to the integration of different sensory information. Starting from the seminal studies by Mountcastle et al. (1975) and Hyvaarinen and collaborators (Leinonen et al. 1979; Hyvärinen 1982), a great deal of research showed that PPC was not only involved in the integration of different sensory modalities, somatic and visual in particular, but it was also involved in the control of somatomotor, visuomotor, oculomotor activities, as well as in the guidance of visuospatial attention (Kalaska 1996; Andersen et al. 1997; Galletti et al. 2003, 2010; Gottlieb 2007; Filimon 2010; Sereno and Huang 2014; Caminiti et al. 2015; Pisella et al. 2017; **Hadjidimitrakis et al. 2019**). In particular, it was demonstrated that most SPL neurons discharged in association with active arm movements performed by monkeys to reach and grasp objects in the peripersonal space, **thus** suggesting that the SPL was selectively involved in processes related to arm movement planning, execution, and **online** control (Andersen et al. 1997; Kalaska et al. 1997; Ferraina et al. 1997a; Galletti et al. 1997, 2003; Battaglia-Mayer et al. 2000; Batista and Andersen 2001; Fattori et al. 2001, 2004, 2005, 2009, 2017; see for a review Andersen and Cui 2009; Galletti and Fattori 2018). **Till a decade ago, IPL was considered to be specifically involved in the distal phase of prehension, i.e. in grasping movements, and SPL in the proximal phase of prehension, i.e** in arm reaching movements (Jeannerod et al. 1995; Wise et al. 1997; Culham et al. 2006; Gallivan et al. 2009; Grafton 2010; Vesia and Crawford 2012). **However, several lines of evidence have** demonstrated that the activity of SPL neurons is also modulated **by the features of the distal phase of prehension, like** wrist orientation and grip formation (Fattori et al. 2004, 2009, 2010; Breveglieri et al. 2016, 2018). The involvement of SPL in the distal phase of prehension has been **also** recently demonstrated in humans (Verhagen et al. 2013; Begliomini et al. 2014; Vesia et al. 2017). At present, it is clear that the act of prehension is controlled by two parieto-frontal circuits, a lateral one **that includes** IPL and ventral premotor cortex **and is** mainly involved in the control of grasping and manipulation, and a medial one including SPL and dorsal premotor cortex that is involved in the control of the entire reach-to-grasp action, particularly when rapid control is required, as when the action **is** time constrained (Galletti et al. 2003; Rizzolatti and Matelli 2003; Borra et al. 2017; Galletti and Fattori 2018).

Regarding the specific functional role **of** the different areas of SPL, the most studied areas to date are PE, PEc, and V6A. Area PE is a somatic area that abuts anteriorly the primary somatosensory cortex SI (Fig. 5A; Brodmann's areas 3, 1, 2). While SI **and** in particular areas 3a and 1 **mainly process tactile stimuli** and host a detailed map of the entire body (Fig. 5A; Pons et al. 1985; Padberg et al. 2007; Krubitzer and Disbrow 2008; Seelke et al. 2012), PE is dominated by proprioceptive representation and hosts a rough topographical map of the body with an over-representation of the arm, particularly of the hand (Fig. 5A; Duffy and Burchfiel 1971; Sakata et al. 1973; Mountcastle et al. 1975; Padberg et al. 2007; Seelke et al. 2012; Baldwin et al. 2018; see also the strong connection with the arm region of F1 in Fig. 4C). Notably, however, only the **antero-**lateral part of area PE has been studied in detail to date (yellow region in **the close-up of** Fig. 5B), **whereas** the medial part of the area **is** still **quite** unexplored. Therefore, it is possible that the lower limb is represented in this **part of PE, given also** the fact that the leg is represented in the adjoining medial part of SI (see

Fig. 5A). **In line with this hypothesis, a very recent report (De Vitis et al. 2019) has shown that in the postero-medial part of PE (orange region in the close-up of Fig. 5B) the lower limb is actually over-represented (Fig. 6 E), although both upper and lower limb representations were found (Fig. 6C, E), and not only the lower limb as it could be expected. In sum, a rough topographical map of the body is present in PE, with an over-representation of the limbs, the upper ones in the antero-lateral part (Fig. 5A) and the lower ones in the postero-medial part (Fig. 6E) of the area.**

**Fig. 5 near here**

**It has been known since a long time that the visual stimulation is ineffective in activating PE neurons (Mountcastle et al. 1975). PE neurons are generally sensitive to multi-joint stimulations and to the posture of limbs (Duffy and Burchfiel 1971; Sakata et al. 1973; Mountcastle et al. 1975; Georgopoulos et al. 1984; Kalaska et al. 1990). According to De Vitis and coworkers (2019), about 90% of PE neurons are sensitive to somatosensory stimulation (Fig. 6A), in particular the joint stimulation of both upper and lower limbs (Fig. 6B, E). Neuronal responses in PE are mainly evoked by somatic stimulation of the contralateral side of the body, or of both sides (Fig. 6D). During arm reaching movements, different populations of cells encode depth and direction of movement, showing an independent processing of these two parameters (Hadjidimitrakis et al. 2015).** It has been demonstrated that PE neurons are involved in preparation and control of limb movements, and become active during skilled actions (Kalaska 1996). **All these data strongly suggest** that PE is a somatomotor area that hosts motor and somatosensory signals from the limbs and **that** is likely involved in the somatomotor guidance of **limb** actions.

Differently from PE, area PEc is an area that hosts a representation of the visual field, together with an incomplete somatosensory map of the body (Gamberini et al. 2018). The visual receptive fields of PEc neurons are quite large and are often sensitive to optic flow (Ferraina et al. 2001; Breveglieri et al. 2008; Raffi et al. 2010, 2011, 2014). **About 65% of PEc neurons are sensitive to somatosensory stimulation (Fig. 6A), in particular the joint stimulation of both upper and lower limbs (Fig. 6B, E).** The map of body is **more** focused on the proximal part of **the** limbs **(Fig. 6E)** and, **differently from PE,** does not show any sign of topographical organization: upper and lower limb representations are intermixed all over the area (Breveglieri et al. 2006, 2008; Gamberini et al. 2018). Somatic PEc neurons respond mostly to single-joint rotations, but also to tactile stimulations of trunk and limbs **(Fig. 6B, E)**. The incidence of joint versus tactile sensitivity is similar to that of PE (**Fig. 6B;** Breveglieri et al. 2008; Gamberini et al. 2018; De Vitis et al. 2019), whereas the contralateral sensitivity is more accentuated than in PE (Fig. 6D). Contrary to PE, several PEc neurons show bimodal somato-visual responses (Breveglieri et al. 2008; Gamberini et al. 2018). Most PEc neurons show arm and/or eye movement-related activity (Ferraina et al. 2001; Battaglia-Mayer et al. 2001; Piserchia et al. 2017), and many PEc neurons are able to encode the direction and depth of arm movements (Hadjidimitrakis et al. 2015). All these data suggest that PEc contributes to the visual guidance of motor behavior and eye-hand coordination (Battaglia-Mayer et al. 2000, 2001; Gamberini et al. 2018). Since area PEc is sensitive to optic flow, receives visual information mostly from the lower visual field, and is more strongly connected with cortical motor/premotor regions that represent the lower limbs, it has been suggested that it is involved in the visual guidance of locomotion (Breveglieri et al. 2008; Bakola et al. 2010; Raffi et al. 2014; Gamberini et al. 2018).

