

# Attention Mechanisms in Visual Search—An fMRI Study

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## Abstract

■ The human visual system is usually confronted with many different objects at a time, with only some of them reaching consciousness. Reaction-time studies have revealed two different strategies by which objects are selected for further processing: an automatic, efficient search process, and a conscious, so-called inefficient search [Treisman, A. (1991). Search, similarity, and integration of features between and within dimensions. *Journal of Experimental Psychology: Human Perception and Performance*, 17, 652–676; Treisman, A., & Gelade, G. (1980). A feature integration theory of attention. *Cognitive Psychology*, 12, 97–136; Wolfe, J. M. (1996). Visual search. In H. Pashler (Ed.), *Attention*. London: University College London Press]. Two different theories have been proposed to account for these search processes. Parallel theories presume that both types of search are treated by a single mechanism that is modulated by attentional and computational demands. Serial theories, in contrast, propose that parallel processing may underlie efficient search, but inefficient searching requires an additional serial mechanism, an attentional “spotlight” (Treisman, A., 1991) that successively shifts attention to different locations in the visual field.

Using functional magnetic resonance imaging (fMRI), we show that the cerebral networks involved in efficient and inefficient search overlap almost completely. Only the superior frontal region, known to be involved in working memory [Courtney, S. M., Petit, L., Maisog, J. M., Ungerleider, L. G., & Haxby, J. V. (1998). An area specialized for spatial working memory in human frontal cortex. *Science*, 279, 1347–1351], and distinct from the frontal eye fields, that control spatial shifts of attention, was specifically involved in inefficient search. Activity modulations correlated with subjects’ behavior best in the extrastriate cortical areas, where the amount of activity depended on the number of distracting elements in the display. Such a correlation was not observed in the parietal and frontal regions, usually assumed as being involved in spatial attention processing. These results can be interpreted in two ways: the most likely is that visual search does not require serial processing, otherwise we must assume the existence of a serial searchlight that operates in the extrastriate cortex but differs from the visuospatial shifts of attention involving the parietal and frontal regions. ■

## INTRODUCTION

Everyday experience confronts our visual system with many different objects simultaneously. While some objects attract our attention instantaneously, we often need to scrutinize a scene to find a particular object. Reaction time studies have revealed two different processes by which an object can be found: an automatic “preattentive” process in which the object “pops out” of the scene, and higher-level, conscious searching (for review see Wolfe, 1996). If the search time is unaffected by the number of distracters in a scene (efficient search, “pop-out”), some kind of parallel processing of all items in the visual field is implied, one that requires very little or no attention. Higher-level conscious search performance, on the other hand, takes longer, depending on the number of distracters and the particular target searched for (inefficient search). The increase in search time with the number of search items remains surprisingly linear, even though processing times per item vary widely for different target/distracter combinations,

indicating different computational demands and correspondingly different processing efficiencies. Interpretations of the linear relationship between search time and number of items differ substantially. Such a relationship might be explained by a number of factors (e.g., Palmer, Verghese, & Pavel, 2000), but most search theories attribute it to attentional demands. Differing views of the way attention is deployed during search broadly divide search theories into serial and parallel models. In more traditional serial theories, efficient and inefficient search types rely on two different processing modes. *Parallel* processing is preattentive and sufficient only for efficient search tasks. Most visual search tasks, however, require additional *serial* processing based on spatial attention, by which an attentional “spotlight” (Treisman, 1991) is successively shifted to different locations in the visual field to process one item or group of items at a time. In serial theories, a linear increase in reaction times for inefficient search tasks reflects the increasing number of spatial attention shifts required to

find the target of interest as the number of distracters increases.

More recent parallel theories question the parallel–serial dichotomy, attributing efficient and inefficient searches to the same parallel mechanism. Theories such as the biased-competition model of Desimone and Duncan (1995) suppose that simultaneous analysis of the whole visual field becomes less efficient, and thus slows down, as a finite processing capacity is approached. Attention modulates the activity of the cortical neurons processing the image, and no specific areas are required for directing attention. Other parallel theories are based on low-threshold theories such as signal detection theory (e.g., Palmer et al., 2000), focussing on the internal–external noise ratio. Parallel models have in common that they do not require different processing modes such as automatic versus attentive or parallel versus serial processing. In these models, it is the increasing effort or global attention, rather than spatial attention, that produces the higher reaction times in inefficient search tasks. Evidence from psychophysical studies showing quantitative but not qualitative differences between efficient and inefficient search types are generally interpreted in favor of parallel theories (e.g., Eckstein, 1998; Joseph, Chun, & Nakayama, 1997; Wolfe, 1992; Bravo & Nakayama, 1992; Cheal & Lyon, 1992; Fahle, 1990; but see Townsend, 1990).

Here, we used functional magnetic resonance imaging (fMRI) to investigate the neural basis of efficient and inefficient visual search, focussing on three aspects of cerebral circuitry that might provide new evidence in favor of parallel or serial processing, respectively. First, we reasoned that if efficient and inefficient search were based on parallel processing, the same cortical network should be activated during either search task. If, in contrast, a searchlight of attention was based on its own spatial attention-specific cortical network, activity in this network should not be observed during efficient search but only during inefficient search. Second, activity in a spatial attention-specific network should increase with increasing numbers of attention shifts and thus with increasing search times. And third, we hypothesized that such a network specific for spatial shifts of attention might resemble the network invoked in overt/covert visuospatial shifts of attention studied with Posner-like paradigms (Corbetta et al., 1998). In particular, inefficient, but not efficient, search should engage the dorsal parietal cortex and frontal eye fields (FEFs), given their important role in the control of spatial shifts of attention. Indeed, imaging techniques and patient studies revealed that similar parietal regions are involved in inefficient conjunction search and covert/overt visuospatial shifts of attention (Corbetta, Shulman, Miezin, & Petersen, 1995; Arguin, Jeanette, & Cavanagh, 1993; Egly, Robertson, & Knight, 1991; Posner, Walker, Friedrich, & Rafal, 1984), but not in efficient search.

