

Neuroimaging of cognitive functions in human parietal cortex

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Functional neuroimaging has proven highly valuable in mapping human sensory regions, particularly visual areas in occipital cortex. Recent evidence suggests that human parietal cortex may also consist of numerous specialized subregions similar to those reported in neurophysiological studies of non-human primates. However, parietal activation generalizes across a wide variety of cognitive tasks and the extension of human brain mapping into higher-order 'association cortex' may prove to be a challenge.

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Abbreviations

AIP	anterior intraparietal area
cIPS	caudal intraparietal sulcus
fMRI	functional magnetic resonance imaging
IPL	inferior parietal lobule
IPS	intraparietal sulcus
IPTO	junction of intraparietal and transverse occipital sulci
LIP	lateral intraparietal area
MIP	medial intraparietal area
PET	positron emission tomography
PRR	parietal reach region
SPL	superior parietal lobule
VIP	ventral intraparietal area

Introduction

Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have provided powerful tools for mapping the human brain. Neuroimaging has been particularly successful in mapping cortical visual areas in the human occipital [1] and temporal [2] lobes. The human parietal lobes (excluding somatosensory regions, which are not discussed here), which traditionally fall into the category of 'association cortex' because of their complex, multimodal responses, provide one of the next challenges for neuroimaging.

Regions of parietal cortex form a major component of the 'dorsal stream', which is thought to be involved fundamentally in spatial localization [3] and the control of action [4] (in contrast to the ventral stream, which is thought to be more involved in perceptual recognition). In patients with parietal damage, human neuropsychology has identified a host of deficits, including attentional disorders (such as hemispatial neglect and simultanagnosia), spatial localization disorders and sensorimotor coordination problems (optic ataxia and apraxia) [5]. Single-neuron recording in macaques has demonstrated numerous regions in parietal

cortex that perform highly specialized spatial and sensorimotor functions (Figure 1a) [6,7].

Although monkey physiology and human neuropsychology have provided invaluable insights, these techniques have important limitations in providing an understanding of human parietal function. Comparisons of brain maps between humans and other primates show striking differences even in early sensory areas [8,9], and one-to-one homologies are even less likely in higher-tier areas. Furthermore, the densely packed areas found in macaque parietal cortex are generally too small to be distinguished by the large lesions typical of most human neuropsychological studies. Neuroimaging thus holds promise for the mapping of human parietal cortex in greater detail than previously possible. What has it delivered so far?

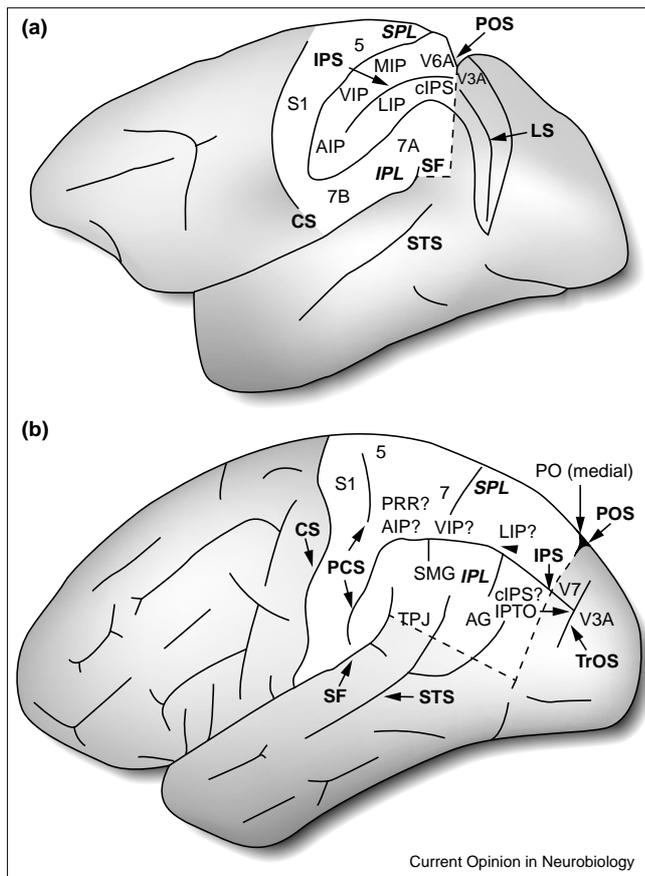
In keeping with findings from human neuropsychology and monkey neurophysiology, numerous articles over the past decade have shown that the parietal lobes are activated in tasks involving visuomotor control, attention and eye movements. Here, we review the main new results in these areas, and also mention some of the other tasks that have been reported to activate parietal cortex. To facilitate localization and cross-species comparisons, Figure 1 illustrates key functional and anatomical areas in macaque cortex (Figure 1a) and the best estimates of homologous regions in human cortex based on the current literature (Figure 1b).

