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REVIEW

Specialization of reach function in human posterior parietal cortex

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Abstract Posterior parietal cortex (PPC) plays an important role in the planning and control of goal-directed action. Single-unit studies in monkeys have identified reach-specific areas in the PPC, but the degree of effector and computational specificity for reach in the corresponding human regions is still under debate. Here, we review converging evidence spanning functional neuroimaging, parietal patient and transcranial magnetic stimulation studies in humans that suggests a functional topography for reach within human PPC. We contrast reach to saccade and grasp regions to distinguish functional specificity and also to understand how these different goal-directed actions might be coordinated at the cortical level. First, we present the current evidence for reach specificity in distinct modules in PPC, namely superior parietal occipital cortex, midposterior intraparietal cortex and angular gyrus, compared to saccade and grasp. Second, we review the evidence for hemispheric lateralization (both for hand and visual hemifield) in these reach representations. Third, we review evidence for computational reach specificity in these regions and finally propose a functional framework for these human PPC reach modules that includes (1) a distinction between the encoding of reach goals in posterior–medial PPC as opposed to reach movement vectors in more anterior–lateral PPC regions, and (2) their integration within a broader cortical framework for reach, grasp and eye–hand coordination. These findings represent both a confirmation and extension of findings that were previously reported for the monkey.

Keywords Reaching · Pointing · Grasping · Saccades · Posterior parietal cortex · Visuomotor control · Eye–hand coordination · TMS · *f*MRI · Optic ataxia

Introduction

A fundamental problem in systems neuroscience is determining *how* and *where* the central nervous system achieves the planning and control of voluntary movement. Converging evidence from nonhuman primate neurophysiology has implicated posterior parietal cortex (PPC) in several aspects of the early transformations for visually guided reach (Kalaska et al. 1997; Rizzolatti et al. 1997; Caminiti et al. 1998; Colby and Goldberg 1999; Andersen and Buneo 2002; Galletti et al. 2003). Human PPC also has been implicated in visuomotor function, primarily through human brain imaging studies (Culham and Kanwisher 2001; Grefkes and Fink 2005; Culham et al. 2006; Culham and Valyear 2006; Iacoboni 2006; Filimon 2010) and patient studies (Perenin and Vighetto 1988; Goodale and Milner 1992; Jeannerod et al. 1995; Rossetti et al. 2003; Coulthard et al. 2006; Pisella et al. 2009). However, the degree of functional specialization for reach within human PPC, that is, as opposed to other motor functions, is less clear than in monkey (Levy et al. 2007); *for review see* (Filimon 2010).

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Much of this controversy is likely due to the spatiotemporal limitations of early approaches in neuroimaging and neuropsychology, but as these techniques continuously advance and are supplemented by techniques such as magnetoencephalography (MEG) and transcranial magnetic stimulation (TMS), a picture of human PPC function is emerging that is compatible with monkey neurophysiology and at times makes new advances.

The purpose of this review is to summarize these recent advances in human systems neuroscience. Parietal cortex is also engaged in other functions (Colby and Goldberg 1999; Husain and Nachev 2007; Bisley and Goldberg 2010; Corbetta and Shulman 2010), but we focus our review to entail the early visuomotor representations in PPC of a simple and well-studied behaviour: hand movements made either directly toward a visual goal or after a brief delay. The latest advances in the study of parieto-frontal connectivity were highlighted recently elsewhere (Andersen and Cui 2009; Koch and Rothwell 2009; Filimon 2010; Grafton 2010; Davare et al. 2011a; Medendorp et al. 2011; Rothwell 2011). We begin by providing an overview of the necessary background of the monkey literature related to visuomotor specificity within PPC before proceeding to these issues in humans with focus on our recent TMS and neuroimaging studies. We then consider three aspects of reach specialization in human PPC: effector specificity, hemispheric laterality and computational specificity, ending with a functional model of the PPC regions involved in the planning and control of visuomotor action.

Overview of visuomotor specificity in monkey PPC

Although this review emphasizes recent advances in human systems neuroscience, neurophysiological studies in nonhuman primates provide a template for our understanding of specialization of human PPC function (Johnson et al. 1996; Andersen 1997; Kalaska et al. 1997; Rizzolatti et al. 1997; Colby and Goldberg 1999; Andersen and Buneo 2002; Galletti et al. 2003; Andersen and Cui 2009). Here, we provide the necessary background of the functional subdivisions for visuomotor control in the monkey (Fig. 1a).

A number of areas in macaque PPC are preferentially active for preparing distinct types of actions involving different body parts, that is, arm, hand, eye (Graziano and Gross 1998; Andersen and Cui 2009; Caminiti et al. 2010), particularly within the intraparietal sulcus (IPS) (Blatt et al. 1990). Areas located in the posteromedial region of IPS contribute to the planning of reaching movements toward objects, whereas a more anterolateral portion of IPS integrate grasp-related information about an object. Specifically, several more medial reach-related clusters (Fig. 1a, red ellipses) have been identified including medial intraparietal area (MIP) (Johnson et al. 1996; Eskandar and Assad 1999), area 5 (Kalaska 1996; Ferraina et al. 2001), area 7A (MacKay 1992; Johnson et al. 1996; Battaglia-Mayer et al. 2000), V6A (situated between V6 and MIP within the superior parietal cortex near the junction of the dorsal parieto-occipital sulcus, POS) (Fattori et al. 2001, 2009a; Galletti et al. 2003) and a putative ‘parietal reach region’ (PRR) that straddles the boundary between MIP and V6A (Batista et al. 1999; Buneo et al. 2002; Chang et al. 2008; Andersen and Cui 2009). PRR is more medial and posterior to the putative ‘parietal eye field’ (PEF) (Andersen et al. 1992), which is situated in approximately the middle third of the lateral bank of IPS (lateral intraparietal area, LIP; Fig. 1a, blue ellipse), and is activated by both saccades (Snyder et al. 1997; Andersen and Buneo 2002; Andersen and Cui 2009) and attention (Colby and Goldberg 1999) Neurons in anterior intraparietal area (AIP) play a key role in hand preshaping and object-directed hand grasping (Fig. 1a, purple ellipse) (Gallese et al. 1994; Baumann et al. 2009); *for recent reviews on grasping see* (Castiello 2005; Tunik et al. 2007; Castiello and Begliomini 2008; Grafton 2010; Davare et al. 2011a). Consistent with these subdivisions, microstimulation of different parts of monkey PPC evokes a vast array of complex movements, including reaching, grasping and eye movements (Stepniewska et al. 2005).

Importantly, these parietal clusters are thought to subtend diverse functions (Averbeck et al. 2009): (1) Mediolateral parietal cluster (i.e. V6A and LIP) is at the core of the visuomotor transformation underlying eye and to some extent hand movements to salient visual targets, as well as belonging to the early stages of eye–hand coordination underlying reaching movements (Battaglia-Mayer et al. 2001; Mascaro et al. 2003); (2) dorsal parietal cluster (i.e. MIP) is crucial for the integration of visual and somatic information, which occurs at the single cell level, for reaching movements (Johnson et al. 1996); and (3) ventral parietal cluster (i.e. AIP) is composed of areas involved in the visual control of hand–object interaction, such as grasping (Rizzolatti and Matelli 2003), and to a certain extent reaching. Further, LIP, PRR and AIP are connected mainly to frontal lobe areas with similar functional selectivity: LIP to the frontal eye fields (FEF) (Fig. 1a, blue arrow) (Pare and Wurtz 2001); the occipito–parietal circuit of V6A and MIP (i.e. PRR) to the dorsal premotor cortex (PMd) (Fig. 1a, red arrow) (Wise et al. 1997); and AIP to the ventral premotor cortex (PMv) (Fig. 1a, purple arrow) (Rizzolatti and Luppino 2001).

