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Human cortical mechanisms of visual attention during orienting and search

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Functional anatomical studies indicate that a set of neural signals in parietal and frontal cortex mediates the covert allocation of attention to visual locations across a wide variety of visual tasks. This fronto-parietal network includes areas, such as the frontal eye field and supplementary eye field. This anatomical overlap suggests that shifts of attention to visual locations or objects recruit areas involved in oculomotor programming and execution. Finally, the fronto-parietal network may be the source of spatial attentional modulations in the ventral visual system during object recognition or discrimination.

Keywords: attention; vision; eye movements; search; cortex; neuroimaging

1. INTRODUCTION

Any visual scene contains numerous objects, where each object comprises several features such as colour, shape, motion and location. Although we can select objects of interest based on any feature or combination of features, the selection of visual objects by location is a powerful way of selecting behaviourally relevant visual information. There are several lines of evidence indicating the importance of spatial selection in vision. First, many studies have shown that attending to a location (spatial cueing) enhances visual performance in a large variety of visual tasks, including threshold and suprathreshold detection of luminance increments, and discriminations involving shape and colour (Eriksen & Hoffman 1972; Posner *et al.* 1980; Prinzmetal *et al.* 1986; Downing 1988; Hawkins *et al.* 1990; Henderson 1996; Luck *et al.* 1996). The widespread effect of attending to location indicates that processes mediating spatial selection have wide access to visual processes specialized for feature and object analysis. Second, locations are also selected in the context of a large class of visuomotor behaviours including orienting to peripheral stimuli. Overt orienting refers to a set of processes by which stimuli of interest in a visual scene are detected in the periphery of the visual field and rapidly brought into the fovea, the retinal region of highest acuity, by means of rapid saccadic eye movements. Overt orienting tasks are dissociable in the laboratory from covert orienting tasks in which behaviourally relevant stimuli can be attended to in the absence of exploratory saccadic eye movements. Third, the role of visual locations is emphasized by several theories of higher vision. For instance, Ullman proposed that the computation of various spatial relations between objects requires the application of visual routines or processes to selected stimulus locations (Ullman 1984). However, because of computational limitations, visual routines can be applied only to one or two locations at any given time. The analysis of the whole visual scene therefore requires a mechanism for selecting and switching the focus of processing from one location to another. Similarly, Treisman's feature integration theory (Treisman & Gelade 1980; Treisman 1991) proposes that the perception of objects in cluttered visual scenes is critically dependent on an attentional mechanism that selects an object location and binds the features at that location into a unified object percept.

The neurophysiological mechanisms underlying spatial selection are under active investigation. Traditionally, failures of spatial attention have been associated with damage to parietal cortex (DeRenzi 1982; Heilman *et al.* 1985; Mesulam 1990; Vallar & Perani 1987). Similarly, single unit analyses in awake behaving monkeys have indicated that neuronal activity in parietal cortex is modulated by the direction of attention (Bushnell *et al.* 1981; Robinson *et al.* 1995; Steinmetz & Constantinidis 1995; Colby *et al.* 1996). Over the past five years, we have studied the neural basis of spatial selection in the normal human brain by combining psychophysics, neuroimaging, and recent image analysis methods for flattening the cortical mantle of the human brain. We have identified a network of parietal and frontal regions that is active whenever attention is directed towards peripheral stimuli, both during cued detection at several locations (Corbetta *et al.* 1993), and visual search of targets in cluttered visual displays (Corbetta *et al.* 1995). The same set of regions is also active during overt orienting to peripheral stimuli via saccadic eye movements (Corbetta 1998). The fronto-parietal cortical network may therefore represent a neural system for selecting spatial locations across a variety of tasks.

2. FUNCTIONAL ANATOMY OF VISUOSPATIAL ATTENTION IN THE HUMAN BRAIN

Several functional anatomical studies have shown that a specific set of frontal and parietal regions is consistently recruited during covert orienting to simple unstructured

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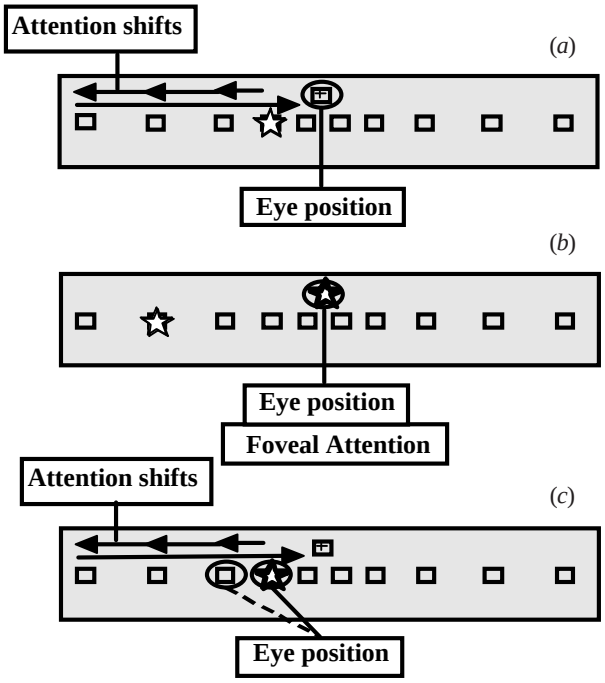

Figure 1. Behavioural tasks for studying covert and overt orienting. (*a*) Shifting attention task. Subjects sequentially shifted attention (arrows) to successive boxes in a predetermined sequence to detect a briefly presented stimulus (star), while maintaining fixation on a central box (oval). (*b*) Central detection with peripheral distractors task. The same sequence of peripheral stimuli was presented as in the shifting attention task, but subjects detected stimuli flashed in the central fixation box. (*c*) Saccadic eye movement task. The same sequence of peripheral stimuli was presented as in the shifting attention task, but before the onset of each stimulus, subjects moved their eyes to the expected location of the stimulus.