Comparisons of human and monkey parietal cortex

Monkey neurophysiology has identified a number of parietal areas within the intraparietal sulcus (IPS) that respond during specific visuomotor processes. Briefly, these include areas specialized for saccades (lateral intraparietal area [LIP]) [10], reaching (parietal reach region [PRR], which includes both area V6A and the medial intraparietal area [MIP]) [11,12], grasping (anterior intraparietal area [AIP]) [13], processing of shape and orientation (caudal IPS [cIPS]) [14], and movements towards and contact with the mouth and head (ventral intraparietal area [VIP]) [15]. These areas have been shown to code space in a variety of coordinate frames [16], including eye-centred (LIP), head-centred (e.g. VIP, V6) [15,17], body-centred (area 5, MIP) [18] or even tool-centred coordinates [19], and many are modulated by factors such as eye position [20]. These areas are not always uniquely specialized or simple; for example, LIP has visual, attentional, memory and saccade-related activation [10], and its receptive fields are dynamic — changing with the intention to make a saccade [21].

We now examine preliminary neuroimaging evidence for potential human homologues of each of the five monkey parietal areas described above. The homologies that we

Figure 1



Comparison of monkey and human parietal lobes. Lateral view of (a) macaque monkey brain (modified with permission from [14]) and (b) human brain (adapted with permission from [102]), showing parietal lobes in white. Bold text indicates major sulci, italicized text indicates lobules, and plain text indicates functional or anatomical areas. Parietal boundaries are based on anatomical criteria rather than on functional attributes [103]. The central sulcus (CS), Sylvian fissure (SF) and parieto-occipital sulcus (POS) provide unambiguous boundaries, with the remaining boundaries extrapolated from other landmarks. The most salient parietal landmark is the intraparietal sulcus (IPS) that divides the parietal lobe into the superior parietal (SPL) and inferior parietal lobules (IPL) in both species [94]. In humans, the IPS is a long (~7 cm), deep (~2 cm) sulcus [102] between the transverse occipital sulcus ([TrOS] near the POS) and the postcentral sulcus (PCS). In the monkey, parietal cortex contains many specialized regions including primary somatosensory cortex (S1); Brodmann's areas 5, 7A and 7B; visual areas V3A (occipitoparietal boundary), V6A and the anterior (AIP), ventral (VIP), medial (MIP) and lateral (LIP) and caudal (cIPS) sections of the IPS [6,7]. The IPS and adjacent lunate sulcus (LS) in the monkey brain have been opened up to reveal the fundus and banks of each sulcus. Human neuroanatomy differs substantially from that of monkey. It is generally believed that the human SPL is homologous to the monkey IPL [104]. Several human areas have been proposed to be putative human homologues of monkey areas (appended with question marks to indicate speculative relationships). Other areas without clear homologues have also been reported, including: V7; the supramarginal (SMG) and angular (AG) gyri; functional areas at the IPS/TrOS junction (IPTO); the temporoparietal junction (TPJ) and parieto-occipital (PO) region. Medial parietal areas have not been well-characterized in either species. STS, superior temporal sulcus.

propose are highly tentative and are offered here merely as a starting point for mapping parietal cortex. Certainly, there are many regions that demonstrate similar properties in both monkeys and humans; however, understanding their precise functions and relationships will require many further experiments.

Lateral intraparietal area

Numerous areas within the IPS (e.g. the junction of the IPS and transverse occipital sulci [IPTO], which may include visual areas V7 and/or V3A; posterior IPS; and anterior IPS) are activated by both saccades and attention [22]. One of these areas may be the homologue of monkey LIP [23**], which is also strongly driven by saccades and attention [10]. The most likely candidate region lies in the mid-posterior IPS, responds strongly even during predictable saccades (which have reduced attentional demands compared with unpredictable ones), and has been proposed as the human homologue of LIP [24]. Putative LIP may contain a retinotopic map of saccade direction [25].

Parietal reach region

Neuroimaging studies have reported activation in the IPS during reaching movements [26]. It is not yet clear whether this region is distinct from other parietal areas. Reach activity was reported anterior to saccade activity in one study [27]. A more recent study using pointing (directing the finger towards a target without reaching to it) found, however, that although pointing and saccade regions overlapped, pointing-related activation was more medial [28]. Interestingly, a reach-related region in the anterior IPS was modulated by eye position [29*,30] and may be the human homologue of the monkey PRR [31].

Anterior intraparietal area

The human anterior IPS is activated during visually guided grasping [32,33], although grasping activity appears to overlap completely with reach-related activity [34]. This area is a probable homologue of monkey AIP, which contains neurons that respond to the visual and motor components of the grasp and that are tuned to specific shapes to be grasped [35]. The human area is also activated by the tactile manipulation of objects [36,37], by the observation of others' hand movements [38], and even by passive viewing of graspable objects, namely tools [39*].