**Fig. 6 near here**

**Area V6A, like PEc,** hosts both visual and somatic neurons. **However, contrary to PEc, visual neurons represent the majority of V6A neurons (about 65%; Gamberini et al. 2011). Visual neurons** mainly represent the contralateral lower part of visual field, partially including also the ipsilateral one. The central part of visual field is more represented in the dorsal part of V6A while the peripheral part, particularly the lower quadrant, in the ventral one (Gamberini et al. 2011). Somatic neurons **are about 40% of V6A cells (Fig. 6A). They** represent almost exclusively the upper limb, and in particular the contralateral arm **(Fig. 6C, D, E).** Most of these neurons are modulated by passive stimulation of proximal joints **(shoulder, elbow)** and some of them by passive stimulation of distal (mainly wrist) joints (**Fig. 6B, E;** Gamberini et al. 2011, 2018). It is worth noticing that the active arm movements are always more effective than passive movements in activating V6A neurons. During active arm movements, about 70% of V6A neurons are modulated by the direction (Fig. **7**A; Fattori et al. 2005) and/or depth (Hadjidimitrakis et al. 2014, **2017**) of reaching movement, and approximately 60% by wrist orientation (Fig. **7**B; Fattori et al. 2009) and grip formation (Fig. **7**C; Fattori et al. 2010; Breveglieri et al. 2016, 2018). **The** presence in V6A of cells modulated by grip formation is in contrast with the common view that this **part** of the brain is only involved in the control of reaching, and strongly supports our view that V6A is also involved in the control of distal aspects of arm movements (**Galletti et al. 2003; Fattori et al. 2004**; see Fattori et al. 2017 for a thorough discussion of this **issue**). Most V6A cells are responsive to both reaching and grasping movements, with some cells more responsive for reaching and others for grasping (Fig. **7**D). About 60% of V6A neurons discharge to object presentation, with about half of them displaying object selectivity (Fattori et al. 2012). Finally, the activity of many V6A cells is also modulated by *the preparation* of prehension action (see for instance the ramp-like activity shown before the onset of grasping, but not of reaching, by the cell in Fig. **7**D; Santandrea et al. 2018). Overall, the functional properties of V6A cells suggest that this medial posterior parietal area is involved in the analysis of vision for action and in the control of all phases of prehension during reach-to-grasp actions (Fattori et al. 2012, 2017), particularly when actions are time-constrained (see Galletti and Fattori 2018). Interestingly, other properties of V6A neurons **supporting these roles are the tuning of activity by** eye position (Galletti et al. 1995; Hadjidimitrakis et al. 2011, **2012**; Breveglieri et al. 2012) **and** the **modulation of** visual response according to gaze direction (Fig. **8**A), **a property that allows neurons to encode spatial locations of visual stimuli** (Galletti et al. 1995). **Further support to the above suggested functional roles comes from the presence in V6A of neurons that respond during** saccadic eye movement**s** and **encode their** direction (Fig. 8B; Kutz et al. 2003), **are modulated by** spatial shift**s** of covert attention (Fig. **8**C; Galletti et al. 2010) and **by** the affordance of graspable objects (Fig. **8**D; Breveglieri et al. 2015).

**Fig. 7 near here**

**Fig. 8 near here**

**Areas** PEip and MIP, hidden into the intraparietal sulcus, and PEci, 31, and PGm located on the mesial surface of the hemisphere (Fig. 2A) **are areas less intensively studied than those described above**. Although specific studies on the functional properties of **PEip** neurons are lacking, **their** properties can be **partially** inferred by data collected in deep electrophysiological penetrations performed in the lateral part of area 5, **since this type** of penetrations could reach area PEip in depth. According to these data, deep area 5 neurons (likely **located** in PEip) were found to respond to somatosensory stimulations of the upper limb (Mountcastle et al. 1975; Iwamura and Tanaka 1996), often in association with arm movements (Kalaska et al. 1990). Neurons in area MIP, instead, respond**ed** not only to somatosensory, but also to visual stimuli (Colby and Duhamel 1991), a bimodal sensitivity that **suggests a similarity with the typical neurons** of Brodmann's area 7 **in the IPL (Leinonen et al. 1979; Hyvärinen 1982)**. Apart from the study of Colby and Duhamel (1991), specific investigations on the functional properties of MIP neurons are still lacking. However, Richard Andersen and his coworkers in the last two decades collected a huge amount of data on the functional properties of neurons of a PPC region, referred to as parietal reach region (PRR; Snyder et al. 1997, 1998; Andersen et al. 2014), that **most** likely included area MIP. According to these studies, the activity of PRR (MIP) neurons **was** strongly modulated by arm movement preparation and execution. In particular, PRR neurons **were** implicated in the sensory-to-motor transformation required for reaching toward visually defined targets **(Buneo and Andersen 2006; Chang and Snyder 2010)**. Single PRR cells integrated target and limb position information across the reaching workspace and seem**ed** to be more involved in encoding the intention to make arm movements rather than the execution of these movements **(Andersen et al. 2014)**.

On the mesial surface of the hemisphere, area PGm codes information related to visually guided navigation and object localization in space (Sato et al. 2006, 2010; Baumann and Mattingley 2010), information useful during planning and execution of arm and/or eye movements (Ferraina et al. 1997a, b). Area 31, anterior to PGm, is likely involved in monitoring eye **position and** movement (Olson et al. 1996), as well as in sensory cognition for the guidance of head and limb movements (Passarelli et al. 2018). Lastly, PEci, anterior to area 31, hosts a somatosensory map of the body (supplementary sensory area; Murray and Coulter 1981a) like area PE, in agreement with our view that PEci and PE are both parts of Brodmann's area 5, **but to our knowledge the functional properties of PEci neurons during active movements have not been explored yet**.

**Overall, the functional properties of SPL summarized in this chapter show that PE, PEip, and PEci are somatomotor areas that are not influenced by visual signals, while PEc, MIP, PGm, and V6A are areas influenced by both somatomotor and visuomotor signals. Since single cell recordings in macaque monkeys have shown that Brodmann's area 5 is a somatomotor cortical region not influenced by visual stimulation (Mountcastle et al. 1975) and Brodmann's area 7 a bimodal somatomotor/visuomotor region (Leinonen et al. 1979; Hyvärinen 1982), we suggest that in SPL the somatomotor areas are parts of Brodmann's area 5 and the bimodal areas of Brodmann's area 7.**

*Comparison with human SPL*

**Since Brodmann's parcellation of the cerebral cortex more than one century ago (Fig. 9A, B; Brodmann 1909)**, **the human** SPL has been considered to be organized **differently** with respect to **monkey** SPL: **in humans, SPL was viewed as hosting both areas 5 and 7, whereas in monkey it seemed to host only area 5** (see Sakata et al. 1973; Mountcastle et al. 1975; Pandya and Seltzer 1982; Battaglia-Mayer et al. 2001). The data reviewed here suggest that this is not the case, **and monkey** SPL **seems likely to have a similar** structure **with** human **SPL**.

**According to Brodmann** (1909), **area 5 is** just posterior to **areas 3, 1, 2 in both monkey and human brains (Fig. 9A, B).** However, while **in monkeys** area 5 extends in the lateral part of the brain (Fig. **9**A, **C**), **in** human **it is confined in** a more medial region **of the brain** (Fig. **9**B, **D**). Since it has been demonstrated that during evolution there has been a high degree of expansion in the associative cortex (Chaplin et al. 2013), particularly in humans (Hill et al. 2010; Gregory et al. 2017), it is plausible that **human** area 5 **was confined within more medial brain locations** because it has been 'pushed' **upwards** and medially by the growing **associative** inferior parietal cortex (Brodmann's areas 39, 40, **Fig. 9B; yellow IPL region in Fig. 9D**). It is worthwhile to notice that the cortex occupying area 5 **in humans** is a region of low evolutionary expansion (blue stripe under the **white** dashed oval in Fig. **9D**, right). It is therefore **reasonable to assume** that the functional properties and role of **the human** area 5 are not significantly different **from those of area 5 of the** non-human primates.

**Fig. 9 near here**

Strong support to the view that human and non-human primates have SPL organized in a similar way also comes from recent neuroimaging data. Sereno and coworkers (see for review Huang and Sereno 2018) have found in humans the presence of a second somatosensory homunculus (Parietal Body Area, PBA) **in the SPL** besides that in the primary somatosensory cortex, **located** at the level of the medial end of the postcentral sulcus, just posterior to the SI (Fig. **10**A, B; Huang et al. 2012). This is the classic location of Brodmann's area 5 in humans (see **Figs. 9D, 10A, B**), and the PBA is reminiscent of the rough topographical map of the body observed in macaque area **PE** (see Fig. 5A; Seelke et al. 2012).

