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Parietal cortex and attention

Marlene Behrmann[1]*, Joy J Geng[2] and Sarah Shomstein[1]

The parietal lobe forms about 20% of the human cerebral cortex and is divided into two major regions, the somatosensory cortex and the posterior parietal cortex. Posterior parietal cortex, located at the junction of multiple sensory regions, projects to several cortical and subcortical areas and is engaged in a host of cognitive operations. One such operation is selective attention, the process where by the input is filtered and a subset of the information is selected for preferential processing. Recent neuroimaging and neuropsychological studies have provided a more fine-grained understanding of the relationship between brain and behavior in the domain of selective attention.

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Abbreviations

aIPS	anterior intraparietal sulcus
CVA	cerebrovascular accident
DMS	delayed match-to-sample
fMRI	functional magnetic resonance imaging
IPL	inferior parietal lobule
SPL	superior parietal lobule
TPJ	temporoparietal junction

Introduction

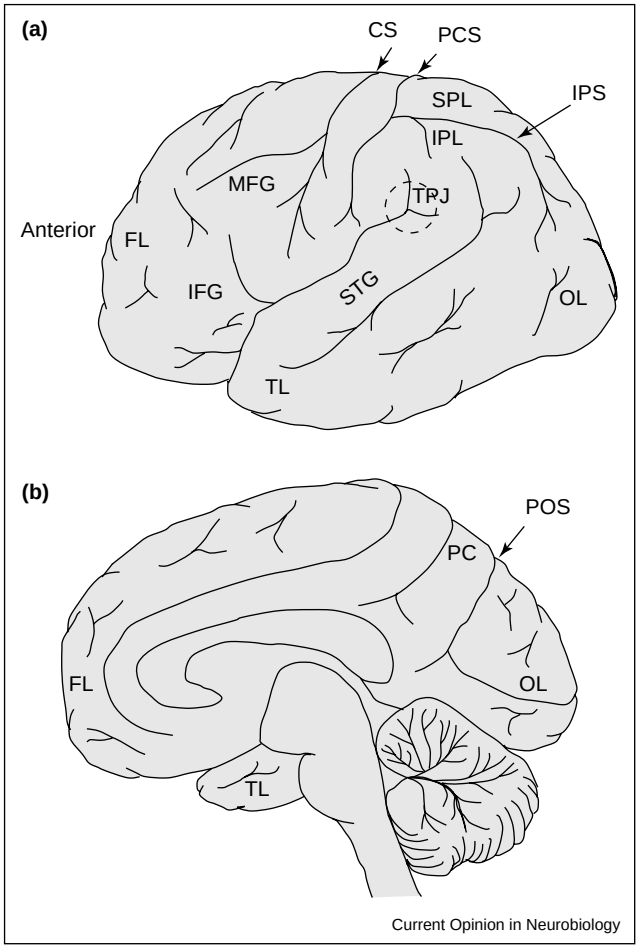
Parietal cortex, situated at the intersection of visual, auditory, and tactile cortices at the 'crossroads of the brain' [1], is 'association' or tertiary cortex. With its requisite connectivity to cortical and subcortical regions associated with motor responses, parietal cortex serves a crucial role in transforming sensory input into motor output. In the course of doing so, a host of cognitive computations are engaged including spatial representation and updating, attention, coordinate transformation, as well as abstract motor planning [2]. Although much progress has been made in demarcating fine-grained anatomical distinctions in parietal cortex and their functional correlates in nonhuman primates [2,3], this has not been possible in humans. In the past, neuropsychological studies in individuals with lesions have been somewhat helpful in this regard; however, in most cases, the lesions are diffuse, precluding definitive conclusions about the structural and functional aspects of human parietal cortex. With the advent of high-resolution functional neuroimaging, this mapping of anatomical areas is now possible. In addition, the development and accessibility of methods for detailed structural analysis of lesions has enabled a more fine-grained demarcation of the lesion site in brain-damaged individuals, and, consequently, a more precise brain–behavior correlation. Here, we review the recent advances that suggest that the role of posterior parietal cortex in selective attention is more specific than was previously assumed.

Parietal cortex and attention

Selective attention is the process whereby a subset of the input is selected preferentially for further processing. A primary focus of several recent neuroimaging investigations of attention has been to determine the anatomical locus within the parietal lobe that gives rise to the attentional biasing signal (i.e. the source) that ultimately initiates the sensory enhancement of the selected stimulus (i.e. the effect). The attentional biasing signal could potentially be generated in one of two ways: first, in a bottom-up or stimulus-driven manner (also referred to as 'attentional capture') that occurs by virtue of an intrinsic property of the stimulus that is sufficiently salient to divert attention from the current focus, or second, in a top-down or goal-directed fashion, resulting from the explicit will of an organism. Both goal-directed and stimulus-driven mechanisms have ecological significance such that, under certain circumstances, attention in one or the other fashion has adaptive value [4], and several recent papers suggest that these two attentional biasing mechanisms map onto distinct loci within the parietal cortex (see Figure 1).

