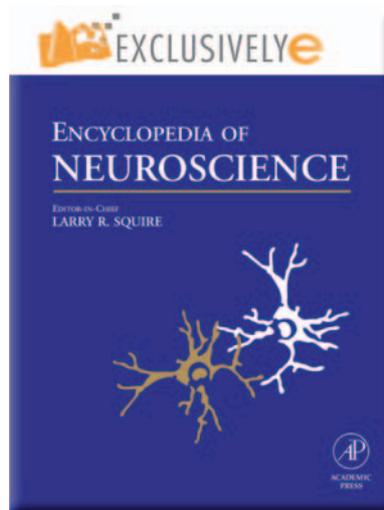


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Spatial Cognition and Executive Function

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Introduction

Representing and exploring the space around us is fundamental to human cognition. The study of spatial cognition, both at the psychological and neural level, is extensive, encompassing parallel investigations of many different types of spatial knowledge and many different spatial tasks. For example, there is now a large literature concerned with the processes involved in deriving spatial relations between objects or between parts of objects, and with the way these processes differ from other mechanisms involved in object recognition, such as the representation of the parts alone.

A rather different form of spatial processing, which is also the topic of much current investigation, concerns the nature of the spatial representations engaged during the learning of the spatial layout of the environment. Two forms of spatial knowledge, both of which are deemed critical for navigation purposes, have been described in these investigations of spatial cognition: survey knowledge (based on an external perspective or an aerial or maplike view), which allows access to the global spatial layout, and route knowledge, which is the perspective represented by a ground-level observer. Recent functional neuroimaging studies have suggested that these two spatial processes recruit both a common network of cortical regions but also additional, differentiable regions of cortex. Consistent with this, in individuals with unilateral hemispheric lesions, several brain areas appear to be involved in retracing a route from the end to the beginning, including the right hippocampal formation, the right posterior parietal cortex, the right dorsolateral prefrontal cortex, and the right temporal lobe. The hippocampus also plays a particular role in path integration; specifically, individuals with lesions to the right (but not left) hippocampus are inconsistent in their navigation to previously viewed targets, and they also show a systematic underregistration of linear displacement (and/or velocity) during walking. Whereas the hippocampal coding appears to be specific to certain places in the field, parietal neurons code route

maps in a more scalable and versatile form, independent of the size and spatial configuration of the navigational field.

A further strand of experimental studies concerned with spatial cognition has explored the psychological and neural mechanisms mediating spatial working memory. Keeping spatial information active online (even for extended periods of time) engages dorsal areas of lateral prefrontal cortex, posterior parietal cortex, and possibly even the hippocampal formation, and damage to these areas significantly impairs working memory. Finally, much research is concerned with delineating the nature of the underlying spatial representations, with specific emphasis on determining the reference frames or spatial coordinates employed for sensory information encoding. In some regions of cortex, the spatial position of the input is defined with respect to an eye-, head-, and/or body-centered frame of reference or sometimes some mixture of these different reference frames. While parietal cortex appears most involved in these egocentric forms of representation, in which the reference frame is centered on the observer, superior parietal cortices represent information allocentrically, independent of the observer, although, of note, these egocentric and allocentric representations appear to be somewhat interdependent. Of great interest, too, are the means whereby spatial information is updated – as the eyes move or as the observer navigates, the spatial positions of items in the environment change. To achieve a stable and robust representation, information must be constantly updated, and studies concerned with spatial updating have been (and continue to be) conducted with humans and nonhuman species, using a variety of methods, including lesion studies, functional magnetic resonance imaging, and single-unit recording.

As is evident from this brief overview, spatial cognition is multifaceted, and spatial representations are derived in the service of many different forms of cognition. Importantly, too, these different spatial representations are not mutually exclusive and much research remains to be done to specify the differences and commonalities among these representations and the spatial tasks in which they are engaged. This article focuses specifically on the spatial representations mediated by parietal cortex, often assumed to be the preeminent area involved in spatial processing. Two major lines of investigation are summarized, with one set of data primarily derived from studies of individuals with parietal lesions and the other set of data acquired from functional brain imaging studies (mostly functional magnetic resonance imaging).

