

**Spatial Selective Attention  
and Spatial Working Memory**

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## **Abstract**

Spatial working memory has previously been dissociated from other working memory systems, but there has been relatively little previous research on the specific *subcomponents* of spatial working memory. In the present paper, we review neuroanatomical evidence that is relevant to a specific model of spatial working memory in which covert shifts of spatial selective attention are hypothesized to mediate the on-line maintenance of location-specific representations.

## 1. Introduction

Consider the following simple memory task: A single dot appears somewhere in the visual field marking a location. That location must be stored in memory for several seconds, after which another dot appears. The subject's task is to decide whether the location of the second dot is identical to that of the first. What processes are involved in this task? A simple analysis suggests that the observer must first encode the location of the memorandum, then store this location in a short-term or working memory for a brief period, and then compare the stored memory representation against the probe-dot that appears thereafter. Of these three processes what is involved in storage? If spatial working memory is at all similar to verbal working memory, there are two components (Awh, Jonides, Smith, Koeppe, Schumacher, & Katz, 1996): One is a set of processes required for the storage of a memory representation of the dot's location. The other is a rehearsal process required to somehow refresh the memory code so that it can be retained with some fidelity in expectation of the upcoming retrieval test. But what is the specific nature of this putative rehearsal process?

Decades of research on spatial selective attention have left little doubt that observers make faster and more accurate responses to stimuli that fall in expected rather than unexpected locations. More recently, there have been compelling demonstrations of location-specific attentional modulation of early-sensory processing, a mechanism that might account for the effects of spatial expectancy (see Mangun, Hansen, & Hillyard, 1987). In other words, spatial selective attention may cause enhanced processing in the specific cortical regions that process an attended region of space. (Recall that independent locations in cortex can be mapped onto independent locations in the environment.) The central theme of this chapter is that this interaction of spatial attention and early visual processing may mediate the rehearsal of information in spatial working memory. Put simply, the hypothesis is that keeping the representation of a location active in memory recruits the same mechanisms that are involved in selectively attending to that location. Awh, Smith, & Jonides (1995) provided a measure of behavioral evidence that renders this hypothesis plausible. They showed that the requirement to

retain a location in memory during a retention interval resulted in a side benefit: When an intervening choice reaction-time stimulus was presented during the retention interval, faster responses were observed for stimuli that fell in *memorized* locations. This is just as it should be if, as a strategy for remembering, subjects allocate their attention to the target location.

If there is a close parallel between spatial selective attention and spatial working memory processes, then the neuroanatomical sites that are activated in tasks of the two types should show a strong overlap. It is this issue that is the focus of our review. We discuss the neuroanatomical basis for tasks that require subjects to engage spatial selective attention versus those that require subjects to engage spatial working memory. The evidence comes from a variety of sources, including studies of the behavior of single cells, studies of the effects of lesions in humans, and neuroimaging studies of humans. To anticipate our conclusions, we find a striking concordance among the various techniques in support of the hypothesis that spatial attention and spatial working memory share a good deal of brain machinery in common. Let us turn to a review of this evidence in detail.

## **2. The Neural Basis of Spatial Selective Attention**

In this section we review the neural circuitry underlying spatial selective attention. Our review is guided by an influential theory of the processes involved in spatial attention that has been proposed by Mesulam (1981, 1990). One essential claim of this theory is that attentional processes are mediated by the activation of a *network* that includes four primary brain regions: (1) a frontal component (the dorsolateral/premotor prefrontal cortex) provides a spatial map for the coordination of exploratory motor processes; (2) a posterior parietal component coordinates the formation of a spatial representation of extrapersonal space; (3) processes of the anterior cingulate gyrus provide a spatial map of motivational valence; and (4) a subcortical reticular component modulates overall arousal and vigilance necessary for attentional processing.

Mesulam asserts that the components of this network mediate two qualitatively different types of attentional processing. One is tonic in nature and involves regulation of the overall

threshold that stimuli must exceed in order to reach consciousness. The reticular component is claimed to mediate this process. The other type is described as phasic, and involves the selection (i.e., location-specific enhancement) of items that will receive the benefits of attentional resources from the multiple items that reach threshold. The frontal, parietal and cingulate components of the network are claimed to subservise this type of attentional processing. Within these areas, Mesulam acknowledges that there is relatively sparse evidence supporting the putative role of the cingulate in motivational valence. Rather, the majority of neuroscientific studies of spatial attention place emphasis on the frontal and parietal components of the model; because of this, we concentrate on these components here.

We note that the four components of Mesulam's model could be said to comprise the *source* of attentional modulation (Posner & Petersen, 1990). The *site* of these effects, however, is likely to be quite different. The beneficial effects of attention may occur at the level of early sensory processing or during later post-perceptual processing stages (for a review see Yantis & Johnston, 1990). Because there is evidence of sensory effects (e.g. Mangun et al., 1987), we include studies of extrastriate and striate participation in spatial selective attention in our review.

## **2.1 Evidence from unit recording**

**2.1.1 Prefrontal regions.** There is an extensive literature demonstrating the participation of prefrontal brain regions in directed visual attention (for a review, see Fuster, 1984). A typical finding is that selected populations of prefrontal neurons show enhanced responses to behaviorally relevant (i.e. attention-attracting) stimuli. For instance, Kodaka, Mikami, and Kubota (1994) identified neurons in the prefrontal cortex of monkeys that showed significant increases in response to extrafoveal stimuli when they were behaviorally relevant compared to when they were not. Mikami, Ito, and Kubota (1982) also identified a relatively small groups of neurons whose response patterns were diagnostic of whether extrafoveal attention was required even before the stimuli appeared. The firing patterns of these neurons were modulated during the

period when relevant stimuli were expected in peripheral space, suggesting a prefrontal mechanism that mediates the tonic engagement of spatial selective attention.

Of course, one might ask of these and other studies that involve responses to relevant and irrelevant stimuli whether the changes in neural activity reflect attentional modulation of sensory processing or response-related processing. An elegant dissociation of these processing components was provided by di Pellegrino and Wise (1993, 1993a), who examined attention-related neurons in both the dorsolateral prefrontal and dorsal premotor areas. Each trial of their experimental task was comprised of the following events: (1) One of eight possible lights was illuminated in the periphery (the prime stimulus, or PS1); (2) Zero to four of the remaining lights were then illuminated, and the monkey was trained not to respond to these distractors; (3) When the prime stimulus was illuminated again (PS2), the monkeys were trained to respond in one of two ways. In one case, the direction of a limb movement was determined by the location of the prime stimulus (compatible condition). In the other case, the direction of the limb movement was fixed, and the reoccurrence of the prime stimulus served only to trigger this movement (incompatible condition). This design allows comparison of responses to attended (PS1 and PS2) and unattended (distractor) stimuli. In addition, the compatible and incompatible conditions constitute a manipulation of the response-related significance of PS1 and PS2, while controlling for the sensory and attentional aspects of the tasks.