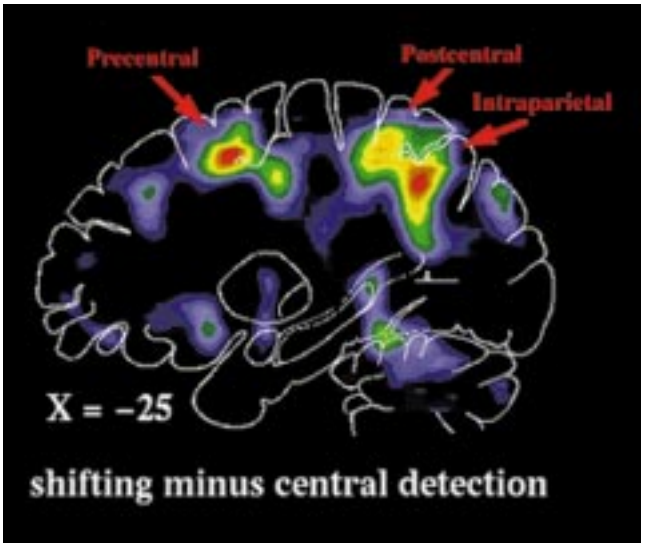

Figure 2. Sagittal PET section, 25 mm left of midline, of group ($n=24$) subtraction image between shifting attention and central detection with peripheral distractors tasks.

peripheral visual stimuli. Corbetta and colleagues (Corbetta *et al*. 1993) measured regional cerebral blood flow with positron emission tomography (PET) in a group of 24 normal subjects during tasks designed to manipulate the direction of spatial attention. In one task, subjects shifted attention voluntarily along a series of locations positioned in the left or right visual field, while maintaining central fixation, to detect brief visual stimuli with a speeded key-press response (shifting attention task; figure 1*a*). In 80% of the trials, the peripheral visual stimuli occurred in a prespecified sequence (see figure 1*a*), allowing subjects to shift attention to the appropriate location before the stimulus appeared. In 20% of the trials, the stimuli were presented at unattended locations, i.e. locations that did not respect the prespecified sequence. For the duration of the actual PET scan (40 s), the percentage of stimuli at unattended locations was decreased to 5% to maximize shifts of attention in a given direction (the direction of attentional shifts was also manipulated in this experiment, but those findings will not be further discussed in this review). As expected, stimuli at attended locations were detected faster than stimuli at unattended locations. In a second task, subjects attended to and manually responded to stimuli in the fovea, while being presented with the same series of peripheral stimuli as in the shifting attention task (central detection with peripheral distractors task; figure 1*b*). Hence, this condition controlled for sensory stimulation of the peripheral visual field, arousal, and visuomotor processes (e.g. motor preparation–execution) recruited by a speeded visuomotor response. The central detection task mostly differed from the shifting attention task in the direction of attention, i.e. foveally maintained against peripherally shifted. In a third task, the same series of peripheral stimuli was presented as in the shifting attention and central detection task, but subjects were instructed to maintain central fixation without responding (passive task). This condition controlled for peripheral sensory stimulation in the absence of a motor response. Because the sudden onset of peripheral stimuli automatically captures attention to those locations (Yantis & Jonides 1990), the passive task also provides an opportunity to image processes related to sensory-driven or reflexive shifts of attention. Finally, in a fourth task (fixation task), no central or peripheral transients occurred and subjects simply maintained fixation. Eye movements were monitored in all conditions with an electro-oculogram (EOG) to ensure proper central fixation. Areas involved in covert orienting were localized by image subtractions between pairs of conditions. In particular, a subtraction image between the shifting attention and central detection task (shifting attention–central detection) controls for peripheral sensory stimulation, arousal, and motor demands, and hence reflects processes specifically involved in shifting attention. Significant blood flow changes were visualized in superior parietal and frontal cortex (figure 2). Interestingly, only the parietal region was active during the passive task, compared with the fixation task. Although we were not able to explicitly compare shifting attention and passive scans, the magnitude of parietal activations in the shifting task was comparable with the passive task (when both tasks were compared with the fixation task).