Parietal Lobe and Spatial Representations

Anatomical Delineation of Parietal Cortex

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 (Figure 1). Posterior parietal cortex, located at the junction of multiple sensory regions and projecting to several cortical and subcortical areas, is engaged in a number of cognitive operations, many of which involve spatial representations. Parietal cortex is separated from the frontal lobes by the central sulcus and from the occipital lobes by the parieto-occipital fissure. Since the 1940s, hundreds of studies have documented the behavioral consequences of parietal lesions in humans and monkeys, with primary emphasis on the perturbation of perceptual and action space following these lesions.

Parietal Lobe and Spatial Representations: Evidence from Hemispatial Neglect

In humans, the deficit that affects the representation of space following unilateral hemispheric lesion is referred to as hemispatial neglect ('neglect,' for short). Following brain damage, particularly to the right hemisphere (see Figure 2 for examples of lesions giving rise to neglect), individuals typically exhibit a variety of symptoms, including impaired representation of information appearing on the side of space contralateral to the lesion. These individuals may fail to report or to orient to sensory information on the contralateral side of space. Standard bedside tests, such as having the patients draw a clock from memory or copy a clock, bisect some lines, or cancel lines on a page, are typically used to elicit neglect (see Figure 2(b) for examples of patients' performance on such tests). Individuals may also show neglect of

information appearing in contralesional personal space, in that they may eat, dress, and/or shave only the ipsilesional side. Furthermore, the eye and hand movements of such individuals may also be somewhat restricted to the ipsilesional side, and there is a perseverative tendency (perhaps induced by the failure to keep track of spatial locations) to revisit the same regions on the ipsilesional side. Interestingly, even in the absence of sensory input, neglect may be evident: the patients report only ipsilesional information in tasks of mental imagery and may show a paucity of contralesional saccades even when moving their eyes in the dark. Note that the neglect disorder does not arise from a primary motor or sensory deficit *per se* and is generally thought to arise from a deficit in attending to and representing the contralateral information.

Neglect also occurs more frequently and with greater severity following right than left hemisphere lesions (see also evidence from functional imaging studies on hemispheric asymmetry of parietal activation), and so we refer to neglect of left-sided information as a convenience throughout the following discussion. The scientific study of hemispatial neglect has been especially captivating over the past few decades and has continued to shed light on the mechanisms supporting spatial representation.

A critical question repeatedly addressed in the neglect literature is whether spatial information from different sensory modalities is processed in similar fashion. Although a majority of the studies have explored visual neglect, the question of interest is whether the underlying spatial map, perturbed by parietal damage, is specifically visual or utilized by other modalities as well. If the latter holds, then one might expect to observe neglect across multiple sensory modalities. Indeed, the consensus is that the representation of and awareness of space involve input from multiple sensory

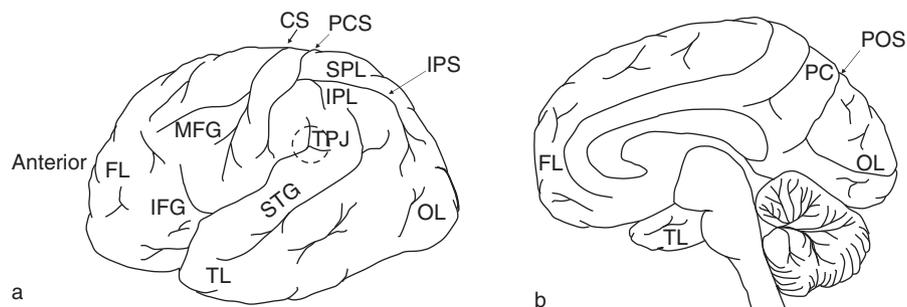


Figure 1 (a) Schematic depiction of relevant anatomical landmarks projected onto the (a) lateral and (b) medial surfaces of the human brain. Parietal cortex (PC) is located posterior to the postcentral sulcus (PCS), which lies posterior to the central sulcus (CS), and superior to the occipital lobe (OL). 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 parieto-occipital 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).

