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Human parietal cortex in action

Jody C Culham and Kenneth F Valyear

Experiments using functional neuroimaging and transcranial magnetic stimulation in humans have revealed regions of the parietal lobes that are specialized for particular visuomotor actions, such as reaching, grasping and eye movements. In addition, the human parietal cortex is recruited by processing and perception of action-related information, even when no overt action occurs. Such information can include object shape and orientation, knowledge about how tools are employed and the understanding of actions made by other individuals. We review the known subregions of the human posterior parietal cortex and the principles behind their organization.

Addresses

Department of Psychology, Social Science Centre, University of Western Ontario, London, Ontario, Canada, N6A 5C2

Corresponding author: Culham, Jody C (culham@imaging.robarts.ca)

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Introduction

Sensory control of actions depends crucially on the posterior parietal cortex, that is, all of the parietal cortex behind primary (SI) and secondary (SII) somatosensory cortex, including both the superior and inferior parietal lobules, which are divided by the intraparietal sulcus. Initially posterior parietal cortex was considered part of ‘association cortex’, which integrates information from multiple senses. During the past decade, the role of the posterior parietal cortex in space perception and guiding actions was emphasized [1,2]. Electrophysiological studies in the macaque monkey defined a mosaic of small areas, each specialized for a particular type of action of the eyes, head, arm or hand [3]. Because neuroimaging in humans has enabled more precise localization of functional areas, it is increasingly apparent that the human parietal cortex contains a similar mosaic of specialized areas. Several years ago we reviewed the early evidence for possible functional equivalencies between macaque and human regions of the posterior parietal cortex, particularly within the intraparietal sulcus [4], however, since then the relationships have become considerably clearer. This

owes, in large part, to the rapid growth of neuroimaging studies, particularly experiments using functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS).

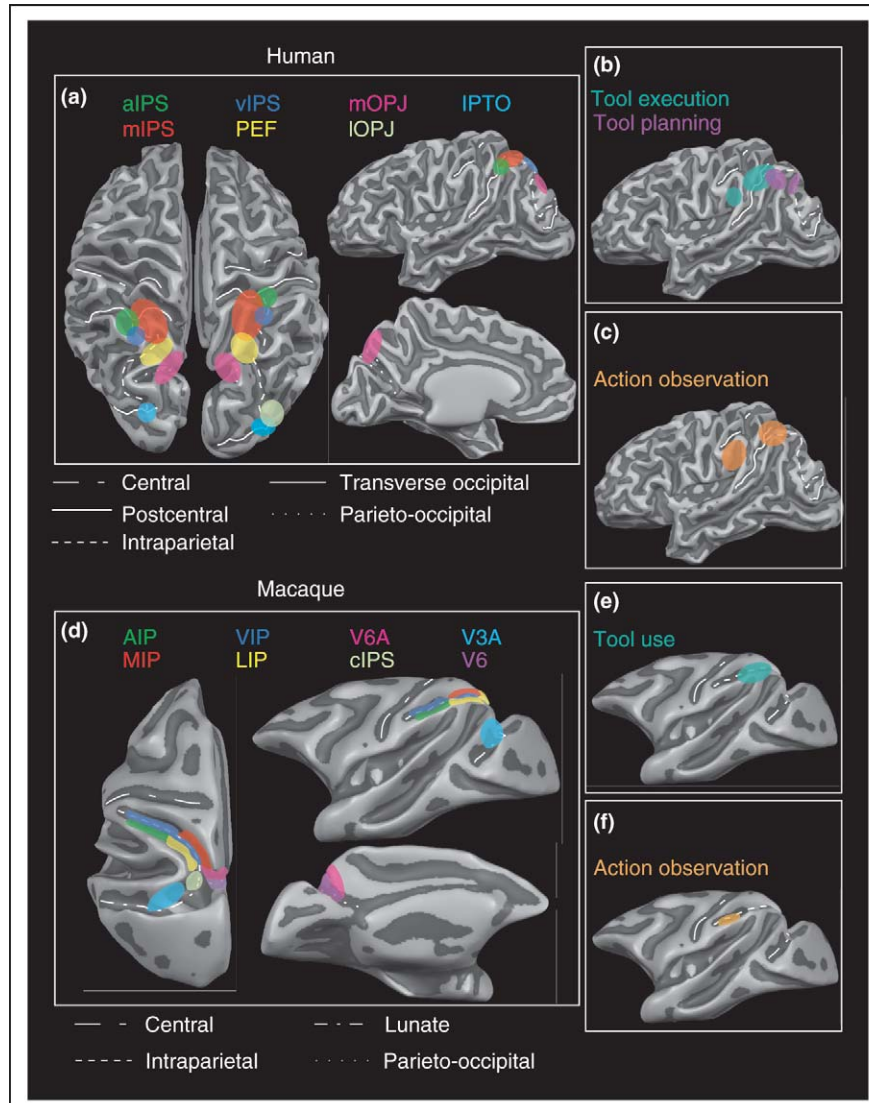
In one popular view of the visual system [1], visual information is segregated along two pathways: the ventral stream (occipito-temporal cortex) computes vision for perception, whereas the dorsal stream (occipito-parietal cortex) computes vision for action. Here, we review recent advances that address the organization of the posterior parietal cortex and the action-related subregions within it. We begin by focusing on the role of the dorsal stream in visually-guided real actions. However, we then discuss a topic that does not fit so easily into the dichotomy: action-related perceptual tasks that invoke the dorsal stream. Growing evidence from studies in both macaque and human brains suggests that areas within the posterior parietal cortex might be active not only when the individual is preparing to act, but also during observation of others’ actions and the perceptual processing of attributes and affordances that are relevant to the actions, even when no actions are executed. We focus largely on the human brain, but include a brief summary of comparable areas in the macaque monkey brain and potential homologies between the two species (See Figure 1). The latest advances in the study of the macaque posterior parietal cortex [3] and issues of macaque–human homology [5–7] were recently highlighted elsewhere.