Prefrontal neurons were analyzed in terms of their phasic responses to the onset of PS1, PS2, and the distractor stimuli (di Pellegrino and Wise, 1993). These observations were consistent with those of Kodaka et al. (1994), who demonstrated enhanced neuronal responses to behaviorally relevant stimuli. Likewise, di Pellegrino and Wise found groups of neurons in both the dorsolateral and premotor parts of prefrontal cortex that showed location-specific, enhanced modulation of responses to PS1 and PS2 relative to those for spatially-identical distractor stimuli. An additional analysis of *tonic* neuronal responses (di Pellegrino and Wise, 1993a) provided further evidence of attentional processing. Cells were identified in both prefrontal and premotor cortex with sustained higher rates of discharge throughout the delay period between PS1-offset

and PS2-onset, suggesting participation in the tonic maintenance of directed spatial attention. However, an analysis of tonic responses as a function of compatibility also suggests an interesting dissociation of prefrontal and premotor function. Modulations of these attentional responses as a function of compatibility were more prevalent for the premotor neurons--where responses tended to decrease in the incompatible condition--than the prefrontal neurons, suggesting that the premotor area is more heavily involved in response-related attentional processing.

It is noteworthy that di Pellegrino and Wise (1993) distinguished between two strategies that the monkeys could use in the performance of these tasks: (1) They might direct *attention* toward the location of the primary stimulus and respond when another stimulus appeared in the attended region, or (2) they might *memorize* the location of the prime stimulus and respond whenever a stimulus was detected at the remembered location. Our model of spatial working memory suggests that these two processes may be one and the same.

**2.1.2 Parietal regions.** Initial studies of the responses of neurons in the parietal cortex for attentional tasks focused on the eye-movement-related responses of these neurons. Lynch, Mountcastle, Talbot, and Yin (1977) studied the activity of neurons in area 7 of parietal cortex in monkeys during tasks that required ocular fixation and tracking of visual targets. They found that most neurons in this area were activated during these ocular activities, but only when the stimuli that the animals were observing were behaviorally relevant. When the identical eye movements occurred spontaneously or during casual inspection of the environment, the parietal neurons did not respond, suggesting a role of attention in describing the behavior of these neurons.

Bushnell, Goldberg and Robinson (1981) went a step beyond the study of Lynch et al. (1977) by dissociating the putative attentional function of parietal neurons from their role in emitting a response. They measured the responses of parietal neurons in area 7 during several tasks that called for a variety of responses--some ocular, and some manual. They replicated

previous findings that a significant portion of these neurons responded in a spatially-specific manner just before saccades to relevant behavioral targets. Beyond this, moreover, they found a strikingly similar profile of responses in the same populations of cells when the animals performed a peripheral attention task that did not require ocular responses. Furthermore, when animals were trained on attentional tasks that required hand-reach responses as well as saccadic responses, there was location-specific enhancement of responses to attended stimuli--within a single neuronal population--in both the saccade task and the hand-reach task. These results provide good support for response-independent mediation of spatial selective attention by cells in parietal cortex.

**2.1.3 Extrastriate regions.** Some of the first evidence from unit-recordings about attentional modulation of early visual processing comes from a study by Moran and Desimone (1984). They recorded activations of cells in the extrastriate cortex (V4) of monkeys during a task that required focal direction of attention. At the start of each trial, two stimuli were presented simultaneously in separate locations within the receptive field of the recorded neuron, one of which was effective in eliciting a response from the cell, the other not. The monkeys had been trained to attend to one of the stimulated locations. Five hundred msec later, a second pair of stimuli appeared and the animals had to indicate whether the stimulus at the attended location matched the initial attended stimulus. Comparing across trials, the experimenters were able to observe neuronal responses to spatially-identical attended and unattended stimuli. They found that when an effective stimulus in the cell's receptive field was attended, the cell responded well. However, when the animal attended to an ineffective stimulus, the response was greatly reduced, despite the presence of an effective stimulus within the receptive field. Thus, the cell's responsiveness was determined by the attended stimulus. The authors suggest that this result may indicate a shrinking of the receptive field of the cell around the attended region.

Notice that this attentional effect is dependent on a number of factors. First, obtaining a good response from a cell required not only directed spatial attention, but also the presence of an



effective stimulus at the attended location. This contrasts with the attentional effects obtained in frontal and parietal cortex, where simple spots of light were adequate to drive the cells' responses. Second, because there were always two stimuli, the observed attentional modulation was dependent on the presence of competing stimuli within the cell's receptive field. The investigators provided direct support for this interpretation by showing that when effective stimuli were presented alone within the receptive field, they always elicited a positive response, regardless of whether they were attended or not. The authors concluded from this result that attention did not serve so much to enhance neuronal responses as to suppress a neuron's response to unattended stimuli within its receptive field.

Using a very different paradigm, Fischer and Boch (1981) had previously shown that extrastriate neuronal responses were enhanced just prior to saccadic eye movements to peripheral stimuli. Moreover, a follow-up study (1985) suggested that these enhancements were dissociable from response-related or visual-sensory aspects of the task. They recorded neuronal responses within the prelunate gyrus (V4) of monkeys during four conditions : (1) During the fixation task, the monkeys fixated a central point and pressed a key to indicate its presence. After a variable period, the spot dimmed and the monkeys had to release the key within 700 msec to get a water reward. Stimuli occurred peripherally as well, but the animals were required to ignore them; (2) During the saccade task, the central fixation point was extinguished simultaneously with the appearance of a peripheral spot. In this case, the monkeys made a saccade to the peripheral stimulus and responded manually when they detected its dimming. The first two tasks allowed a comparison of responses to peripheral stimuli that were either ignored or the target of a saccade; (3) A delayed saccade task was similar to the saccade task, except that the offset of fixation occurred one second after the onset of the peripheral target stimulus, and the dimming always occurred at fixation. In this task, the monkeys maintained fixation and detected the dimming at the central location; then they executed a saccade to the peripheral stimulus when the central spot was extinguished. (4) The fourth task, the suppressed saccade task, was a modified version of the delayed saccade task, in which the offset of the central fixation was only temporary. If the

offset were short enough (about 400-600 msec), the animals tended not to execute the saccade to the peripheral target. Tasks 3 and 4 allowed observation of neuronal responses to identical series of stimulus events, with and without eye movements.

The results of the fixation and saccade tasks replicated their earlier findings; neuronal responses to the onset of peripheral stimuli were enhanced in a spatially specific manner when the fixation point was extinguished, and a saccade to the peripheral stimulus was triggered (in 74% of cells tested). While this enhancement could have been driven by a direction of attention to the peripheral stimulus, it is also possible that the increased response was due simply to the onset of the peripheral target (regardless of whether attention was directed to its location). The results of the delayed saccade task suggest that this explanation is unlikely, however. Recall that the peripheral stimulus appeared before the offset of the fixation point, during a period when the monkey was still motivated to attend centrally. Although there was an initial increase in response when the peripheral stimulus appeared, it was transient and activation quickly returned to baseline. However, after the offset of the fixation point, the response to the peripheral stimulus was enhanced again until the saccade occurred (in 76% of the cells tested). These results show a clear dissociation of enhanced neuronal responses and the onset of the peripheral stimulus. Finally, the results of the suppressed saccade task are crucial. Although the first three experiments suggest that the enhancement is not related to stimulus-onset alone, there is still a confounding of neuronal enhancement and the execution of a saccade. The results of the suppressed saccade task show that even when the monkey did not choose to make a saccade to the peripheral stimulus, there was a reliable enhancement of the response to the peripheral stimulus after the offset of the central fixation dot (in 80% of cases without eye movements). In addition, further control experiments provided evidence that the offset of the fixation point was not the causal factor in these enhancements. A reasonable interpretation of these results is that the offset of the central fixation point directly precedes a redirection of visual attention to the peripheral target, which causes enhanced extrastriate responses to the attended stimulus.