As shown in Fig. **10**C, the parietal cortex *posterior* to PBA is activated by **goal-directed** limb movements (in particular by reaching), but it is not organized topographically (Fig. **10**B), similarly to what has been observed in macaque **in the postero-medial part of PE (De Vitis et al. 2019) and in** PEc (Gamberini et al. 2018). Huang et al. (2012) found that the part of PBA representing leg and toe and the cortical region that abuts posteriorly PBA overlap with a region representing the lower visual field (Fig. **10**A, B). This suggested to the authors that this parietal region could be involved in the control of **locomotion** (Fig. **10**C), similarly to macaque area PEc (Breveglieri et al. 2008; Bakola et al. 2010; Raffi et al. 2014; Gamberini et al. 2018).

Overall, the activation by reaching movements, the representation of both lower- and upper-limb movements, the lacking of somatotopic organization, and the lower field representation of the parietal region abutting posteriorly PBA are reminiscent of the functional properties of the **homologous SPL region (postero-medial part of PE and area PEc) in the macaque.**

**Fig. 10 near here**

Further support to the view of a strict homology between human and non-human primate SPLs comes from a very recent neuroimaging study (Pitzalis et al. 2019) reporting that the medial SPL cortex in humans hosts the same areas described in macaque SPL, that is V6A, PEc, and PE (compare Fig. **11**B and **11**E). As shown in Fig. 1**1E**, **human (h)** V6A is located in the posterior portion of SPL, **anterior to the parieto-occipital sulcus,** in a cortical territory that includes the caudalmost portion of the precuneate cortex; hV6A is anterior to hV6 (Pitzalis et al. 2006) and posterior to hPEc, which occupies the dorsalmost portion of the anterior precuneus, just behind the dorsal tip of the cingulate sulcus; area **h**PE **is anterior to hPEc and** occupies the dorsomedial portion of the post-central gyrus, just over the tip of the cingulate sulcus. It is worthwhile noticing that while **h**V6 is **part** of Brodmann's area 19 (compare Fig. **11**C and **11**E), areas hV6Ad **and** hPEc are **parts** of area **7, and hPE part of area 5** (compare Fig. 1**1C** and 11**E**). **Quite recently, Scheperians and coworkers (2008) reported the presence of several cytoarchitectonic fields within the limits of Brodmann's areas 7 and 5 in human. A comparison of this anatomical parcellation (Fig. 11D) with the functional parcellation by Pitzalis and colleagues (Fig. 11E) strongly suggest that hV6A is within the limits of Scheperians' area 7P, hPEc within the limits of area 7A, and hPE within those of areas 5L-5M. Tab.1 provides a comparison between present suggestions and existing nomenclatures in macaque and human SPL.**

**Fig. 11 near here**

**Tab 1**

### *Conclusions*

Most studies in the last century claimed that macaque SPL was entirely occupied by Brodmann's area 5. Recent data, however, show that **in the caudal part of SPL a cortical region larger than that originally indicated as area 7 by Brodmann (1909) has** structural and functional features typical of area 7. Within this region that occupies **roughly** the caudal **half** of SPL, **four cytoarchitecturally and functionally distinct** areas have been **identified**: PEc, V6A, **PGm, and MIP (see orange region in Fig. 11A). In the anterior half of SPL, within the cortical region indicated by Brodmann as area 5, three cytoarchitecturally and functionally distinct areas have been recognized: PE, PEip, PEci (see blue region in Fig. 11A).** The **comparison of macaque with human SPL presented here (Fig. 11)** strongly supports the view that **they** have similar structural organization, **with a somatosensory-dominated anterior sector and a bimodal, visual-somatosensory caudal part.**

The here suggested macaque-human homology could address future neuroimaging experiments in humans aimed at understanding the **largely unknown** functional role of **the various sectors lying** within the wide sheet of cortex **indicated as** area 7 in **humans**. Furthermore, if human SPL, like macaque SPL, is involved in the control of arm reaching and reach-to-grasp movements, as suggested by many brain imaging studies (e.g. Astafiev et al. 2003; Connolly et al. 2003; Filimon et al. 2009; Cavina-Pratesi et al. 2010; Galati et al. 2011; Gallivan et al. 2011; Fabbri et al. 2014; Tosoni et al. 2015; Heed et al. 2016) and by the effects of caudal SPL lesions (Optic ataxia: Perenin and Vighetto 1988; Karnath and Perenin 2005), we could use the huge amount of data collected **from** single **cells in** different areas of macaque SPL to verify their efficacy in **encoding reach-to-grasp actions (e.g., see Filippini et al. 2017, 2018),** so to decide whether and how to use neural signals from human SPL to guide artificial arms in tetraplegic patients.

**Ethical approval:** This article does not contain any new, previously unpublished study with human participants or animals performed by any of the authors.

**List of References**

Andersen RA, Andersen KN, Hwang EJ, Hauschild M (2014) Optic ataxia: from Balint’s syndrome to the parietal reach region. Neuron 81:967–983. doi: 10.1016/j.neuron.2014.02.025

**Andersen RA, Cui H (2009) Intention, action planning, and decision making in parietal-frontal circuits. Neuron 63:568–83. doi: 10.1016/j.neuron.2009.08.028**

Andersen RA, Snyder LH, Bradley DC, Xing J (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. Annu Rev Neurosci 20:303–330. doi: 10.1146/annurev.neuro.20.1.303

Astafiev S V, Shulman GL, Stanley CM, et al (2003) Functional Organization of Human Intraparietal and Frontal Cortex for Attending, Looking, and Pointing. J Neurosci 23:4689–4699. doi: 10.1523/JNEUROSCI.23-11-04689.2003

Bakola S, Gamberini M, Passarelli L, et al (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. doi: 10.1093/cercor/bhq007

Bakola S, Passarelli L, Gamberini M, et al (2013) Cortical connectivity suggests a role in limb coordination for macaque area PE of the superior parietal cortex. J Neurosci 33:6648–58. doi: 10.1523/JNEUROSCI.4685-12.2013

Bakola S, Passarelli L, Huynh T, et al (2017) Cortical Afferents and Myeloarchitecture Distinguish the Medial Intraparietal Area (MIP) from Neighboring Subdivisions of the Macaque Cortex. eNeuro 4:ENEURO.0344-17.2017. doi: 10.1523/ENEURO.0344-17.2017

Baldwin MKL, Cooke DF, Goldring AB, Krubitzer L (2018) Representations of Fine Digit Movements in Posterior and Anterior Parietal Cortex Revealed Using Long-Train Intracortical Microstimulation in Macaque Monkeys. Cereb Cortex 28:4244–4263. doi: 10.1093/cercor/bhx279

Batista AP, Andersen RA (2001) The parietal reach region codes the next planned movement in a sequential reach task.

J Neurophysiol 85:539–544. doi: 10.1152/jn.2001.85.2.539

Battaglia-Mayer A, Ferraina S, Genovesio A, et al (2001) Eye-hand coordination during reaching. II. An analysis of the relationships between visuomanual signals in parietal cortex and parieto-frontal association projections. Cereb Cortex 11:528–44. doi: 10.1093/cercor/11.6.528

Battaglia-Mayer A, Ferraina S, Mitsuda T, et al (2000) Early coding of reaching in the parietooccipital cortex. J Neurophysiol 83:2374–2391. doi: 10.1152/jn.2000.83.4.2374

Baumann O, Mattingley JB (2010) Medial Parietal Cortex Encodes Perceived Heading Direction in Humans. J Neurosci 30:12897–12901. doi: 10.1523/JNEUROSCI.3077-10.2010

**Begliomini C, De Sanctis T, Marangon M, et al (2014) An investigation of the neural circuits underlying reaching and reach-to-grasp movements: from planning to execution. Front Hum Neurosci 8:676. doi: 10.3389/fnhum.2014.00676**

Borra E, Gerbella M, Rozzi S, Luppino G (2017) The macaque lateral grasping network: A neural substrate for generating purposeful hand actions. Neurosci Biobehav Rev 75:65–90. doi: 10.1016/j.neubiorev.2017.01.017

Bremner LR, Andersen RA (2012) Coding of the reach vector in parietal area 5d. Neuron 75:342–351. doi: 10.1038/nmeth.2250.Digestion

Breveglieri R, Bosco A, Galletti C, et al (2016) Neural activity in the medial parietal area V6A while grasping with or without visual feedback. Sci Rep 6:28893. doi: 10.1038/srep28893