Posterior parietal cortex in action

Reaching and pointing

The role of the posterior parietal cortex in reaching is evident from the deficits in patients with optic ataxia [8]. Typically these patients show inaccurate reaches only when visual targets are viewed in peripheral vision. The lesions underlying optic ataxia were classically assigned to the parietal lobe, always including the intraparietal sulcus and sometimes extending into the inferior or superior parietal lobules [9]. Karnath and Perenin [10^{*}] were recently able to identify more specific parietal foci by contrasting the lesions in patients with parietal damage who were diagnosed with optic ataxia against lesions in parietal patients who did not demonstrate the disorder. Their data revealed that optic ataxia was commonly associated with several lesion foci in the parietal cortex: the medial occipito-parietal junction (mOPJ), the superior occipital gyrus, the intraparietal sulcus, and the superior parietal lobule (particularly in the left hemisphere) or inferior parietal lobule (particularly in the right hemisphere). These results agree remarkably well with the activation foci found in a recent study using fMRI that

Figure 1



Schematic representation of action-related areas shown on the cortical surface of a human brain (a, b, c) and a macaque monkey brain (d, e, f). The cortical surfaces were defined at the gray–white matter boundary and have been partially inflated to reveal regions within the sulci while preserving a sense of curvature. Sulci (concavities) are indicated in dark gray; gyri (convexities) are indicated in light gray. White lines indicate labelled sulci.

(a) Human parietal areas involved in actions, as identified with neuroimaging. The two hemispheres are shown from above, along with lateral and medial views of the left hemisphere. The schematic is not intended to veridically show the extent and overlap of activation, which would require systematic comparisons within the same subjects. Although right IOPJ is activated during passive viewing rather than in an action task, the dorsal view in (a) was the most appropriate for highlighting its location. **(b)** Human parietal areas activated during the planning and execution of tool use movements. **(c)** Human parietal areas activated during action observation. **(d)** Macaque parietal areas involved in actions, as identified with neurophysiological recordings. The left hemisphere is shown from dorsal, lateral and medial views. **(e)** Macaque parietal areas involved in tool use. **(f)** Macaque parietal areas involved in action observation.

Areas are coded with similar colors to suggest possible functionally equivalent areas between species; however, such comparisons must always be undertaken with considerable caution (for an extended discussion of the issues, see Culham *et al.* [5]). For grasping, there is one reliably activated area in the human brain, aIPS, that is probably the equivalent of macaque AIP [23,90]. Similarly, both the human PEF and the macaque LIP have regularly been shown to be involved in saccadic eye movements [41], so there is a reasonable argument for equivalence. Both human vIPS [44] and macaque VIP [91] show multimodal responses to moving stimuli, and, therefore, might be functionally equivalent. Both human IOPJ [49] and macaque cIPS [92] have demonstrated orientation-selectivity; however, any suggestion of functional equivalence is tentative at this time. Retinotopic mapping suggests equivalence between macaque V3A and a human area around the junction of the intraparietal and transverse occipital sulci (IPTO) [40]; the IPTO is also activated in studies of attention and saccades [41]. Similarities between reach-related areas in the two species are particularly confusing [12,13,19]. In the macaque, areas MIP and V6A are adjacent to one another and, because both show reach-related activation, together they are often labelled the parietal reach region. In humans, both the mIPS and the mOPJ demonstrate reach-related activation but they are not directly adjacent to each other. It is possible that functional equivalencies exist between the mIPS and the MIP and between the mOPJ and V6A; however, additional evidence is needed to substantiate such claims.

