Human Parietal Cortex in Action

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Summary

Functional neuroimaging and transcranial magnetic stimulation experiments 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, human parietal cortex is also recruited by the processing and perception of action-related information, even when no overt action occurs. Such information may 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 human posterior parietal cortex and the principles behind their organization.

Introduction

The sensory control of actions depends critically upon the posterior parietal cortex, that is, all of parietal cortex behind primary (SI) and secondary (SII) somatosensory cortex, including both the superior and inferior parietal lobules, divided by the intraparietal sulcus. Initially, posterior parietal cortex was recognized as "association cortex" that integrated information from multiple senses. Over the past decade, the role of posterior parietal cortex in space perception and guiding actions has been emphasized [1,2]. Electrophysiological studies in the macaque monkey have defined a mosaic of small areas, each specialized for a particular type of action with the eyes, head, arm or hand [3]. As human neuroimaging has enabled more precise localization of functional areas, it has become 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 is due in large part to the rapid growth of neuroimaging studies, particularly functional magnetic resonance imaging (fMRI) experiments, as well as transcranial magnetic stimulation (TMS) experiments.

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 while the dorsal stream (occipito-parietal cortex) computes vision-for-action [1]. 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 next discuss a topic that does not fit so easily into the dichotomy: action-related perceptual tasks that invoke the dorsal stream. There is growing evidence in both the macaque and human brain that areas within the posterior parietal cortex may be active not only when the individual is preparing to act, but also during observation of others' actions and during the perceptual processing of attributes and affordances that are relevant for 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 macaque posterior parietal cortex [3] and issues of macaque-human homologies [5-7], have recently been highlighted elsewhere.

--------- Insert Figure 1 about here ---------

Posterior Parietal Cortex in Action

Reaching and Pointing

The role of the posterior parietal cortex in reaching is evident from the deficits of patients with optic ataxia [8]. These patients show inaccurate reaches to visual targets, typically only when those targets are viewed in peripheral vision. The lesions underlying optic ataxia have classically been 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 fMRI study investigating visually-guided reaching. Prado and colleagues [11] reported activation in the medial intraparietal sulcus (mIPS, near the intraparietal sulcus lesion site identified in Karnath & Perenin), dorsal premotor cortex (dPM), and in the mOPJ, near reach-related activation reported by others [12,13]. Moreover, they found that whereas mIPS was activated regardless of whether the target was presented in foveal or peripheral vision, mOPJ only responded (and 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 may play a critical role in decoupling eye-hand coordination. In addition, their results may explain the peripheral vision deficits of optic ataxic patients, as well as the strange phenomenon of magnetic misreaching in which parietal patients reach to the location of their gaze even when instructed to reach elsewhere [14]. These results are also consistent with new TMS findings showing that disruption of posterior parietal cortex function led to a tendency to reach closer toward fixation, leading "the hand to be a slave to the eye" [15]. TMS has also found that posterior parietal cortex disruption interferes with corrections to

compensate for jumps in target location [16] and with 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 toward the target without extending the arm. These studies have also reported activation in mOPJ [12,13], but only when targets were presented in peripheral vision [11], as well as within mIPS [18]. The relationships between the various reach- and pointing-related parietal regions in the human and the more well-established parietal reach region in the macaque monkey awaits clarification. Although one group has suggested that mOPJ as a homologue of the macaque parietal reach region (which includes areas V6A and MIP) [13], another group has proposed that mIPS in the human is a functional equivalent of macaque area also in the medial intraparietal sulcus (area MIP), based on similarities in responses to a visuomotor joystick task [19].

A growing body of literature is further characterizing the role of 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 those movements were planned than during subsequent times, suggesting that the region is also activated by movements to bodily targets as well as visual targets. An ambitious fMRI study of various types of reaching errors suggested that mOPJ encodes the current target of a reach [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]. In addition to demonstrations that human patients with aIPS lesions have grasping deficits, TMS applied to aIPS [28] and the superior parietal lobule [29] disrupts online 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 vs. reaching despite damage to an object-selective area in the ventral stream, the lateral occipital cortex [30].