A number of functional magnetic resonance imaging (fMRI) studies have documented that bottom-up attentional capture, mediated by stimulus salience and/or relevance, is subserved by the temporoparietal junction (TPJ; see Figure 1a). For example, when subjects attend to and monitor a change in either a visual or an auditory stimulus presented simultaneously, blood oxygenation level dependent (BOLD) activation of the TPJ region of the right parietal lobe is enhanced; this only happens, however, when the stimulus change occurs in the modality that is relevant to the current behavior [5]. In addition to the apparent sensitivity to relevant stimuli, the TPJ is also activated in response to potentially novel

Figure 1



Anatomical regions and boundaries of human parietal cortex. **(a)** Schematic depiction of relevant anatomical landmarks projected onto the (a) lateral and **(b)** medial surface of the human brain. Parietal cortex is located posterior to the postcentral sulcus (PCS), which lies posterior to the central sulcus (CS), and superior to the occipital lobe (OL). It is divided by the intraparietal sulcus (IPS) into the superior parietal lobule (SPL) and the inferior parietal lobule (IPL). The continuation of the SPL on the medial side, anterior to the parietooccipital sulcus (POS), is called the cuneus. The frontal lobe (FL) is divided into the middle frontal gyrus (MFG) and the inferior frontal gyrus (IFG). The superior temporal gyrus (STG) runs along the superior extent of the temporal lobe (TL) and terminates at the temporoparietal junction (TPJ).

(unexpected or infrequent) events when an organism is engaged in a neutral behavioral context (i.e. not performing a specific task) [6••]. This activation occurs independent of the modality (auditory, tactile, visual) in which the input is delivered, which reflects the multisensory attentional role played by the TPJ.

When the source of the attentional signal is top-down or goal-directed, the superior parietal lobule (SPL; see Figure 1a) and the precuneus (PC; see Figure 1b) region are engaged [7••,8••,9•,10•]. In a typical task, individuals are shown two streams of input presented peripherally to the left and right of fixation and are initially instructed to monitor one stream for a cue (a digit among the stream of letters). The identity of the cue indicates to the subject whether they should maintain attention on the current stream or shift attention to the other stream [7••,8••]. In comparison to the activity levels in extrastriate cortex when maintaining attention on the contralateral field, there was an increase in activation when attention shifted to the contralateral visual field. Similarly, activation in extrastriate cortex decreased following a shift of attention to the ipsilateral visual field and remained relatively low when the attentional focus was maintained on the ipsilateral target stream. This result corroborated earlier findings suggesting that the strength of the sensory representation of an item is enhanced when an item is the object of attention [11,12]. An interesting finding emerged when the authors compared activity related to shifting the attentional focus from one spatial location to another with activity during a condition in which subjects were instructed to remain focused within the stream. It was observed that the time course of the BOLD signal in the right SPL and inferior parietal lobule (IPL; see Figure 1a) exhibited transient activity when attention was shifted between spatial locations. The transient nature of the signal elicited by the SPL suggests that this area of the parietal cortex is the source of a brief attentional control signal to shift attentive states, and is not the source of a continuous signal to actively maintain the new attentive state.

SPL activation is not apparently restricted to spatial shifts alone and this region is activated when subjects shift their attention between any two dimensions of the input; for example, shifts between superimposed houses and faces [8••], shifts between two different features of an object [9•] or shifts between two different sensory modalities [13•] all activate SPL. Whereas spatial shifts are accompanied by increased activation in the SPL region of the parietal lobe [7••], non-spatial shifts are accompanied by increased activity in the precuneus region, the continuation of the SPL on the medial side of the parietal lobe. This anatomical distinction between spatial and nonspatial shifts of attention deserves a more thorough investigation [10•].

We should note that additional attentional functions could be mediated by the same subareas of parietal cortex. For example, both an anterior part and an inferior part of the intraparietal sulcus appear to be activated in a visual conjunction task, even in the absence of multiple distractors [14•], and this occurs to a greater extent in the left than right hemisphere (see also Shulman *et al.* [15]). By contrast, activation of a more posterior region of the intraparietal sulcus appears to be contingent on the presence of distractors.