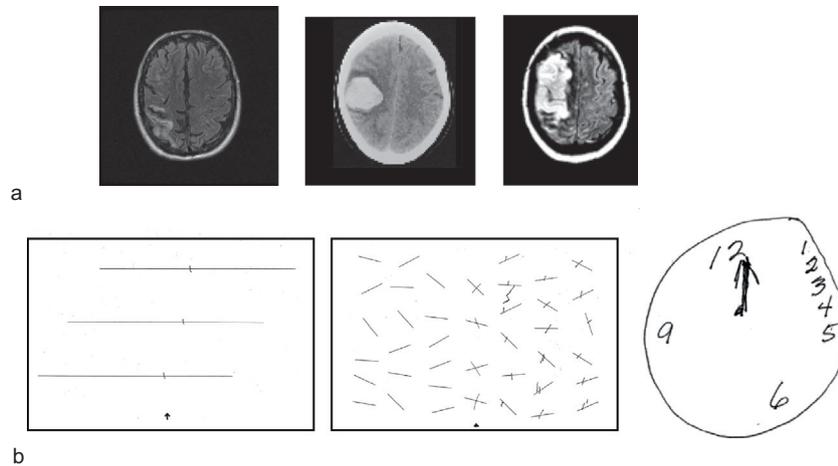


Figure 2 (a) Examples of structural scans from three different individuals, all of whom show hemispatial neglect following right parietal lobe lesions. Note that the right hemisphere is on the left of the image. (b) Examples of performance of three different patients with hemispatial neglect, using bedside tests of line bisection, line cancellation, and clock drawing from memory.

modalities: patients with visual neglect have difficulty localizing sounds and also experience problems in specifying the location of tactile input. Also, prism adaptation (see later for more details) appears to affect visual as well as proprioceptive input, further attesting to the cross-modal nature of spatial representation. Of course, one cautionary note in reaching this conclusion is that the lesions in humans are typically large and may implicate many regions of parietal cortex (in contrast to the lesions in nonhuman primates or the single-unit recording studies wherein the target areas are more circumscribed). With the advent of high-resolution structural imaging, we can start delineating better, in the neglect patient, the exact site of the lesion, the extent to which different parietal regions are affected, and the consequences of these more limited lesions on behavior.

Given that parietal cortex appears to derive a representation of space, one issue that has been under considerable investigation concerns the nature of competitive interactions between information appearing further on the ipsilesional or contralesional side of space. Consistent with ideas emerging from ‘biased competition’ accounts, there is a view that suggests that information appearing more contralesionally is assumed to compete with more rightward information, perhaps ‘extinguishing’ it entirely. If the contralesional information appears temporally in advance of the more rightward information or is much more salient than the rightward information, it might not be so readily extinguished and might ultimately be reported. It is also the case that if the contralesional information can be integrated or perceptually grouped with the rightward information, it, too, might survive the competitive interaction and be

reportable. Although much of the emphasis has been on a spatial gradient with greater activation as one proceeds from left to right, there is also growing consensus that there is a temporal delay in representing spatial information (enhanced or prolonged ‘attentional blink’), even when the information appears in the midline.

One recent domain in which considerable progress has been made concerns the nature of recovery of spatial attention deficits in individuals with hemispatial neglect. An intervention procedure used in some recent studies to ameliorate hemispatial neglect is to adapt the patients to prisms, which serves to induce a rightward displacement of the visual field. Several studies have successfully reported reduction in the severity of hemispatial neglect following prism adaptation and have shown that the eye movements postadaptation (in individuals with right-sided lesions and left-sided neglect) are significantly more rightward deviated than was the case prior to the intervention. Although many questions remain as to the mechanisms that give rise to this lateral-displacement postadaptation (Is it a redistribution of spatial attention? Is it visuomotor in nature?), and even though the consequences of adaptation are not very prolonged, the technique has proved to be remarkably valuable in flexibly altering the behavior of the patients with neglect, and much remains to be done in this domain.

Even without prism adaptation, following standard rehabilitation procedures, individuals with hemispatial neglect do show a decrement in the bias to orient rightward as well as showing a significant improvement in attention reorienting to the contralateral space. Of particular interest in recent investigations, as revealed in functional imaging studies, is that the

behavioral improvement even in these standard treatment procedures is correlated with reactivation of multiple cortical areas, which previously evinced weak or no task-related activity (even though some of these areas were anatomically intact). The opportunity to use functional imaging procedures to track recovery and perhaps to identify the optimal procedures for reinstating cortical activation is promising and offers a new method for developing and assessing rehabilitation procedures.