**2.1.4 Striate regions.** While the studies reported here demonstrate attentional influences on extrastriate processing, similar effects are elusive in the earliest processing areas (V1 and V2). For example, Moran and Desimone (1984) tested V1 neurons in the same paradigm described above and failed to observe similar attentional modulation (see also Mohler and Wurtz, 1977). One possibility is that attentional effects within striate cortex are dependent on specific testing conditions, perhaps different from those required in extrastriate studies. Evidence supporting this possibility comes from a study by Motter (1993). He recorded the responses of cells in V1, V2, and V4 during a focal attention task. Two tasks were employed: (1) The first was used to assess the baseline response of these neurons to visual stimulation. At the start of each trial, the monkeys fixated a central spot and depressed a key. While they maintained fixation and held down the key, peripheral stimuli were presented that the monkey had been trained to ignore. Then a small bar was superimposed on the fixation target. The onset of the bar was the monkey's signal to release the key and depress either a right or left key (within 600 msec) to indicate the orientation of the bar. This task allowed measurement of responses to unattended peripheral stimuli as well as identification of the optimal orientations and receptive fields of the tested cells. (2) The second task required responses to the peripheral stimuli, and manipulated whether the relevant stimulus was attended or not. Once again, the monkeys fixated centrally and depressed a key. Then, an array of small dot-cues was presented in the periphery. Each dot marked the potential location of a relevant behavioral stimulus. After a variable period of time, all but one of the dots were extinguished. The remaining dot marked the position of the relevant stimulus in an array that appeared 200-400 msec later. The number of stimuli in the array varied from 3 to 8 in 85% of the trials, and was restricted to a single stimulus in 15% of the trials. Manipulating the location of the final dot allowed comparison of neuronal responses when attention was directed toward or away from the cell's receptive field.

In 35% of the V1 neurons tested, there was a spatially specific modulation of responses to stimuli depending on whether attention was directed toward or away from the neuron's receptive field. The same effect was observed in 39% and 45% of the cells tested in V2 and V4

respectively. While attentional effects were observed in all three cortical areas tested, there were important qualitative differences among these areas. The effects observed in V1 and V2 interacted strongly with the nature of the receptive field stimulus. In both of these regions the attentional effects were usually limited to stimuli near the optimal orientation of the tested cell. By contrast, the effects in V4 typically extended over a broader range of orientations, sometimes including all of the tested values. Also, the nature of the attentional modulation differed among the cortical areas. In V1 and V2, 70% of the neurons showed enhanced responses when attention was directed toward the receptive field. However, in area V4, the effect of attention was more evenly split between enhancement (58%) and suppression of neuronal responses. Furthermore, while the variation of array size from 3 to 8 stimuli had little effect on the responses of V1 and V2 neurons, V4 neurons usually required the larger arrays to show significant attentional effects. Finally, in all three areas, the attentional effects were partially dependent on the presence of competing stimuli. Approximately 67% of attention-sensitive cells in each area failed to demonstrate these effects when the array contained only a single stimulus.

**2.1.5 Summary of evidence from unit recordings.** The unit recording studies of spatial selective attention reveal a network of cortical sites that is generally consistent with the model proposed by Mesulam. There are prefrontal areas whose activations are directly correlated with motor-related attentional processing. In addition, the dorsolateral prefrontal cortex is implicated in the tonic maintenance of directed spatial attention, independent of response activities. Studies of neuronal responses in parietal cortex also suggest a direct role in the control of spatial attention, independent of any specific response modality. Finally, there is compelling evidence that processing within striate and extrastriate regions is directly modulated by spatial attention, although this effect occurs only under relatively specific experimental conditions.

It should be noted that the appropriate homology between nonhuman primate and human cortical areas is an unresolved issue. For instance, while the inferior parietal lobe in humans was identified by Brodmann as areas 39 and 40, he found no architectonic equivalent to these regions

in the monkey. Instead, Brodmann designated the inferior parietal region in monkeys as area 7, and it has been argued that this region may be homologous to area 7 (*superior* parietal) in humans (see Mesulam, 1981). As we shall see below, this hypothesis is in accord with the evidence from human neuroimaging studies (where area 7 activations are consistently associated with shifts of spatial attention), as well as with human lesion evidence that relates superior parietal damage to visual extinction (e.g. Posner, Walker, Friedrich, & Rafal, 1984; Vallar, 1993). Nevertheless, the syndrome that is classically associated with impaired spatial attention is hemineglect, and here it is the *inferior* parietal region that is the most consistent site of lesion overlap (Vallar, 1993). In line with this, it has been pointed out that the cytoarchitecture of human areas 39 and 40 is most similar to area 7 in monkeys (see Mesulam, 1981). Clearly, the issue of the human homolog to the monkey inferior parietal lobe is unresolved. Hence, caution is required when using nonhuman primate evidence to make inferences about functional localization in humans.

## **2.2 Evidence from Studies of Human Lesions**

Our discussion of human lesion studies is abbreviated because numerous general reviews can be consulted about this topic (e.g. Vallar, 1993; DeRenzi, 1982). Some of the earliest evidence from human lesions regarding spatial attention focused on the role of the parietal cortex, particularly in the right hemisphere (for a review, see Weinstein and Friedland, 1977). There is also ample evidence suggesting that right frontal regions are important for directed attention (for a review, see Foster, Eskes, & Stuss, 1994). However, while both areas are implicated, studies that include patient populations with frontal or parietal lesions indicate that attentional deficits are most prevalent in parietal cortex (e.g. Vallar and Perani, 1987). Finally, there are also reports associating attentional deficits and subcortical lesions. These data implicate posterior and medial thalamic areas as well as the basal ganglia in processes of spatial attention (for a review of the neural correlates of hemineglect, see Vallar, 1993). Overall, the

data from human lesions are generally consistent with those from unit recordings in animals in implicating frontal and parietal sites in attentional processes. A point of divergence is the oft-cited importance of right-hemisphere lesions in disrupting attentional processing in humans. Some have argued, though, that this is a bias in selecting patients for study, in that patients with severe enough lesions in left hemisphere to cause attentional deficits may also have lesions sufficiently severe to cause language-related deficits, making these patients difficult to study systematically.

There is evidence that distinct attentional disorders result from lesions of the inferior and superior areas of parietal cortex. In particular, right *inferior* parietal lesions are the most frequent correlate of hemineglect, which may be defined as the failure to explore the contralesional side of space, while elementary sensory/motor processing remains intact. But *superior* parietal lesions are instead associated with symptoms such as visual extinction or mislocalization (Vallar, 1993). Thus, while it appears that both the superior and inferior aspects of parietal cortex are important for intact attentional processing, the specific roles of each region may be functionally dissociable.