## RESULTS

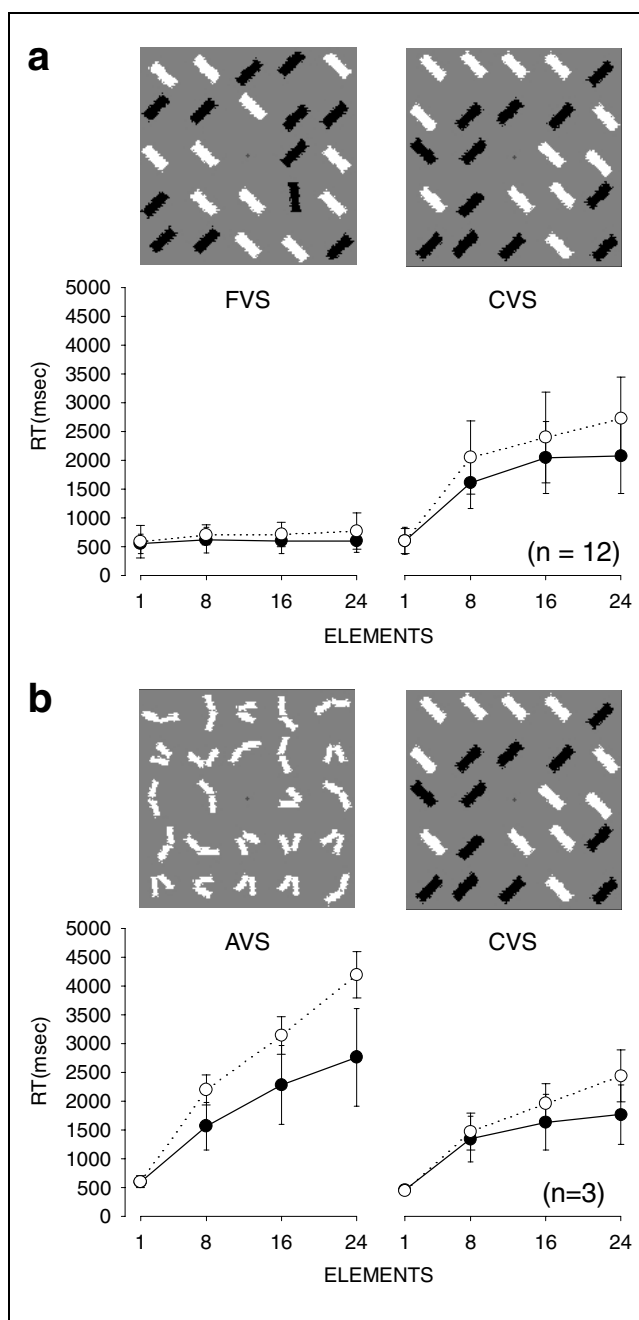
### Experiment 1

While maintaining fixation, subjects searched for targets that differed from surrounding distracters either by orientation or luminance (feature visual search, FVS), or by a conjunction of orientation and contrast polarity (conjunction visual search, CVS).

#### *Psychophysical Training Prior to Functional Imaging*

To ensure visual search performance under steady fixation, subjects underwent two 1-hr training sessions before being scanned (see Methods section). Figure 1 shows the mean increase in reaction time with the number of items obtained during the last training session. Subjects performed the different search tasks without eye movements. Feature search (Figure 1a left panel) invoked a search pattern in which reaction times did not increase with the number of distracters, corresponding to an efficient search pattern. During conjunction search (Figure 1a right panel), reaction times increased with the numbers of distracters and were longer for target-absent (open symbols) than for target-present (filled symbols) conditions, corresponding to an inefficient search pattern. Mean error rates (in %) were  $2.7 \pm 2.9$  SD and  $6.4 \pm 3.2$  SD for feature and conjunction search, respectively, revealing only a slight difference in difficulty for the two tasks.

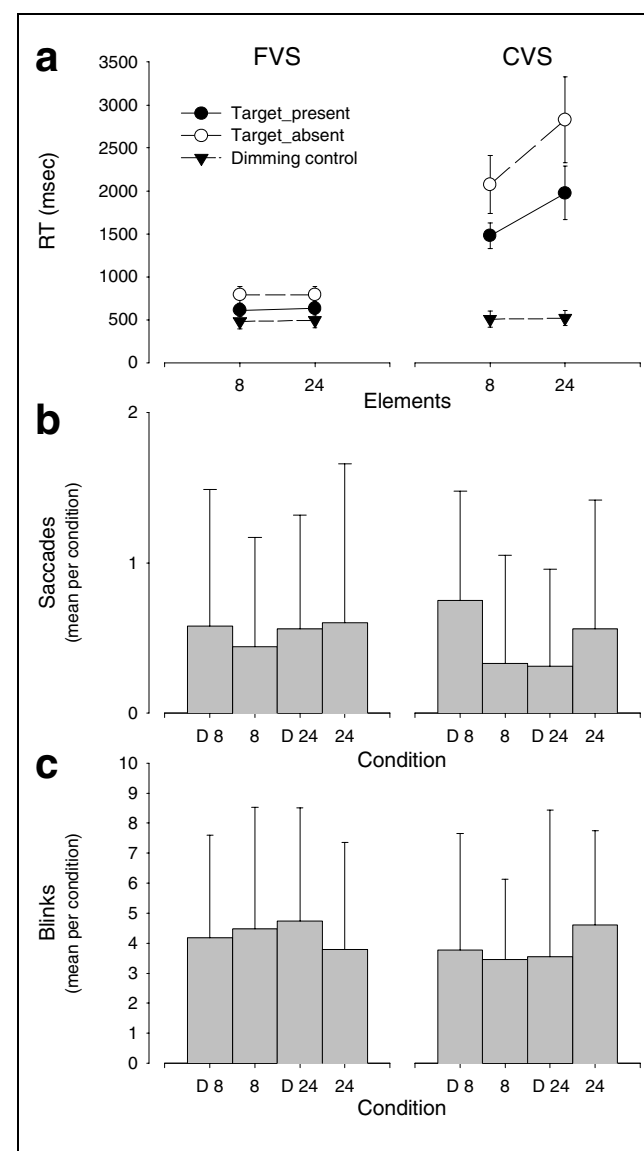
Even though data in Figure 1 mirror classical results for an efficient and an inefficient search, our stimulus design might have induced undesired side effects (see Methods section for details concerning stimulus choice). First, two distracter types of orthogonal orientation were used in feature search. Second, since the target was not consistently mapped in conjunction search and could serve as distracter in the next trial, subjects had to identify the target by comparing the target with surrounding elements (“rule finding”). And third, the introduction of fixation cross dimming might have contaminated visual search tasks with additional focal attention. To estimate influences of these three factors on search performance, we analyzed the behavioral data in more detail. First, separate analysis of each stimulus series within the two training sessions revealed that in all subjects, reaction times decreased with training in both search types, but that the reaction time pattern of Figure 1 was present from the first stimulus series. Thus feature search was efficient from the beginning, excluding the possibility that the feature search may have become parallel with training due to consistently mapped targets (Sigman & Gilbert, 2000; Shiffrin & Schneider, 1977) or global learning effects (Sireteanu & Rettenbach, 1995). Second, independent analysis of white and black target trials during conjunction search revealed that 7 of the 12 subjects developed a strategy of searching through light and dark elements sequentially.