Breveglieri R, De Vitis M, Bosco A, et al (2018) Interplay Between Grip and Vision in the Monkey Medial Parietal Lobe. Cereb Cortex 2028–2042. doi: 10.1093/cercor/bhx109

Breveglieri R, Galletti C, Bosco A, et al (2015) Object affordance modulates visual responses in the macaque medial posterior parietal cortex. J Cogn Neurosci 27:1447–55. doi: 10.1162/jocn_a_00793

Breveglieri R, Galletti C, Gamberini M, et al (2006) Somatosensory Cells in Area PEc of Macaque Posterior Parietal Cortex. J Neurosci 26:3679–3684. doi: 10.1523/JNEUROSCI.4637-05.2006

Breveglieri R, Galletti C, Monaco S, Fattori P (2008) Visual, Somatosensory, and Bimodal Activities in the Macaque Parietal Area PEc. Cereb Cortex 18:806–816. doi: 10.1093/cercor/bhm127

Breveglieri R, Hadjidimitrakis K, Bosco A, et al (2012) Eye Position Encoding in Three-Dimensional Space: Integration of Version and Vergence Signals in the Medial Posterior Parietal Cortex. J Neurosci 32:159–169. doi: 10.1523/JNEUROSCI.4028-11.2012

Brodmann K (1909) Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues.

Brunamonti E, Genovesio A, Pani P, et al (2016) Reaching-related Neurons in Superior Parietal Area 5: Influence of the Target Visibility. J Cogn Neurosci 28:1828–1837. doi: 10.1162/jocn_a_01004

**Buneo CA, Andersen RA (2006) The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. Neuropsychologia 44:2594–2606. doi: https://doi.org/10.1016/j.neuropsychologia.2005.10.011**

Caminiti R, Innocenti GM, Battaglia-Mayer A (2015) Organization and evolution of parieto-frontal processing streams in macaque monkeys and humans. Neurosci Biobehav Rev 56:73–96. doi: https://doi.org/10.1016/j.neubiorev.2015.06.014

Cavada C, Goldman-Rakic PS (1989) Posterior parietal cortex in rhesus monkey: I. Parcellation o f areas based on distinctive limbic and sensory corticocortical connections. J Comp Neurol 287:393–421. doi: 10.1002/cne.902870402

Cavina-Pratesi C, Monaco S, Fattori P, et al (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. doi: 10.1523/JNEUROSCI.2023-10.2010

**Chang SWC, Snyder LH (2010) Idiosyncratic and systematic aspects of spatial representations in the macaque parietal cortex. Proc Natl Acad Sci U S A 107:7951–6. doi: 10.1073/pnas.0913209107**

Chaplin TA, Yu H-H, Soares JGM, et al (2013) A Conserved Pattern of Differential Expansion of Cortical Areas in Simian Primates. J Neurosci 33:15120–15125. doi: 10.1523/JNEUROSCI.2909-13.2013

Colby CL, Duhamel JR (1991) Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. Neuropsychologia 29:517–37. doi: 10.1016/0028-3932(91)90008-V

Colby CL, Gattass R, Olson CR, Gross CG (1988) Topographical organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. J Comp Neurol 269:392–413. doi: 10.1002/cne.902690307

Connolly JD, Andersen RA, Goodale MA (2003) FMRI evidence for a ‘parietal reach region’ in the human brain. Exp Brain Res 153:140–145. doi: 10.1007/s00221-003-1587-1

Culham JC, Cavina-Pratesi C, Singhal A (2006) The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? Neuropsychologia 44:2668–2684. doi: 10.1016/j.neuropsychologia.2005.11.003

**De Vitis M, Breveglieri R, Hadjidimitrakis K, et al (2019) The neglected medial part of macaque area PE: segregated processing of reach depth and direction. Brain Struct Funct 224:2537–2557. doi: 10.1007/s00429-019-01923-8**

Duffy FH, Burchfiel JL (1971) Somatosensory system: organizational hierarchy from single units in monkey area 5. Science 172:273–5. doi: 10.1126/science.172.3980.273

Fabbri S, Strnad L, Caramazza A, Lingnau A (2014) Overlapping representations for grip type and reach direction. Neuroimage 94:138–146. doi: 10.1016/j.neuroimage.2014.03.017

Fattori P, Breveglieri R, Amoroso K, Galletti C (2004) Evidence for both reaching and grasping activity in the medial parieto-occipital cortex of the macaque. Eur J Neurosci 20:2457–2466. doi: 10.1111/j.1460-9568.2004.03697.x

Fattori P, Breveglieri R, Bosco A, et al (2017) Vision for Prehension in the Medial Parietal Cortex. Cereb Cortex 27:1149–1163. doi: 10.1093/cercor/bhv302

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. doi: 10.1523/JNEUROSCI.4998-08.2009

Fattori P, Breveglieri R, Raos V, et al (2012) Vision for action in the macaque medial posterior parietal cortex. J Neurosci 32:3221–3234. doi: 10.1523/JNEUROSCI.5358-11.2012

**Fattori P, Gamberini M, Kutz DF, Galletti C (2001) ‘Arm-reaching’ neurons in the parietal area V6A of the macaque monkey. Eur J Neurosci 13:2309–2313. doi: 10.1046/j.0953-816x.2001.01618.x**

Fattori P, Kutz DF, 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. doi: 10.1111/j.1460-9568.2005.04288.x

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. doi: 10.1523/JNEUROSCI.3800-09.2010

Ferraina S, Battaglia-Mayer A, Genovesio A, et al (2001) Early Coding of Visuomanual Coordination During Reaching in Parietal Area PEc. J Neurophysiol 85:462–467. doi: 10.1152/jn.2001.85.1.462

Ferraina S, Brunamonti E, Giusti MA, et al (2009) Reaching in depth: hand position dominates over binocular eye position in the rostral superior parietal lobule. J Neurosci 29:11461–70. doi: 10.1523/JNEUROSCI.1305-09.2009

Ferraina S, Garasto MR, Battaglia-Mayer A, et al (1997a) Visual control of hand-reaching movement: activity in parietal area 7m. Eur J Neurosci 9:1090–1095. doi: 10.1111/j.1460-9568.1997.tb01460.x

Ferraina S, Johnson PB, Garasto MR, et al (1997b) Combination of hand and gaze signals during reaching: activity in parietal area 7 m of the monkey. J Neurophysiol 77:1034–8. doi: 10.1152/jn.1997.77.2.1034

Filimon F (2010) Human Cortical Control of Hand Movements: Parietofrontal Networks for Reaching, Grasping, and Pointing. Neurosci 16:388–407. doi: 10.1177/1073858410375468

Filimon F, Nelson JD, Huang R-S, Sereno MI (2009) Multiple parietal reach regions in humans: cortical representations for visual and proprioceptive feedback during on-line reaching. J Neurosci 29:2961–71. doi: 10.1523/JNEUROSCI.3211-08.2009

**Filippini M, Breveglieri R, Akhras MA, et al (2017) Decoding information for grasping from the macaque dorsomedial visual stream. J Neurosci 37:4311–4322. doi: 10.1523/JNEUROSCI.3077-16.2017**

**Filippini M, Breveglieri R, Hadjidimitrakis K, et al (2018) Prediction of Reach Goals in Depth and Direction from the Parietal Cortex. Cell Rep 23:725–732. doi: https://doi.org/10.1016/j.celrep.2018.03.090**

Galati G, Committeri G, Pitzalis S, et al (2011) Intentional signals during saccadic and reaching delays in the human posterior parietal cortex. Eur J Neurosci 34:1871–1885. doi: 10.1111/j.1460-9568.2011.07885.x

Galletti C, Battaglini P, Fattori P (1995) Eye position influence on the parieto-occipital area PO (V6) of the macaque monkey. Eur J Neurosci 7:2486–2501. doi: 10.1111/j.1460-9568.1995.tb01047.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. doi: 10.1371/journal.pone.0015078

Galletti C, Fattori P (2018) The dorsal visual stream revisited: Stable circuits or dynamic pathways? Cortex 98:203–217. doi: 10.1016/j.cortex.2017.01.009