One might ask whether the deficits studied in humans reflect damage to the same selective attention mechanism under study in the unit recording experiments. While the paradigms rely on very different methodologies, of course, there are reasons to believe that they may indeed tap the same functional network. First, both paradigms implicate a frontal-parietal attentional network. Second, the effects of frontal and parietal lesions in humans have been studied using "attentional spotlight" paradigms. These tasks are more directly comparable to the single-cell studies than the typical clinical assessments of neglect. Posner et al. (1984) showed that patients with parietal damage had **difficulty** with a spatial precuing task, in which the brightening of one of two peripheral boxes informed subjects of the most likely location of a target for detection. When an invalid precue appeared in the ipsilesional visual field, these subjects had great difficulty responding to the contralesional targets. Both right and left parietal patients showed this "extinction-like" **reaction time** pattern, but it was more pronounced in the

right parietal group. Posner et al. suggest that these results reflect impairment of a disengagement mechanism that must be initiated before shifts of spatial attention can occur. Alivisatos and Milner (1989) also used a spatial precuing experiment to examine the effects of unilateral frontal lobectomy. Their subjects performed a choice reaction time task and were given precues regarding the location of the impending stimulus. Patients with unilateral damage showed significantly less benefit from the spatial precues (relative to a neutral, uninformative condition) than either normal subjects or controls with temporal lobectomies. It appears, then, that the evidence from human lesions is in good agreement with the data from recordings of cells in infrahuman animals. Both sets of studies implicate frontal and parietal mechanisms in a way that is consistent with the putative network proposed by Mesulam (1981).

### **2.3 Evidence from Human Neuroimaging**

We turn next to studies of spatial selective attention using neuroimaging techniques. These studies are an important source of converging evidence because they allow whole-brain assessments of the substrate of spatial selective attention in normal human populations. An important consideration as we examine the overlap between the brain regions implicated in these and other neuroscientific studies concerns the dependence of most neuroimaging studies on the use of a subtraction methodology (Fox, Mintun, Reiman & Raichle, 1988). This technique allows experimenters to uncover differential activations between an experimental and a control condition; consequently, the interpretation of the observed areas of activation in any particular study must be considered in the context of the specific subtraction that was employed.

Using positron emission tomography (PET), Corbetta, Miezin, Shulman & Petersen (1993) examined activations related to spatial selective attention using a precuing task that required subjects to track the onset of a series of peripheral targets. During each trial, subjects fixated centrally while a series of targets was illuminated. Eighty percent of the time each stimulus appeared in a predictable location relative to the last one, allowing subjects to shift attention toward the locations of the ensuing targets, which appeared either on the left or right of

fixation. Behavioral testing demonstrated that subjects were reliably faster to respond to validly cued targets, showing that subjects were shifting attention to the cued locations as planned. In order to determine the brain regions activated by the attentional components of this task, activations when subjects had to shift attention were compared with activations in a central detection task, in which subjects detected the onset of a central target while randomly flashed peripheral targets were to be ignored. The central detection task was intended to control for the peripheral sensory stimulation and the response-related processing found in the shifting task. (Because subjects had an intended central focus of attention, the irrelevant peripheral stimuli were unlikely to attract attention automatically: Yantis and Jonides, 1990.) Subjects were also scanned during passive viewing of a similar display (random peripheral locations were stimulated). It should be noted that both the shifting task and the passive viewing task might cause shifts of visual attention; however, only the shifting condition should have activated brain regions that coordinate motor-related attentional processing since subjects were not making responses to attended stimuli in the passive viewing condition.

Subtraction of activations in the central detection task from those in the shifting task revealed significant changes in superior parietal cortex, superior frontal cortex, inferior frontal cortex, and anterior cingulate cortex (area 24). Note that while superior parietal and superior frontal sites are a common theme in neuroimaging studies of selective attention (as we shall see below), the foci reported by Corbetta et al. are significantly anterior to those that are commonly observed. The sites of frontal and parietal activation were contralateral to the field of visual presentation, with the exception of bilateral parietal responses to right visual field stimulation. The superior frontal responses were absent in the passive viewing task relative to the central detection task. Two main differences between the shifting and passive conditions might explain the difference in effect with respect to the frontal responses: (1) These regions may mediate motor-related attentional processing, or (2) Frontal regions may be more important for voluntary shifts of attention (rather than any automatic ones that might have been elicited in the passive viewing task). The fact that the parietal activations were present in both the shifting and passive



viewing conditions suggests that this region is generally involved in shifting of spatial attention, whether it is voluntary or automatic.

The experiments just reviewed were designed to reveal effects of attention that one might call phasic in character. That is, in these experiments, subjects were required to shift their attention from one location to another. By contrast, Heinze, Mangun, Burchert, Hinrichs, Scholz, Münte, Gös, Scherg, Johannes, Hundeshagen, Gazzaniga & Hillyard (1994) used both PET and ERP techniques to observe brain responses during the tonic maintenance of attention. Subjects attended to the right or left side of a bilateral stimulus array, and they made judgments about stimuli appearing on the attended side. Each condition involved attention to only a single location with no shifts of attention required. When a condition that required just passive viewing was subtracted from the conditions involving unilateral attention, PET revealed contralateral activation in the fusiform gyrus of extrastriate visual cortex in the attentional conditions, suggesting a location-specific enhancement of visual response to the bilateral stimulus array. In addition, the subtraction of the passive viewing condition from that in which subjects had to attend to the left revealed activation in anterior cingulate cortex and left superior frontal cortex (supplementary motor area 6), while the attend-right-minus-passive subtraction revealed a further site of activation in the thalamus. The ERP recordings confirmed the early attentional modulations in extrastriate cortex, by revealing signals of significantly larger amplitude at a latencies of 80-130 msec; these ERP effects were also localized to occipital cortex contralateral to the attended side. Thus, both the timing and localization of these attentional responses suggest enhancement of early visual processing by the tonic allocation of spatial selective attention. Furthermore, the lack of parietal activation in these conditions is consistent with the notion that superior parietal cortex is involved in shifting attention rather than in tonically maintaining it on a single location.

Duncan, Orban, Vandenberghe, Ward, Dupont, Bormans and Mortelmans (unpublished manuscript) have also used neuroimaging to examine the brain regions involved in spatial directed attention. Subjects made visual discriminations of either the orientation or displacement

(or both) of **peripheral stimuli**. When PET activations related to simple detection of the same stimuli were subtracted from those in the discrimination conditions, a network of activations was observed in bilateral superior parietal cortex, right lateral frontal cortex, right occipital-temporal-parietal (OPT) junction, anterior cingulate, left motor/premotor cortex, basal ganglia, pulvinar and bilateral cerebellum. Presumably, the discrimination conditions required relatively more allocation of attention to the periphery than the detection condition, and therefore should have activated the areas that mediate spatial selective attention. However, these activations reflect not only the relatively higher peripheral attention demands of the discrimination tasks, but also the processing of orientation and displacement information about the stimuli. In order to pinpoint the activations related to spatial attention, the investigators examined the relative increases in activation between detection, judgments of orientation or displacement, and judgments of both orientation and displacement. The rationale here was that each increase in processing demands would be accompanied by a corresponding increase in attentional processing; thus, areas that showed monotonic increases in activation across these three conditions respectively are likely to play a role in spatial attention. By contrast, this pattern of results would not be expected in the areas related to stimulus presentation or the discrimination of specific stimulus characteristics. The bilateral superior parietal focus showed the monotonic increases associated with attentional processing. While the type of discrimination did not affect the level of activity in this region, the number of peripheral discriminations was a key factor. This region showed greater activation in all single-discrimination conditions than control, and the greatest activation in the task that required concurrent judgments of orientation and displacement. The authors point out that this result mirrors that of Bushnell et al. (1981), where area 7 parietal responses were enhanced by attention, regardless of the specific task performed. The same pattern of increased activation during dual discriminations was observed in left premotor and nearby lateral prefrontal cortex (but in no other regions). These results suggest that superior parietal regions and left premotor and lateral prefrontal areas participate directly in the allocation of spatial attention to peripheral locations.