Despite this dissociation, reach- and saccade-related activity in monkey is relative and not absolute (Snyder et al. 1997, 2000; Calton et al. 2002). Similarly, recent findings in neurons in macaque area V6A challenge the view that reach and grasp components are processed independently (Fattori et al. 2009b, 2010) and are

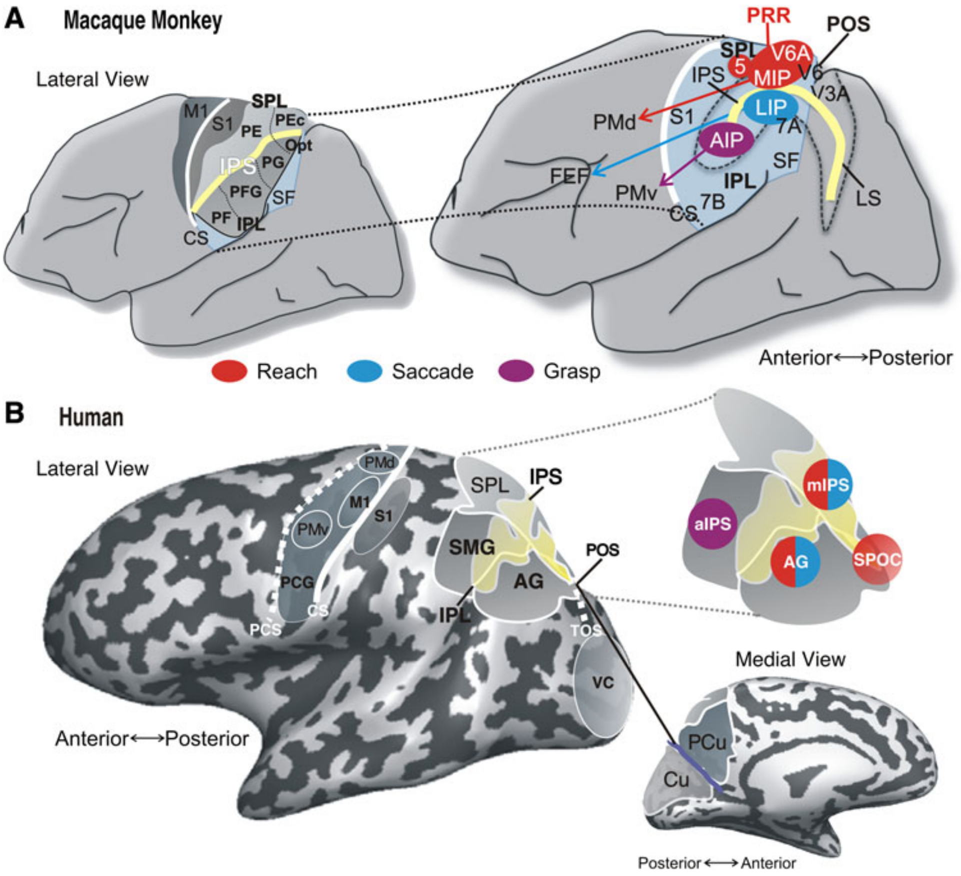


Fig. 1 Comparison of monkey and human parietal lobes. **a** Macaque monkey brain showing basic anatomy and putative specialization of visuomotor function in posterior parietal cortex for saccade, reach and grasp. Intraparietal sulcus (IPS) and lunate sulcus (LS) of monkey brain in rightmost panel have been opened up to reveal the fundus and banks of each sulcus. **b** Human brain neuroanatomy differs substantially from that of monkey. *CS* central sulcus, *SF* sylvian fissure, *POS* parieto-occipital sulcus, *TOS* transverse occipital sulcus, *PCS* postcentral sulcus, *SPL* superior parietal lobule (PE, PEc), *IPL* inferior parietal lobule (Opt, PG, PFG, PF), *S1* primary somatosensory cortex, *M1* primary motor cortex, *Brodmann's areas 5* 7A and 7B, *visual areas V3A* V6A, *AIP* anterior, *MIP* medial, *LIP* lateral sections of IPS, *VC* visual cortex, *AG* angular gyrus, *aIPS* anterior part of IPS, *mIPS* midposterior part of IPS, *SPOC* superior parieto-occipital cortex, *PMd* dorsal premotor cortex, *PMv* ventral dorsal premotor cortex, *FEF* frontal eye fields, *SMG* supramarginal gyrus, *PCG* postcentral gyrus, *PCu* precuneus, *Cu* cuneus (*see text for details*)

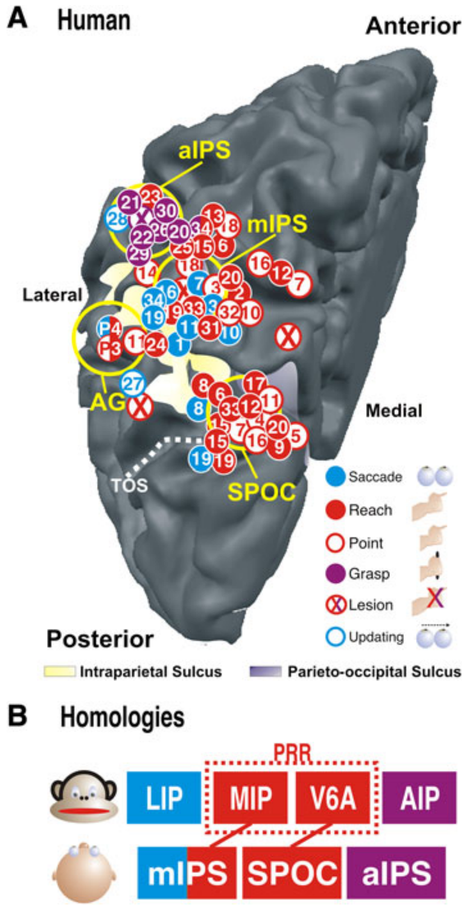
consistent with recent anatomical evidence showing connectivity between V6A and AIP (Borra et al. 2008).

The corresponding human anatomical areas are shown in Fig. 1b. Opportunities to record from individual neurons in humans are very limited, but current human neuroscience techniques provide an opportunity to identify homologies in regional specialization between the two species (Fig. 2b). In the subsequent sections, we delve into this topic in some detail, focusing on recent evidence for reach specificity from neuroimaging, patient and TMS studies (Fig. 2a),

Reach effector specificity in human PPC

Reach versus saccades

Reach-related signals have been surprisingly difficult to dissociate from saccade signals in human PPC. In humans, functional neuroimaging has revealed a large overlap of PPC activation during the planning of hand and eye movements (Fig. 3a) (Beurze et al. 2007, 2009; Levy et al. 2007; Hinkley et al. 2009). Several different nonmutually exclusive factors may account for this phenomenon. First, these undifferentiated activations for distinct movements could be explained by the fact that traditional functional magnetic resonance imaging (*f*MRI) approaches show the average activity within a given area and might be unable to distinguish the neural information contained in distributed patterns of voxel activity (Gallivan et al. 2011a, b). Second, given that the close neuroanatomical location of MIP and LIP and the dissociation of reach- and saccade-related activity in monkey PPC is not strict (Snyder et al. 1997, 2000; Calton et al. 2002), similar levels of detection might be difficult to distinguish in the blood oxygenation level-dependant (BOLD) *f*MRI signal (Logothetis 2008) because the BOLD effects caused by the functionally different