Parietal Lobe and Spatial Representations: Evidence from Lesion Analyses

The advent of high-resolution imaging (and its relative ease of accessibility) has also enabled investigators to track the lesion site in greater detail than has been possible in the past and to reevaluate the anatomical underpinnings of hemispatial neglect. While neglect has been most commonly associated with the inferior parietal lobule and also the temporoparietal junction (TPJ; see [Figure 1](#)), the underlying anatomical substrate has come under increased scrutiny. For example, some findings suggest that the superior temporal gyrus (STG) is the critical site of cortical damage associated with neglect and subcortical sites, including the putamen, and, to a lesser extent, the caudate nucleus within the basal ganglia and the pulvinar within the thalamus have also been implicated. Yet others have argued that a disconnection between the frontal and the inferior parietal region, brought about by a lesion of the superior longitudinal fasciculus, gives rise to chronic neglect. A further set of investigations has suggested that parietal cortex has a more dorsal and a more ventral stream and that each may play a slightly different role, with more superior regions engaged in voluntary, goal-directed attention and more inferior regions more engaged in bottom-up detection of salience or novelty. Finally, large-scale studies report that neglect arises after lesions to any one of multiple nodes making up a distributed spatial-attentional network, including temporal, parietal, frontal, and occipital cortices as well as basal ganglia and thalamus (in order of incidence). The continued development of more sophisticated imaging techniques and methods of lesion analysis will be critical in outlining the neural substrate of spatial representation and possibly even in differentiating subtypes of neglect and their cortical signatures.

Parietal Lobe and Spatial Representations: Evidence from Functional Imaging Studies

Thus far, the role of parietal cortex in spatial representation has been considered based on findings from human lesion studies. Converging evidence

from functional imaging studies has recently contributed enormously to elucidating the mechanisms underlying spatial representation. For example, one robust finding is that when cues direct an observer to a spatial location in which an upcoming target is likely to appear, activation is noted in superior frontal, inferior parietal, and superior temporal cortices. Spatial attentional selection serves to facilitate perception of stimuli (e.g., objects), as reflected in enhanced speed of processing of attended information. Given the increased access to functional imaging, researchers have spent considerable effort to shed light on the mechanism subserving spatial attentional orienting. A primary focus of such studies has been to determine the anatomical loci within the human cortex that give rise to the attentional biasing signal (i.e., the source or process that directs or shifts attention) that ultimately initiates the sensory enhancement of the selected stimulus (i.e., the effect). In this next section, we summarize findings from these studies, showing the differential involvement in the source versus the effects of attentional manipulations.

Effects of Spatial Selection: Enhancement of Sensory Signals

Studies of the effects of visual attentional selection have revealed behavioral facilitation and enhanced cortical responses to information appearing in attended spatial locations. Neurophysiological studies investigating the effects of top-down attentional bias have demonstrated that when a cell is presented with a stimulus in its receptive field (RF), the neural response to that stimulus is increased when attention is covertly directed to it as compared to when the stimulus is in the RF but attention is either unfocused or is diverted elsewhere. For example, in their seminal study, Moran and Desimone first identified the classical RF of a V4 neuron and its corresponding effective and ineffective stimuli (i.e., stimuli that drive the cell strongly and weakly, respectively). The monkeys were trained to attend to stimuli in a specific location within the visual field while ignoring stimuli at another location. Both effective and ineffective stimuli were presented within the RF and the responses of the V4 neurons were strongly modulated by the spatial attentional locus: the firing rate to the preferred stimulus was only one-third as great when the monkey did not attend to it as compared to when the preferred stimulus was attended. In fact, what was particularly interesting about this study is that when attention was directed to one of two stimuli in the receptive field of a V4 cell, the effect of the unattended stimulus was attenuated, as if the receptive field had contracted to include only the attended stimulus. This type of spatial

attentional enhancement was found to increase with task difficulty and was observed throughout early sensory regions within the visual cortex.

Several neuroimaging studies in humans have also documented early sensory enhancement following top-down spatial attentional allocation. In the majority of these experiments, individuals are presented with stimuli appearing to the left or right of fixation and are asked to direct their attention to either side of the fixation point (i.e., shifting their attention either to the left or the right side of space) (Figure 3). Directing spatial attention to the left hemifield results in increased stimulus-evoked neural activity of the early visual areas in the right hemisphere, whereas directed spatial attention to the right hemifield is accompanied by increase of activity in the early visual areas of the left hemisphere. Studies employing event-related potentials (ERPs) take advantage of the fact that visual stimuli typically elicit two early waveform components, which are termed P1 (first positive, occurring 100–200 ms after stimulus onset) and N1 (first negative). These effects are robust and are observed even during passive viewing of input. Of relevance, the P1 and N1 components are modulated (i.e., increase in negativity and/or positivity) when visual stimuli are being attended to, as opposed to when spatial attention is diverted elsewhere in the scene. The modulation is manifest by a change in the amplitude of these components, while the component latency remains the same when the stimuli are attended or ignored.