Vandenberghe, Dupont, De Bruyn, Bormans, Mortelmans, & Orban (unpublished manuscript) applied PET measurements to a paradigm similar to that of Duncan et al. Subjects in the study of Vandenberghe et al. made either detection or orientation-discrimination responses for stimuli that were presented either centrally or peripherally, with or without accompanying distractor stimuli. Subtraction of the activations in the detection conditions from those in the conditions requiring orientation discriminations showed relative increases in superior parietal lobule (bilaterally), right supplementary motor cortex, left premotor cortex, anterior cingulate, inferior occipital cortex (bilaterally), and right putamen. In right and medial superior parietal regions, the difference between discrimination and detection was larger when peripheral as opposed to central stimuli were presented; in fact, there was no significant difference in the activation of these regions between detection and orientation judgments with central stimuli. It is possible that the superior parietal cortex is particularly important when attention must be shifted peripherally; this would be consistent with the Corbetta et al. (1993) finding that detection of centrally appearing targets does not cause greater superior parietal responses than passive viewing of a similar stimulus display. Vandenberghe et al. argue against this possibility by pointing out that detection of peripheral targets in their experiment resulted in smaller superior parietal responses than detection of central targets. However, tasks involving only detection of stimuli in fixed, predictable locations may be inappropriate for testing such a hypothesis because they may require only limited allocation of directed spatial attention.

The bilateral increases in inferior occipital cortex may reflect attentional enhancement of visual responses, or alternatively, the effects of making orientation judgments. There are two arguments for the former: (1) **The** activation differences between orientation and detection judgments were greater with **central** than peripheral stimulus presentations. It is unclear why this interaction would occur if these activations were driven by orientation processing, given that the peripheral presentations probably entailed more difficult discriminations. Indeed, performance accuracy with the peripheral stimuli was 6% lower than accuracy with central presentations. (2) The sites of extrastriate enhancement in this study are remarkably similar to those localized in

the Heinze et al. experiment, in which response selection characteristics were completely matched. Overall, then, this study implicates a network of regions in selective attention that includes frontal and superior parietal regions, as well as evidence of attention-enhanced extrastriate responses.

Despite the use of widely varying experimental paradigms, the neuroimaging studies reviewed here consistently implicate a frontal-parietal network of activations in the control of spatial selective attention. The superior parietal activations are perfectly correlated with the requirement of shifting attention. The frontal responses are less reliable, and the specific localization of these responses is more variable. Although all studies included frontal activations around Brodmann area 6, the specific focus varied between the superior and inferior aspect of this region (i.e. between premotor and supplementary motor areas). Also, some conditions entailing allocation of spatial attention failed to activate any part of area 6. It is also noteworthy that while unit-recording studies consistently implicate dorsolateral prefrontal regions in spatial selective attention, the neuroimaging studies included no evidence of such activations.

Finally, while only two of the four reviewed studies showed evidence of attentionally-enhanced visual responses, there is an underlying consistency in these data. In particular, the rate of stimulus presentation was predictive of whether modulations of visual responses were observed. The interstimulus intervals employed by Heinze et al. and Vandenberghe et al. average 300 msec and 550 msec, respectively, and both studies include evidence of enhanced visual responses. On the other hand, the Corbetta et al. and Duncan et al. studies had much longer average interstimulus intervals (1500 msec and 1656 msec, respectively), and no visual enhancement was observed in these studies. It is possible that faster presentation rates drive visual responses more effectively, and are therefore more likely to reveal modulations of these responses. Another possibility--perhaps directly related to the rate of stimulus presentation--is that the tasks were more difficult in the studies that demonstrated enhanced visual processing. The average behavioral accuracy in the Vandenberghe et al. and Heinze et al. studies (where attention-enhanced visual responses were observed) was only 79% and 57%, respectively. By

contrast, the average accuracy in the Duncan et al. study was 87%, and the Corbetta et al. task resulted in near-ceiling performance levels, and no attentional enhancement of visual response was observed in these studies.

### **3. The Neural Basis of Spatial Working Memory**

Next we turn to the neuroanatomical evidence regarding spatial working memory. The bulk of evidence regarding this memory system has been generated through unit-recording and lesion studies in nonhuman primates, and, more recently, through neuroimaging studies of humans. Having considered the network of cortical sites that mediate spatial selective attention, we can now review evidence about spatial working memory with an eye toward the possible correspondence between attention and memory.

#### **3.1 Evidence from Nonhuman Primates**

Spatial memory is a long-standing topic of research with nonhuman primates, and numerous reviews exist of this research. We report here only the highlights of this work, and we direct readers to other sources for a more in-depth review (e.g. Goldman-Rakic, 1987; Fuster, 1995; Ungerleider 1995).

A prototypical paradigm for spatial working memory studies has been the delayed-response task. Trials begin with a cue that indicates a location to be remembered for several seconds, after which a response based on this spatial memory is required. Both lesion studies and single-unit recordings have consistently shown that the regions surrounding the principal sulcus in monkeys (putatively homologous to the dorsolateral prefrontal cortex in humans) is of primary importance in the performance of these tasks (Goldman-Rakic, 1987). More recent studies have also implicated regions of the parietal cortex in spatial working memory. Chafee, Funahashi & Goldman-Rakic (1989) observed neuronal responses in posterior parietal cortex during the performance of an oculomotor delayed-response task. They found that 28% of the neurons tested showed sustained activations during the delay period of the memory task. These

response patterns mirror those that have been observed in neurons of the dorsolateral prefrontal cortex (for a review see Fuster, 1984 ), and suggest that parietal cortex is also directly involved in short-term maintenance of spatial information. The extensive connectivity between the frontal and parietal regions is well-known (e.g. Petrides and Pandya, 1984) and suggests that these areas are central nodes in a highly-interactive network mediating spatial cognition (Goldman-Rakic, 1987; Fuster, 1995). A compelling picture of frontal-parietal interactions has emerged, in which parietal cortex serves as a receiving area of sensory information and calculates spatial coordinates that are then transmitted to prefrontal regions. The prefrontal regions, through extensive reciprocal connections with parietal regions, mediate the continued activation of this posterior sensory representation. Recently, direct tests of the interaction between prefrontal and parietal regions have been carried out. Goldman-Rakic and Chafee (1994) observed neuronal responses in posterior parietal cortex during performance of an oculomotor delayed-response task. These measurements were carried out before, during, and after the dorsolateral prefrontal cortex was cryogenically suppressed. They found that the magnitude of the responses of most parietal responses (previously demonstrated to play a role in spatial memory) were significantly reduced during prefrontal cooling. These results support the notion that prefrontal cortex mediates posterior parietal memory activations through reciprocal feedback connections.