Crossmodal and unimodal attentional enhancement

Most studies of parietal cortex and attention have focused on visuospatial tasks, and, unsuprisingly, the neural systems associated with attention have been tightly coupled with the saccadic eye-movement system [16,17•]. However, findings from the monkey physiology literature as well as recent fMRI data in humans [18,19] suggest functional specialization within the parietal lobe in mapping between different sensory modalities and different motor effectors. Although crossmodal effects have been explored quite extensively in behavioral psychology (e.g. Driver and Spence and Kennett *et al.* [20,21]), the neural representation of these processes using fMRI has only started recently [13•].

Two recent studies report considerable agreement in their findings of crossmodal representations in the anterior intraparietal sulcus (aIPS; see Figure 1a) [22••,23••]. In the Macaluso *et al.* study [22••], an auditory tone cued participants to the side of a space where a target was likely to appear. Unimodal targets in all conditions were embedded within bilateral and bimodal (visual and tactile) stimulation. Contralateral aIPS and middle lateral occipital gyrus activation were recorded during the delay period when the expected target was both visual and tactile. (It is worth noting that the Talairach coordinates for the middle lateral occipital location correspond well with those of the tactile and visual representation of objects in the lateral occipital cortex (LOC) reported by Amedi *et al.* [24].) Grefkes *et al.* [23••], by contrast, used a delayed match-to-sample (DMS) task in which the sample and target stimuli were either crossmodal (tactile and visual) or intramodal (tactile or visual), and greater activation was observed in the left aIPS (tactile stimuli presented to the right hand) for the crossmodal condition compared with that in the intramodal condition.

Although Macaluso *et al.* [22••] and Grefkes *et al.* [23••] agree that aIPS and, to a lesser degree, other areas are involved in multimodal representation, it is unclear whether these activations reflect the crossmodal representation of contralateral space [22••,25] or they reflect the spatially nonspecific transfer of information among modalities [23••]. A further possibility is that this activation reflects the imagery of self-generated movements [26]; in a DMS task in which the sample and target were tactile, activation of the aIPS and fusiform gyrus were also found during the delay period. Similarly, in a study that was not designed to investigate attentional effects per se but was rather an attempt to localize the anterior intraparietal region (AIP) in humans [27], subjects performed a DMS task in which they performed a visual orientation task, a color discrimination task, an orientation plus imagined grasping task, or an orientation discrimination plus pantomimed grasping task. There was condition-dependent modulation of the aIPS such that the grasping condition produced the most activation, followed in descending order by imagined grasping, visual discrimination, and color discrimination, which produced the least activation. The aIPS in humans might also be involved in preparatory activity for multi-effector action [28]; the investigators observed activation in the aIPS when a lateralized visual target was covertly attended, fixated with a saccade, or pointed to with a finger ([29] see also Macaluso *et al.* [25]). Interestingly, the aIPS was activated in tasks that involved a delay period between presentations of task-associated visual and/or tactile information, which suggests a role in sensorimotor transformation.

The question of whether or not the human aIPS is homologous to monkey AIP, which is involved in visually guided grasping, is still very much open [27,28,30]. In addition to the disagreement regarding the functional nature of aIPS, there is also variance in the peak Talairach coordinates listed for aIPS in each of these papers. Nevertheless, these recent papers begin to address the question of how multimodal sensory information is transformed into multiple output systems by considering shared spatial coordinates and temporal constraints.

The parietal lobe and neuropsychology

Spatial neglect has long been considered a visual attentional disorder because the deficit in processing information on the contralesional side of space can occur without any visual field deficits. Spatial neglect can occur after damage to several areas [31,32], but it has been associated most frequently with the parietal cortex and the TPJ [33,34]. Recently, several studies have attempted to determine the crucial anatomical correlates of neglect to better understand both the behavioral deficit and the functional role of the underlying anatomical substrate. Controversy over the anatomical substrates giving rise to neglect has highlighted the heterogeneity of the behavioral deficit and has also contributed to the controversy over the functional roles of different regions of parietal cortex.

Karnath *et al.* recently argued that the superior temporal gyrus (STG; see Figure 1a) and not the IPL was the site of cortical damage associated with neglect [35]. They excluded from the sample all neglect patients with visual field deficits, arguing that damage associated with visual field deficits artificially shifted the average site of the lesion associated with neglect. In a recent related study [36•], the same group identified subcortical sites as relevant for neglect, including the putamen and, to a lesser extent, the caudate nucleus within the basal ganglia, and the pulvinar within the thalamus. This was achieved using the same method they had previously employed: the authors created an anatomical map of maximal lesion overlap from neglect patients and subtracted from this map the areas of damage in non-neglect control patients.