◀ **Fig. 2** Comparison of fMRI, patient and TMS studies. **a** Parietal sites discussed in current review (*open yellow circles*): AG, aIPS, mIPS and SPOC, shown on a dorsomedial view of the *left hemisphere*. A summary of peak activation, lesion and stimulation sites for saccade (*solid blue circle*), reach- (*red filled circle*), pointing- (*open red circle*) and grasp-selective (*solid purple circle*) regions identified in PPC by previous key studies in visuomotor control is listed below. Note that foci were based on reported Talairach coordinates transformed to surface locations on a subject's pial surface and represent averaged group peaks of activity, lesion overlap and stimulation area; *shaded yellow area*, intraparietal sulcus; *shaded blue area*, parieto-occipital sulcus; *dotted white line*, temporal occipital sulcus (TOS). *f*MRI activation, lesion foci and TMS sites are as follows: *Saccade*: 1 (Sereno et al. 2001; Merriam et al. 2003), 8 (Schluppeck et al. 2005, 2006), P4 (Elkington et al. 1992; Müri et al. 1996; Müri et al. 2000; Kapoula et al. 2001; Yang and Kapoula 2004; Nyffeler et al. 2005); *Saccade and Reach*: 8 (Levy et al. 2007), 19 (Beurze et al. 2009), 33 (Vesia et al. 2010); *Saccade and Point*: 3 (Medendorp et al. 2003), 7 (Zettel et al. 2007), 10 (Hagler et al. 2007), 11 (Fernandez-Ruiz et al. 2007), 16 (Tosoni et al. 2008); *Reach*: 2 (Pellijeff et al. 2006), 6 (Prado et al. 2005), 9 (Culham et al. 2008; Gallivan et al. 2009), 12 (Filimon et al. 2009), 13 (Beurze et al. 2007), 15 (Blangero et al. 2009), 17 (Busan et al. 2009b; Busan et al. 2009a), P3 (van Donkelaar and Adams 2005; Vesia et al. 2006, 2008; Koch et al. 2008), 31 (Striemer et al. 2011); *Point*: 3 (Medendorp et al. 2005), 4 (Astafiev et al. 2003), 5 (Connolly et al. 2003), 14 (DeSouza et al. 2000), 32 (Davare et al. 2012); *Grasp*: 21 (Davare et al. 2007), 29 (Culham et al. 2003), 30 (Frey et al. 2005); *Grasp and Reach*: 20 (Cavina-Pratesi et al. 2010b); *Saccade, Grasp and Reach*: 34 (Hinkley et al. 2009); *Spatial Updating*: 27 (Morris et al. 2007), 28 (Chang and Ro 2007); *Online Control*: 22 (Rice et al. 2006), 23 (Desmurget et al. 1999), 24 (Della-Maggiore et al. 2004), 25 (Glover et al. 2005), 26 (Tunik et al. 2005; Rice et al. 2007; Cohen et al. 2009); *Eye–Hand Coordination*: P3 (van Donkelaar et al. 2000); *Joystick*: P3 (Smyrnis et al. 2003), 18 (Grefkes et al. 2004); *Lesion*: X (Binkofski et al. 1998; Karnath and Perenin 2005). **b** Possible homologies between monkey and human brain (*see text for details*)

types of neurons may blend (Bartels et al. 2008). Finally, this clustering could be due to the need to minimize axonal wiring across neural populations involved in body movements (Levy et al. 2007), analogous to frontal motor regions (Graziano and Aflalo 2007; Meier et al. 2008).

Despite this overlap, effector-specific signals for either hand or eye movements have also been shown in Fig. 3b; (Connolly et al. 2003; Medendorp et al. 2005; Connolly et al. 2007; Hinkley et al. 2009; van der Werf et al. 2010; Gallivan et al. 2011a), and candidate homologues for macaque areas LIP and PRR have been proposed (Connolly et al. 2003; Schluppeck et al. 2005; Beurze et al. 2007; Hagler et al. 2007). These findings have led to the view that PPC is organized in an effector-specific manner, with distinct subregions mediating spatially guided movements for each effector (Andersen and Cui 2009; Hinkley et al. 2009). More specifically, neuroimaging research has identified a cluster of activation for both saccades and attention (Corbetta et al. 1998; Nobre et al. 2000), possibly analogous to monkey LIP (Fig. 2b) (Colby and Duhamel 1991; Colby et al. 1996), in human PPC; however, the putative PEF in humans is located medial to IPS (mid-posterior IPS; mIPS), along its anterior–posterior axis (Fig. 2a) (Muri et al. 1996; Sereno et al. 2001; Astafiev et al. 2003; Merriam et al. 2003; Schluppeck et al. 2005, 2006; Tosoni et al. 2008). It is also generally thought that the human superior parietal lobule (SPL) is homologous to the monkey inferior parietal lobule (IPL) (Milner 1996).

Indeed, in patients with parietal damage, the neural substrates of reaches and saccades are difficult to dissociate because of typically widespread lesions and variability in the pattern of deficits—likely reflecting the heterogeneity of the lesions. For instance, lesions of both human IPL and SPL impair reach (Perenin and Vighetto 1988; Milner and Goodale 1995) and saccadic eye movements (Pierrot-Deseilligny et al. 1991, 2004; Muri and Nyffeler 2008). In spite of this, a recent case study with a parietal patient with optic ataxia shows a functional dissociation of reach and saccade control: lesions in the medial region rather than lateral bank of IPS impaired visually guided reaching movements with preserved saccadic metrics (Trillenberg et al. 2007); *cf*. (Gaveau et al. 2008). Interestingly, TMS of regions in both the vicinity of mIPS and AG also disrupts saccades (Fig. 2a) (Elkington et al. 1992; Oyachi and Ohtsuka 1995; Muri et al. 1996, 2000; Kapoula et al. 2001; Nyffeler et al. 2005; Ryan et al. 2006; Vesia et al. 2010).

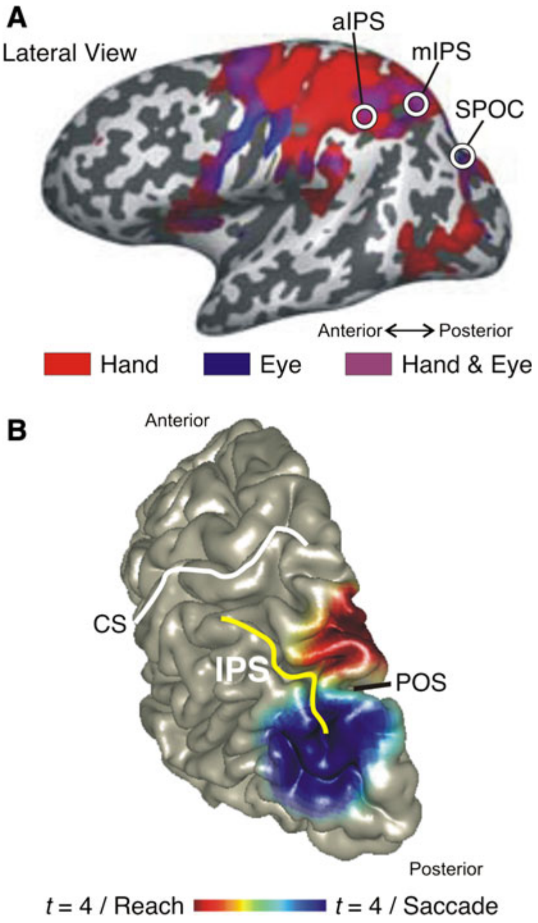
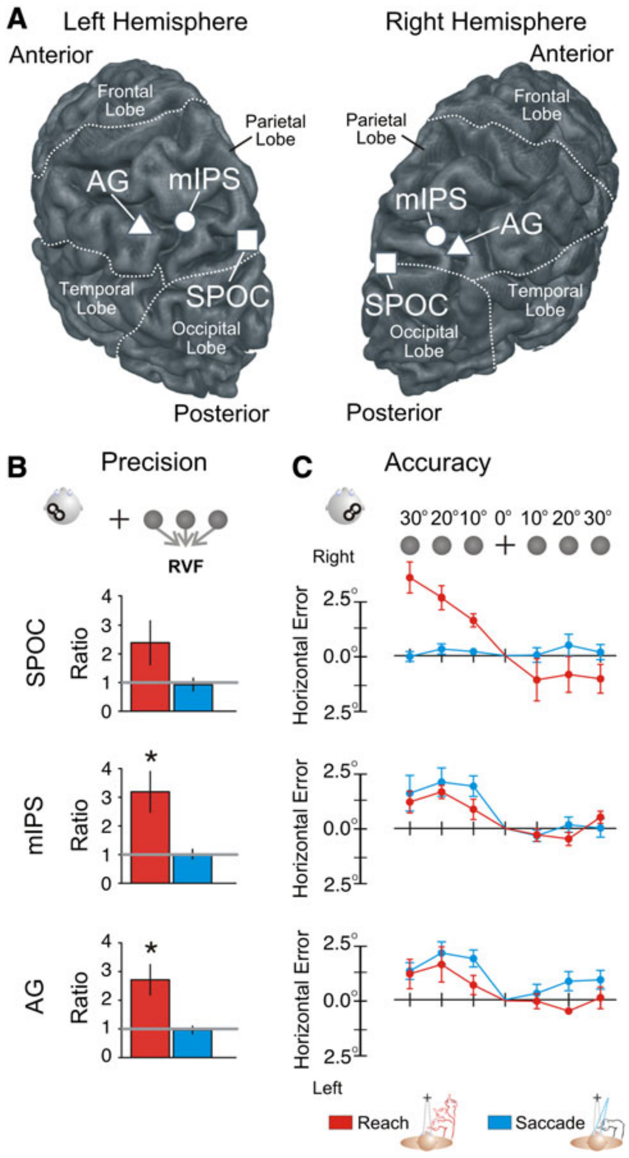