### **3.2 Evidence from Human Neuroimaging**

Studies in humans using neuroimaging measurements of brain activity also provide support for the role of parietal and prefrontal structures in spatial working memory, and they suggest a role for occipital structures as well, a role that has not been investigated in studies of animal models. As few in number as the neuroimaging studies of spatial working memory are in humans, they nonetheless fall into two classes based on the type of task that has been used and the resulting pattern of brain activations that result (a distinction first articulated by Owen, Evans, and Petrides, 1996). One type of task requires subjects to store spatial information during a retention interval and then to retrieve all or part of that information. The second type requires

not only storage, but also some manipulation or monitoring of that information to satisfy task requirements. Thus, the two types of task share encoding, storage, and possibly retrieval processes in common, but the second type also includes processes responsible for the *manipulation* of spatial information as well. Let us examine tasks of the two types, and we shall see that they share many parts of a working memory circuit in common, while differing in the nature of prefrontal activation.

**3.2.1 Tasks that involve storage.** Jonides, Smith, Koeppe, Awh, Minoshima, and Mintun (1993) used PET to measure brain activations during the performance of a spatial working memory task that required storage and retrieval of three spatial locations. Each trial of the memory task began with the presentation of three target-dots appearing on the circumference of an imaginary circle surrounding a fixation point. A three-second delay followed, after which a probe circle appeared on the screen. The task was to indicate whether the probe surrounded the location of one of the previously presented dots. The activations in this memory task were compared to those in a control task that involved nearly identical stimulus presentations, but the target-dots and the probe circle were presented *simultaneously after* the delay interval. Thus, the control task involved similar stimulus presentations and responses, but it did not require active maintenance of information about spatial locations in memory. The memory task caused significantly higher activations than the control task in four right hemisphere regions: a ventral prefrontal region (area 47), premotor cortex (area 6), inferior parietal cortex (area 40), and extrastriate cortex (area 19). It should be noted that the field of view of the PET camera in this experiment was somewhat restricted in that the most superior aspects of posterior cortex were not clearly observable. Thus, there was no opportunity to observe activations in superior parietal cortex (area 7), an area that we have cited as central to spatial attentional processes. Nevertheless, this study does provide evidence of a frontal-parietal circuit involved in spatial working memory in humans.. In addition, the study reports activations in extrastriate cortex, consistent with the idea that early visual circuits may be involved in spatial working memory as well.

This pattern of activations is echoed in an experiment by Courtney, Ungerleider, Keil, and Haxby (1996), who also used PET to observe brain regions activated by working memory for spatial locations. During each spatial memory trial, subjects saw an array of 24 irregularly-positioned boxes. Three faces appeared one at a time for 1500 msec each in three of the boxes, followed by a 500 msec delay, and then a single probe-face (faces were used as stimuli to compare these results to those from a face-memory task). Subjects had to indicate whether the probe occupied one of the memorized locations. This task was compared to a control task, in which subjects simply indicated when the fourth stimulus in the sequence appeared by pressing the right or left response button. Two subtractions were reported: (1) Comparison of the memory activations to those in the control task revealed memory-related activations in right and left superior parietal cortex (area 7), and right occipital cortex (area 19). (2) The activations in the location-memory condition were also directly compared with those in a face-memory condition in which subjects had to match the probe against the target-faces on the basis of identity, not location. The location-memory condition showed relatively higher activations in right and left supplementary motor cortex (area 6), right and left superior and inferior parietal cortex (areas 7 and 40, respectively), left extrastriate cortex (area 19), and striate cortex (area 17). The data of Courtney et al. (1996) suggest a more bilateral role of memory structures in a spatial storage task than do the data of Jonides et al. (1993). Nevertheless, there is good agreement between the studies about the involvement of structures in superior posterior prefrontal cortex, in extrastriate cortex, and in posterior parietal cortex. Notice that the data of Courtney et al. (1996) also implicate area 7 of parietal cortex, consistent with the proposed relationship between processing in spatial working memory and spatial attention.

Perhaps the most wide-ranging of the studies of spatial working memory is that by Owen, Evans, and Petrides (1996). They took PET measurements of brain activations during the performance of several varieties of spatial working memory tasks intended to tap either simple storage or storage-plus-monitoring processes. The storage tasks were these. In the *Spatial Span* task, eight red circles were presented in random locations on a screen. Subsequently, a



sequence of five of these circles changed from red to blue and then back to red at the rate of 500 msec each. Immediately after the fifth circle turned back to red, subjects were required to touch each of the five circles in any order they wished. In the *Fixed Spatial Sequence* task, eight randomly positioned red circles were presented. Subjects simply had to touch the circles in a well-learned fixed sequence. When each circle was touched, it turned blue for 500 msec and then returned to red to indicate that the next circle in the sequence should be touched. Both of these conditions were compared to a baseline control condition in which eight red circles were presented in random locations, except for one centrally located one. Subjects monitored the central circle, which turned from red to blue once a second; they had to touch the circle each time it changed colors. This task was intended to involve similar perceptual and response requirements as the experimental tasks.

The two storage tasks of Owen et al. (1996) resulted in activations in right ventrolateral prefrontal cortex (area 47), bilateral premotor cortex (area 6, Spatial Span task only), bilateral superior parietal cortex (area 7), and bilateral occipital cortex. This pattern of results is very similar to those of Jonides et al. (1993), and it accords well with some of the activations found in the study by Courtney et al. (1996) as well. The bulk of the evidence from these three experiments (from different laboratories and with different tasks) is in good agreement about the nodes involved in a circuit concerned with the storage of spatial information in working memory. These nodes include premotor cortex, inferior frontal cortex, superior parietal cortex, posterior parietal cortex, and occipital cortex. Furthermore, it appears that right-hemisphere structures in these areas are more activated during spatial working memory than those in left-hemisphere.

**3.2.2 Tasks that involve storage and manipulation.** Going beyond tasks that require just storage of spatial information, Smith, Jonides, and Koeppel (1996) used PET to observe brain activations during the performance of a continuous spatial working memory task. Subjects saw a series of single stimuli appear in various locations around the circumference of an imaginary circle (The stimuli were letters to compare this task with a verbal memory task used in another condition of the experiment, but we shall ignore the verbal nature of the stimuli here and treat

them simply as markers for location.) The task was to indicate whether or not each stimulus occupied the same location as the stimulus presented three items back in the sequence. This is a demanding task for which subjects must maintain three spatial locations in working memory at any moment to be successful, and the memory load is continuous because each older letter is replaced by a newer letter as the sequence continues. Activations in the spatial memory condition were compared to those in a control condition that required subjects to monitor a similar sequence of stimuli presented in various locations; in this case, subjects were required to discriminate only whether each stimulus occupied one of three unchanging locations that had been committed to long term memory prior to the beginning of the sequence. Thus, the need for working memory in this control condition was minimal. Subtraction of the activations in the control condition from those in the spatial memory condition revealed a bilateral pattern of activations (with right dominance) in dorsolateral prefrontal cortex (areas 9,10 and 46), supplementary motor area, and superior and inferior parietal cortex (areas 7 and 40, respectively). In addition, a unilateral right hemisphere activation was observed in premotor cortex (area 6). Note that the activations seen in this experiment bear a striking similarity to those found by Jonides et al. (1993), Courtney et al. (1996), and Owen et al. (1996; their storage tasks) with one exception: The continuous working memory task of Smith et al. (1996) recruited activations in dorsolateral prefrontal cortex, an area that was not activated in the pure storage tasks.