**Figure 1.** Search slopes for different visual search tasks. Stimulus display examples and subjects' mean reaction times for the last training session plotted as a function of the number of items in the display. (a) Experiment 1: FVS (left panel) and CVS (right panel) and (b) experiment 2: AVS (left panel) and CVS (right panel). ● = target-present trials, ○ = target-absent trials,  $n$  = number of subjects. Error bars indicate *SEM*. Statistical comparison of search slopes for all three search tasks revealed significant differences (Wilcoxon  $\alpha < 0.01$ ; AVS > CVS; CVS > FVS).

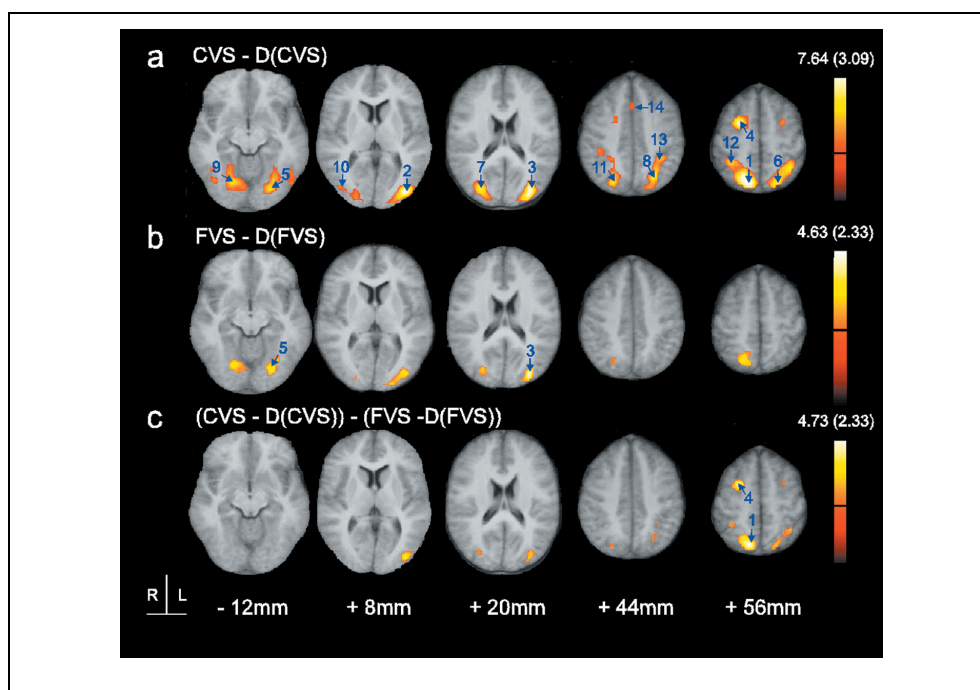
Such feature switching might activate an additional search process, not directly related to spatial attention shifts, during conjunction search. Since the general pattern of a classical inefficient search was preserved, with reaction times proportional to the number of elements and longer reaction times for target-absent

trials, we feel that the additional “rule finding” process did not change subjects' basic search behavior. Third, search trials with and without dimming were analyzed subject by subject to assess any interference due to the dimming of the fixation cross. Analysis revealed neither differences in mean reaction time and standard deviation nor in the distribution of the shortest reaction times. Furthermore, error rates for feature and conjunction search remained unaffected by dimming. It is therefore unlikely that dimming had captured attention (e.g., Yantis & Egeth, 1999), contaminating the search process with extraneous focal attention.

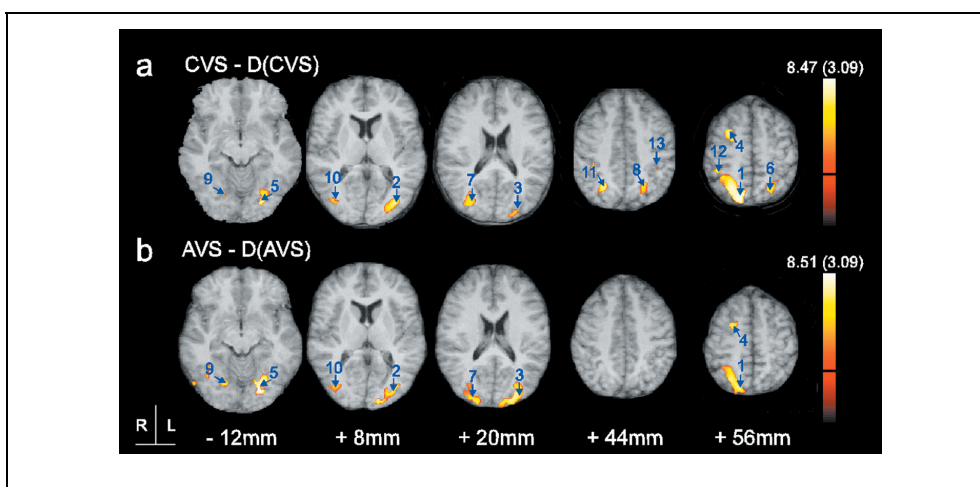


**Figure 2.** Search behavior during scanning. Subjects' mean reaction times (a) for feature (FVS, left panel) and conjunction (CVS, right panel) search; ● = target-present search, ○ = target-absent search, and ▼ = dimming control. Subjects' mean saccadic rate (b) and blink rate (c) per time series per condition for feature search (left panel) and conjunction search (right panel). The numbers 8 and 24 indicate the number of elements searched through, D8 and D24 are the corresponding control conditions. Error bars indicate *SEM*.