Eye Movements and Topographic Maps

There is an extensive literature on human areas involved in eye movements [reviewed in 31]. fMRI studies have 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 demonstrates spatial updating when gaze changes [34,35,37]. The map in each hemisphere represents the contralateral visual field, which has led to the suggestion that the region is functionally similar to macaque parietal eye fields (in the lateral intraparietal sulcus) [33].   This suggestion is bolstered by an fMRI study that directly compared saccade-related activation in humans and macaques. 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. Based on similarities in their retinotopic maps [39], IPTO is comparable to macaque V3A [40]. Two additional human parietal areas with topographic representations have been reported posterior to the PEF [41,42]. Other preliminary evidence suggests that putative human equivalents of V6 and the ventral intraparietal area, VIP [43], may also contain topographic maps [44,45]. Indeed, it now appears that parietal cortex is tiled with spatiotopic maps that were not previously reported by simple visual mapping (typically using flickering checkerboard stimuli) but 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 have focused on areas within the ventral stream [46], neuroimaging has also revealed shape-selective activation for objects within the dorsal stream of both monkeys and humans [47]. These regions have tended to be ignored because of concerns regarding attentional confounds, which could be more problematic for parietal areas. Given the importance of actions in the dorsal stream, we hypothesize that these regions likely 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 [48,49] but not object identity [48], consistent with the

fact that orientation is critical to action planning whereas identity may not always be

essential. fMRI adaptation has also been used to investigate the selectivity of aIPS,

finding that aIPS is sensitive to the grasp posture, whereas object-selective ventral stream

regions are not [50]. Furthermore, aIPS, or a nearby region, demonstrates a preference for

shapes with 3D information defined by motion or pictorial cues [51]. 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., 52], regions in the dorsal stream remain activated by objects

even when those objects are not consciously perceived [53]. 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 for action were

indeed being processed in the dorsal stream. These results could account for the ability of

patients (such as D.F. or patients with blindsight) and normal subjects [e.g., 54] to

accurately act upon objects without explicit awareness [53].

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 review, see 55]. 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, tool-selective areas in the dorsal stream are thought to be related to the motor representations associated with familiar tools and their usage [56].

However, the nature of the tool-selective activation within the dorsal stream is not yet certain. Since tools are graspable, and typical control stimuli (e.g., animals [56]) are not, tool-related parietal activations near aIPS may 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 [57]. 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). Moreover, we found that the tool-selective parietal region is typically posterior to aIPS, as defined by grasping (vs. reaching) [58]. 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 Fig. 1b) [59,60]. It is likely that some of these posterior parietal activations directly correspond to those representations which 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 critical sites of damage associated with

ideomotor apraxia [61,62]. It is worth noting that some apraxic patients have no troubles preshaping their hand in accordance with the physical attributes of an object but yet are unable to form the correct hand postures when attempting to utilize these same objects based on their learned functional attributes [63-65]. Thus, it appears as though the tool-related representations within the left posterior parietal cortex play a critical 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 [66].

Action Observation

Within the grasping circuit of the macaque, including aIPS and the adjacent inferior parietal lobule [67], as well as area F5 in frontal cortex [68], 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 [69]. Such mirror responses have also been reported in human parietal and frontal cortex during action observation [for review, see 70]. In the human [71], as in the macaque [67], action observation responses appear to be tuned to the ultimate goal of the action rather than specifics such as the hand's trajectory. In human parietal and ventral premotor cortex, activation for passive observation of others' actions partially overlaps with activation for execution of those same actions [72]. Mirror responses can also be driven by sounds or verbal descriptions that imply others' actions [73,74].

Action observation responses may depend on the richness of the observer's own experience with such actions. An fMRI study found that expert dancers showed greater mirror responses to watching another dancer perform movements in their trained style than in another style [75]. These enhanced responses were observed across the network of action observation areas, including posterior parietal cortex. Another fMRI study had subjects observe biting actions and communicative mouth gestures made by humans, monkeys, or dogs [76]. Two regions of the left posterior parietal cortex became active not only while observing human feeding actions, but also during the observation of feeding actions performed by the other species. Interestingly, although parietal activations were always observed in both hemispheres, right parietal areas preferred the viewing of human actions compared to 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 may be critical in imitating and learning new actions [77]. Some intriguing results from Buccino et al. [78] suggest that the parietal cortex plays a special role in observing actions when the observer intends to later imitate those actions. When non-musicians had to observe a musician playing a guitar chord and then plan to imitate the action, parietal cortex was more activated than when they had to observe one chord but then prepare 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, due in large part to the technical challenges of using action paradigms for neuroimaging, perhaps accompanied by a general neglect of the study of action in cognitive science [79]. In some ways, however, this may be an advantage, because the study of the ventral stream has revealed general principles which may 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 have been dissenting views on whether visual processing occurs within specialized modules dedicated to processing specific stimulus categories [80] or whether overlapping activation across multiple stimulus types reflects a distributed representation of all categories [81,82]. 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 have been studied largely in isolation, in the real world, these actions often co-occur in a carefully choreographed movement, as when one saccades to, reaches toward 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 may be greatly simplified through the determination of general organizational principles. For example, areas within