Galletti C, Fattori P, Gamberini M, Kutz DF (1999a) The cortical visual area V6: Brain location and visual topography. Eur J Neurosci 11:3922–3936. doi: 10.1046/j.1460-9568.1999.00817.x

Galletti C, Fattori P, Kutz DF, Battaglini PP (1997) Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule. Eur J Neurosci 9:410–3. doi: 10.1111/j.1460-9568.1997.tb01410.x

Galletti C, Fattori P, Kutz DF, Gamberini M (1999b) Brain location and visual topography of cortical area V6A in the macaque monkey. Eur J Neurosci 11:575–582. doi: 10.1046/j.1460-9568.1999.00817.x

Galletti C, Fattori 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. doi: 10.1111/j.1460-9568.1996.tb01165.x

Galletti C, Gamberini M, Kutz DF, et al (2005) The relationship between V6 and PO in macaque extrastriate cortex. Eur J Neurosci 21:959–970. doi: 10.1111/j.1460-9568.2005.03911.x

Galletti C, Kutz DF, Gamberini M, et al (2003) Role of the medial parieto-occipital cortex in the control of reaching and grasping movements. Exp Brain Res 153:158–170. doi: 10.1007/s00221-003-1589-z

Gallivan JP, Cavina-Pratesi C, Culham JC (2009) Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. J Neurosci 29:4381–91. doi: 10.1523/JNEUROSCI.0377-09.2009

Gallivan JP, McLean DA, Valyear KF, et al (2011) Decoding action intentions from preparatory brain activity in human parieto-frontal networks. J Neurosci 31:9599–610. doi: 10.1523/JNEUROSCI.0080-11.2011

Gamberini M, Dal Bò G, Breveglieri R, et al (2018) Sensory Properties of the Caudal Aspect of the Macaque Superior

Parietal Lobule. J Neurosci 223:1863–1879. doi: 10.1007/s00429-017-1593-x

Gamberini M, Galletti C, Bosco A, et al (2011) Is the medial posterior parietal area V6A a single functional area? J Neurosci 31:5145–57. doi: 10.1523/JNEUROSCI.5489-10.2011

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. doi: 10.1002/cne.21980

Georgopoulos AP, Caminiti R, Kalaska JF (1984) Static spatial effects in motor cortex and area 5: quantitative relations in a two-dimensional space. Exp brain Res 54:446–54. doi: 10.1007/bf00235470

Gottlieb J (2007) From thought to action: the parietal cortex as a bridge between perception, action, and cognition. Neuron 53:9–16. doi: 10.1016/j.neuron.2006.12.009

Grafton ST (2010) The cognitive neuroscience of prehension: recent developments. Exp Brain Res 204:475–491. doi: 10.1007/s00221-010-2315-2

Gregory MD, Kippenhan JS, Eisenberg DP, et al (2017) Neanderthal-Derived Genetic Variation Shapes Modern Human Cranium and Brain. Sci Rep 7:6308. doi: 10.1038/s41598-017-06587-0

**Hadjidimitrakis K, Bakola S, Wong YT, Hagan MA (2019) Mixed Spatial and Movement Representations in the Primate Posterior Parietal Cortex. Front Neural Circuits 13:15. doi: 10.3389/fncir.2019.00015**

Hadjidimitrakis 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. Cereb Cortex 24:1645–57. doi: 10.1093/cercor/bht021

**Hadjidimitrakis 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. doi: 10.1007/s00429-016-1319-5**

**Hadjidimitrakis K, Breveglieri R, Bosco A, Fattori P (2012) Three-dimensional eye position signals shape both peripersonal space and arm movement activity in the medial posterior parietal cortex. Front Integr Neurosci 6:37. doi: 10.3389/fnint.2012.00037**

Hadjidimitrakis K, Breveglieri R, Placenti G, et al (2011) Fix Your Eyes in the Space You Could Reach: Neurons in the Macaque Medial Parietal Cortex Prefer Gaze Positions in Peripersonal Space. PLoS One 6:e23335. doi: 10.1371/journal.pone.0023335

Hadjidimitrakis K, Dal Bo' G, Breveglieri R, et al (2015) Overlapping representations for reach depth and direction in caudal superior parietal lobule of macaques. J Neurophysiol 114:2340–52. doi: 10.1152/jn.00486.2015

Heed T, Leone FTM, Toni I, Medendorp WP (2016) Functional versus effector-specific organization of the human posterior parietal cortex: revisited. J Neurophysiol 116:1885–1899. doi: 10.1152/jn.00312.2014

Hill J, Inder T, Neil J, et al (2010) Similar patterns of cortical expansion during human development and evolution. Proc Natl Acad Sci 107:13135–13140. doi: 10.1073/pnas.1001229107

Huang R-S, Chen C -f., Tran AT, et al (2012) Mapping multisensory parietal face and body areas in humans. PNAS 109:18114–18119. doi: 10.1073/pnas.1207946109

Huang R-S, Sereno MI (2018) Multisensory and sensorimotor maps. Handb Clin Neurol 151:141–161. doi: 10.1016/B978-0-444-63622-5.00007-3

Hyvärinen J (1982) Posterior parietal lobe of the primate brain. Physiol Rev 62:1060–1129. doi: 10.1152/physrev.1982.62.3.1060

**Impieri D, Zilles K, Niu M, et al (2019) Receptor density pattern confirms and enhances the anatomic-functional features of the macaque superior parietal lobule areas. Brain Struct Funct 224:2733–2756. doi:**

**10.1007/s00429-019-01930-9**

Iwamura Y, Tanaka M (1996) Representation of reaching and grasping in the monkey postcentral gyrus. Neurosci Lett 214:147–150. doi: https://doi.org/10.1016/0304-3940(96)12911-6

Jeannerod M, Arbib MA, Rizzolatti G, Sakata H (1995) Grasping objects: the cortical mechanisms of visuomotor transformation. Trends Neurosci 18:314–320. doi: 10.1016/0166-2236(95)93921-J

Kalaska JF (1996) Parietal cortex area 5 and visuomotor behavior. Can J Physiol Pharmacol 74:483–98. doi: 10.1139/y96-040

Kalaska JF, Caminiti R, Georgopoulos AP (1983) Cortical mechanisms related to the direction of two-dimensional arm movements: relations in parietal area 5 and comparison with motor cortex. Exp brain Res 51:247–60. doi: 10.1007/bf00237200

Kalaska JF, Cohen DA, Prud'homme M, Hyde ML (1990) Parietal area 5 neuronal activity encodes movement kinematics, not movement dynamics. Exp brain Res 80:351–64. doi: 10.1007/bf00228162

Kalaska JF, Scott SH, Cisek P, Sergio LE (1997) Cortical control of reaching movements. Curr Opin Neurobiol 7:849–859. doi: 10.1016/S0959-4388(97)80146-8

Karnath H-O, Perenin M-T (2005) Cortical control of visually guided reaching: evidence from patients with optic ataxia. Cereb cortex 15:1561–1569. doi: 10.1093/cercor/bhi034

Krubitzer L, Disbrow E (2008) The evolution of parietal areas involved in hand use in primates. In: The senses: a comprehensive reference (Kaas J, Gardner E, eds), Elsevier. London, pp 183–214

Kutz DF, Fattori P, Gamberini M, et al (2003) Early- and late-responding cells to saccadic eye movements in the cortical area V6A of macaque monkey. Exp brain Res 149:83–95. doi: 10.1007/s00221-002-1337-9

Lacquaniti F, Guigon E, Bianchi L, et al (1995) Representing spatial information for limb movement: role of area 5 in the monkey. Cereb Cortex 5:391–409. doi: 10.1093/cercor/5.5.391

Leinonen L, Hyvärinen J, Nyman G, Linnankoski I (1979) I. Functional properties of neurons in lateral part of associative area 7 in awake monkeys. Exp Brain Res 34:299–320. doi: 10.1007/bf00235675

Lewis JW, Van Essen DC (2000a) Mapping of architectonic subdivisions in the macaque monkey, with emphasis on parieto-occipital cortex. J Comp Neurol 428:79–111. doi: 10.1002/1096-9861(20001204)428:1<79::aid-cne7>3.0.co;2-q

Lewis JW, Van Essen DC (2000b) Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. J Comp Neurol 428:112–137. doi: 10.1002/1096-9861(20001204)428:1<112::aid-cne8>3.0.co;2-9