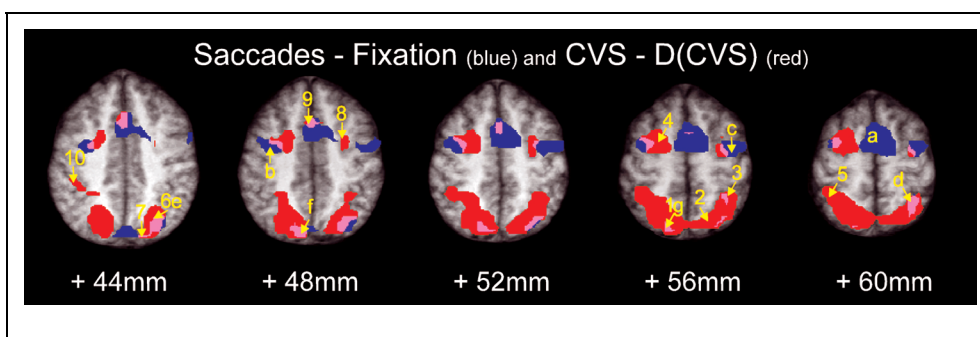
**Figure 3.** Cortical activation during performance of feature and conjunction search. Group ( $n = 12$ ) statistical parametric maps (SPMs) indicating brain areas more active during search than during corresponding control (D-) conditions: search for (a) conjunctions (CVS); (b) features (FVS), and regions more active during conjunction search compared to feature search (c). SPMs are superimposed on transverse sections through the average structural MRI at levels indicated. Displayed regions exceed a threshold of  $Z > 3.09$  ( $Z > 2.33$  for b and c, see color bars). In all three subtractions, regions with a  $Z > 4.6$  were taken as significant, and were numbered according to their Z scores for conjunction search. (1) R DIPSM / DIPSL; (2) L LOS; (3) L TRIPS; (4) R SFS; (5) L COLS; (6) L DIPSL / DIPSM; (7) RTRIPS; (8) L MIPS; (9) R COLS; (10) R LOS; (11) R MIPS / VIPS; (12) R DIPSA; (13) L DIPSA; (14) anterior cingulate. R/L = right and left hemisphere. Talairach coordinates of activated regions are listed in Table 1.



**Figure 4.** Cortical activation during performance of conjunction and angle search. Group ( $n = 3$ ) statistical parametric maps (SPMs) indicating brain areas more active during search than during corresponding control (D-) conditions: search for (a) conjunctions (CVS) and (b) angles (AVS). Same conventions and numbering as in Figure 3a. Inefficient conjunction and inefficient angle search had most of their activation sites in common.



**Figure 5.** Cortical activation for oculomotor compared to search performance. Comparison of group SPMs ( $n = 6$ ) contrasting activations during saccades versus fixation (blue) and conjunction search versus dimming (red). Pink regions show regions of overlap. Visualization conventions are the same as in Figure 3. Numbers indicate significant activation sites for conjunction search: (1) R DIPSM; (2) L DIPSM; (3) L DIPSL; (4) R SFS; (5) R DIPSA; (6) L MIPS; (7) L POIPS; (8) L SFS; (9) anterior cingulate; (10) R DIPSA. Letters indicate saccadic activation sites (with Talairach x/y/z coordinates): (a) SEF (-4/-4/64); (b) R FEF (36/-4/48); (c) L FEF (-32/-8/56); (d) L DIPSL (-32/-52/68); (e) L MIPS (-28/-72/44); (f) R precuneus (8/-80/48); (g) R DIPSM (20/-72/56).



# Functional Magnetic Resonance Imaging

In the scanner, subjects were tested with eight conditions: two versions of feature search (FVS), with 8- and 24-element displays designated FVS8 and FVS24, respectively, and their corresponding dimming conditions [D(FVS8), D(FVS24)], and two versions of conjunction search (CVS), again with 8- and 24-element displays, termed CVS8 and CVS24, and their corresponding dimming conditions [D(CVS8), D(CVS24)].

Subjects' search performance during scanning was comparable to that during training. Reaction times of the feature search (FVS) did not increase with the number of elements presented (Figure 2a left column), but reaction times of the conjunction search (CVS) did (Figure 2a right column) (compare with Figure 1a).

To estimate differences in oculomotor activity that might interfere with search performance, saccades and

eye blinks were tallied for the different search and dimming control conditions, for 8 and 24 elements. Neither the occurrence of rare accidental saccades (Figure 2b) nor the number of blinks (Figure 2c) differed between search and dimming control conditions. We can therefore assume that no observed cortical activation was the result of differences in oculomotor behavior.

In the initial analysis, we concentrated on the effect of task, irrespective of display size, comparing feature search with its dimming [FVS – D(FVS)] and conjunction search with its dimming [CVS – D(CVS)]. A number of areas located in the parietal lobe, a region generally thought to be involved in spatial processing, were consistently activated in all participants during conjunction search compared to its control condition [Figure 3a, Table 1 CVS – D(CVS)]. Regions along the intraparietal sulcus (IPS) were activated bilaterally,

**Table 1.** The Z Scores and Mean Signal Changes (in %) for Regions Activated During Efficient (FVS) and Inefficient (CVS) Visual Search