the ventral stream appear to follow a quasi-retinotopic organization, with adjacent representations for stimuli that are processed in the fovea (faces), mid-periphery (objects) and far periphery (scenes) [83]. Moreover, multiple areas selective for those categories are arranged in a mirror-symmetric organization, a principle which minimizes connection lengths in the brain [84]. One very intriguing and comprehensive neuroimaging study suggests that general organizational principles and mirror symmetry may explain the arrangement in parietal and frontal cortex [85]. It may be that the human parietal cortex is organized by broader principles, perhaps including factors such as the relative contribution of somatosensory (anterior) vs. visual (posterior) information, the importance of motor execution (anterior) vs. planning (mid-anterior) [59,60], sensorimotor (superior) vs. cognitive (inferior) processing [85], or coding of action space in particular coordinate frames [e.g., 86]. Although more abstract cognitive functions, such as numerical representations [87], may be greatly expanded in humans compared to nonhuman primates, they may ultimately also fit into a general organizational framework [85,88].

Acknowledgements

Figure Captions.

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 lOPJ 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 in the two species to suggest *possible* functional equivalents between species; however, such comparisons must always be done with considerable caution [for an extended discussion of the issues, see 5]. For grasping, there is one reliably-activated area in the human brain, aIPS, that is a likely equivalent of macaque AIP [23,89]. Similarly, both the human, PEF and macaque LIP have regularly

been shown to be involved in saccadic eye movements [40], so there is a reasonable argument for equivalence. Both human vIPS [43] and macaque VIP [90] show multimodal responses to moving stimuli and may be functionally equivalent. Both human lOPJ [48] and macaque cIPS [91] have demonstrated orientation-selectivity; however, any proposals for functional equivalence are very 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) [39], which is also activated in studies of attention and saccades [40]. Equivalencies between reach-related areas in the two species are particularly confusing [12,13,19]. In the macaque, adjacent areas MIP and V6A both show reach-related activation and together they are often labelled the parietal reach region. In the human, both mIPS and mOPJ both demonstrate reach-related activation but they are not directly adjacent. It is possible that functional equivalencies exist between mIPS and MIP and between mOPJ and V6A; however, additional evidence would be needed to substantiate such claims.

Sources for human activation foci: aIPS [24,25], mIPS [11], PEF [33,34], mOPJ [11-13], lOPJ [48], IPTO [92], tool execution and planning [60], action observation [76]. Sources for macaque activation foci: AIP, MIP, LIP and VIP [93], V6 and V6A [94], V3A [91,95], cIPS [91], action observation [67], tool use [96,97].

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Annotations (i.e. recommended reading)

• Karnath HO, Perenin MT: **Cortical control of visually guided reaching: evidence from patients with optic ataxia**. *Cereb Cortex* 2005.

This neuropsychological study utilized a "lesion subtraction" analysis to re-

evaluate the common lesion site for patients with reaching deficits in optic ataxia.

•• Prado J, Clavagnier S, Otzenberger H, Scheiber C, Perenin MT: **Two cortical systems for reaching in central and peripheral vision**. *Neuron* 2005, **48**:849-858.

This elegant fMRI experiment greatly clarified the pattern of reach-related

activation in parietal cortex, showing a dissociation between areas depending on

eye position. One area (mIPS) was activated by reaching regardless of the

subject's eye position during target presentation. A second area (mOPJ) was

activated when the target was presented peripherally but not when it was

presented foveally. Moreover mOPJ was activated when the target was presented

very briefly in the periphery and the eyes made a saccade to its location after it

disappeared but before the reach occurred. This suggests that the activation did

not depend on the occurrence of a saccade, but rather on whether the target was

"captured by the fovea" before the reach.

• Tunik E, Frey SH, Grafton ST: **Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp**. *Nat Neurosci* 2005, **8**:505-511.

By applying TMS to aIPS, the authors disrupted subjects' ability to adjust hand

posture to a change in the orientation of an object to be grasped.

•• Shmuelof L, Zohary E: **Dissociation between ventral and dorsal fMRI activation during object and action recognition**. *Neuron* 2005, **47**:457-470.

The authors presented subjects with videos of hands grasping objects to provide converging evidence that dorsal and ventral stream areas are tuned to fundamentally different aspects of an observed movement. First, whereas the dorsal stream showed a greater response when the acting hand was in the contralateral visual field, the ventral stream showed a greater response when the target object was in the contralateral visual field. Second, whereas dorsal stream activity was elevated when subjects attended to the acting hand, ventral stream activity was elevated when subjects attended to the target object. Third, whereas fMR-adaptation indicated that the dorsal stream was sensitive to both the form of the grasp and the object shape, the ventral stream was tuned only to object identity.