This pattern of results indicated that both superior parietal and frontal regions were related to endogenous

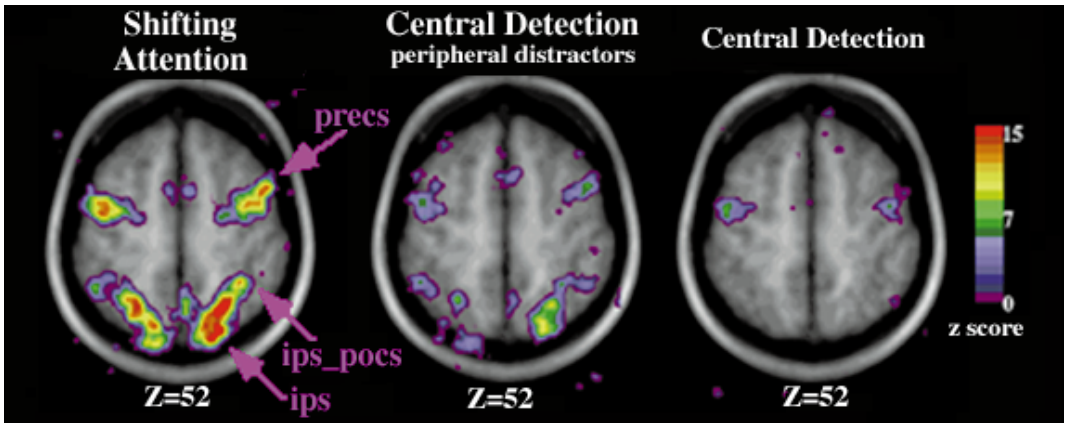

Figure 3. Group fMRI activity superimposed on anatomical MRI during shifting attention, central detection with peripheral distractors, and central detection tasks in the left visual field. In the fixation control common to all tasks, the array of boxes was displayed, no stimuli were presented, and subjects maintained fixation on the central box. Transverse section, $z=52$. Abbreviations: precs, precentral sulcus; ips_pocs, intraparietal sulcus–postcentral sulcus; ips, intraparietal sulcus.

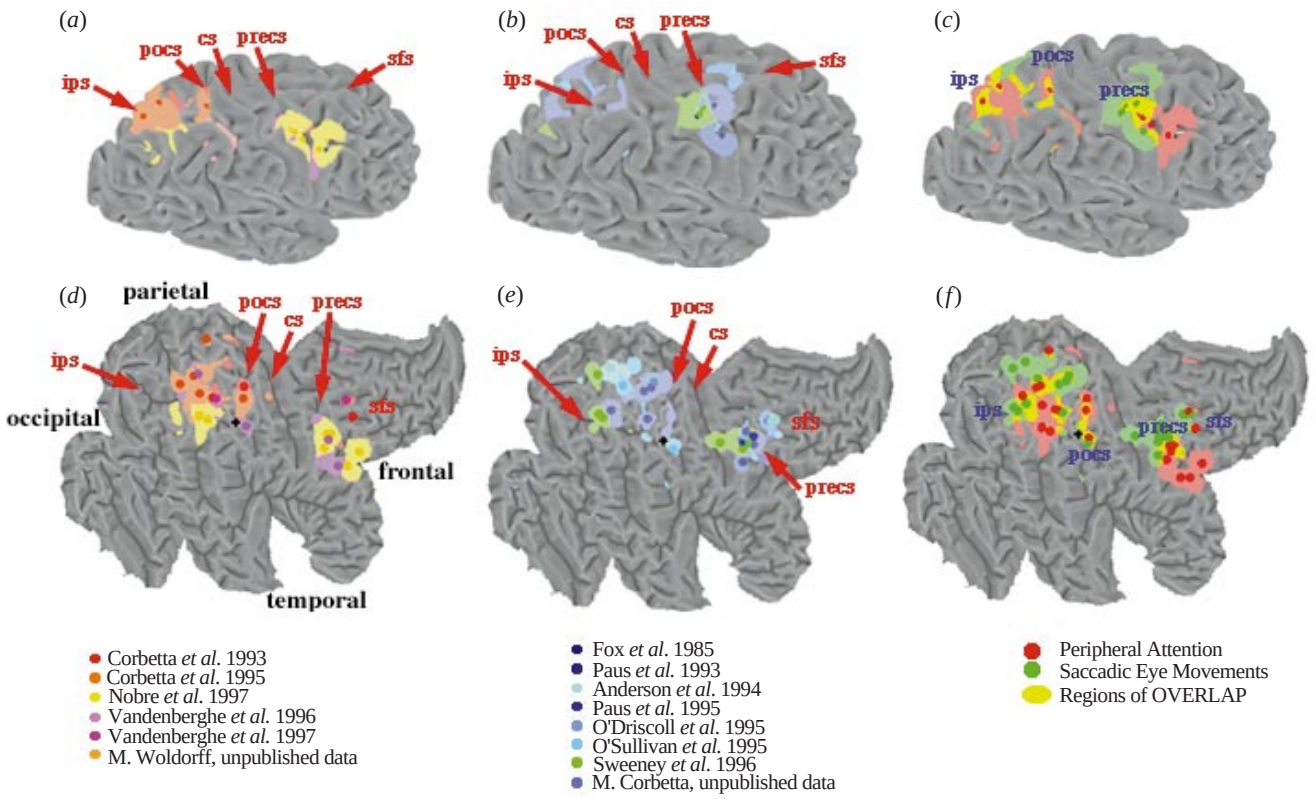

Figure 4. 3D rendering (*a–c*) and 2D flattened surface (*d–f*) of the Visible Man brain atlas, right hemisphere only. Lobes are indicated in 2D surface. Sulci are indicated as follows: sfs, superior frontal sulcus (s.); precs, precentral s.; cs, central s.; pocs, postcentral s.; ips, intraparietal s. (*a*, *d*): areas of activation during peripheral attention. (*b*, *e*): areas of activation during saccadic eye movements. (*c*, *f*): anatomical overlap of areas active during peripheral attention and saccadic eye movements.

shifts of attention. In both regions neural activity may reflect instruction signals for covertly (without change in eye fixation) shifting attention to peripheral locations. In parietal cortex, activity could also reflect a modulation (enhancement) of the sensory component of the peripheral visual stimuli, and/or sensory-driven shifts of attention induced by the sudden onset of those stimuli given the activation in the passive task (Yantis & Jonides 1990). In frontal cortex, activity could also reflect visuomotor processes, that are specifically related to the preparation–execution of a key-press response to peripheral visual stimuli, because no significant activity was observed when subjects did not respond (passive task) or responded to central stimuli (central detection task).