The authors suggest that this result is consistent with their previous claim that the STG is the crucial cortical component of neglect, in that there are dense anatomical pathways connecting the STG and the putamen, the caudate nucleus, and the pulvinar, and that damage to this network is crucial for neglect. It is worth noting, however, that the subcortical areas identified by Karnath *et al.* [35,36•] have connections with many cortical regions, including the parietal and occipital lobes, and therefore do not unequivocally support the notion that the STG is the natural cortical component of the neural network involved in neglect.

By contrast with the STG hypothesis, others have reinforced the idea that the IPL is the crucial anatomical correlate of neglect [37••]. Using high resolution (isotropic 1 mm voxels) magnetic resonance imaging (MRI) scans, Mort *et al.* [37••] found that all 14 of their neglect patients had damage to the angular gyrus, whereas only one of the control patients did. In addition, when looking at the individuals with neglect, damage to the TPJ and the IPS was found in nine patients, the supramarginal gyrus and the inferior frontal gyrus in eight patients, the STG in seven patients and the SPL and the middle frontal gyrus (MFG; see Figure 1a) in only four patients. None of the control subjects had damage to either the TPJ or the STG, whereas two or more had damage to each of the other areas. Furthermore, a recent anatomical study has revealed that a disconnection between the frontal and the inferior parietal region, brought about by a lesion to the superior longitudinal fasciculus, gives rise to chronic neglect in the absence of a visual field defect ([38•] see also Leibovitch *et al.* [39]).

Although the debate regarding the crucial cortical anatomical correlate of neglect is ongoing, the idea that lesion volume might be predictive of the manifestation of neglect has been raised. In all individuals with neglect persisting beyond three months post-cerebrovascular accident (CVA), three or more cortical lobes were damaged with the right CVA lesion volumes ranging from 42 to 111 cm^3 and the left CVA resulting in a lesion volume of 14 cm^3 [40•]. The only region of damage that was common to all patients involved the basal ganglia, specifically the globus pallidus and the putamen.

The investigators who report lesion volume as being correlated with neglect or a spatial bias raise the interesting possibility that neglect might only be apparent if multiple cognitive or functional abilities are damaged. Although not incompatible with the idea that certain neural structures are sufficient or necessary to produce neglect, the results do suggest the need for a better understanding of the cognitive and behavioral subcomponents of neglect as well as the functional characteristics of putative correlated areas. These studies have started towards that aim by emphasizing the role of implicated areas in the representation of both dorsal and ventral stream information as well as by testing the subcomponents of neglect in terms of formal theories of visual attention (see also Shapiro *et al.* [41] for a study of nonspatial attentional blink in patients with damage to IPL and STG with and without neglect; [42•,43]).

Conclusions

Although much less is known about human parietal cortex than homologous monkey cortex, recent studies, employing neuroimaging and neuropsychological methods, have begun to elucidate increasingly fine-grained functional and structural distinctions. This recent emphasis on demarcating subregions of parietal cortex is especially important given that the surface area of this region is 20 times larger in humans than in macaque monkeys and deserves close scrutiny. In this review, we have focused on recent studies that have outlined the role of distinct regions of parietal cortex in attentional biasing, in cross-modal processing and in the emergence of hemispatial neglect. We should note that our emphasis has been predominantly on spatial attention but several interesting recent studies explore the relationship between spatial and object attention [44••,45] and the role of the ventral cortex in attention-based feature binding.

As is evident from this review, significant progress has been made in detailing the anatomical and corresponding functional roles of different regions of human parietal cortex. The work, however, is still in its infancy and there remain not only open questions but points of divergence that need to be reconciled. As alluded to above, for example, the distinction between the neural substrate mediating spatial and nonspatial shifts of attention is yet to be fully elucidated, as is the extent to which lesion volume is a critical predictor of the presence and persistence of hemispatial neglect. Functional imaging work has become increasingly sophisticated over the past few years and the full power of this method is yet to be realized in the exploration of human parietal cortex. Furthermore, the use of this method in individuals who have sustained brain damage will help to resolve some of the ongoing discrepancies between neuropsychological investigations and functional imaging studies in normal individuals.

Acknowledgements

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Papers of particular interest, published within the annual period of review, have been highlighted as:

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In this important event-related fMRI study the authors demonstrated that the temporoparietal junction (TPJ) is activated by novel and salient stimuli. In addition, it was demonstrated that the TPJ was sensitive not only to the novel and salient visual stimuli but also to novel and salient auditory and tactile stimulation. This finding suggests a more general involvement of the TPJ in goal-directed attentional orientation.