	Region		<i>x/y/z</i> coordinates	CVS		FVS	
				<i>Z</i>	<i>Mean ± SD</i>	<i>Z</i>	<i>Mean ± SD</i>
<i>Occipital</i>	COLS	L	–28/–72/–20	<b>6.91</b>	0.36 ± 0.20	<b>4.49</b>	0.21 ± 0.13
		R	20/–68/–12	<b>5.65</b>	0.35 ± 0.25	3.73	0.20 ± 0.18
	LOS	L	–36/–84/8	<b>7.57</b>	0.47 ± 0.21	3.88	0.19 ± 0.19
		R	44/–76/4	<b>5.52</b>	0.38 ± 0.28	2.76	0.18 ± 0.21
	TRIPS	L	–28/–84/20	<b>7.45</b>	0.49 ± 0.25	<b>4.63</b>	0.25 ± 0.14
		R	28/–76/20	<b>6.43</b>	0.41 ± 0.27	3.21	0.19 ± 0.14
<i>Parietal</i>	MIPS	R	24/–64/40	<b>5.47</b>	0.35 ± 0.25	2.93	0.18 ± 0.16
	VIPS	R	28/–76/32	<b>5.40</b>	0.43 ± 0.29	–	–
		L	–24/–68/44	<b>6.00</b>	0.38 ± 0.22	2.68	0.18 ± 0.12
	DIPSM	R	16/–72/56	<b>7.64</b>	0.74 ± 0.31	3.97	0.23 ± 0.19
	DIPSL	R	24/–60/52	<b>7.47</b>	0.49 ± 0.23	3.65	0.19 ± 0.16
		L	–20/–72/56	<b>6.45</b>	0.50 ± 0.33	2.65	0.18 ± 0.13
		L	–32/–56/60	<b>6.60</b>	0.44 ± 0.37	–	–
	DIPSA	R	36/–44/56	<b>5.38</b>	0.25 ± 0.23	–	–
		L	–32/–44/44	<b>5.32</b>	0.26 ± 0.19	–	–
<i>Frontal</i>	SFS	R	28/4/56	<b>7.23</b>	0.23 ± 0.13	–	–
	Anterior cingulate		0/16/48	<b>4.64</b>	0.16 ± 0.13	–	–

Feature search (FVS) compared to its control D(FVS), and conjunction search (CVS) compared to its control D(CVS). Numbers in bold indicate regions significant at a  $p \leq .05$  corrected level ( $Z > 4.6$  for CVS,  $Z > 4.4$  for FVS), the remaining numbers indicate significance at a  $p \leq .01$  uncorrected level.

with the strongest changes in the right medial and lateral dorsal parts of the IPS, corresponding to DIPSM and DIPSL (Sunaert, Van Hecke, Marchal, & Orban, 1999). These activation sites are in agreement with earlier findings (Corbetta et al., 1995). Additional activations in the IPS were observed at the junction with the postcentral sulcus (DIPSA, Sunaert et al., 1999), and with the transverse occipital sulcus (TRIPS, Orban, Sunaert, Todd, Van Hecke, & Marchal, 1999) as already described for other attention tasks (Wojciulik & Kanwisher, 1999). We further observed a right-hemispheric activation slightly dorsal to TRIPS in the occipital extension of the IPS that had been previously labeled VIPS (Sunaert et al., 1999), and a bilateral activation in the medial ventral part of the IPS referred to as the medial intraparietal sulcus region (MIPS). Significant activation in the occipital lobe was found in the lateral occipital sulcus (LOS), and along the posterior part of the collateral sulcus (COLS). In the frontal lobe, we observed a bilateral activation site in the superior frontal sulcus (SFS) anterior to the junction with the precentral sulcus, again predominantly in the right hemisphere, as well as an anterior cingulate activation.

**Table 2.** Activation Differences Between Inefficient Conjunction Search (CVS) and Efficient Feature Search (FVS)

	<i>Region</i>		<i>x/y/z coordinates</i>	<i>CVS-FVS, Z</i>
<i>Occipital</i>	LOS	L	−36/−84/8	4.17
	TRIPS	L	−32/−80/20	3.39
		R	32/−76/20	2.89
<i>Parietal</i>	VIPS	R	28/−76/32	2.73
	MIPS	L	−24/−68/44	2.91
	DIPSM	R	16/−72/56	4.79
	DIPSL	R	24/−60/52	4.08
		L	−16/−76/52	3.30
		L	−32/−56/60	3.51
	DIPSA	R	36/−48/56	2.89
		L	−28/−44/44	2.73
<i>Frontal</i>	SFS	R	28/4/56	4.63
		L	−28/4/56	2.70

The Z scores for regions more activated (at  $p \leq .01$  uncorrected,  $Z > 2.33$ ) during conjunction search (CVS) than during feature search (FVS). Search types were compared only after subtracting their corresponding dimming conditions. No region was more activated during feature search (FVS) than during conjunction search (CVS).

We obtained similar activation sites for efficient feature search compared to its corresponding control condition, including the right DIPSM/DIPSL sites [Figure 3b, Table 1, FVS − D(FVS)]. These were not observed in an earlier study (Corbetta et al., 1995), in which only four-element displays were used. Efficient and inefficient searches in fact shared large parts of the same cortical network. Most regions in which activity was significantly stronger for inefficient search (contrast ((CVS − D(CVS)) − (FVS − D(FVS))), Figure 3c, Table 2) were also active in efficient search (Figure 3b), at least for a significance level of  $p = .01$  uncorrected for multiple comparison. This indicates that a similar network was active in the two types of search, and that activity within the network increased with search inefficiency. It should be noted that activation patterns for the search types were compared only after subtracting their corresponding dimming conditions. These subtractions should have removed any confound resulting from differences in exposure duration between the two types of search (see Methods section). Moreover, contrasting activation patterns during dimming for conjunction search [D(CVS)] with those for feature search [D(FVS)] revealed no significant differences, even though the exposure time for the former was also about four times longer.

Exceptions to the common activation pattern for feature and conjunction search included the IPS regions DIPSA, L DIPSL, R VIPS, as well as the SFS and to a lesser degree, anterior cingulate. In all these regions significant activity could be detected only during conjunction search. No region displayed stronger or even specific activity for feature search compared to conjunction search.