Sources for human activation foci: aIPS [24,25], mIPS [11**], PEF [33,34], mOPJ [11**,12,13], IOPJ [49], IPTO [39], tool execution and planning [61*], action observation [77]. Sources for macaque activation foci: AIP, MIP, LIP and VIP [93], V6 and V6A [94], V3A [92,95], cIPS [92], action observation [68], tool use [96,97].

investigated visually-guided reaching. Prado *et al.* [11^{••}] reported activation in the medial IPS (mIPS; near the intraparietal sulcus lesion site identified in Karnath and Perenin), dorsal premotor cortex (dPM) and in the mOPJ, near reach-related activation reported by others [12,13]. Moreover, they found that whereas the mIPS was activated regardless of whether the target was presented in foveal or peripheral vision, the mOPJ only responded (and the dPM responded more) when the target was initially presented in peripheral vision (even if the eye subsequently looked directly at the location where the target had been). They suggested that the mOPJ and dPM might have crucial roles in decoupling eye-hand coordination. In addition, their results could explain the deficits of peripheral vision in patients with optic ataxia, in addition to the strange phenomenon of magnetic misreaching, in which patients with parietal damage reach to the location of their gaze, even when instructed to reach elsewhere [14]. These results are also consistent with new TMS findings, which showed that disruption of posterior parietal cortex function led to a tendency to reach closer towards fixation and for ‘the hand to be a slave to the eye’ [15]. TMS studies also found that posterior parietal cortex disruption interfered with corrections to compensate for jumps in target location [16] and the learning of new movement trajectories [17].

In contrast to reaching, in which subjects extend the arm to touch a target, many recent neuroimaging studies have employed pointing, in which the index finger is directed towards the target without extending the arm. These studies also reported activation in the mOPJ [12,13], but only when targets were presented in peripheral vision [11], as well as within the mIPS, regardless of whether the targets were in foveal or peripheral vision [18]. The relationships between the various reaching- and pointing-related parietal regions in humans and the more well-established parietal reach region in macaque monkeys await clarification. Although one group has suggested that the mOPJ is a homologue of the macaque parietal reach region (which includes areas V6A and MIP) [13], another group has proposed that the mIPS in the human is a functional equivalent of the macaque area also in the medial intraparietal sulcus (area MIP), on the basis of similarities in the responses to a visuomotor joystick task [19].

A growing body of literature is further characterizing the role of the mOPJ in reaching. One study examined reaching movements directed toward body parts (the chin or the thumb of the other hand) when subjects had their eyes closed [20]. They found that the mOPJ was more active the first time the movements were planned than it was for subsequent movements, suggesting that, in addition to activation in response to visual targets, this region is also activated by movements to bodily targets. An ambitious fMRI study of various types of reaching errors

suggested that the mOPJ encodes the current target of a reaching movement [21].

Grasping

Converging evidence suggests that a region in the human anterior intraparietal sulcus (aIPS) is involved in visually-guided grasping [22–26] and cross-modal (visual-tactile) integration [27]. Not only do humans with aIPS lesions demonstrate grasping deficits [22], TMS applied to aIPS [28[•]] and the superior parietal lobule [29] disrupts on-line hand-preshaping adjustments to sudden changes in object orientation. fMRI experiments in the well-studied patient, D.F., have shown that her aIPS is activated during object grasping but not during reaching, despite damage to an object-selective area in the ventral stream (the lateral occipital cortex) [30].

Eye movements and topographic maps

There is extensive literature on the areas involved in eye movements in humans (reviewed in [31]). Studies using fMRI reliably demonstrated saccade-related activation midway up the intraparietal sulcus [32] and somewhat medial to it, in the superior parietal lobule [33–37]. One saccade-related focus in the superior parietal lobe contains a topographic map that represents memory-driven saccade direction [33], the focus of attention [38] or the direction of a pointing movement [34,36]. Moreover, activation in this area demonstrated spatial updating when the gaze changed [34,35,37]. The map in each hemisphere represents the contralateral visual field, which led to the suggestion that the region is functionally similar to the parietal eye fields (in the lateral intraparietal sulcus) of the macaque [33]. This suggestion is bolstered by an fMRI study that directly compared saccade-related activation in humans and macaques [39]. Note that whereas macaque LIP is on the lateral bank of the intraparietal sulcus, the human area is medial to the intraparietal sulcus. Thus, we have called the human area ‘the parietal eye fields’ (PEF) to avoid any confusion regarding its laterality.