Fig. 3 Brain activation during saccade and reach planning in humans. **a** Brain activation for movement planning, presented on the semi-inflated hemisphere of a single subject, for saccades (*blue voxels*) versus right-hand movements (*red voxels*) and movement preparation of both hand and eye movements (conjunction analysis, *purple voxels*) for regions along the intraparietal sulcus (i.e. mIPS; aIPS) and parieto-occipital sulcus (i.e. SPOC). Modified, with permission, from (Beurze et al. 2009). **b** Effector specificity of gamma-band power in space and time. *Positive t values* represent specificity for contralateral reach goals; *negative values* represent specificity for contralateral saccade goals. *CS* central sulcus, *IPS* intraparietal sulcus, *POS* parieto-occipital sulcus, *aIPS* anterior portion of IPS, *mIPS* midposterior IPS, *SPOC* superior parieto-occipital cortex. Modified, with permission, from (van der Werf et al. 2010)

Further, numerous neuroimaging studies also have systematically characterized two distinct reach-related modules in human PPC (Fig. 2a): one cluster of activation, similar to the parietal region activated by saccades in humans, around the mIPS that encodes both pointing and reaching preparation (DeSouza et al. 2000; Medendorp et al. 2003; Grefkes et al. 2004; Medendorp et al. 2005; Prado et al. 2005; Beurze et al. 2007; Fernandez-Ruiz et al. 2007; Hagler et al. 2007; Levy et al. 2007; Zettel et al. 2007; Tosoni et al. 2008; Beurze et al. 2009); the other, a yet more medial–posterior cluster in superior parieto-occipital cortex (SPOC) that selectively encodes contralateral pointing and reaching actions to peripheral locations (Astafiev et al. 2003; Connolly et al. 2003; Prado et al. 2005; Fernandez-Ruiz et al. 2007; Zettel et al. 2007; Culham et al. 2008; Tosoni et al. 2008; Beurze et al. 2009; Filimon et al. 2009; Bernier and Grafton 2010; Cavina-Pratesi et al. 2010b) and is more strongly activated during passive viewing of tools when they are within graspable range (Gallivan et al. 2009). The former region, mIPS, may represent the putative homologue of macaque MIP component of PRR (Johnson et al. 1996; Eskandar and Assad 1999), whereas the latter, SPOC, might be homologous to reach-specific regions in monkey (Fig. 2b; PO sulcus), which contains areas V6 and V6A component of PRR (Galletti et al. 2003; Pitzalis et al. 2006; Fattori et al. 2009a). Lesions of SPL and to the region including and surrounding IPS may induce a deficit in visually guided movements, namely pointing and reaching, referred to as optic ataxia (Perenin and Vighetto 1988). Furthermore, temporary 'virtual lesions' of AG, mIPS and SPOC using TMS perturb reach performance (Fig. 2a) (Smyrnis et al. 2003; Vesia et al. 2006, 2008; Busan et al. 2009a, b; Davare et al. 2012; Striemer et al. 2011; van Donkelaar and Adams 2005).

Our recent TMS work systematically determined the effector specificity in human PPC. Using 'on-line', event-related rTMS, we were the first to causally demonstrate regional effector (reach versus saccade) specificity in healthy human PPC (Vesia et al. 2010), confirming previous monkey electrophysiological results. Furthermore, using control experiments, we were also able to demonstrate that different parietal regions involved in reaching actually process different information associated with the movement. As we alluded to, compared to monkey electrophysiology (Fig. 1a), studies in humans have provided conflicting evidence for strong effector specificity in PPC. Overcoming the limitations of traditional *f*MRI approaches, our study compared the behavioural effect of short trains of TMS pulses delivered to three different parietal sites (AG, mIPS and SPOC) (Fig. 4a) during a brief memory interval in which subjects plan either a saccade or a reaching movement toward peripheral visual targets. We found differences between the effects of stimulation of more lateral and anterior regions (AG and mIPS) and the stimulation of a more medial and posterior region (SPOC). In particular, stimulation of the mIPS and the AG had very similar effects, increasing end-point variability for reaches and decreasing reach and saccade accuracy for contralateral targets. In contrast, stimulation of the SPOC caused only a deviation of reach end points toward visual fixation but did not affect saccades (Fig. 4b, c). More recently, Gallivan et al. (2011a) reported similar findings that suggest that *f*MRI spatial activity patterns preceding



◀ **Fig. 4** Specificity of human parietal saccade and reach regions during transcranial magnetic stimulation. **a** Three-dimensional rendering of a typical subject's structural MRI with marked cortical sites in *left* and *right hemispheres*: *square* SPOC, *circle* mIPS, *triangle* AG (dorsal–lateral view). **b** Reach precision plots for reaches (*solid red bar*) and saccades (*solid blue bar*) with the right hand for all targets in right visual hemifield (RVF) for each subject and then averaged across all six subjects. *Bar graphs* plot the precision ratio (mean elliptical area with rTMS as a ratio of the mean baseline no rTMS condition) for *left* PPC stimulation, for SPOC (*top*), mIPS (*middle*) and AG (*bottom*). *Solid grey line* (baseline no rTMS condition) indicates a ratio value equal to one and reflects identical elliptical areas, whereas values greater than this value indicate that parietal rTMS increased end-point variability. *Asterisks* indicate values showing significant differences ($p < 0.05$) using Tukey's post hoc tests. *Error bars* represent SE. **c** Saccade and reach accuracy plots. The magnitude of the rTMS-induced effects on horizontal error (relative to baseline no rTMS condition) is plotted for reaches (*solid red circle and line*) and saccades (*solid blue circle and line*) with the right hand for all subjects. These plots show the change in *horizontal error* for all targets for SPOC (*top*), mIPS (*middle*) and AG (*bottom*) after stimulation of right PPC. Stimulation of mIPS and AG produced similar patterns: increased end-point variability for reaches and decreased saccade accuracy for contralateral targets. In contrast, stimulation of SPOC deviated reach end points toward visual fixation and had no effect on saccades. *Error bars* represent SE. Modified, with permission, from (Vesia et al. 2010)

movement onset in these different human PPC regions are predictive of upcoming reaches and saccades and their intended directions using a multivariate technique sensitive to spatially distributed *f*MRI patterns.

These findings strongly support a clear degree of effector specificity between the encoding of reach and saccades in human PPC, although there is still substantial overlap. Several caveats remain. First, it may be that even a greater degree of local effector specificity will emerge (i.e. as in LIP versus MIP in monkey) as human neuroscience techniques continue to advance. Second, we cannot know how effector specific these regions are until *all* effectors have been tested. For example, Heed et al. (2011) recently tested parietal effector specificity during saccades, hand pointing and foot pointing and found no separation between the latter two, suggesting that PPC effector specificity may be more related to a functional specificity between pointing with the eye versus skeletomotor structures, rather than reach per se.

Reach versus grasp

The classical model of the neural control of reaching and grasping movements proposes that areas located in the posteromedial portion of the IPS contribute to the planning of reaching movements toward an object, whereas a more anterolateral region of IPS integrates grasp-related information about an object (Jeannerod et al. 1995). Similarly, in human PPC, both an anterior–lateral cluster (mIPS and AG) and a more medial–posterior region (SPOC) have been implicated in pointing and reach (*see above*), whereas the anterior part of IPS (aIPS) has shown grasping-related responses (Fig. 2a; (Grafton et al. 1996; Binkofski et al. 1998; Culham et al. 2003; Frey et al. 2005), the possible homologue of macaque AIP (Nelissen and Vanduffel 2011); Fig. 2b). Further, patients with lesions involving the anterior portion of the IPS have selective deficits in grasping, whereas reaching is much less disturbed (Binkofski et al. 1998). Interestingly, when the most anterior parietal region (aIPS) is spared in parietal patients (Fig. 5b, *rightmost panel*), corresponding to the area isolated by Binkofski et al. (1998), grasping deficits are not observed (Cavina-Pratesi et al. 2010a). Likewise, TMS delivered to aIPS disrupts grasp (Fig. 2a) (Rice et al. 2006; Davare et al. 2007).