To further investigate the relation between endogenous shifts of attention and the preparation–execution of a motor response, we have recently studied a 'no-response' version of the shifting attention task (Corbetta *et al.* 1998),

in which subjects shifted attention voluntarily between peripheral locations and detected visual stimuli, but did not press a key to signal stimulus detection. Shifts of attention were therefore entirely decoupled from motor responses. To have some measure of performance, manual reaction times were measured in a prior psychophysical session in which subjects were trained to covertly shift attention to different locations in the periphery of the visual field. In addition to the shifting attention task, subjects were also scanned during a no-response central detection task, and a new no-response control task in which subjects detected foveal stimuli during central fixation (as in the central detection with peripheral distractors task), but no peripheral stimuli were simultaneously presented (central detection). This experiment was done by using functional magnetic resonance imaging (fMRI), which allows a more precise localization of functional activity in relation to the underlying anatomy in both single subjects and groups of subjects. The experiment was run as a blocked design in which each task was compared to a fixation control baseline. As in the PET experiment, regions in superior frontal and parietal cortex were strongly active when attention was directed toward the peripheral visual stimuli (figure 3, left), even in the absence of an overt motor response. Much weaker activations were evident in both frontal and parietal cortex during the central detection with peripheral distractors condition, i.e. when the same stimuli were unattended (figure 3, centre). Finally, only frontal cortex was weakly active during foveal attention without peripheral distractors (central detection, figure 3, right), suggesting that the parietal activity in the central detection with peripheral distractors task was related to the peripheral distractors. Although eye movements could not be recorded in the MR scanner, subjects were trained on these tasks in a prior behavioural session in which eye movements were monitored with EOG. Furthermore, the data from the fMRI experiment was very similar to the data from the PET experiment, in which eye movements were monitored during the scanning session. These fMRI findings confirm that activity in frontal and parietal cortex is unrelated to visuomotor manual processing *per se*, but is driven by the purely mental process of directing and shifting attention to different visual locations.

How general is the conclusion that a fronto-parietal cortical network is active during the allocation of attention to peripheral visual stimuli? To answer this question a meta-analysis of all published studies involving peripheral attention was done by using a new brain atlas (the Visible Man atlas) developed at Washington University by Heather Drury and David Van Essen. This atlas is based on the digital reconstruction of the anatomical sections of an adult male brain (Visible Human project, National Library of Medicine) (Drury *et al*. 1996; Van Essen & Drury 1997). The digital brain has been normalized to a standard 3D atlas space which is routinely used to localize responses in neuroimaging studies (Talairach & Tournoux 1988). The cerebral cortex has been flattened by using a reconstruction of layer 4 and foci of activation from all studies on peripheral attention have been plotted onto the 3D and 2D brain atlas representation. Each focus (indicated by a small sphere whose centre corresponds to x-, y-, z-coordinates of the activation in Talairach & Tournoux (1988) is surrounded by a 10-mm radius, which accounts for the variability in the mean location estimate (see Van Essen & Drury 1997). This variability has several sources: (i) imperfect registration of the functional data during the normalization to Talairach space; (ii) variability in the position of identified cortical areas in relation to nearby geographical landmarks; (iii) limited spatial resolution of the PET techniques; and (iv) variability in the anatomy of different groups of subjects.

This analysis involved studies that manipulated spatial attention in various ways: attention was dynamically shifted between different visual locations (Corbetta *et al*. 1993; Nobre *et al*. 1997), or maintained at a single peripheral location (Heinze *et al*. 1994; Woldorff *et al*. 1995; Vandenberghe *et al*. 1996, 1997), target locations were explicitly (spatial cueing) (Corbetta *et al*. 1993; Nobre *et al*. 1997), or implicitly cued (visual search) (Corbetta *et al*. 1995), and tasks required detection (Corbetta *et al*. 1993; Nobre *et al*. 1997) or discrimination (Heinze *et al*. 1994; Corbetta *et al*. 1995, 1996; Woldorff *et al*. 1995; Vandenberghe *et al*. 1996, 1997). All studies also differed in terms of the display characteristics and rate of stimulation. Overall, this analysis showed a very strong overlap in the pattern of cortical activation under all conditions (figure 4*a*,*d*). In parietal cortex, activity localizes along post-central and intraparietal sulci. In frontal cortex, two distinct foci of activations are evident: one near the precentral sulcus–gyrus, the other near the posterior tip of the superior frontal sulcus. The similarity in the functional anatomy of shifting and tonic attention paradigms suggests that this fronto-parietal network controls the allocation of attention to peripheral locations. Furthermore, in experiments that involve object discrimination, the dorsal fronto-parietal network is active concurrently with ventral occipito-temporal regions involved in object analysis. Here, the direction of attention modulates both psychophysical performance and brain activity. Object targets presented at the attended location are discriminated more accurately, and produce stronger blood flow responses in ventral object-related regions, than targets presented at the unattended location (Heinze *et al*. 1994; Vandenberghe *et al*. 1996, 1997). Correspondingly, powerful neuronal enhancement of visual responses for the attended object have been recorded in occipital visual areas with scalp and single unit recordings in virtually the same paradigm (Hillyard & Picton 1987; Luck *et al*. 1997). We propose that attentional modulation in the ventral visual system reflects an interaction with a selective location signal from the fronto-parietal spatial network.