## Experiment 2

Feature and conjunction searches largely activated overlapping cortical regions. Even with lowered activation thresholds some regions showed no activation during feature search, and thus seem to be uniquely activated during inefficient conjunction search. To test whether these observations hold for inefficient search in general, we retested three subjects with conjunction search and a second inefficient search task, in which the target had an included angle of  $90^\circ$  among distracters with angles of  $140^\circ$  and  $40^\circ$  (angle visual search (AVS), Figure 1b). As can be seen in Figure 1b for the last training session, angle search (left panel) invoked an even more inefficient search pattern than conjunction search (compare to the data for conjunction search in Figure 1b right panel, obtained in the same subjects). Angle search can thus be assumed to require even more attentional resources than conjunction search.

As pointed out earlier, the conjunction search used here differs from other types of inefficient search in the

need to compare the target with surrounding elements (“rule finding”). Activity in cortical regions during conjunction but not feature search could thus be due to the specificity of our conjunction search paradigm but not to inefficient search in general. On the other hand, grouping of similar elements during conjunction search could have reduced the number of attention shifts, and consequently, the amount of serial processing required. The number of covert attention shifts might thus have been insufficient to evoke significant activation in areas specifically controlling attention. Such areas might be detectable with angle search.

As in experiment 1, we tested eight conditions: two versions of angle search (AVS), with 8- and 24-element displays respectively (AVS8, AVS24), and their corresponding dimming conditions [D(AVS8), D(AVS24)], and the two versions of conjunction search (CVS), with 8- and 24-element displays (CVS8, CVS24), and their corresponding dimming conditions [D(CVS8), D(CVS24)]. Again, data were analyzed according to the search type irrespective of display size: angle search minus its dimming [AVS – D(AVS)] and conjunction search minus its dimming [CVS – D(CVS)].

Comparison of Figure 4a and Figure 3 shows that the cortical regions of the three subjects involved in conjunction search nicely matched those of the 12 subjects in the first experiment. Only activation in the anterior cingulate could not be observed in the group analysis,

but was confirmed in two of the three subjects by individual analysis (see Table 3).

Most activation sites for angle search (Figure 4b) resembled those associated with conjunction search (Figure 4a) with significant activations in the right DIPSM/L and SFS, bilateral TRIPS, LOS, and COLS. Activation in areas MIPS and the left DIPSL/DIPSM were significant only at a  $p \leq .01$  uncorrected for multiple comparison. Moreover, angle search activated neither DIPSA nor anterior cingulate as confirmed by individual analysis (Table 3). The general activation pattern of angle search with its low activation of MIPS and left DIPSL/M and lack of activation in DIPSA and anterior cingulate thus resembled that of efficient feature search more than conjunction search. All three subjects, however, showed strong activation of the SFS during the angle search, but not in the feature search. Direct statistical comparison between the two inefficient search tasks for group as well as individual data revealed no additional activation site specific for angle search.

We therefore assume that inefficient search-specific areas were not missed due to insufficient numbers of attention shifts during conjunction search. In contrast, conjunction search led to stronger activation than angle or feature search in several regions (MIPS, DIPSL/DIPSM), and even seemed to uniquely activate regions such as DIPSA and anterior cingulate. These

**Table 3.** The Z Scores for Regions Activated During Inefficient Conjunction (CVS) and Inefficient Angle (AVS) Visual Search

				CVS, Z			AVS, Z		
	Region		<i>x/y/z</i> <i>coordinates</i>	<i>S1</i>	<i>S2</i>	<i>S3</i>	<i>S1</i>	<i>S2</i>	<i>S3</i>
Frontal	SFS	R	28/4/56	<b>6.24</b>	<b>6.90</b>	<b>5.75</b>	<b>5.96</b>	<b>7.37</b>	<b>5.41</b>
	Anterior cingulate	–		<b>5.27</b> (4/8/46)	<b>5.58</b> (2/18/44)	3.51 (4/14/50)	–	–	–
Parietal	MIPS	R	22/–64/40	<b>6.92</b>	<b>7.57</b>	<b>6.05</b>	–	<b>5.04</b>	3.51
	VIPS	R	34/–76/26	<b>5.60</b>	<b>7.66</b>	<b>6.98</b>	4.17	<b>7.3</b>	<b>5.25</b>
		L	–22/–58/44	<b>5.53</b>	<b>8.47</b>	<b>7.29</b>	4.15	<b>6.09</b>	3.09
	DIPSM	R	14/–76/54	4.51	<b>8.44</b>	<b>7.38</b>	3.38	<b>7.67</b>	2.63
	DIPSL	R	28/–68/62	<b>7.54</b>	<b>8.29</b>	<b>8.44</b>	<b>7.37</b>	<b>6.36</b>	<b>6.72</b>
		L	–18/–66/58	<b>6.62</b>	<b>7.90</b>	<b>7.36</b>	4.87	4.76	<b>6.79</b>
		L	–26/–62/56	<b>6.58</b>	3.97	<b>7.15</b>	3.95	–	3.93
	DIPSA	R	42/–44/58	<b>7.39</b>	<b>7.25</b>	<b>7.03</b>	3.08	–	–
		L	–40/–38/54	<b>6.94</b>	<b>7.68</b>	–	–	–	–

Data of individual subjects S1, S2, and S3. Conjunction search (CVS) compared to its control D(CVS), and angle search (AVS) compared to its control D(AVS). Numbers in bold indicate regions significant at a  $p \leq .05$  ( $Z > 5.0$ ) corrected level, the remaining numbers indicate significance at a  $p \leq .01$  uncorrected level.

differences between the two inefficient search types might reflect behavioral processes, such as search strategy or target selection that were specific for our conjunction search design but that were not general for inefficient search. In particular, the anterior cingulate activation in conjunction search probably reflects the need to reject inappropriate responses, akin to its activation in a variety of Stroop tests (Peterson et al., 1999; Bush et al., 1998). Those regions common to conjunction and angle search, however, were also involved in efficient search (with exception of the SFS), generalizing our findings of a common visual search network in experiment 1.