How functionally specialized are the parietal regions for reaching and grasping? Although recent findings support

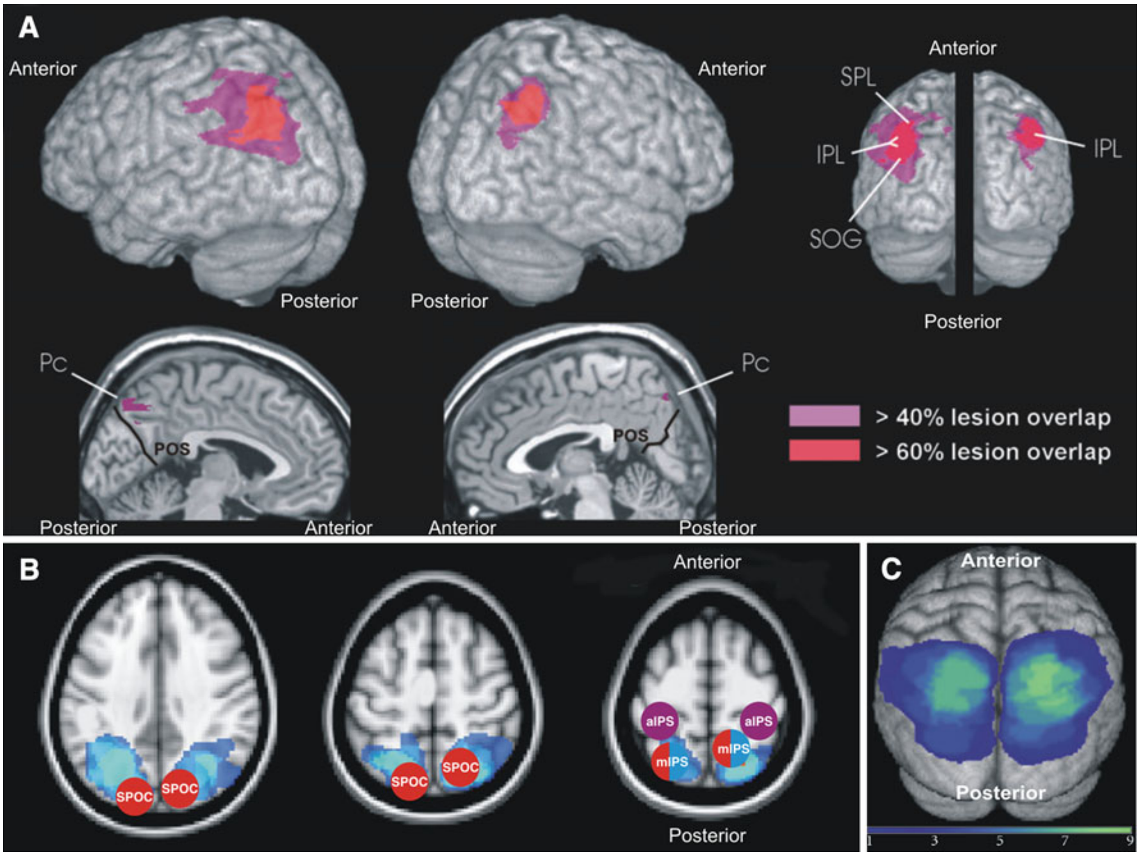


Fig. 5 Lesion overlap in patients with optic ataxia. **a** Lateral and medial surface views of the centre of lesion overlap in patients with unilateral optic ataxia. The percentage of lesion overlap in these patients has been calculated after the subtraction of control subjects with unilateral lesions but without optic ataxia. *SOG* superior occipital gyrus, *IPL* inferior parietal lobule, *SPL* superior parietal lobule, *Pc* precuneus. Parieto-occipital sulcus (POS) is marked by a *black contour*. Modified, with permission, from (Karnath and Perenin 2005). **b** Overlay of the main regions damaged in three (*dark blue*) to eight (*light blue*) optic ataxia patients. *Symbols* represent the clusters identified in a meta-analysis by (Blangero et al. 2009). *aIPS* anterior portion of IPS; *mIPS* midposterior IPS, *SPOC* superior parieto-occipital cortex. Modified, with permission. **c** Three-dimensional rendering of the area of lesion overlap, posterior view of the brain. Lesions are centred in the parieto-occipital regions, including SPOC and mIPS. The centre of the maximum overlay zone is situated just in front of the parieto-occipital junction (*left hemisphere*: $x = -24$, $y = -66$, $z = 44$; *right hemisphere*: $x = 30$, $y = -68$, $z = 46$; MNI space). Note that most of the IPS (i.e. mIPS) is included in the maximum lesion overlap, whereas more anterior parts (i.e. aIPS) are excluded. Brighter (*more green*) the region indicates greater number of patients with lesions in the given area from 0 to 8. Modified, with permission, from (Pisella et al. 2009)

the existence of functionally distinct parietal regions for controlling reach-to-grasp movements, the overlap between these parietal regions may also reflect the different functional and computational constraints that need to be satisfied when planning reach-to-grasp movements. For instance, previous conventional *f*MRI work has found differences between arm transport and grip formation in distinct regions of the PPC during the execution phase of reach-to-grasp actions in humans (Cavina-Pratesi et al. 2010b). Different regions may be involved in controlling proximal arm/shoulder muscles that drive the hand to the target location (transport component) and distal hand/finger muscles that exert fingertip forces to the object (grip component). TMS studies have shown that stimulation to a yet more anterior–lateral region (aIPS), and not to mIPS and caudal IPS regions, disrupts grasping (Rice et al. 2006; Davare et al. 2007). However, as suggested by recent monkey single-unit recordings (Fattori et al. 2009b, 2010) and human functional neuroimaging (Gallivan et al. 2011b), it is possible that grasping recruits multiple PPC regions. Therefore, although TMS enables us to conclude about the necessity of a particular brain region for a given behaviour, other brain regions may also be necessary for this behaviour (Chouinard and Paus 2010). Indeed, these findings do not necessarily preclude the involvement of other PPC regions in grasping but rather suggest that aIPS is critically involved in grasping (Cohen et al. 2009).

Perhaps, their functional specialization is not simply a matter of encoding reach versus grasp parameters. It appears that the dorsomedial pathway contributes to the integration of the grasp with the reaching component (Fattori et al. 2010), probably to ensure smooth coordination between both components. In contrast, the dorsolateral pathway may be specialized in the fast processing of the object properties, allowing online control of hand–object interactions (Grol et al. 2007). Taken together, it is plausible that PPC does not follow a strict effector-specific organization per se, but rather might reflect the different computational constraints that are required when planning eye and different limb movements.

Hemispheric lateralization

Limb-specific representation for reach

The majority of functional neuroimaging studies have reported bilateral activation in response to pointing and reaching movements of either arm or hand, but that the modulation is stronger for contralateral movements (Sereno et al. 2001; Astafiev et al. 2003; Connolly et al. 2003; Medendorp et al. 2003; Merriam et al. 2003; Medendorp et al. 2005; Beurze et al. 2007). TMS in humans has also revealed similar lateralized deficits in mIPS and AG for reaching (Desmurget et al. 1999; van Donkelaar and Adams 2005; Vesia et al. 2010) and rostral IPS for grasping (Rice et al. 2007); *cf.* (Vesia et al. 2006). A recent TMS study also demonstrated that AG is critical in the early stages of planning contralateral reaches with the contralateral hand (Koch et al. 2008). This limb specificity is also consistent with reaching deficits in optic ataxia (Perenin and Vighetto 1988; Rossetti et al. 2003; Blangero et al. 2007; Khan et al. 2007; Blangero et al. 2008; Pisella et al. 2009), neuronal activity found in monkeys (Chang et al. 2008), and BOLD activation in the mIPS and AG regions of human PPC (Medendorp et al. 2003, 2005; Beurze et al. 2007). Thus, hemispheric specialization for limb-specific representations (i.e. ipsilateral-versus contralateral-limb movements) arises at a very early stage of visuomotor control.