3. THE RELATION BETWEEN VISUOSPATIAL ATTENTION AND OCULOMOTOR PROCESSES

The existence of a set of psychological and neural processes for covertly (without changes in eye position) directing attention to locations raises the question of their relation to mechanisms responsible for saccadic generation, because under normal conditions attention and the eyes move together when peripheral targets are selected in the visual field. Early papers provided

conflicting evidence on whether preparing an eye movement toward a location enhanced the visual processing of stimuli presented at the same location, and vice versa whether a shift of attention facilitated oculomotor execution (Klein 1980; Remington 1980). More recent work, however, has established that attention and eye movements are closely related. Shepherd and colleagues (Shepherd *et al.* 1986) separately manipulated the direction of spatial attention, by varying the probability that peripheral probe stimuli would appear in different positions, and the direction of saccades, by using a central arrow cue. They found that the preparation and execution of a saccadic eye movement enhanced the manual detection of stimuli presented at the saccadic target location, independently of probe probability. That is, even when attention and eye movements were cued to opposite locations, the effect of eye movement preparation–execution was predominant. Chelazzi and co-workers (Chelazzi *et al.* 1995) showed that the facilitation from saccadic preparation–execution extends to other locations in the same direction as the location of the saccade. Hoffman & Subramian (1995) confirmed in a dual task paradigm that target detection is superior at the saccade location regardless of the location at which attention was cued. Based on these new findings, the current view is that attention and saccadic systems are tightly related. For example, during the preparation of a saccade, the selection of a location is controlled by the oculomotor system, even when attempts are made to bias attention to different locations through experimental manipulations. It is still under discussion whether attentional processes may be separate when a saccade is planned but not performed, or when the eyes are fixated (Rafal *et al.* 1989; Klein 1994).

Areas of the human brain involved in oculomotor processing have been identified by a variety of imaging studies that have used different types of oculomotor tasks including voluntary, visually guided, memory-guided and conditional saccades (Fox *et al.* 1985; Anderson *et al.* 1994; O'Sullivan *et al.* 1995; O'Driscoll *et al.* 1995; Sweeney *et al.* 1996; Bodis-Wallner *et al.* 1997; Darby *et al.* 1996; Lang *et al.* 1994; Law *et al.* 1997; Luna *et al.* 1998; Muri *et al.* 1996; Paus *et al.* 1993, 1995; Petit *et al.* 1993, 1996, 1997). Figure 4*b*,*e* summarizes selected studies from the early PET literature (until about mid-1996), that reported activations in Talairach atlas, plus those from our own laboratory that involved visually guided and memory-guided saccades. Preliminary analysis showed no consistent difference in the pattern of activation between different types of saccades. The only exception was the presence of prefrontal activity (not plotted) in some experiments that involved memory-guided saccades. In the frontal lobe activity centres on the precentral gyrus, extending from the central sulcus to the precentral sulcus. A second cluster is evident near the posterior tip of the superior frontal sulcus. Similar activations have been reported by PET studies that have not used Talairach-based analysis (e.g. Petit *et al.* 1993), and more recent fMRI studies in single subjects (e.g. Luna *et al.* 1998; Petit *et al.* 1997). These regions are thought to contain the human homologue of the monkey's frontal eye field (FEF) (Paus 1996; Petit *et al.* 1997; Luna *et al.* 1998). Lesions in the FEF cause acutely an eye deviation toward the side of the lesion, and chronically the inability to suppress reflexive saccades (DeRenzi 1982; Henik *et al.* 1998). A third cluster (not shown) involves a region on the medial wall of the frontal lobe, probably corresponding to the supplementary eye field (SEF) (Shook *et al.* 1991; Schlag *et al.* 1992; Luna *et al.* 1998). In parietal cortex activity is again distributed near intraparietal and post-central sulci, and adjacent gyri, but extends also toward the precuneus.

To directly compare eye movement- and attention-related activations, foci for attention have been coloured in red, foci for eye movements in green, and areas of anatomical overlap in yellow. Areas of large overlap occur bilaterally in intraparietal and postcentral regions, and frontally in the precentral region and superior frontal sulcus region. Exclusive eye movement activity is evident dorsally in the right precuneus, and left postcentral gyrus. Exclusive attention activity is evident ventrally in the intraparietal sulcus. Overall, this analysis shows both overlap and segregation in the spatial distribution of cortical activity when attention- and eye movement-related foci are compared across PET experiments. The biological interpretation of these findings must be cautious given the presence of non-biological variability. Although the 10-mm radius of uncertainty associated with each focus should account for most of the methodological variability, differences in experimental variables across experiments (e.g. eccentricity of stimuli, rate of stimulus presentation) can also increase variability. However, if one emphasizes anatomical overlap, all three main sites of activation for attention (intraparietal, post-central, and precentral) show convergent activation during eye movements. Vice versa, if one emphasizes anatomical segregation there appear to be large sections of parietal and frontal cortex that are uniquely active for each condition. For example, attention foci are more anteriorly located in frontal cortex than eye movement foci. In conclusion, this meta-analysis of PET experiments suggests that attention and eye movements share neural substrates. However, the variability in the data does not allow one to conclude that these two sets of processes involve identical cortical regions. As attention is generally shifted during an eye movement, some overlap is expected. It is unclear, however, whether making an eye movement adds any unique regions in parietal or frontal cortex.