### Experiment 3

A notable exception to the common activation pattern for efficient and inefficient search was the activation site in the SFS, which was strongly active during the two inefficient searches but not during efficient feature search. According to serial theories, inefficient search differs from efficient search by serial shifts of attention (Treisman, 1991). Other components specific for inefficient search include a memory component for holding on-line information about the searched target (Desimone & Duncan, 1995; Treisman, 1991), or a decision component for terminating the search if no target is found (Chun & Wolfe, 1996). We therefore reasoned that the SFS activation during inefficient search might reflect these memory or decision components, or might be related to spatial shifts of attention. Recently, it has been shown that regions involved in explicit covert spatial shifts of attention (Posner-like paradigms), anatomically overlap those involved in overt shifts of attention (saccades) (Gitelman et al., 1999; Corbetta et al., 1998). In fact, the FEFs were shown to be even more active during covert attention shifts than during saccades (Corbetta et al., 1998). Moreover, activation in the FEFs was shown to be independent of whether covert shifts of attention were performed automatically or voluntarily (Rosen et al., 1999). Single-cell studies have also implicated the FEFs in control of covert attention shifts (Thompson, Bichot, & Schall, 1997). To test whether the SFS activation observed only during inefficient search overlapped with the FEFs and was thus caused by covert shifts of attention, we compared, within a single session (experiment 3), activation sites related to inefficient conjunction search [CVS – D(CVS), see experiment 1] with those evoked by self-induced saccades, comparing activity during horizontal and vertical saccades with that during fixation (saccades–fixation, see Methods section).

In line with other studies (Petit, Clark, Ingeholm, & Haxby, 1997; Paus, 1996), saccadic eye movements were associated with activation in the precentral sulcus at the junction with the SFS, corresponding to the FEFs

(Figure 5). A group analysis showed that this site (b and c in Figure 5) overlapped only slightly with the main SFS activation obtained during conjunction search (4 and 8 in Figure 5). Individual analysis of the six subjects (6 mm effective smoothing) revealed significant distances between FEF and SFS activation sites (mean distances:  $15.2 \text{ mm} \pm 4.2 \text{ SD}$  and  $16.7 \text{ mm} \pm 3.2 \text{ SD}$  for right and left hemisphere, respectively). Thus, the SFS activation during conjunction search was clearly distinct from the FEFs, active during self-induced, overt shifts of attention. The same distinction was observed for the SFS activation during angle search and the FEFs. It is therefore unlikely that the SFS activity during inefficient search reflects covert shifts of attention, at least not covert shifts in the classical sense as evoked by Posner-like paradigms.

### Additional Analysis of Experiments 1 and 2

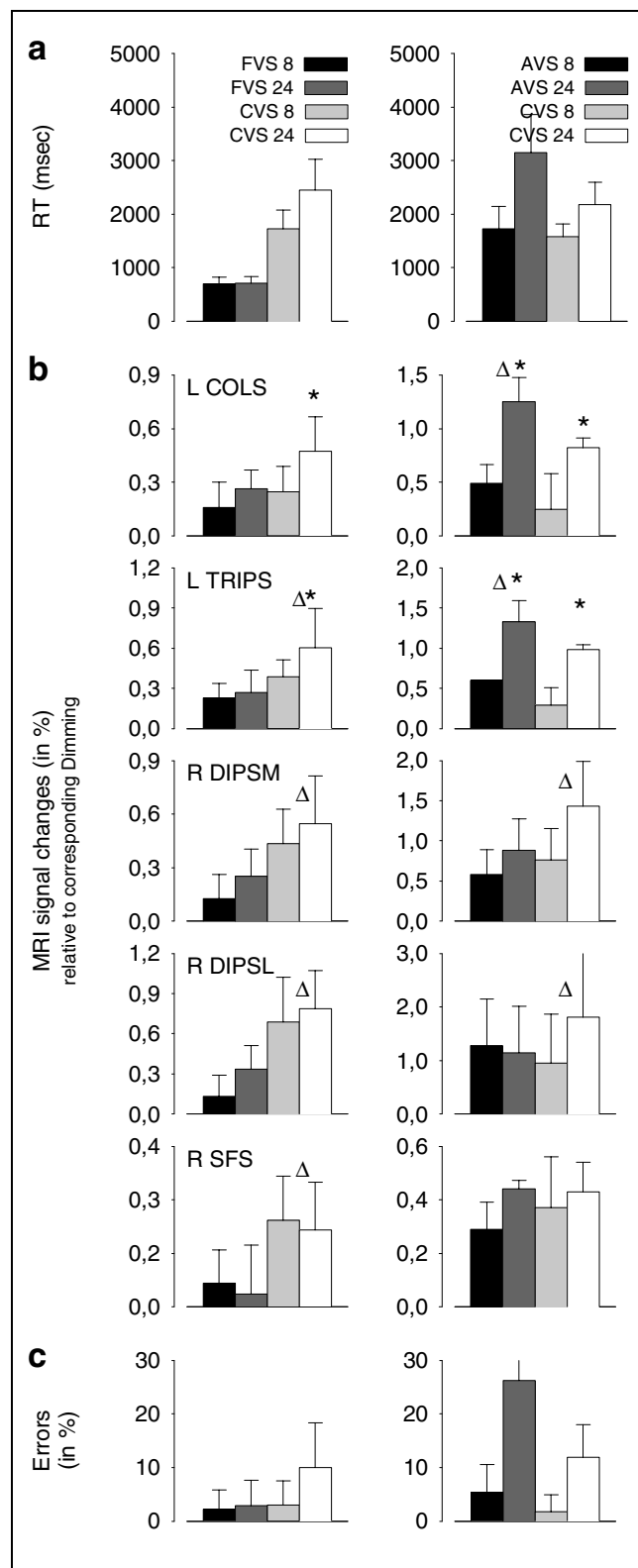
In inefficient search, it is often implied that a serial mechanism specifically involves cortical regions controlling attention, as revealed by imaging studies using visual tasks that explicitly demand spatial shifts of attention and by lesion studies (e.g., Posner, 1995; Mesulam, 1990). In addition to the FEFs, the parietal cortex also plays an important role in the control of attention and is a likely host for a serial mechanism (Nobre et al., 1997; Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta et al., 1998). Earlier studies (Corbetta et al., 1995; Arguin et al., 1993; Egly et al., 1991) have implicated the parietal cortex involvement in conjunction but not in feature search. In our study, however, the dorsal parietal cortex was involved in both efficient and inefficient search, even to the extent of having the same activation maxima (DIPSL, DIPSM). If, as proposed by Wolfe (1996), parallel and serial mechanisms contribute to both efficient and inefficient search, or if feature search had been contaminated by focal attention in our stimulus design, we might have observed attention-shift related parietal activity during both inefficient and efficient search. Specifically, attention shifts towards a “pop-out” target and back to the fixation point or, less likely (see experiment 1), dimming-induced attention shifts, might have been sufficient to activate the parietal cortex during efficient feature search. If the parietal activity observed during efficient search reflected such a relatively low number of spatial attention shifts, we reasoned that activity levels in the parietal cortex should then closely mirror the number of attention shifts, unless these few shifts had already saturated the parietal cortex. The latter possibility can be dismissed, however, since the parietal activity increased significantly between efficient and inefficient search (see Figure 3). Similar rate–activity relationships have been documented with stimulus and motor response rates (Vafaer et al., 1999; Orban, Dupont, Vogels, Bormans, & Mortelmans, 1997; Rao et al., 1996; Fox & Raichle, 1984). Depending on the precise