In addition, there appears to be a rostro-caudal gradient of upper-limb specificity within parietal cortex. Overall, both *f*MRI and lesion data are consistent with the notion that there is a greater lateralization for contralateral hand movements in more anterior–lateral than medial–posterior foci (Blangero et al. 2009). Consistent with this, our recent TMS studies of reach support a gradient of hand specialization running from SPOC (least arm/hand effector specificity) toward mIPS and angular gyrus (highest degree of arm/hand effector specificity) (Vesia et al. 2010).

Visual hemifield specificity

Several regions within PPC encode target direction relative to gaze direction (the fovea) (Medendorp et al. 2008), which begs the question of whether these areas show retinotopic organization. Several *f*MRI studies have identified a simple contralateral topography along the intraparietal reach and saccade areas (Sereno et al. 2001; Medendorp et al. 2003; Fernandez-Ruiz et al. 2007), and at least one has suggested a more complete directional topography (Sereno et al. 2001). Other *f*MRI findings support the existence of two different cortical systems of reach—mIPS and SPOC—differently modulated by whether targets are presented in central or peripheral vision, respectively (Prado et al. 2005; Clavagnier et al. 2007).

Our recent TMS work and lesions to these different regions in PPC provides further evidence in favour of this scheme. In particular, we showed that, during TMS over SPOC, reach is deviated toward gaze (Fig. 4c) (Vesia et al. 2010). This resembles the gaze-dependent deviation in reaching induced by TMS over PPC by van Donkelaar and Adams (2005) and the inability of patients with optic ataxia (damage to PPC) to decouple reach from gaze (Carey et al. 1997; Jackson et al. 2005; Granek et al. 2009; Sergio et al. 2009)—expressed as hypometria in gaze-centred coordinates (Blangero et al. 2010). This effect is expected if foveal representations are preserved at the expense of disrupted peripherally retinal representations (Crawford et al. 2004) and is consistent with selective activation of SPOC for peripherally retinal targets (Prado et al. 2005). In fact, a recent study (Karnath and Perenin 2005) (Fig. 5a) using lesion superimposition of stroke patients with, and without, optic ataxia suggests that damage of SPOC may be specific to optic ataxia deficits in reaching to peripheral targets (Himmelbach et al. 2009) and agree well with the multiple reach-related clusters (modules) for central and peripheral vision (Prado et al. 2005; Clavagnier et al. 2007).

Based on these findings, some authors further suggest that reach errors in optic ataxia induced by mIPS may represent mainly the ‘hand effect’ (i.e. the hand-eye-vector), whereas the more posterior–medial cluster (SPOC) may cause the ‘field effect’ (i.e. the target-eye-vector) (Blangero et al. 2007, 2009; Pisella et al. 2009) (Fig. 5b, c). Indeed, the ‘hand’ and ‘field’ effects revealed in optic ataxia reaching behaviour can be explained by the disruption of the parietal target-hand integration regions that are organized along a postero-anterior gradient of visual-to-somatic information integration (Blangero et al. 2009).

Computational specificity for reach control

Reach involves a number of specific computations, which are perhaps best illustrated by contrasting with the saccade system. First, whereas saccades are thought to be ballistic, one can usually see the hand, and if it moves slowly enough, this visual feedback can influence the trajectory of the hand (Elliott et al. 1999). Second, whereas early saccade planning is thought to occur in eye-centred coordinates, both eye- and body-related reference frames are probably used for limb movement planning (Pesaran et al. 2006; Marzocchi et al. 2008; Chang et al. 2009; Ferraina et al. 2009; McGuire and Sabes 2009; Bernier and Grafton 2010; Chang and Snyder 2010; Pesaran et al. 2010). Third, unlike eye movements, which necessarily always begin from the current foveated target, hand position is dissociated from the eye—so one must incorporate information of initial hand position into the motor plan for reach. We will consider each of these topics below in turn.

Feed-forward versus feedback visuomotor control of reach

In theory, parietal cortex may be involved in both transformation of initial visual information into a motor plan for reach (Crawford et al. 2011) and in the use of visual feedback to guide an ongoing movement (Iacoboni 2006). To monitor the performance of a reach, the brain needs to predict the consequences of its motor commands prior to their execution (Wolpert 1997; Desmurget and Grafton 2000). Further, visual and proprioceptive feedback signals need to be integrated with efference copies of ongoing motor commands, as well as information about limb dynamics and visual feedback of the hand, to generate an estimate of the current state of the limb as the movement unfolds (Desmurget and Grafton 2000; Wolpert and Ghahramani 2000).

This function is highly reliant on the integrity of PPC. For instance, both lesions and TMS to multiple regions in PPC, namely aIPS, AG and adjacent sites along the IPS, disrupt online control of grasping and reaching (Wolpert et al. 1998; Desmurget et al. 1999; Pisella et al. 2000; Della-Maggiore et al. 2004; Glover et al. 2005; Tunik et al. 2005; Rice et al. 2007). In addition, Filimon et al. (2009) compared visible and nonvisible reaching movements to saccades to identify reach-selective areas and regions modulated by visual feedback of the hand. Their findings showed that SPOC, mainly a more posteriorly located region at the superior end of parieto-occipital sulcus, possibly homologous to macaque V6A (Fattori et al. 2001), is more active for visual than for nonvisual reaching and may process visual feedback from the hand during online reaching or calculate the visual distance between the effector and target. In contrast, the anterior part of the precuneus, along with mIPS, responds equally during visual and nonvisual reaches, as well as saccades, suggesting a proprioceptive input from the moving arm during the reach. This suggests that SPOC plays a different role in reach control, a theme that will be explored more thoroughly in the next section.

Goal encoding versus movement vector encoding

To perform a goal-directed action toward a visual target, a series of feed-forward computational processes are required to convert its early representation into the pattern of muscular contractions required for the movement, including the construction of internal representations of the target position and effector position to compute a desired reach vector (Buneo and Andersen 2006; Blohm and Crawford 2007; Blohm et al. 2009). Figure 7a provides a flow diagram of the computation of the reach movement vector that we discuss. Although a complete model of the sensorimotor transformations for reach would include a complete model of limb dynamics (Todorov 2000; Todorov and Jordan 2002), including visual feedback control loops (Gomi 2008), we focus on the feed-forward mechanisms required for rapid, accurate action. Once a goal has been selected (Schall and Thompson 1999), and a desired action chosen (Cisek and Kalaska 2010), the computation of movement vectors requires knowledge of both the desired goal and the internal estimate of initial hand position, derived from either vision or proprioception, or both (Sober and Sabes 2003, 2005; Khan et al. 2007). Whereas the target location is determined generally from visual information, the brain can either visually encode the position of the viewed hand or extract hand position through proprioceptive information from the arm itself (Prablanc et al. 1979; Lackner 1988; Rossetti et al. 1995; Graziano et al. 2000; Buneo et al. 2002; Crawford et al. 2004; Buneo and Andersen 2006). When vision is available, humans compare the target to both visual and proprioceptive sensation of hand position and optimally integrate these signals depending on the stage of motor planning; however, they tend to rely more on vision especially in the early stages of motor planning (Sober and Sabes 2005).