A more precise test of the relation between saccadic eye movements and attention is provided by functional mapping experiments in which covert (attentional) and overt (saccadic) visual orienting mechanisms are compared in the same subject. Subjects were scanned with fMRI in separate blocks during the no-response shifting attention task, in which attention was shifted sequentially along a series of predictable locations and stimuli were covertly detected, and during an eye movement task (figure 1*c*) in which voluntary saccades were done along the same series of locations as in the no-response shifting attention task. In both tasks subjects shifted attention (shifting attention task), and attention and eye position (eye movement task) in anticipation of the sensory stimulus. Visual stimuli were therefore presented in the periphery of the visual field in the shifting attention task, and in the fovea in the eye movement task. The fixation

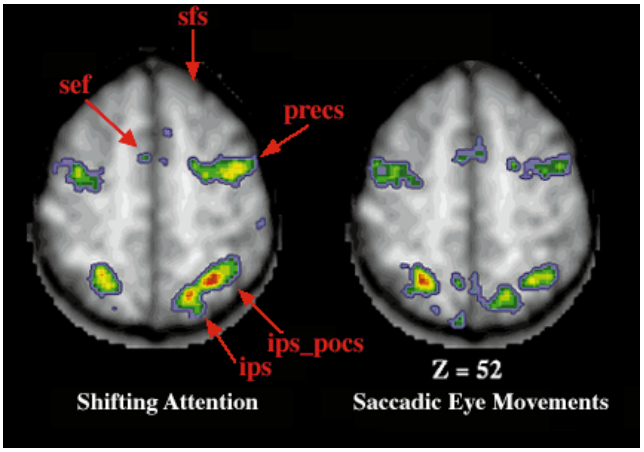

Figure 5. Group ($n=5$) fMRI activity superimposed on anatomical MRI during shifting attention and saccadic eye movement tasks in left visual field. A fixation control was common to both tasks. Anatomical regions as in figures 3 and 4. Abbreviations as in figure 3, and sef, supplementary eye field.

task described earlier, in which no peripheral transients were presented and subjects maintained fixation, served as a control. Although eye movements could not be monitored in the MR scanner, subjects were trained on all tasks during a prior behavioural session in which eye movements were monitored via EOG, and behavioural effects measured in the shifting attention task. Subjects moved their eyes appropriately during the eye movement task and maintained fixation during the attention task. In the attention task, all subjects showed robust behavioural effects for attended against unattended stimuli. In this experiment, we found very similar activations during attention and eye movement shifts both in parietal and frontal cortex (figure 5). The frontal activation centred on the precentral region and extended to the posterior tip of the superior frontal sulcus, and probably involved several areas. The activation of the precentral region corresponds to the FEF activation found in other oculomotor tasks (see figure 4). A medial frontal focus probably corresponds to SEF (Shook *et al.* 1991; Schlag *et al.* 1992; Luna *et al.* 1998). The parietal activations may correspond to areas in macaque that contain both oculomotor and attentional signals (e.g. LIP and 7a) (Andersen *et al.* 1990; Andersen 1995; Colby *et al.* 1995, 1996). The eye movement condition also yielded several activations not found in the attention condition, including the medial cerebellum and occipital cortex. The cerebellar activations presumably reflected the presence of eye movements while the occipital activations presumably reflected the presence of foveal transients. Both results confirm that subjects were maintaining fixation during the attention condition.

The extensive anatomical overlap of the neural systems for attention and eye movements is reminiscent of their tight functional relation at the behavioural level. In addition, the discovery of attention-related activity in the FEF suggest that covert attention processes involve oculomotor areas. The FEF is one of the cortical oculomotor centres of the brain. Neurons in the FEF are monosynaptically connected with the superior colliculus and pontine nuclei for eye movement control (Astruc 1971; Leichnetz *et al.* 1984). Microstimulation of the FEF with threshold electrical currents specifically produces contralateral saccades (Robinson & Fuchs 1969; Bruce & Goldberg 1985). A total of three populations of neurons have been described in the FEF: motor, visual, and visuomovement neurons (Bruce & Goldberg 1985). The motor neurons fire before and during a saccade, code target locations in motor parameters, i.e. direction and amplitude, and project to subcortical structures. Visual neurons respond to the onset of visual stimuli, and their response is enhanced when the visual stimulus is the target for a saccade. Visual neurons may provide sensory information about the target to motor neurons. Visuomovement neurons begin to discharge after the presentation of a visual stimulus, and remain active until a saccade is made into their movement field (refs). Recently, Schall and colleagues have shown that during a pop-out visual search task, the activity of these neurons signals the location of a target before a saccade, or during a fixation task (Schall & Hanes 1993; Thompson *et al.* 1997). These modulations indicate that FEF may participate in target selection aside from motor programming.