Caudal intraparietal sulcus

Human neuroimaging has identified a region in the caudal end of the IPS that is activated during object matching and grasping [32], as well as during discriminations of object size and orientation [40]. This area may be a homologue of monkey cIPS, an area that contains neurons selective to binocular disparity, shape and three-dimensional orientation, and that may send projections to AIP to provide information for the visual guidance of hand action [14,41]. The relationship of cIPS to other areas in the vicinity (V3A, V7 and IPTO) has yet to be determined.

Ventral intraparietal area

Preliminary data suggest an area in human IPS that may correspond to monkey VIP. Like the monkey area, putative VIP in humans responds to visual motion towards the face as well as tactile stimulation of the face (SP Dukelow *et al.*, unpublished data) and has multimodal responses [42**].

Attention and eye movements

Few would challenge the claim that the parietal lobes play an important role in visual attention [6,43], the mechanism that enables us to direct our processing resources to a subset of the available information. Most physiological research on attention has focused on area 7 in the monkey inferior parietal lobule (IPL), which is believed to be homologous with area 7 in the human superior parietal lobule (SPL; Figure 1) [44]. In the human, attention-related activation has been reported throughout the parietal lobe, specifically in the IPS (ranging between IPTO and the postcentral sulcus), the postcentral sulcus, the SPL and IPL (including the supramarginal gyrus), and the temporo-parietal junction [22,45,46,47**,48**,49,50**]. As yet, the precise role of these parietal regions in attention is a matter of substantial debate. We consider here three recent developments in the neuroimaging literature on attention.

First, research during the past year has strengthened the evidence that regions in parietal cortex produce the top-down signals that modulate activity elsewhere in the visual system. In particular, several studies have demonstrated ‘baseline shift’ attention signals [10] in which neural activity in visual and association areas, including SPL, IPS and in some cases IPL, increases as a function of attentional preparation even before the target stimulus appears [23**,48**,49,51,52*]. Importantly, these baseline signals can be larger in SPL [23**] or IPS [48**,52*] than in other visual areas, suggesting that the parietal lobes may be a source of attentional control signals.

Second, several studies have implicated parietal regions not only in visual attention, but also in auditory [53] and haptic attention [54]. One study [55**] found overlapping activations in parietal (and frontal) regions for a change detection (‘oddball’) task (see also [56**]) with visual, auditory and tactile stimuli, as well as unimodal activations in visual, auditory and somatosensory association cortex (see also [57*]). These findings suggest that at least some parietal regions may be involved in attentional selection independent of modality.

Third, new findings indicate that not all attentional activations of the parietal lobe reflect a spatial component, and not all such activations can be accounted for in terms engaging the eye movement system. Visual attention and saccades [22,58], as well as smooth pursuit eye movements [59,60], activate largely overlapping networks, including areas within the IPS. Two recent studies suggest that attention yields greater activity than saccades in several regions, including the SPL, IPS and frontal eye fields

(FEF) [61,50**]; however, another report suggests that a network of areas responds more to overt saccades than covert attentional shifts [62]. Nevertheless, eye movement factors cannot account for all attentional activations in the parietal lobes. Foveal attention tasks that have little or no spatial component and do not involve the making, planning or suppression of eye movements can nonetheless produce substantial activation throughout the IPS and in other parietal regions [47**,63–65]. These findings indicate that attention per se can strongly activate parietal regions, independently of any involvement of spatial or eye movement processes.

Other functions

In addition to the functions reviewed above, parietal activation has also been reported for a stunningly diverse range of stimuli and tasks. These include motion processing [52*,66*,67,68], stereo vision [69], spatial [70,71] and non-spatial working memory (which shows considerable overlap with visual attention activation [72**]), mental imagery [73], mental rotation [74], response inhibition [75,76], task switching [77], alertness [78], calculation [79,80], and even functions not typically attributed to parietal cortex such as pain processing [81], swallowing [82] or meditation [83]. Clearly, it would be absurd to claim that parietal areas are specialized for any one of these processes and some means of integrating the diversity of findings is required.

Conclusions

Why is parietal activation so general?

The most striking finding in a review such as this is the heterogeneity of stimuli and tasks that produce parietal activation. Why is parietal activation so general? We propose several possible explanations.