Owen et al. (1996) included three tasks in their experiment that, by their analysis, also involved more than simply the storage of spatial information. In the first, each trial started with the sequential presentation of three blue circles (for 250 msec each) in random locations of a blank screen. After a three-second delay, eight red circles were simultaneously presented on the screen, and the task was to touch the three red circles that matched the memorized locations. Owen et al. (1996) assert that this task involves not only the storage of spatial information, but also processes necessary to pick these locations out from among a number of distractors. In a second task, a random arrangement of eight red circles was presented on the screen, and subjects

"searched" through the array by touching individual circles until one of them turned blue. After the blue circle changed back into a red one, the subjects were instructed to continue searching for the new "target", while avoiding touching the circles that had already turned blue (similar to the task of McCarthy et al., 1994, discussed below). Subjects were explicitly instructed not to use any systematic spatial strategies, but to search in a "random fashion." This task also involves more than mere storage because subjects must devise search strategies to sample the locations that have not already been selected in the display. The third task was similar to the second except that an array of 12 instead of 8 circles was presented.

All three of these tasks generated very similar patterns of activation; each task resulted in bilateral activations in superior parietal cortex (area 7), and occipital cortex. In addition there were sites of activation in right inferior parietal cortex (area 40, all tasks), left ventrolateral prefrontal cortex (area 47, in tasks 2 and 3), right premotor activation (area 6, in tasks 1 and 3), left premotor cortex (area 6, all tasks), anterior cingulate cortex (area 32, tasks 2 and 3). Except for the site in anterior cingulate, these activations are consistent with the tasks described earlier that involve storage alone. In addition to these, however, Owen et al. (1996) also found activations in dorsolateral prefrontal cortex in their three tasks, consistent with a role for this area in manipulating spatial information that is stored. The nature of the manipulation involved in these three tasks appears quite different, and there is no clear account of how they share similarities; nevertheless, by the account of Owen et al. (1996), all the tasks involved a sort of monitoring function that might recruit dorsolateral prefrontal processes.

The role of dorsolateral prefrontal structures in spatial working memory tasks has also been investigated by McCarthy, Blamire, Puce, Nobre, Block, Hyder, Goldman-Rakic, and Shulman (1994) using functional MRI. They required subjects to monitor a sequence of stimuli that appeared in a set of haphazard locations. Subjects were required to respond whenever the current stimulus appeared in a location that had already been occupied. In order to perform accurately, subjects had to keep in memory the set of previously stimulated locations. Activations in the memory condition were compared to a baseline of activation with no task

requirements. Two additional control tasks were also included, both of which required peripheral attention to the locations of visually identical stimuli, but no memory of those stimuli.

The window of view in this experiment was restricted to a single anterior coronal slice that included only parts of areas 9, 46, 23, and 47. Thus, the posterior areas (in parietal and occipital cortex) that may have been activated by the spatial memory task were not observed. Comparison of the memory task to the baseline condition revealed significantly higher activations in mid-dorsolateral prefrontal cortex (area 46) and the cingulate gyrus (area 23). The activations in area 46 were bilateral but dominant in the right hemisphere. These results are consistent with the second and third spatial monitoring tasks of Owen et al. (1996) described above, who also found activations in dorsolateral prefrontal cortex. In addition, however, the *control* tasks used by McCarthy et al. (1994) also showed activations in dorsolateral prefrontal cortex, in the same region activated in the memory task. This is consistent with the possibility that the memory and control tasks in this experiment had overlapping functional profiles; that is, perhaps both tasks required allocation of peripheral attention.

**3.2.3 Summary of neuroimaging experiments.** Data from the set of neuroimaging experiments on spatial working memory are in remarkably good agreement. This can be seen by inspecting Table 1, which lists the various experiments and notes the areas of activation found in each. This table makes apparent that only a small number of sites of activation have been found in spatial working memory experiments. The sites include inferior prefrontal, premotor, supplementary motor, superior parietal, posterior parietal, and occipital areas in cortex. In addition, when the task involves more than just storage of information, there is evidence of dorsolateral prefrontal activation as well.

To summarize the table, the studies by Jonides et al. (1993) and Courtney et al. (1996) used tasks that could be described as "pure storage" tasks; accordingly, the prefrontal activations in these tasks were restricted to premotor and ventrolateral prefrontal cortex. By contrast, due to the continuous nature of the memory task used by Smith et al. (1996), constant updating of the memory set was required; the presentation of each new stimulus necessitated dropping the first

item in memory and adding a new one (while preserving the temporal order of the memorized items). Thus, this task requires significant manipulation of the items in spatial working memory, and the results show that there were strong bilateral activations in dorsolateral prefrontal cortex. The interpretation of the task by McCarthy et al. (1994) is somewhat less clear. While this task does require updating of spatial memory as new items are presented (and added to the list of memorized positions), it may be that this type of "manipulation" is qualitatively different from the temporal ordering required in the continuous task of Smith et al. (1996). Likewise, the interpretation of the dorsolateral prefrontal activations noted by Owen et al. (1996) in their spatial monitoring tasks also assumes that these tasks share some processes in common with the very different continuous working memory task of Smith et al. (1996).

However this issue resolves itself, there is at least clear unanimity about the remaining areas of activation, and it is these that are most germane to the hypothesis under discussion in this paper. Four areas in particular were activated in at least three of the four studies reported: (1) bilateral superior parietal cortex (area 7, three of three studies where it was observable); (2) right inferior parietal cortex (area 40, all studies, bilaterally in two studies); (3) superior frontal (area 6, all studies, bilaterally in three studies); (4) extrastriate cortex (three of four studies). Note that the experiment by McCarthy et al. (1994) could not be included in this summary due to the restricted field of view of their fMRI camera. However, when this experiment is considered, three of five studies showed activation of dorsolateral prefrontal cortex (areas 9, 10, and 46), and anterior cingulate cortex (area 32). It is interesting to note that with the single exception of the experiment by Courtney et al. (1996), every spatial working memory study reported here showed a striking right-hemisphere dominance. Right-hemisphere dominance is defined here as greater right-hemisphere activation than left (as judged by the reported z-values) for any bilateral area of activation, as well as a larger incidence of unilateral activations in the right hemisphere. The right-hemisphere dominance aside, the data from these experiments, taken together, show that a frontal-parietal circuit is a prominent feature of the neuroanatomical substrate of spatial working memory.

The specific sites of activation in frontal cortex are somewhat variable (again reminiscent of the selective attention evidence); this may reflect the current imprecision in our understanding of the functional categories subserved by this part of the brain. Activations in superior and inferior parietal cortex, however, are quite robust; it seems clear that at least two sites in parietal cortex are essential nodes in the network subserving spatial working memory. Finally, activations in extrastriate cortex are abundant in these studies and may reflect enhanced visual responses during the memory conditions. Interestingly, these extrastriate activations seem to be more prevalent in spatial memory conditions (three of four studies) than they were in the spatial selective attention studies reviewed here (two of four studies). One possibility is that the memory tasks constituted a more challenging load on the selective attention system, causing a greater allocation of attentional resources. We have already seen that the incidence of visual activations within neuroimaging work on selective attention varies directly with task difficulty. The relative prevalence of visual enhancements in the spatial memory conditions over the spatial attention conditions may reflect differences in task difficulty--and thus the degree of attentional allocation--rather than an underlying functional difference.