Haemodynamic activity in the FEF during covert attention may reflect three separate neuronal signals. Shifts of attention may enhance visual responses of visual or visuomovement neurons. Alternatively, or in addition, shifts of attention may involve saccadic preparation that drives motor neurons in the FEF. This would imply that both saccades and attentional shifts are planned in motor coordinates (e.g. amplitude and direction from the current position) (Rizzolatti *et al.* 1987). A similar conclusion was reached by Kustov & Robinson (1996) who found that covert shifts of attention modify the vector of saccadic eye movements induced by the microelectrical stimulation of the deep layer of the superior colliculus, the other oculomotor centre of the brain. Finally, FEF activity might reflect a fixation or suppression signal for preventing reflexive saccades to peripheral stimuli in the attention task. These latter possibilites are less likely as FEF activity is very weak in other tasks that require, as the shifting attention task, fixation during the presentation of peripheral stimuli (e.g. central detection or passive tasks in the PET experiment).

4. FRONTO-PARIETAL SPATIAL NETWORK, VISUAL SEARCH AND THE FOCUS OF PROCESSING

The functional link between shifts of visual attention and eye movements, and activity within a fronto-parietal cortical network provides important neurobiological constraints for unresolved issues in psychology and vision. We are referring in particular to the long-standing discussion about 'serial' and 'parallel' models of visual search. The basic phenomenon is well-known: while the search time for a high saliency target, e.g. a red triangle among green triangles (or feature search), is independent of the number of distractors, the search time for a low saliency target, e.g. a red triangle among green triangles and red squares (or conjunction search), increases with the number of distractors (Treisman & Gelade 1980; Duncan & Humphreys 1989; Wolfe *et al.* 1989). The biased competition model of Desimone & Duncan (1995) proposes that visual analysis proceeds in parallel (parallel search) across the field in both cases, but that its

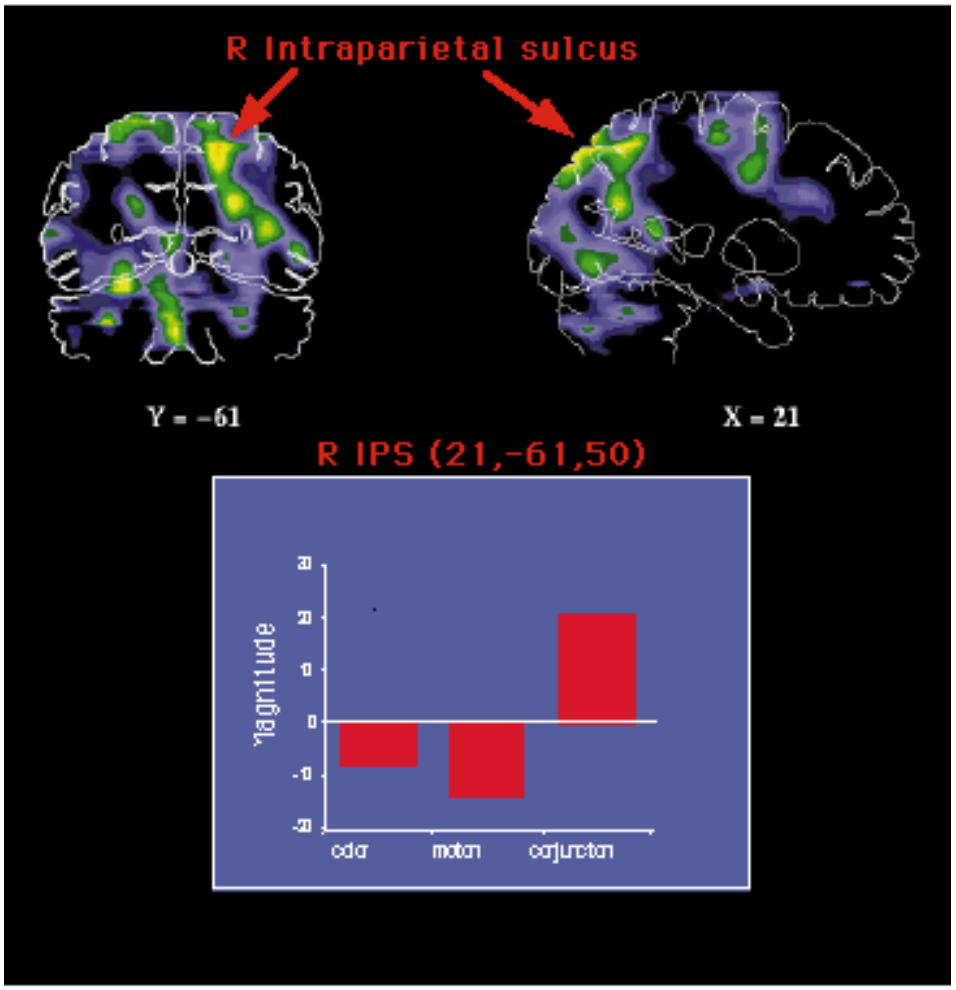

Figure 6. Top: group ($n=17$) PET activity from coronal (left) and sagittal (right) sections in the right intraparietal sulcus during visual search for targets defined by a conjunction of colour and motion speed. The control condition is passive viewing of the same display. Bottom: magnitude of blood flow responses (in PET counts) in the feature (colour, motion) and conjunction conditions for the intraparietal region maximally activated in the shifting attention task (figure 1).