Other human parietal areas also contain spatiotopic maps. One saccade-related focus at the junction of the intraparietal sulcus and transverse occipital sulcus (IPTO) demonstrates stronger activation for saccades into the contralateral visual field, as do the PEF. The human IPTO region is likely to correspond to macaque V3A, which also contains a retinotopic map [40,41]. Two additional human parietal areas with topographic representations were reported posterior to the PEF [42,43]. Other preliminary evidence suggests that putative human equivalents of V6 and the ventral intraparietal area, VIP [44], might also contain topographic maps [45,46]. Indeed, it now seems that the parietal cortex is tiled with spatiotopic maps that were not previously reported by simple visual mapping (typically using flickering checkerboard stimuli), but that can be revealed with appropriate action-related tasks.

Posterior parietal cortex in action-related functions

Object-selective areas

Although the vast majority of human studies on object selectivity focused on areas within the ventral stream [47], neuroimaging has also revealed shape-selective activation for objects within the dorsal stream of both monkeys and humans [48]. These regions tend to be ignored because of concerns regarding attentional confounds, which could be more problematic for parietal areas than for occipito-temporal areas. Given the importance of actions in the dorsal stream, we hypothesize that these regions probably encode the action-related attributes of objects, such as orientation, depth and motion. For example, in fMRI adaptation studies, one region at the lateral occipito-parietal junction (LOPJ) shows sensitivity to object orientation [49,50] but not object identity [49], consistent with the fact that orientation is crucial to action planning, whereas identity might not always be essential. fMRI adaptation was also used to investigate the selectivity of aIPS, finding that aIPS is sensitive to the grasp posture, whereas object-selective ventral-stream regions are not [51^{••}]. Furthermore, aIPS, or a nearby region, demonstrated a preference for shapes in which 3D information was defined by motion or pictorial cues [52]. Taken together, these results suggest that object-selectivity in the dorsal stream warrants further investigation, particularly with a view to its possible relevance to action planning.

Unlike category-selective regions in the ventral stream, which require awareness to become activated (e.g. [53]), regions in the dorsal stream remain activated by objects, even when those objects are not consciously perceived [54^{••}]. Moreover, the activation to unperceived stimuli in the dorsal stream occurred for manipulable objects but not faces. This result strongly suggests that the 'invisible' stimuli that are relevant to actions were, indeed, processed in the dorsal stream. These results could account for the ability of patients (e.g. D.F. or patients with blindsight) and normal subjects (e.g. [55]) to accurately act on objects, without explicit awareness [54].

Tools

For the dorsal stream, tools, because of their obvious ties to action, represent a particularly significant category of objects. Indeed, neuroimaging investigations reliably report a left-lateralized network of areas, including areas within the posterior parietal cortex, as underlying the representation(s) of knowledge about familiar tools (for a review, see [56]). Tool-selective areas in the dorsal stream are thought to be related to the motor representations associated with familiar tools and their usage, in contrast to the role of tool-selective areas within the ventral stream, which are thought to be involved with the semantic associations of tools [57].

However, the nature of the tool-selective activation within the dorsal stream is not yet known. Because tools are graspable, and typical control stimuli (e.g., animals [57]) are not, tool-related parietal activations near aIPS might simply be driven by the graspable properties of tools, perhaps reflecting a covert plan to manipulate the object. This hypothesis does not appear likely, however, given the results of two recent fMRI studies. One study showed that an area in the vicinity of aIPS was active during the passive viewing of familiar tools but did not respond to unfamiliar shapes that were potentially graspable [58]. A study from our lab has also found that this tool-selective parietal region does not generalize to other objects that are graspable (e.g., an apple) [59]. Moreover, we found that the tool-selective parietal region is typically posterior to aIPS, as defined by grasping (versus reaching) movements. In addition, two recent imaging studies found that left parietal areas involved in the planning of tool use gestures are posterior to those involved in the execution of those gestures (See Figure 1b) [60[•],61[•]].

It is likely that some of these posterior parietal activations directly correspond to those representations that are impaired in patients suffering from ideomotor apraxia, a disorder of skilled object-related movements. Consistent with this hypothesis, lesion analyses implicate the left inferior parietal lobule and intraparietal sulcus as the most crucial sites of damage associated with ideomotor apraxia [62,63]. Although some apraxic patients have no trouble preshaping their hand in accordance with the physical attributes of an object, they might be unable to select the functionally correct posture for the object. For example, they might pick up a hammer using stable grasp points, but not in such a way that it could be used for hammering [64–66]. Thus, it appears that the tool-related representations within the left posterior parietal cortex play a crucial role in the storage and integration of knowledge about learned hand–object interactions, and that these representations are distinct from those mediating the visuomotor transformations underlying simple grasping actions [67].