Using *f*MRI (Fernandez-Ruiz et al. 2007) and TMS (Vesia et al. 2010), our recent work suggests that the spatial goal for movement is primarily encoded in the posterior part of IPS (i.e. SPOC), whereas more rostral parietal regions along IPS, namely the medial (mIPS) and AG, might be specific for the visual and somatosensory calculation of the reach vector, respectively (Fig. 7a). Specifically, when subjects were trained to point while looking through left–right reversing prisms, the spatially selective activity in most PPC areas (SPOC, mIPS, visual areas V3, 7) remained tied to the visual direction of the goal, not the movement direction (Fig. 6a, c) (Fernandez-Ruiz et al. 2007). Only one PPC region—the angular gyrus (Fig. 6b, d)—showed the opposite effect. Likewise, the

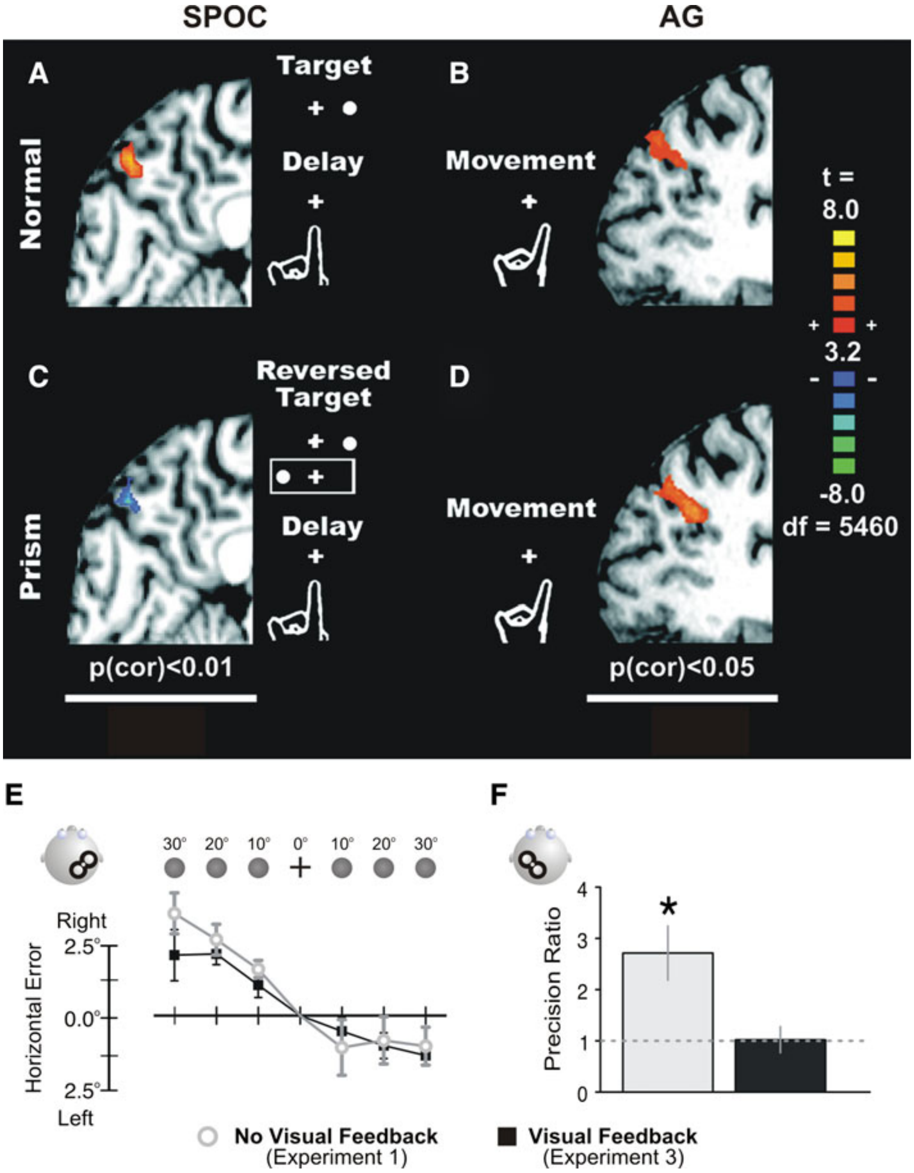


Fig. 6 Goal encoding versus sensory and motor encoding. Effect of the reversing prism on SPOC response during the memory delay period (**a** and **c**), and absence of prism effect on AG response during the movement period (**b** and **d**). Lateral views of left occipital–parietal region average activations for all subjects are shown in each condition. *Top row* shows the activations that are the result of the statistical GLM predictor contrast of rightward (intended) movements + and leftward (intended) movements − without the prism, and *bottom row* shows activations in response to the same contrast after adaptation with the prism in place. Note that the pattern of activation reversed for SPOC during the memory period (**a** and **c**) but not for AG during the movement period (**b** and **d**). Modified, with permission, from (Fernandez-Ruiz et al. 2007). **e** Comparison between data (magnitude of parietal rTMS-induced effects) obtained in experiment 1 (no visual feedback of hand) and experiment 3 (visual feedback of hand) for reaches with the *right hand*. The figure plots the magnitude of the rTMS-induced effects (relative to their respective baseline no rTMS conditions) on accuracy for reaches with (*open grey circle*) and without (*filled black square*) visual feedback of the right hand for the right SPOC across targets. rTMS over the more posterior–medial region, SPOC, deviated end points similarly toward visual fixation, and they were not found to be significantly different for these visual conditions. **f** Reach precision with and without visual feedback of the right hand. The precision ratio for the mean elliptical area for reaches with (*solid grey bar*) and without (*solid black bar*) visual feedback of the hand compared to baseline no rTMS trials (*dashed grey line*) for left PPC stimulation in the right visual hemifield for AG. *Error bars* represent SE. Modified, with permission, from (Vesia et al. 2010)

directionality of reach errors during AG stimulation did not reverse after adaptation to left–right reversing prisms (Vesia et al. 2006). Thus, both mIPS and SPOC maintain a visual directional tuning after adaptation to left–right reversing prisms, whereas the spatial selectivity of AG remained fixed in somatosensory coordinates. Similarly, our recent TMS findings showing that visual feedback of the hand did not correct errors induced by TMS over SPOC (Fig. 6e) also suggest that this region is involved with goal encoding (Vesia et al. 2010). In contrast, visual

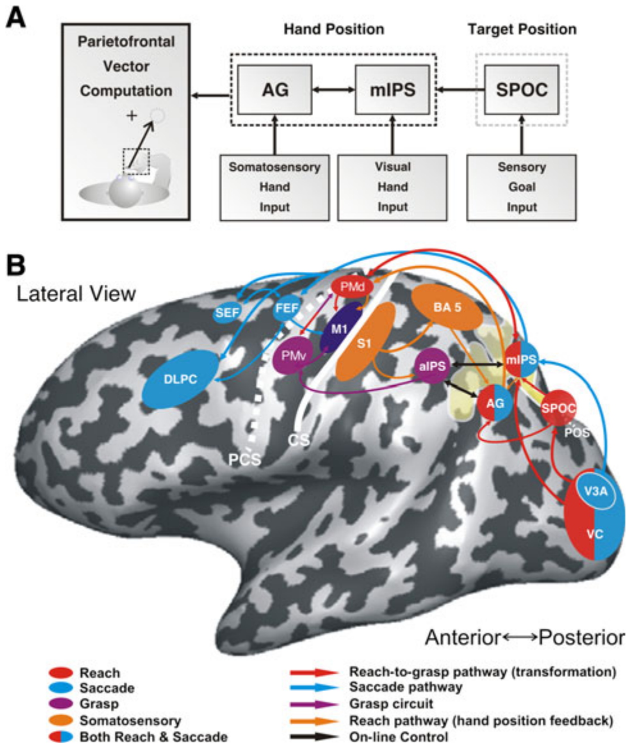


Fig. 7 Overview of reach vector computation and visuomotor brain areas. **a** Computation of reach (movement) vectors requires knowledge of both the desired goal and the internal estimate of initial hand position, derived from either vision or proprioception, or both. Whereas SPOC encodes sensory goal signals (i.e. target position), AG and mIPS likely encode somatosensory and visual input signals of the initial hand position, respectively. Goal and hand position signals could then be combined to comprise parietal–frontal loops for the computation of the movement vector (i.e. subtraction of target position from initial hand position to generate desired hand motor error. **b** Schematic representation of human brain (*lateral view*) regions involved in processing of visuomotor actions and eye–hand coordination: *VC* visual cortex (V3A), *AG* angular gyrus, *aIPS* anterior part of IPS, *mIPS* midposterior IPS, *SPOC* superior parieto-occipital cortex, *S1* primary somatosensory area for arm movements (proprioception), *BA5* Brodmann's area 5, *M1* primary motor cortex, *PMd* dorsal premotor cortex, *PMv* ventral premotor cortex, *FEF* frontal eye fields, *SEF* supplementary eye fields, *DLPC* dorsolateral prefrontal cortex, *PCS* precentral sulcus, *CS* central sulcus, *IPS* intraparietal sulcus, *POS* parieto-occipital sulcus (*see text for details*)

feedback of the hand not only corrects reach errors induced by TMS over mIPS and AG (Fig. 6f) (Vesia et al. 2008, 2010) but also the 'hand effect' reach errors in optic ataxia (Blangero et al. 2007). This suggests that these anterior–lateral PPC regions are involved in calculating the motor vector from the sense of initial hand position. This effect cannot be attributed to a perturbation of the internal representation of the reach goal, because goal feedback remains constant in both tasks. Overall, these data suggest a computational distinction between the encoding of reach goals in SPOC and reach vectors in more anterior–lateral PPC sites.