First, the parietal lobes may really be purely ‘association cortex’, a zone in which many related functions such as attention, spatial representation, working memory, eye movements and the guidance of actions come together. Although these topics have been treated traditionally as separate domains in cognitive science, they may be highly integrated in their underlying neuroanatomy. Second, the processing performed in parietal cortex may be of such a general nature (e.g. attention, coordinate transformation) that parietal cortex is recruited by a wide range of tasks. Third, some have suggested that the factors that enhance the baseline firing rate of a large number of neurons, such as attention [10], may lead to large increases in the population responses measured by neuroimaging [84**]. Thus, parietal functions such as attention may be particularly effective at producing activation. Fourth, functional specialization in the parietal lobes may be at a finer grain than is typically resolved with current imaging techniques [85], or neurons within areas may be specialized but interdigitated such that they cannot be resolved by fMRI. Last, current hypotheses concerning parietal function may not be the actual dimensions along which the parietal lobes are functionally

organized; on this view, what we are lacking is a conceptual advance that leads us to test better hypotheses.

How can future research better investigate parietal function?

Even a cursory review of the parietal neuroimaging literature to date suggests that perhaps the appropriate question to ask is not ‘what activates parietal cortex?’, but rather ‘what does not activate parietal cortex?’. For example, in the case of visual attention, it is enlightening to find not only that multiple forms of attention activate equivalent regions but also that a challenging language task does not, indicating that the area is not simply driven by general difficulty or arousal [47**].

Comparisons between tasks are most fruitful when performed within subjects. Although meta-analyses of the imaging literature may suggest similarities or differences in activation across tasks [86,87*], these typically only report the centroids of group activation without considering the extent (often large for parietal regions), individual variability, or specifics of the subtractions used. Experiments that analyze overlapping activation across many tasks in individual subjects appear particularly valuable in elucidating parietal processing [22,47**,72**], as they have been in mapping earlier visual areas [1].

Perhaps the greatest challenge in mapping parietal cortex is that many of the functions that it probably subserves are a vital component in many cognitive tasks. Specifically, most tasks involve one or more of the following components: shifting and maintaining attention; directing eye movements and generating motor plans, either explicitly or implicitly; using working memory; and coding and transforming space [88] in input (e.g. retinotopic) or output (e.g. arm-centred) coordinates. Thus, in any comparisons between two states, it is important to control for these general factors (e.g. attention) before drawing conclusions about parietal function. Even in cases when indirect factors may play a role, attempts to control them may fail.

For instance, it is common practice to require subjects to maintain fixation throughout an experiment in an attempt to minimize eye-movement-related activation. However, the requirement to fixate may lead to greater peripheral attention and suppression of eye movements that are planned but not executed, potentially producing greater activation confounds than free viewing [50**]. Alternative approaches include the use of parametric designs where fixation requirements are comparable across task loads [89] or free viewing of stimuli with post hoc analyses to determine whether eye movements differed between conditions [90].

With the advent of more sophisticated techniques in neuroimaging, more rigorous tools are available to decode parietal function. Whereas PET and many traditional fMRI experiments have used blocked designs, event-related designs have recently used analyses based on individual

trials [91]. One particularly promising technique available with event-related designs is the use of adaptation. Just as psychophysics has used adaptation to determine whether two stimuli are processed by the same mechanism, neuroimaging has used adaptation to determine whether two stimuli are processed by the same brain region. Specifically, fMRI adaptation has been used to study invariance in ventral stream areas [92**]. If dorsal stream areas also demonstrate adaptation, the technique might provide a powerful means to determine whether two functions, such as attention and eye movements, really do activate the same neural subpopulations.

Neuroimaging of human brain functions is also likely to benefit from crosstalk with related disciplines. Neurophysiology has been reasonably successful at mapping monkey parietal cortex by combining functional data from single units with precise anatomical localization [93], architectonic parcellation [94] and information about regional connectivity [95]. Its limitations come from the fact that experimenters must have a priori hypotheses about which regions perform which functions. Neuroimaging enables researchers to determine which regions carry out a given function in the absence of prior anatomical hypotheses. The future may lie not only in more systematic functional mapping, but also in combining activation data with human architectonics [94] and functional connectivity [57*,96,97]. Neuroimaging in primates also holds much promise for identifying homologies by using comparable techniques in the two species [98–100].

Can association cortex be mapped?

Functional imaging is pushing the boundaries of human brain mapping from the relatively well-established primary cortical areas to secondary and tertiary ‘association cortex’. It remains to be seen how far such functional mapping will go, particularly for areas where monkey homologies are unknown or nonexistent. Research in occipital and temporal cortex suggests that functional imaging can make a valuable contribution in identifying human homologues of cortical areas identified previously in the macaque, and in discovering novel functionally defined regions.

As discussed here, however, parietal cortex may be particularly challenging for a number of reasons. The parietal lobes are not the only region of the brain where researchers are struggling to understand overlapping activations across apparently very different tasks; a similar pattern of results is found in the frontal lobes [101]. Our hope is that more sophisticated experimental designs and converging techniques will aid in dissociating association cortex.

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