In summary, spatial attention serves to modulate sensory signals elicited by the stimuli in the early sensory cortex (i.e., areas V1–V4) and also in higher order areas such as the motion-sensitive region (MT+), fusiform face area (FFA) selective for face processing, and other higher order regions within the human cortex.

Sources of Spatial Orienting Signal

Several regions within monkey and human posterior parietal cortex (PPC) have been identified as coarsely representing spatial topography as it relates to the source or trigger of a spatial attentional orienting signal. For example, neurons in the lateral intraparietal area (LIP) of the monkey cortex fire in response to the location in space to which attention was cued, representing the voluntary allocation of attention to a specific region in space. Several regions within the human parietal and frontal cortices – inferior parietal sulcus (IPS), superior parietal lobule (SPL), and the frontal eye fields (FEFs) – are also identified as playing a critical role in spatial attentional selection. Functional magnetic resonance imaging (fMRI) studies have demonstrated that activity in these frontal and parietal regions is spatially selective, such that stronger activity is noted when attention is directed toward spatial locations in the contralateral field.

Several fMRI studies support the proposal that the top-down attentional signal (the implementation of the cue) arises at least partially from the parietal

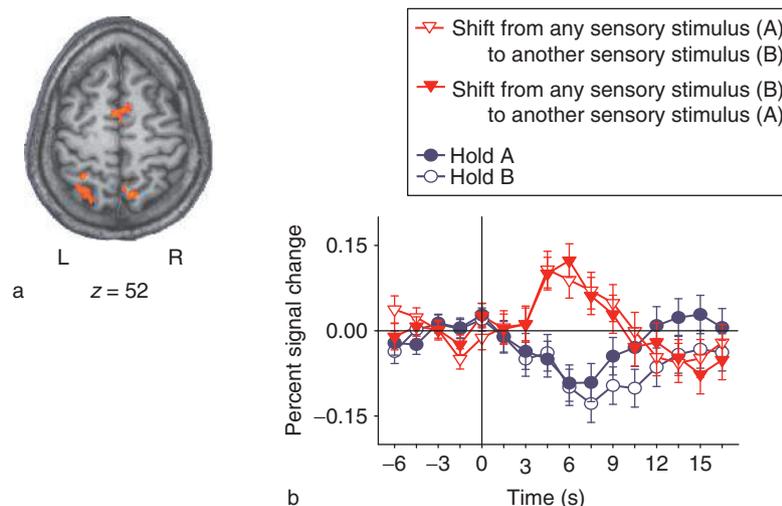


Figure 3 (a) A representative slice through a high-resolution reconstructed brain of an individual performing an attentional shifting task. The activation (shown in red) is obtained by contrasting activity during shifts of attention between the sensory stimuli (could be, for example, from left side of space to right side of space, or from auditory stimuli presented to the left ear and to the right ear) with activity when holding attention within a sensory stimulus. The cluster of activated voxels encompassed within the white circle is in the right superior parietal lobule. (b) Blood oxygen-level-dependent signal extracted from the right superior parietal lobule reflects transient activity elicited within this region following shifts of attention from one sensory stimulus to another. Note that activity within this region remains low for sustained attention (hold trials). From Shomstein S and Yantis S (2006) Parietal cortex mediates voluntary control of spatial and nonspatial auditory attention. *Journal of Neuroscience* 26(2): 435–439.

cortex, with an additional contribution from the frontal cortex – what has been termed the frontoparietal attentional network. For example, when individuals are asked to covertly direct their attention following a cue to a spatial location in the visual display in preparation for a target, areas in the occipital lobe respond transiently to the cue, while areas in the posterior parietal cortex along the inferior parietal sulcus exhibit a more sustained response. The sustained activity in the PPC is assumed to reflect the source of the attentional orienting signal: it could not be linked to either visual stimuli or motor responses *per se* and its activity was time locked to the period during which individuals paid attention to the peripheral future target location.