Functional overview for reach and eye–hand coordination

Based on these considerations and our recent TMS and *f*MRI studies, Fig. 7b summarizes the hypothetical flow of signals for reach between aIPS, mIPS, AG and SPOC, their interactions with other cortical reach regions, and other cortical regions necessary for coordinating reach with grasp and eye movements. We propose that information about target location flows from early visual areas into SPOC to form a high-level internal representation of the reach-to-grasp goal. The equivalent for the saccades system might be area V3A (Galletti and Battaglini 1989; Colby and Duhamel 1991; Colby and Goldberg 1999; Sereno et al. 2001; Medendorp et al. 2005). In contrast, visual information of initial hand position from visual cortex might flow to mIPS, while proprioceptive information encoded in the postcentral sulcus might travel to AG. We speculate that this information is integrated with goal information from SPOC (and V3A in the case of saccades) to comprise parietal–frontal loops for the computation of the movement vector (Beurze et al. 2007, 2009).

A yet more anterior portion of IPS (aIPS) is selective for the planning of grasp and may perform iterative comparisons during an ongoing movement between an efference copy of the motor command and incoming sensory information to ensure that the current reach-to-grasp plan matches the current context and sensorimotor state (Tunik et al. 2005). Thus, aIPS may perform an online computation of a difference vector based on the motor goal, efference copy and sensory inputs by outputting either an evaluative description of the mismatch, such as a difference vector, or perhaps even a solution to resolve it (Tunik et al. 2007). Further, we propose that these distinct parietal subregions may target different premotor areas that may possess dissociable processes: PMv is more involved in distal components (i.e. hand preshaping and grip-specific responses), whereas PMd is more involved in proximal components (i.e. power-grip or reach-related hand movements; (Tanne-Gariepy et al. 2002; Davare et al. 2006; Cavina-Pratesi et al. 2010b). Thus, PMv and PMd may form the anterior components of dissociable parieto-frontal networks involved in visuomotor control: the dorsolateral circuit comprising connections from posterior portions of IPS including a caudal part of IPS; (Taira et al. 1990; Shikata et al. 2003) to aIPS and then to PMv for grasping (grip component); and the dorsomedial circuit involving connections between SPOC to mIPS (AG) and then to PMd for arm transport component in reach-to-grasp (*for review, see* Rizzolatti and Matelli 2003; Grafton 2010). Importantly, while the substreams may show relative degrees of specialization, anatomical connectivity data also suggest crosstalk between dorsolateral and dorsomedial streams

(Borra et al. 2008; Gamberini et al. 2009). Further, the contribution of these circuits might also be a function of the degree of online control (finger precision) required by the reach-to-grasp movement (Grol et al. 2007). Perhaps, with simple tasks, it can be possible to find a double dissociation of the two systems, whereas more complex tasks may require greater interaction between the systems and significant coordination between these regions (Cavina-Pratesi et al. 2010b).

These circuits also can be considered from the viewpoint of eye–hand coordination. Some tasks require a decoupling of hand and eye movements (Henriques and Crawford 2000, 2002; Gorbet and Sergio 2009), which in turn would require the functional separation between reach and saccade goals (Gorbet et al. 2004; Prado et al. 2005). For example, as you read this, you may have a cup of coffee nearby, and easily can reach for the cup without explicitly directing your eyes at it. However, reaching to and manipulating objects are degraded when the eyes are deliberately deviated from normal fixation patterns (Bock 1986; Henriques and Crawford 2000; Terao et al. 2002; Henriques et al. 2003). Thus, many tasks require specific eye–hand coupling mechanisms (Fisk and Goodale 1985; Neggers and Bekkering 2000; Johansson et al. 2001; Land and Hayhoe 2001; Neggers and Bekkering 2001). Eye and arm movements, for instance, show mutual facilitation in their kinematic profiles (van Donkelaar 1998; Snyder et al. 2002; Thura et al. 2008). Eye movements typically precede the hand (Prablanc et al. 1979), with eye fixation normally ‘anchored’ to a target until the end of the reach movement (Neggers and Bekkering 2000, 2001), and improve their accuracy (Prablanc et al. 1979; Vercher et al. 1994; Henriques et al. 1998).

Given the dual behavioural needs of decoupled and coupled eye–hand movements, it should not be surprising that evidence is accumulating for neural circuitry to subserve both of these actions. If SPOC is associated with reaches toward retinally peripheral targets, particularly eye and hand decoupled, then it makes sense for this region to have a more reach-specific function independent of gaze signals. In contrast, if mIPS is more specialized for reach toward foveated targets, then it seems reasonable for gaze and reach signals to intermingle at this point. Clearly, many other areas of the brain are involved in these processes, but it is notable that effector-specific mechanisms for both feed-forward visuomotor control and eye–hand coordination are already present in human PPC.

Closing remarks

In the course of reviewing the literature on reach specificity versus other visuomotor actions within human PPC, several themes have emerged. First, although the degree of local functional specificity for reach is still not as clear as that in the nonhuman primate, the gap in understanding these two species has narrowed rapidly in the past few years, largely due to advances in human neuroscience technologies and the application of multiple techniques to examine particular questions. Second, although the human PPC is not just a larger monkey PPC, there are remarkable homologues between the two, such as the functional anatomy for reach, grasp and saccades. Moreover, the neuroscience of human PPC has progressed beyond the point where it is only replicating animal neurophysiology; it is now bringing about new advances (such as the role of AG in reach). Third, certain trends emerge such as the progression from a more posterior–medial hand-independent reach target system to a more anterior–lateral hand-dependent reach vector system, with more complex postural and gaze-dependent signals in the latter. As outlined in the previous section, it is now possible to construct a hypothetical circuitry for visuomotor transformations for reach-to-grasp actions and eye–hand coordination from the functional regions within this progression, simply not possible a decade ago.

This level of detail does not contradict the overarching theories of parietal function that have been proposed in the past (Critchley 1953; Mountcastle et al. 1975; Andersen 1997; Colby and Goldberg 1999), but rather tends to reconcile them. It is not possible to construct a realistic computational model for reach without accounting for signals related to attention, sensory integration and intention (Andersen and Cui 2009; Desmurget and Sirigu 2009; Bisley and Goldberg 2010; Cisek and Kalaska 2010). At the same time, there is a danger in overreaching with functional specificity. For example, SPOC, an area related to visually guided reach, is also activated for pointing with the foot (Heed et al. 2011) and can switch from gaze-centred encoding to gaze-independent encoding for somatosensory targets (Bernier and Grafton 2010). Both AG and mIPS are involved during the planning stages of saccades (Vesia et al. 2010), but TMS disruption of this area also interferes with perception and memory across saccades (Prime et al. 2008). These apparent contradictions disappear if we consider PPC to be composed of modules specialized for specific computational transformations of sensory inputs into outputs (i.e. target location, saccade-related signals) that can be used whenever required. Similarly, this tends to reconcile overarching theories of parietal function based on descriptions of input (Ungerleider and Mishkin 1982) versus output (Milner and Goodale 2008).

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