efficiency declines in conditions of low target discriminability when more noise (distractors) is added to the system. Other models, such as Treisman's feature integration theory propose that a spatial attention mechanism is recruited in conditions of low discriminability and serially inspects individual items or groups of items in the field, to discriminate between target and distractors (Treisman & Gelade 1980; Treisman & Gormican 1988). 'Pure' versions of these two competing models make different predictions about the underlying functional anatomy. Parallel models predict that feature and conjunction search should yield similar regions of activation, perhaps stronger in the conjunction search because of the longer time on task. As the target is defined by a non-spatial feature (e.g. colour) these models predict either no activation of the fronto-parietal network, or activation during both feature and conjunction tasks. In contrast, serial models predict a dissociated pattern of activation with the conjunction task uniquely recruiting a spatial selection mechanism. If the fronto-parietal network, active during visual orienting, also controls the focus of processing during visual search tasks, then this network should be preferentially recruited by the conjunction task.

To address this issue we compared blood flow (measured with PET) during visual search tasks involving either targets defined by colour or by motion, or targets defined by a conjunction of colour and motion (Corbetta *et al.* 1995). The visual display contained four square windows (4° eccentricity from fixation, 2° length), and each window contained coloured (red, orange), moving (fast, slow) dots. In the colour task subjects searched for a red window among orange windows. In the motion task subjects searched for the fast window among slow windows. In the conjunction task subjects searched for the red–fast window among orange–slow, orange–fast, and red–slow windows. All search tasks were compared with a common control condition, in which similar displays were passively viewed. In a separate behavioural session, the feature task yielded a flat search function relating response latencies to the number of items in the display, while the conjunction task yielded the expected increasing search function. Across the entire brain, feature and conjunction search were best distinguished by activity in posterior parietal cortex corresponding to regions that were also active for attentional and oculomotor shifts during the visual orienting tasks discussed here. Blood flow in posterior parietal cortex was strongly increased when subjects searched for conjunction targets of colour and motion, and was slightly decreased when they searched for feature targets of either colour or motion, as compared with a control condition that involved passive viewing of the same set of stimuli (see figure 6). This basic observation has been confirmed by other experiments involving the conjunction of colour and orientation (Hunton *et al.* 1995) and is further supported by recent

transcranial magnetic stimulation (TMS) experiments. TMS is a relatively new technique in which radio-frequency single pulses are applied through the skull via a magnetic stimulator to limited parts of the cortex. These magnetic pulses transiently disrupt neuronal activity in the stimulated brain region, and produce a transient functional deficit at different time points during the performance of a particular task. Ashbridge and co-workers (1997) stimulated posterior parietal cortex during various visual search tasks that involved either feature or conjunction targets. They showed that TMS stimulation of posterior parietal cortex significantly delayed search time for conjunction targets, whereas it did not influence search time for feature targets. The unique role of posterior parietal cortex during conjunction search, and its anatomical overlap with regions involved in shifting attention and eye movements to peripheral locations, is therefore consistent with models of search that predict the recruitment of a spatial attentional mechanism. It is important to note that this finding does not necessarily imply that subjects are serially shifting attention between all items in the display. For example, this finding is also consistent with hybrid parallel-serial models (Hoffman 1979; Wolfe *et al.* 1989), in which 'candidate targets' that pass an initial parallel screen are evaluated by a spatially selective, limited capacity mechanism.

Although the data indicate that the parietal component of the spatial attention network was selectively involved during the conjunction condition that yielded a serial search function, they do not indicate why this condition required spatial attention. Spatial attention may be required during any difficult search task that yields a serial search function (e.g. parietal activity might be present during a difficult feature search condition), and/or may be required to bind visual features at a certain spatial location. The greater PET activation in the conjunction task, for example, may reflect the 'binding' of colour and motion targets, which is not necessary when targets are defined by a single feature such as colour or motion alone. This view is consistent with a recent behavioural analysis of a patient with bilateral occipital–parietal lesion and Balint's syndrome (Friedman-Hill *et al.* 1995). This patient showed profound deficits in encoding and using locations for visual behaviour, as well as problems in binding the features of simple visual objects, e.g. he might report seeing a green X when presented with a red X and a green O. Posterior parietal cortex may contain a spatial map, topographically connected (directly or indirectly through other structures, such as the pulvinar) to various feature maps (colour, motion, shape), which provides a location signal that is used during visual orienting tasks, difficult search tasks, or conjunction tasks involving the integration of several features at one location.

5. CONCLUSIONS

This review highlights psychological, functional anatomical, and cellular levels of the analysis of spatial visual selection. There are three main conclusions which can be derived from this body of results. First, there appears to be a robust set of neural signals in parietal and frontal cortex that reflect spatial attentional processes across a variety of detection and discrimination tasks. These signals occur during tonic and dynamic allocation of attention to a location, and during tasks that explicitly (cueing) and implicitly (search) direct attention to a location. Second, psychological and physiological data indicate that attentional processes are closely linked to oculomotor processes. Third, these selective spatial neural signals bias visual processing at selected locations in ventral visual areas related to object analysis.

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