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. doi: 10.1111/j.1460-9568.2005.04149.x

Luppino G, Rizzolatti G (2000) The Organization of the Frontal Motor Cortex. News Physiol Sci 15:219–224. doi: 10.1152/physiologyonline.2000.15.5.219

Mackay WA, Mendonça AJ, Riehle A (1994) Spatially modulated touch responses in parietal cortex. Brain Res 645:351–355. doi: 10.1016/0006-8993(94)91673-X

Matelli M, Govoni P, Galletti C, et al (1998) Superior area 6 afferents from the superior parietal lobule in the macaque monkey. J Comp Neurol 402:327–352. doi: 10.1002/(SICI)1096-9861(19981221)402:3<327::AID-CNE4>3.0.CO;2-Z

Matelli M, Luppino G, Rizzolatti G (1991) Architecture of superior and mesial area 6 and the adjacent cingulate cortex in the macaque monkey. J Comp Neurol 311:445–462. doi: 10.1002/cne.903110402

McGuire LMM, Sabes PN (2011) Heterogeneous representations in the superior parietal lobule are common across reaches to visual and proprioceptive targets. J Neurosci 31:6661–73. doi: 10.1523/JNEUROSCI.2921-10.2011

Menzer DL, Rao NG, Bondy A, et al (2014) Population interactions between parietal and primary motor cortices during reach. J Neurophysiol 112:2959–84. doi: 10.1152/jn.00851.2012

Morecraft RJ, Cipolloni PB, Stilwell-Morecraft KS, et al (2004) Cytoarchitecture and cortical connections of the posterior cingulate and adjacent somatosensory fields in the rhesus monkey. J Comp Neurol 469:37–69. doi: 10.1002/cne.10980

Mountcastle VB, Lynch JC, Georgopoulos A, et al (1975) Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. J Neurophysiol 38:871–908. doi: 10.1152/jn.1975.38.4.871

Murray EA, Coulter JD (1981a) Supplementary Sensory Area BT - Cortical Sensory Organization: Volume 1: Multiple Somatic Areas. In: Woolsey CN (ed). Humana Press, Totowa, NJ, pp 167–195

Murray EA, Coulter JD (1981b) Organization of corticospinal neurons in the monkey. J Comp Neurol 195:339–365. doi: 10.1002/cne.901950212

Olson CR, Musil SY, Goldberg ME (1996) Single neurons in posterior cingulate cortex of behaving macaque: eye movement signals. J Neurophysiol 76:3285–3300. doi: 10.1152/jn.1996.76.5.3285

Padberg J, Cooke DF, Cerkevich CM, et al (2019) Cortical connections of area 2 and posterior parietal area 5 in macaque monkeys. J Comp Neurol 527:718–737. doi: 10.1038/nmeth.2250.Digestion

Padberg J, Franca JG, Cooke DF, et al (2007) Parallel Evolution of Cortical Areas Involved in Skilled Hand Use. J Neurosci 27:10106–10115. doi: 10.1523/JNEUROSCI.2632-07.2007

Pandya DN, Seltzer B (1982) Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. J Comp Neurol 204:196–210. doi: 10.1002/cne.902040208

Passarelli L, Rosa MGP, Bakola S, et al (2018) Uniformity and Diversity of Cortical Projections to Precuneate Areas in the Macaque Monkey: What Defines Area PGm? Cereb Cortex 28:1700–1717. doi: 10.1093/cercor/bhx067

Passarelli L, Rosa MGP, 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. doi: 10.1523/JNEUROSCI.4784-10.2011

Penfield W, Welch K (1951) The supplementary motor area of the cerebral cortex: a clinical and experimental study. AMA Arch Neurol Psychiatry 66:289–317. doi: 10.1001/archneurpsyc.1951.02320090038004

Perenin M-T, Vighetto A (1988) Optic Ataxia: a specific disruption in visuomotor mechanisms. Brain 111:643–674. doi: 10.1093/brain/111.3.643

Pisella L, Rossetti Y, Rode G (2017) Optic ataxia in Bálint-Holmes syndrome. Ann Phys Rehabil Med 60:148–154. doi: https://doi.org/10.1016/j.rehab.2016.01.003

Piserchia V, Breveglieri R, Hadjidimitrakis K, et al (2017) Mixed Body/Hand Reference Frame for Reaching in 3D Space in Macaque Parietal Area PEc. Cereb Cortex 27:1976–1990. doi: 10.1093/cercor/bhw039

Pitzalis S, Galletti C, Huang R-S, et al (2006) Wide-field retinotopy defines human cortical visual area v6. J Neurosci 26:7962–73. doi: 10.1523/JNEUROSCI.0178-06.2006

**Pitzalis S, Serra C, Sulpizio V, et al (2019) A putative human homologue of the macaque area PEc. Neuroimage 202:116092. doi: 10.1016/j.neuroimage.2019.116092**

Pons TP, Garraghty PE, Cusick CG, Kaas JH (1985) The somatotopic organization of area 2 in macaque monkeys. J

Comp Neurol 241:445–466. doi: 10.1002/cne.902410405

Raffi M, Carrozzini C, Maioli MG, Squatrito S (2010) Multimodal representation of optic flow in area PEc of macaque monkey. Neuroscience 171:1241–1255. doi: 10.1016/j.neuroscience.2010.09.026

**Raffi M, Maioli MG, Squatrito S (2011) Optic flow direction coding in area PEc of the behaving monkey. Neuroscience 194:136–149. doi: 10.1016/j.neuroscience.2011.07.036**

Raffi M, Persiani M, Piras A, Squatrito S (2014) Optic flow neurons in area PEc integrate eye and head position signals. Neurosci Lett 568:23–28. doi: 10.1016/j.neulet.2014.03.042

Riehle A, Vaadia E (2004) Motor cortex in voluntary movements: a distributed system for distributed functions. CRC Press

Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: Anatomy and functions. Exp Brain Res 153:146–157. doi: 10.1007/s00221-003-1588-0

Sakata H, Takaoka Y, Kawarasaki A, Shibutani H (1973) Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. Brain Res 64:85–102. doi: 10.1016/0006-8993(73)90172-8

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. doi: 10.1038/s41598-018-25117-0

Sato N, Sakata H, Tanaka YL, Taira M (2006) Navigation-associated medial parietal neurons in monkeys. Proc Natl Acad Sci U S A 103:17001–6. doi: 10.1073/pnas.0604277103

Sato N, Sakata H, Tanaka YL, Taira M (2010) Context-Dependent Place-Selective Responses of the Neurons in the Medial Parietal Region of Macaque Monkeys. Cereb Cortex 20:846–858. doi: 10.1093/cercor/bhp147

Scheperjans F, Eickhoff SB, Hömke L, et al (2008) Probabilistic maps, morphometry, and variability of cytoarchitectonic areas in the human superior parietal cortex. Cereb cortex 18:2141–2157. doi: 10.1093/cercor/bhm241

Scott SH, Sergio LE, Kalaska JF (1997) Reaching movements with similar hand paths but different arm orientations. II. Activity of individual cells in dorsal premotor cortex and parietal area 5. J Neurophysiol 78:2413–26. doi: 10.1152/jn.1997.78.5.2413

Seelke AMH, Padberg JJ, Disbrow E, et al (2012) Topographic Maps within Brodmann's Area 5 of Macaque Monkeys. Cereb Cortex 22:1834–1850. doi: 10.1093/cercor/bhr257

Sereno MI, Huang R-S (2014) Multisensory maps in parietal cortex. Curr Opin Neurobiol 24:39–46. doi: 10.1016/j.conb.2013.08.014

Shipp S, Blanton M, Zeki S (1998) A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: Cortical connections of areas V6 and V6A. Eur J Neurosci 10:3171–3193. doi: 10.1046/j.1460-9568.1998.00327.x

Snyder LH, Batista AP, Andersen RA (1997) Coding of intention in the posterior parietal cortex. Nature 386:167–70. doi: 10.1038/386167a0

Snyder LH, Batista AP, Andersen RA (1998) Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. J Neurophysiol 79:2814–2819. doi: 10.1152/jn.1998.79.5.2814