#### **4. Conclusions**

Our review of the literature concerned with the anatomical substrates of spatial selective attention and spatial working memory was motivated by a simple hypothesis: that spatial selective attention may be recruited in the service of spatial working memory. In the form of an analogy, this hypothesis amounts to the claim that there is a rehearsal process involved in spatial working memory, similar to the role that rehearsal is claimed to have for verbal working memory. For spatial working memory, the assumption is that processes involved in spatial selective attention operate during the retention interval of a spatial working memory task to allocate attention in turn to each location that must be retained, keeping the representation of that location activated in memory. According to this hypothesis, there should be some overlap in the brain circuitry that is activated during spatial attention and spatial working memory tasks.

Our review suggests that there is. The major nodes in each processing network lie in frontal and parietal regions, and there is also considerable evidence of enhanced extrastriate responses to attended or memorized locations. Whether there are two overlapping circuits, or a singular memory/attention circuit is unclear. While it is apparent that there is a core set of brain regions that are reliably activated by both spatial memory and attention paradigms, there are possible exceptions. Multiple neuroimaging experiments have identified inferior parietal (area 40) and dorsolateral prefrontal areas in spatial working memory experiments; but we have not yet seen these areas activated by spatial selective attention tasks. Thus, it is possible that the circuitry subserving spatial selective attention comprises a *subset* of the overall spatial working memory network. For example, it may be that processes of spatial attention are responsible for a maintenance or rehearsal function in spatial working memory but that there are other processes that are involved in memory tasks in addition (such as creating the code that represents the spatial array or storing this code) that are not shared with spatial selective attention tasks.

We should note, of course, that the activation differences between memory and attention tasks may be in part an artifact of the specific paradigms that have been employed in tests of working memory and selective attention. For instance, as we've already discussed, there may have been differences in task difficulty between the memory and attention experiments. Other potentially relevant differences include faster stimulus presentation rates and the consistent presence of landmarks (by which subjects guided their attentional shifts) in the selective attention tasks. Future within-study analyses of the relationship between working memory and attention may provide clearer leads about the effects of these task-factors. Nevertheless, the overall pattern of results suggests a similarity in neuroanatomical substrates between attention and spatial working memory that goes beyond mere artifact.

In addition to the demonstration of similar neuroanatomical substrates, it can be argued that there is functional correspondence between the roles suggested for the individual areas within these networks. The attentional literature has converged upon a role for the superior parietal cortex in formation of high-level spatial representations required by shifts of attention

while the prefrontal regions have been implicated in the tonic maintenance of directed spatial attention. Similarly, spatial working memory paradigms have suggested a role for prefrontal cortex in the tonic activation of posterior parietal sensory representations. While this highly-interactive relationship between the frontal and parietal regions has been interpreted as the cortical instantiation of spatial *working memory* (Goldman-Rakic, 1987; Fuster, 1995; Ungerleider, 1995), we suggest that the label spatial *selective attention* may also provide a fruitful means of interpreting this phenomenon. Thus, the major premise of this review is that the neuroanatomical correspondence between spatial working memory and spatial selective attention is a direct reflection of an underlying *functional* correspondence. Future investigations may help to reveal the full extent of this correspondence.



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## Activations Across 5 Neuroimaging Studies of Spatial Working Memory

### Pure Storage Tasks

	dorsolateral	prefrontal	ventral	superior area 6	superior parietal	inferior parietal	early visual regions	anterior cingulate
<b>Jomides et al. (1993)</b> spatial memory		R				R	R	
<b>Courtney et al. (1996)†</b> location memory-control					R & L		R	
<b>Owen et al. (1996)</b> location memory - face memory				R & L	R & L	R & L	L & midline	
<b>Fixed Array</b>		R		R & L			R & L	midline
<b>Fixed Span</b>		R		R & L			R & L	midline

### Tasks Requiring Manipulation

<b>Smith et al. (1996)</b> 3-back task	R & L			R & L		R & L		midline
<b>Owen et al. (1996)</b> Spatial monitoring I	R			R & L		R	R & L	
Spatial monitoring II	R	L		R & L		R	R & L	midline
Spatial monitoring III	R	L		R & L		R	R & L	midline
<b>McCarthy et al. (1994)</b> memory vs. baseline	R & L							midline

**Note.** This table displays every region significantly activated by these spatial working memory tasks, with the following exceptions: Owen et al. also observed significant activations in sensorimotor cortex (Spatial monitoring I), and precuneus (Spatial monitoring III, and Fixed Span). However, to our knowledge, these activations have not appeared in any other studies of spatial working memory. R = right; L = left; shaded regions were outside of that experiment's field of view.

† Note that the Courtney et al. subtractions we have listed are drawn from a single spatial memory condition.

figure 1

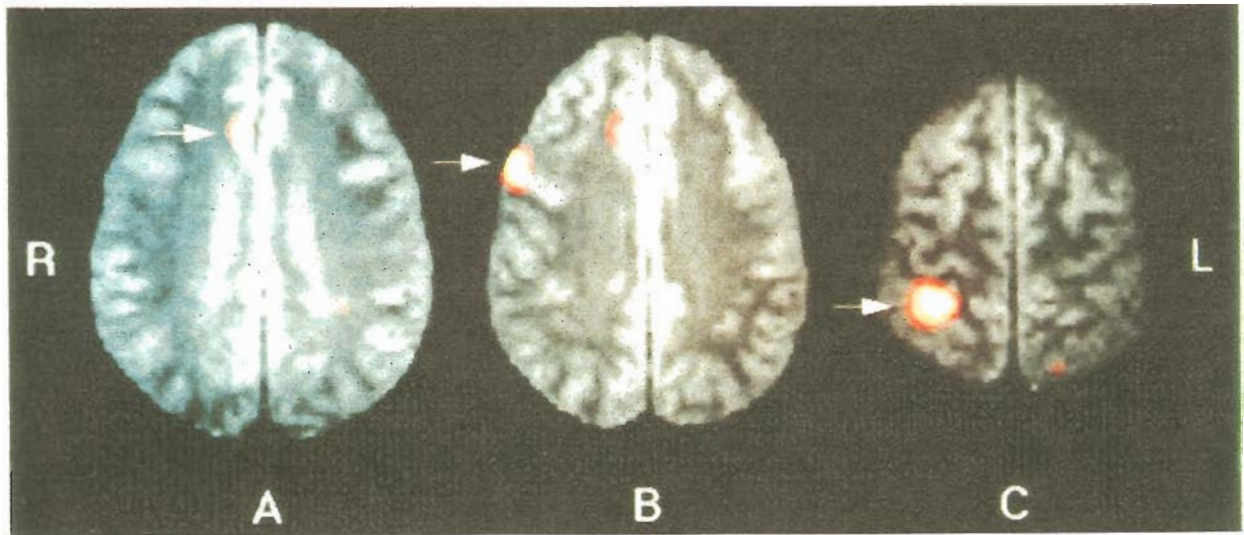


figure 2