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In this important study, the authors demonstrated both the effects of attentional modulation and the sources of an attentional biasing signal. It was observed that when attention was re-directed to the contralateral visual field, activity in extrastriate cortex increased and remained high. In addition, they showed that the superior parietal cortex was probably the source of the attentional biasing signal given the transient increases in activation in this area following spatial shifts of attention.

8. •• Yantis S, Serences JT: **Cortical mechanisms of space-based and object-based attentional control**. *Curr Opin Neurobiol* 2003, **13**:187-193.

An increase in the response of the parietal cortex following shifts of attention between two superimposed objects led the authors to conclude that superior parietal cortex (SPL) subserves both spatial and non-spatial attentional biasing signals.

9. • Liu T, Slotnick SD, Serences JT, Yantis S: **Cortical mechanisms of feature-based attentional control**. *Cereb Cortex* 2003, **13**:1334-1343.

The authors examined the neural mechanisms of feature-based attentional control in human cortex. Subjects were asked to shift their attention from one feature of an object to another — color and its direction of motion (the stimulus consisted of an array of moving dots). It was observed that multiple areas within the fronto-parietal network exhibited transient and sustained responses following attentional shifts.

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The purpose of this study was to compare directly the neural mechanisms of spatial and non-spatial control of attention. It was observed that even though both types of orienting recruited similar portions of the fronto-parietal network, under a direct comparison, spatial orienting appeared to activate regions within the fronto-parietal network to a greater extent than nonspatial orienting.

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In this study, the authors examined human brain activity during attention shifts between vision and audition. Attention shifts from vision to audition caused increased activity in auditory cortex and decreased activity in visual cortex, and vice versa, reflecting the effects of attention on sensory strength. Posterior parietal and superior prefrontal cortex exhibited transient increases in activity that were time-locked to the initiation of voluntary attention shifts between vision and audition. These findings show that posterior parietal and superior prefrontal cortex mediate the control of crossmodal shifts of attention.

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One role attributed to parietal cortex is the inhibition of distractors during visual search. In this study, cortical activation was measured during visual search in the absence of distractors. Anterior and inferior parts of the intraparietal sulcus were activated, showing that the contribution of parietal cortex is not restricted to counteracting the effects of distractors.

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The authors presented bilateral and bimodal (visual, tactile) stimuli following a spatial auditory cue. Target modality was blocked. Preparatory activation was found following the spatial cue and before stimulus onset for both visual and tactile targets in the contralateral anterior intraparietal sulcus and lateral occipital gyrus. Modality specific activation was also found in primary visual and somatosensory cortex.

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The authors employed a delayed match to sample task with visuo-tactile stimuli. Visual stimuli were presented centrally and tactile stimuli to the right hand. Left anterior intraparietal activation was found in the crossmodal conditions in which either a visual or a tactile stimulus was compared with a subsequent tactile or visual stimulus, respectively.

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Using a similar technique to their previous study [35], the authors identified the subcortical regions involved in neglect. The identified regions have reciprocal connections with the superior temporal gyrus, which they previously identified as the crucial cortical substrate that underlies neglect.

37. •• Mort DJ, Malhotra P, Mannan SK, Rorden C, Pambakian A, Kennard C, Husain M: **The anatomy of visual neglect**. *Brain* 2003, **126**:1986-1997.
The authors used high-resolution anatomical MRI images of the middle cerebral artery (MCA) and the posterior cerebral artery (PCA) in neglect patients to determine the crucial anatomical locations underlying neglect. All patients with lesions of MCA suffered damage to the angular gyrus, whereas PCA patients had all suffered damage to the parahippocampal gyrus. The authors also outlined anatomical markers for defining the temporal parietal junction, which has previously been implicated in neglect, but not defined anatomically.

38. • Doricchi F, Tomaiuolo F: **The anatomy of neglect without hemianopia: a key role for parietal-frontal disconnection?** *Neuroreport* 2003, **14**:2239-2243.
The focus of this study was defining the region of maximum overlap in a group of 10 individuals with hemispatial neglect and no visual field defect. The region of maximum overlap was in the superior longitudinal fasciculus. In those patients without subcortical lesions, an additional maximum overlap region was in the rostral part of the supramarginal gyrus. The crucial point made in this paper is the fronto-parietal disconnection and its central role in hemispatial neglect.

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The authors examined the anatomical scans of patients with persisting neglect and concluded that chronic neglect was correlated with the extent of the lesion. All patients involved in their study suffered damage to at least three major cortical lobes and subcortical structures. The only area of overlap in all patients involved the basal ganglia.

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