Tosoni A, Pitzalis S, Committeri G, et al (2015) Resting-state connectivity and functional specialization in human medial parieto-occipital cortex. Brain Struct Funct 220:3307–21. doi: 10.1007/s00429-014-0858-x

Verhagen L, Dijkerman HC, Medendorp WP, Toni I (2013) Hierarchical organization of parietofrontal circuits during goal-directed action. J Neurosci 33:6492–503. doi: 10.1523/JNEUROSCI.3928-12.2013

Vesia M, Barnett-Cowan M, Elahi B, et al (2017) Human dorsomedial parieto-motor circuit specifies grasp during the planning of goal-directed hand actions. Cortex 92:175–186. doi: 10.1016/j.cortex.2017.04.007

Vesia M, Crawford JD (2012) Specialization of reach function in human posterior parietal cortex. Exp brain Res 221:1–18. doi: 10.1007/s00221-012-3158-9

Vogt C, Vogt O (1919) Allgemeinere Ergebnisse unserer Hirnforschung. Zweite Mitteilung. Das Wesen der topischen architektonischen Differenzen des Cortex cerebri. J Psychol Neurol 25:292–360.

von Economo CF, Koskinas GN (1925) Die cytoarchitektonik der hirnrinde des erwachsenen menschen. J. Springer

Wise SP, Boussaoud D, Johnson PB, Caminiti R (1997) Premotor and parietal cortex: Corticocortical Connectivity and Combinatorial Computations. Annu Rev Neurosci 20:25–42. doi: 10.1146/annurev.neuro.20.1.25

## Legends

**Fig. 1** Parietal cortex **in Old World monkey**.
(A) Lateral view of the **left** hemisphere **of an Old World monkey brain**. Top: **the** anterior parietal cortex **is** colored in yellow; superior and inferior parietal lobules in **the** posterior parietal cortex in green and red, respectively. Bottom: close-up showing, enlarged, **a brain** region **including** SPL, **with the original Brodmann's parcellation (Brodmann 1909);** area 5 **is colored** in blue, area 7 in orange. (B) Vogt and Vogt's parcellation of posterior parietal cortex (modified from Vogt and Vogt 1919). Top: drawings of medial and lateral surfaces of **left** cerebral hemisphere. Bottom: close-up showing, enlarged, the SPL in color, with areas 5a and 5b colored in blue being indicated by Vogt and Vogt as parts of area 5. (C) Pandya and Seltzer's parcellation of posterior parietal cortex (modified from Pandya and Seltzer 1982). Top: drawings of medial and lateral surfaces of **left** cerebral hemisphere, with cingulate and intraparietal sulci open to show the areas hidden inside (see close-up on the bottom). Bottom: close-up showing, enlarged, the region of areas PE, PEc, PEci and PEa, all colored in blue being indicated by Pandya and Seltzer as parts of area 5.
Abbreviations: as, arcuate sulcus; cgs, cingulate sulcus; cs, central sulcus; lf, lateral fissure; ls, lunate sulcus; sts, superior temporal sulcus; ips, intraparietal sulcus; pcd, post-central dimple; pos, parieto-occipital sulcus; cc, corpus callosum; PGm, PEc, PE, PEci, PEa, 5a, 5b, 7a, 7b: areas PGm, PEc, PE, PEci, PEa, 5a, 5b, 7a, 7b.

**Fig. 2** Areal parcellation of macaque superior parietal lobule.
(A) Posterolateral view of macaque brain. The right hemisphere has been partially dissected at the level of the fundus of intraparietal, parieto-occipital, and lunate sulci to show the hidden cortex of SPL. The medial surface of the left hemisphere is also visible, with the cingulate sulcus open to show area PEci hidden inside. **Dashed lines delimit different cortical areas of SPL. Labels 'B' and 'C' indicate the regions of the brain whose cyto- and myeloarchitectures are illustrated below in panels B and C, respectively.** (B) High power photomicrographs of the cytoarchitectonic organization of V6 and V6A (modified from Luppino et al. 2005). Pictures show the major features that distinguish the occipital pattern of V6 from the parietal pattern of V6A (see text for details). Scale bar, 200 µm. (C) High power photomicrographs of representative myeloarchitectonic fields of areas MIP and PEip (modified from Bakola et al. 2017), showing the well-separated bands of Baillarger of area MIP, and the relatively light myelination of area PEip (Scale bar, 1 mm).
Abbreviations: cal, calcarine sulcus; ios, inferior occipital sulcus; ots, occipito-temporal sulcus; ps, principal sulcus; pre-cd, precentral dimple; V6, V6A, 31, MIP, PEip: areas V6, V6A, 31, MIP, PEip. Other abbreviations as in Fig. 1.

**Fig. 3** Summary of **the** main cortico-cortical connections of areas PE, PEc, V6A, PGm, MIP.
(A-E) Cortical connections of areas PE, PEc, V6A, PGm, and MIP, respectively. For each area, only projections representing more than 1% of the total cortical connections of that area are reported. The thickness of connecting lines is proportional to the strength of connections, as indicated in the legend within the figure, averaged across all cases with injections in the same area (data obtained from Gamberini et al. 2009; Bakola et al. 2010, 2013, 2017; Passarelli et al. 2011, 2018).
Abbreviations: D, dorsal; P, posterior; F1, F2, F3, F4, F5, F7, FEF, 23, 24, PFop, PGop, PG, Opt, Ri, 46, AIP, LIP, VIP, V2, V3, V4, MST: areas F1, F2, F3, F4, F5, F7, FEF, 23, 24, PFop, PGop, PG, Opt, Ri, 46, AIP, LIP, VIP, V2, V3, V4, MST; PFC, prefrontal cortex areas 8, 9, 10 and 12; RSC, retrosplenial cortex **(**areas 29, 30**);** 23i, 23v, **posterior cingulate cortex**; Vis, visual cortex ventral to area PGm; cST, caudal superior temporal areas MST and TPO; EXT, extrastriate areas V2, V3, V4, MST, V6, PIP, and TEO; ParOp, parietal operculum. Other abbreviations as in Figs. 1 and 2.

**Fig. 4** Frontal connections of areas PE, PEc, V6A.
(A) Posterolateral view of left hemisphere of macaque brain partially dissected as in Figure 2 to show the cortex hidden into parieto-occipital and intraparietal sulci. Colored zones represent the injected areas PE (red), PEc (green), V6A (yellow). (B) Lateral view of macaque's left hemisphere, with highlighed the frontal lobe enlarged in (C). (C) Frontal lobe

with cells (colored dots) labeled after **retrograde** tracer injection in areas PE (red; three injections), PEc (green; three injections), V6A (yellow; five injections) **(data obtained from Gamberini et al. 2009; Bakola et al. 2010, 2013; Passarelli et al. 2011).** (D) Parcellation of agranular frontal cortex showing, overimposed, the representations of various body parts (modified from Matelli et al. 1991; Luppino and Rizzolatti 2000). Other details and abbreviations as in Figs. 1-3.

**Fig. 5** Functional organization of **Brodmann's** areas 1, 2, 3, 5 **in macaque monkey**.
(A) Summary of the functional subdivisions of anterior parietal areas 3a, 3b, 1, 2, and of posterior parietal area 5 (area PE). Notice that the medial part of area 5 has not been studied (modified from Seelke et al. 2012). (B) Dorsolateral view of macaque's left hemisphere. The enlarged close-up on the bottom shows in yellow the part of area 5 recorded from, in the whole, by the following studies (Kalaska et al. 1983, 1990; Mackay et al. 1994; Lacquaniti et al. 1995; Scott et al. 1997; Ferraina et al. 2009; McGuire and Sabes 2011; Bremner and Andersen 2012; Seelke et al. 2012; Menzer et al. 2014; Brunamonti et al. 2016; Padberg et al. 2019). **In orange, it is reported the recording site of a recent study focused on the medial part of PE (De Vitis et al. 2019).**
Abbreviations: IPS, intraparietal sulcus; PCS, post-central sulcus. Other details and abbreviations as in Figs. 1-3.