•• Fang F, He S: **Cortical responses to invisible objects in the human dorsal and ventral pathways**. *Nat Neurosci* 2005, **8**:1380-1385.

The authors investigated whether fMRI activation in object-selective areas within the ventral (fusiform and lateral occipital areas) and dorsal (intraparietal sulcus) streams would be modulated by "interocular suppression" whereby stimuli could be made 'invisible' to conscious perception. Dorsal but not ventral stream activations remained elevated for intact objects as compared to scrambled images even when the stimuli were not consciously perceived.

• Fridman EA, Immisch I, Hanakawa T, Bohlhalter S, Waldvogel D, Kansaku K, Wheaton L, Wu T, Hallett M: **The role of the dorsal stream for gesture production**. *Neuroimage* 2005.

This fMRI study examined the neural substrates associated with the planning and execution of both transitive (i.e. object related) and intransitive (i.e. non-object

related) gestures. For both types of gestures, parietal activity associated with planning was localized more posterior/inferior to that associated with execution. For ventral premotor areas the relationship was reversed. In addition, parietal (and frontal) areas were recruited more for transitive actions as compared to intransitive actions, consistent with findings that parietal patients have more problems with object-related actions than other gestures.

• Johnson-Frey SH, Newman-Norlund R, Grafton ST: **A distributed left hemisphere network active during planning of everyday tool use skills**. *Cereb Cortex* 2005, **15**:681-695.