Action observation

Within the grasping circuit of the macaque, including aIPS and the adjacent inferior parietal lobule [68], in addition to area F5 in frontal cortex [69], a subset of visuomotor neurons (known as 'mirror neurons') respond not only during the execution of goal-directed actions, but also during the observation of another individual making those same actions [70]. Such mirror responses were also reported in the parietal and frontal cortices of humans during action observation (reviewed in [71]). In the human [72], as in the macaque [68], action observation responses appear to be tuned to the ultimate goal of the action rather than specifics such as the trajectory of the hand. In the parietal and ventral premotor cortices of humans, activation resulting from the passive observation

of others' actions partially overlaps with activation resulting from the execution of those same actions [73]. Mirror responses can also be driven by sounds or verbal descriptions that imply others' actions [74,75].

Responses to action observation might depend on the richness of the observer's own experience with such actions. A study using fMRI found that expert dancers showed greater mirror responses to watching another dancer perform movements in their trained style than in another style [76]. These enhanced responses were observed across the network of action-observation areas, including posterior parietal cortex. Another study using fMRI involved subjects observing biting actions and communicative mouth gestures made by humans, monkeys or dogs [77]. Two regions of the left posterior parietal cortex were active not only while subjects observed human feeding actions, but also during the observation of feeding actions performed by the other species. Interestingly, although parietal activation was always observed in both hemispheres, right parietal areas preferred the viewing of human actions compared with both monkey and dog behaviors. The posterior parietal areas showed little or no activation for oral communication movements made by any of the three species. These two experiments suggest that parietal responses to action observations are most strongly activated when those actions are within the observer's repertoire.

The mirror system might be crucial in imitating and learning new actions [78]. Some intriguing results from Buccino *et al.* [79] suggest that the parietal cortex has a special role in observed actions that the observer intends to later imitate. The parietal cortex was more activated if nonmusicians observed a musician playing a guitar chord and planned to imitate the action than if they observed a chord being played but prepared a previously learned, but unrelated, action. Interestingly, these effects were more pronounced in the left hemisphere, perhaps because of the role of the left hemisphere in the acquisition and storage of skilled-movement representations.

Conclusions

Mapping of the human dorsal stream has progressed at a slower pace than mapping of the ventral stream, largely because of the technical challenges of using action paradigms for neuroimaging, perhaps accompanied by a general neglect of the study of actions in cognitive science [80]. In some ways, however, this might be an advantage, because the study of the ventral stream has revealed general principles that might also be helpful in elucidating organization within the dorsal stream.

Within both streams, it remains unclear whether regions of activation are truly distinct for particular stimuli or tasks. Within the ventral stream, there are dissenting views on whether visual processing occurs within

specialized modules dedicated to processing specific stimulus categories [81] or whether overlapping activation across multiple stimulus types reflects a distributed representation of all categories [82,83]. Similarly, within the dorsal stream, it is not yet clear how distinct the representations for specific actions, such as grasping, reaching and saccades, really are. Although these actions were studied largely in isolation, in the real world these actions often co-occur in a carefully choreographed movement; for example, when an individual saccades to, reaches towards and then grasps an object. Newer findings, such as the dependence of reach-related activation on eye position during target presentation [11], suggest interdependence of regions controlling different effectors.

The confusing plethora of regions in both streams could be greatly simplified by the determination of general organizational principles. For example, areas within the ventral stream seem to follow a quasiretinotopic organization, with adjacent representations for stimuli that are processed in the fovea (faces), midperiphery (objects) and far periphery (scenes) [84]. Moreover, multiple areas that are selective for those categories have a mirror-symmetric organization, a principle that minimizes connection lengths in the brain [85]. One highly intriguing and comprehensive neuroimaging study suggested that general organizational principles and mirror symmetry might explain the arrangement in the parietal and frontal cortices [86]. It could be that the human parietal cortex is organized by broader principles, perhaps including factors such as the relative contribution of somatosensory (anterior) versus visual (posterior) information, the importance of motor execution (anterior) versus planning (midanterior) [60,61], sensorimotor (superior) versus cognitive (inferior) processing [86] or coding of action space in particular coordinate frames (e.g. [87]). Although more abstract cognitive functions, such as numerical representations [88], might be greatly expanded in humans compared with those in nonhuman primates, they ultimately might also fit into a general organizational framework [86,89].

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