**Fig. 6 Somatic representations in areas PE, PEc, V6A.**
**A posterolateral view of the left hemisphere of a macaque brain, partially dissected as in Figure 2, is shown on the top left of the figure to show the cortex hidden into parieto-occipital and intraparietal sulci. Dashed lines delimit different cortical areas of SPL. Areas PE, PEc, and V6A are indicated in red, green, and yellow, respectively.**
**(A-D) Column plots reporting the incidence of somatosensory cells (A), different submodalities of somatosensory responses ("more" are cells driven by more than one type of stimulation, as for instance joint and deep stimulations) (B), body part representation (C), and laterality of somatosensory responses (D), in areas PE, PEc, V6A; the results of $\chi 2$ test are indicated by asterisks, ***$p < 0.005$; *$p < 0.05$. (E) Body locations of somatosensory (patches) and joints (circles) RFs in PE (red), PEc (green) and V6A (yellow). All RFs have been reported on the animal's right side. RFs reported on the left arm represent RFs located on the internal part of the arm (not visible if drawn on the right arm). Boxes to the right of monkey's silhouettes report close-up view of the hand in V6A and foot in PEc.**
**Data for PE have been obtained by De Vitis and coworkers (De Vitis et al. 2019), for PEc and V6A by Gamberini and coworkers (Gamberini et al. 2018).**

**Fig. 7** Reaching and grasping properties of area V6A neurons.
(A) Cell tuned by the direction of arm movement. (B) Cell modulated by wrist orientation. (C) Cell modulated by the grip type. (D) Cell modulated by both reaching and grasping activities (notice that it is the same cell shown in (A)). Cell responses are shown as peri-event time histograms and raster displays of impulse activity, aligned at the arm movement onset (black triangle). Below cell responses, recordings of X and Y components of eye positions are reported. Reach-to-grasp arm movements were performed in the dark during foveal reach-to-grasp tasks. To the left and right of cell responses, the sketches of hand actions performed by monkey are shown.
Scale: vertical bar on histograms, 113 spikes/s; eye traces, 60°/ per vertical division. Modified from Fattori et al. (2009, 2010, 2017).

**Fig. 8** Functional properties of V6A neurons.
(A) Cell modulated by eye position. The figure shows the visual responses of a cell evoked by receptive field stimulation (peri-event time histograms, raster-plots of cell activity) while animal gazed at nine different positions on a frontal screen, in darkness (modified from Galletti et al. 1995). (B) Cell modulated by saccadic eye movements performed in different directions (towards 8 different positions on a frontal screen, in darkness). For each saccade direction, the peri-saccade time histogram, raster-plot of cell activity, and eye-traces aligned to saccade onset are reported. The central polar plot shows the entity of cell activity for saccades performed in the different tested directions (modified from Kutz et al. 2003). (C) Cell modulated by covert spatial attention: the animal gazed at a stationary fixation point in the central part of a frontal screen (cross) while attending to one of 8 different screen positions (spots), in darkness; the grey level of the 8 spots indicates the entity of cell activity while the animal covertly attended to that spatial location (attending to the bottom parts of the screen increased cell activity). On the bottom of the figure, spike density functions of cell activity for each of the 8 cued positions are superimposed and aligned at the cue onset: cell discharge was strongly modulated by the covertly attended spatial position (modified from Galletti et al. 2010). (D) Cell sensitive to the object affordance. The cell strongly discharged when the animal grasped a handle, but not when it grasped a plate (bottom part of the figure), despite the similarity of the two objects from the animal point of view (see top left). Cell response was about the same no matter whether the grasped object was thin or thick (see the bottom part of the panel). In other words, since from the point of view of the animal the handle and plate looked very similar when of the same thickness, this cell discharged according to the affordance (graspability) of the object, not according to the visual features of it. Neural activity is shown as peri-stimulus time histograms aligned at the onset of object illumination (dark bars under peri-stimulus time histograms; modified from Breveglieri et al. 2015).

Scale: (A) 12 spikes/s per vertical division, 400 ms per horizontal division. (B-D) 75, 70, 45, spikes/s, respectively, per vertical division; eye traces in B, 60°/ per vertical division.

**Fig. 9 Brodmann's parcellation of the cerebral cortex and p**ostnatal cortical expansion **in the** human brain.
**(A-B) Brodmann's parcellation of the cerebral cortex in monkey and human (Brodmann 1909). Red outlines enclose area 5 in monkey and human brains. (C)** Lateral and dorsal views of the **left** hemisphere of the F99 macaque atlas with a number of typical ROIs labeled. (**D**) Lateral and dorsal views of the **left** hemisphere of a human brain showing with different colors the postnatal surface expansion of brain cortex, overlaid with the same ROIs showed in (**C**) for macaque brain. Yellow areas indicate the regions of maximum postnatal cortical expansion. The **approximate** location of Brodmann's area 5 is indicated **in the dorsolateral cortical surface of the brain by dashed red outlines** in macaque (**C**) and dashed oval white outline in human (**D**) brains (modified from Hill et al. 2010).
Abbreviations: BA5, Brodmann area 5; 10, 21, Brodmann area 10, 21; FEF, frontal eye fields; HG, Heschl's gyrus; **IPL, inferior parietal lobule;** LIPv, ventral part of lateral intraparietal cortex; 7a and 7b, parietal areas 7a and 7b; MFG, anterior third of the middle frontal gyrus; MT, medial temporal visual region; PFC, prefrontal cortex; STPp, visual region on anterior bank of superior temporal sulcus; TEa, visual region on the posterior bank of the superior temporal sulcus; TEpd, visual region on the inferior temporal gyrus; V1, primary visual cortex; V2, secondary visual cortex.

**Fig. 10** Somatotopic and visuotopic representations in human frontal, parietal, and occipital cortex.
(A) Group-average somatotopic ROIs overlaid on group-average retinotopic maps displayed on single subject cortical surface (left hemisphere). Colored contours and areas indicate somatotopic and visual representations, respectively, as indicated in the legend within the figure (modified from Huang et al. 2012). (B) Group-average map of somatotopic areas activated by passive tactile stimulation, superimposed on a faded retinotopic map. (C) Map of action representations in parietal and frontal cortices. Yellow labels indicate specific actions activating that part of cortex (according to the abbreviations reported here below). Data shown in B-C are from Huang & Sereno (2018).
Abbreviations: PBA, parietal body area; VIP+, human parietal face area; M, medial; A, anterior;
IFS and SFS, inferior and superior frontal sulci; LH, left hemisphere; LIP+, human homolog of macaque lateral intraparietal area; LoVF, lower visual field; OPA, occipital place area; UpVF, upper visual field; D, defense; E, eye movements; F, feeding; G, grasping; P, pointing; R, reaching; T, touching; W, walking.

**Fig. 11 The** SPL in human and non-human primates.
**(A) Posterolateral view of a partially dissected macaque brain, showing the different SPL areas as in Fig. 2A. The region colored in light blue (area V6) is a visual cortex that is likely part of Brodmann's area 19; the region colored in orange (areas V6A, MIP, PEc, PGm) is responsive to both visual and somatosensory stimulations and according to the present data is likely part of Brodmann's area 7; the region colored in blue (areas PE, PEip, PEci) is responsive to somatosensory stimulations but not to visual stimulations, and is likely part of Brodmann's area 5. (B)** Dorsal view of macaque brain showing the location and extent of **a number of** SPL areas and of **part of** Brodmann's area 19 **in the fundus of the parieto-occipital sulcus. (C)** Dorsal view of human brain showing the location and extent of Brodmann's areas 5 (blue), 7 (orange), and 19 (light blue). (**D**) Maximum probability map of areas of the human superior parietal cortex **according to Scheperjans et al. (2008)**. The point of view is posterior with an elevation of 45° from the horizontal plane, as shown by the arrow in the inset in the left upper corner. Modified from Scheperjans et al. (2008). (**E**) Dorsal view of the inflated representation of the left hemisphere of Conte69 surface-based atlas showing the location and extent in the human brain of areas hPE, hPEc, hV6A (data obtained from Pitzalis et al. **2019**), and V6 (data obtained from Pitzalis et al. 2006).
Abbreviations: 5L and 5M, lateral and medial subdivision of area 5; 7PC, 7A, 7P, 7M, postero-caudal, anterior, posterior and medial subdivision of area 7. **Other details and abbreviations as in Figs. 1-2.**