It is important to understand the precise function of the parietal lobe's involvement in attentional control. At least two possibilities regarding the time course of parietal lobe activity following spatial shifts of attention must be considered. The first possibility is that the PPC provides a continuous signal that maintains the locus of attention at a specific spatial location – the 'sustained hypothesis.' In other words, once the individual has decided to change the locus of spatial attention, the PPC issues a signal that will be sustained until another change in the locus of spatial attention is made (i.e., sustained increase in neural activity). Another possibility is that the PPC issues a transient brief signal to shift the attentional state – the 'transient hypothesis,' such that once the locus of spatial attention needs to be redirected elsewhere, the PPC issues a transient signal that dissipates quickly once the attentional shift has been made. This latter hypothesis also predicts that the locus of attention is maintained by other areas, presumably frontal areas within the frontoparietal network.

Several recent studies examined the exact involvement of the PPC in attentional shifting tasks by adjudicating between these two hypotheses. 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 (for example, a digit among the stream of letters). The identity of the cue indicates to the individuals whether they should maintain attention on the current stream or shift attention to the other stream. The critical finding is revealed when one compares cortical activity related to shifting the attentional focus from one spatial location to another with activity related to maintaining the attentional focus on a single stream. When attention was shifted between spatial locations, the time course of the blood oxygen-level-dependent (BOLD) signal in the right SPL and inferior parietal lobule (IPL) exhibited transient activity (see [Figure 3](#)). 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 to a new spatial position, and is not the source of a continuous signal to actively maintain the new attentive state.

Sources of Nonspatial Orienting Signal

Although the focus thus far has been on spatial representation and attending to spatial regions containing input, the top-down attention-shifting signal is not restricted to spatial shifts alone, and this region is activated when individuals shift their attention between any two dimensions of the input. For example, shifts between superimposed houses and faces, shifts between two different features of an object, or shifts between two different sensory modalities all selectively activate the PPC. Whereas spatial shifts are accompanied by increased activation in the SPL region of the parietal lobe, nonspatial shifts are accompanied by increased activity in the precuneus region, the continuation of the SPL on the medial side of the parietal lobe (see [Figures 1 and 3](#)). This anatomical distinction between spatial and nonspatial shifts of attention clearly deserves a more thorough investigation. We should note that additional attentional functions could be mediated by some of the same subareas of parietal cortex already described. 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, and this occurs to a greater extent in the left than in the right hemisphere. By contrast, activation of a more posterior region of the intraparietal sulcus appears to be contingent on the presence of distractors. Much work remains to be done to outline the various attentional functions mediated by the parietal cortex and also, in parallel, to map out the behavioral and neural mechanisms associated with spatial representation.

Conclusion

Spatial cognition is a complex, multifaceted set of processes that are engaged in a large variety of tasks, including, for example, mental rotation, spatial navigation, and spatial working memory. The exact nature of the spatial knowledge implicated in these different tasks remains to be determined. We have focused on behavioral and neural mechanisms involved in representation of spatial locations, with evidence drawn from neuropsychological studies of individuals with hemispatial neglect and neuroimaging studies of spatial attentional selection (and the ensuing sensory enhancement). As is evident, the

findings are probably more complicated than we might have thought, given the progress made to date on these topics. In particular, better use of structural and functional imaging has led to fine-grained reconsideration of previous findings. Some of the received wisdoms regarding hemispatial neglect have come under scrutiny, and the fMRI findings have opened new avenues of investigation. Among the outstanding issues are the mechanisms giving rise to the neglect in the first place (for example, a deficit in spatial attention, a problem in spatial updating, or competition between inputs). The neural locus of neglect has also come under reconsideration and many questions remain. Findings from functional imaging studies have also opened new domains of investigation. In particular, the imaging studies have suggested that spatial positions in the world can be selectively attended and that these attentional effects are robust and are present throughout the visual (and auditory) system, and attending to specific stimuli modulates the cortical areas involved in processing the input. The posterior parietal cortex appears to play a dominant role in signaling and implementing the attentional shift from one location (or feature or object) to another, as reflected in the transient activity in posterior parietal cortex.

See also: Attentional Networks in the Parietal Cortex; Cognition: An Overview of Neuroimaging Techniques; Executive Function and Higher-Order Cognition: Neuroimaging; Neglect Syndrome and the Spatial Attention Network; Neural Coding of Spatial Representations; Parietal Cortex and Spatial Attention; Spatial Orientation: Our Whole-Body Motion and Orientation Sense; Spatial Memory: Assessment in Animals; Spatial Transformations for Eye-Hand Coordination; Spatial Cognition; Spatial Cognitive Maps.

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