This fMRI study disentangled activity associated with the planning of tool use pantomimes from that associated with their execution. A left lateralized network of areas was identified during the planning of tool-use pantomimes relative to the planning of meaningless arm movements. Within parietal cortex, the planning-related activation showed partial overlap with execution-related activation, but also included more posterior regions. Importantly, the same network was active during the planning and execution of tool use gestures with either hand.
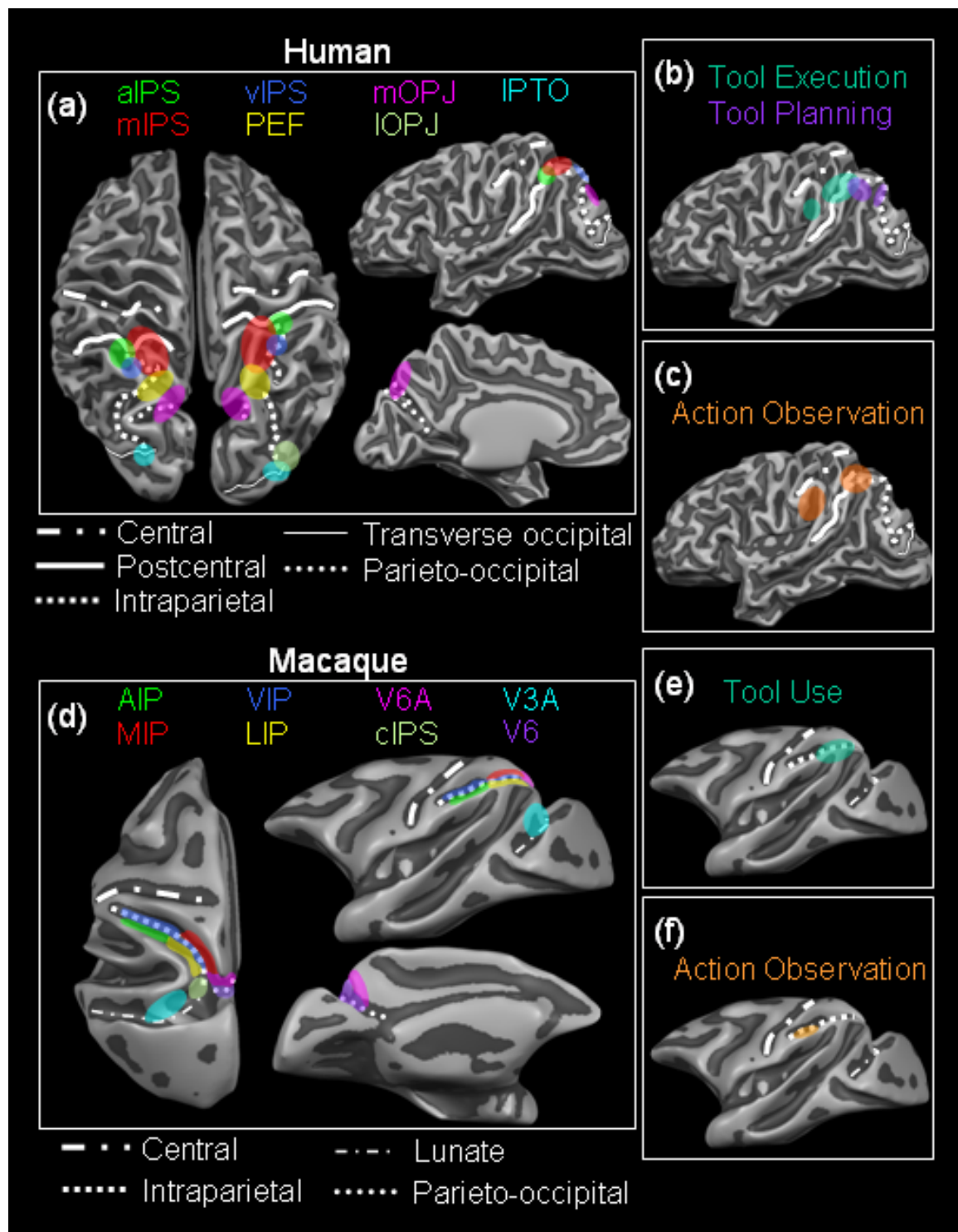
• Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund HJ, Rizzolatti G: **Neural circuits underlying imitation learning of hand actions: an event-related fMRI study**. *Neuron* 2004, **42**:323-334.
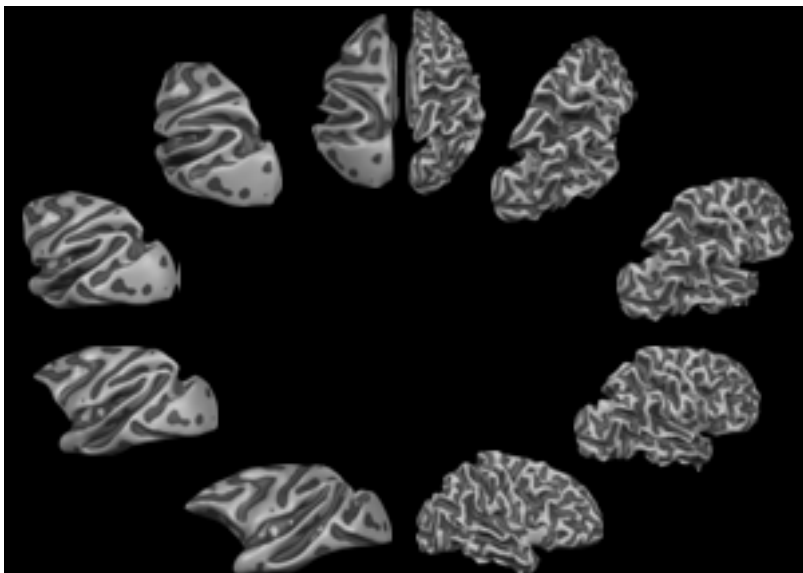
Subjects in an fMRI experiment were asked to observe a 'model' play a guitar chord and either imitate that action after a delay period or instead execute a completely different 'nonchord' action. A condition whereby the subject simply viewed a guitar, without any associated action, and then later played a guitar chord of their choice was also included. The results suggest that the mirror

system, including inferior parietal and ventral premotor cortices, plays a critical role in imitative learning. Specifically, the authors propose that the vision-to-action transformations needed to successfully imitate an observed behavior are carried out within the mirror neuron system and this information is then fed into other regions for the guidance and execution of those actions.

•• Simon O, Kherif F, Flandin G, Poline JB, Riviere D, Mangin JF, Le Bihan D, Dehaene S: **Automatized clustering and functional geometry of human parietofrontal networks for language, space, and number**. *Neuroimage* 2004, **23**:1192-1202.

This impressive reanalysis of earlier fMRI data suggests general organizational principles within parietal cortex. The original experiment [98] included six different tasks within the same group of subjects: saccades, attention shifts, pointing, grasping, calculation and a language task. In the reanalysis, an automatic clustering algorithm was used to categorize voxels within the parietal and frontal lobes based on the pattern of responses across all six tasks. The authors suggest that whereas visuospatial and manual tasks activate more superior regions of posterior parietal cortex (in the intraparietal sulcus and superior parietal lobule), calculation and language activate more inferior regions (in the inferior parietal lobule). Furthermore, they note that the ordering of activations in parietal and frontal cortex, particularly for language and calculation tasks, occurs in a mirror-symmetric arrangement.

[potential cover image]