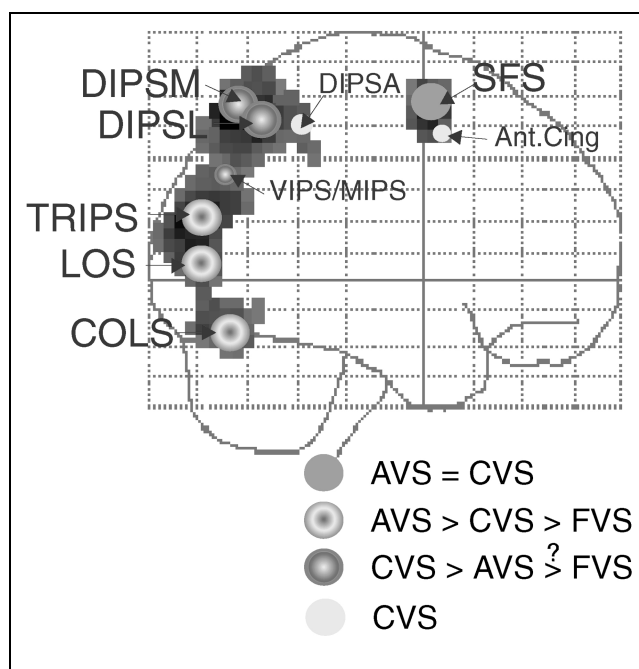
interpretation of the serial mechanism, the number of shifts is either (i) proportional to the number of elements in the display (assuming fixed processing time) or (ii) to reaction times (allowing for revisiting and unequal processing time). Since reaction times

differed consistently for all three search tasks (feature search: 2.87 msec/item; conjunction search: 60 msec/item, angle search: 123 msec/item), we tested both hypotheses by contrasting reaction time (Figure 6a) and fMRI-signal intensities in the visual search network (Figure 6b) for the three tasks and the two array sizes tested.

Both dorsal parietal regions, DIPSM and DIPSL (Figure 6b), showed significantly higher activity levels for conjunction and angle search than for feature search, but neither the number of items in the display nor reaction time was significantly correlated with the activity level associated with the two inefficient search tasks. On the contrary, activity in the dorsal parietal area DIPSL was significantly higher during the performance of conjunction search than during angle search despite the fact that angle search produced significantly longer reaction times. Thus, even though DIPSM and DIPSL anatomically overlapped with regions activated during saccades (Figure 5) and were active during all three searches, activity in these regions seemed to be unrelated to the (assumed) numbers of spatial shifts of attention. In fact, the parietal activity in general seemed unrelated to reaction times and thus to the main correlate for subjects' search behavior. SFS activity displayed equally little correlation with reaction times or number of elements in the display. Distinctly behavior-related activity was observed exclusively in occipital regions such as COLS, right LOS, and TRIPS. In these regions, activity levels increased significantly with the number of elements in the display for both angle and conjunction search (as indicated by asterisks in Figure 6b) but not for feature search. Moreover, activity levels depended on reaction times, leading to significant activation differences between angle and conjunction search and conjunction and feature search (as indicated by triangles in Figure 6b). A close look to activity profiles in Figure 6b might give the impression that activity in the dorsal parietal regions DIPSL and DIPSM also tends to increase with the number of elements in the display. Further lowering of the activation threshold ( $p \leq .01$ ,  $Z > 2.33$ ) for the data of experiment 1 did not support this observation, how-



**Figure 6.** Search behavior and cortical activity modulations. (a) Mean reaction times during scanning for feature (FVS) compared to conjunction search (CVS) ( $n = 12$ , left panels), and angle (AVS) compared to conjunction search ( $n = 3$ , right panels). Error bars indicate standard errors. Note that reaction times for trials with and without target were averaged to compare more easily with functional data. (b) Corresponding mean MR signal changes (compared to D) plotted as a function of search type and number of items, in areas L COLS, L TRIPS, R DIPSM, R DIPSL and R SFS. Significant differences ( $p \leq .001$  uncorrected) between array sizes of a given search type or between search types are indicated by stars and triangles, respectively. (c) Error rates as a function of search type and number of elements. Activation profiles in the parietal and frontal regions (b) did not correlate with error rates, indicating that activation differences were not due to differences in difficulty.



**Figure 7.** Summary scheme of activation sites during visual search. Regions are grouped depending on their relative activity in the three types of search: feature search (FVS), conjunction search (CVS), and angle search (AVS). Most regions were active during all three search types; ">" significantly larger activation, "=" nonsignificant differences, "?" changes undetermined. A few regions were active in only one or two types of search.

ever. Thus, the extrastriate regions COLS, R LOS, and TRIPS were the only regions where activity followed search inefficiency.

## DISCUSSION

In this fMRI study, we investigated the cortical networks involved in different types of visual search, concentrating on predictions derived from parallel and serial models. Scanning the whole brain revealed that both efficient and inefficient types of visual searches activate a single complex cortical network, albeit to different degrees, favoring the concept of a single parallel processing mode (see question 1 in the Introduction section). This common network includes regions along the IPS and several extrastriate regions. Figure 7 summarizes cortical activity during visual search and its modulations according to the type of search performed. Activity in the extrastriate but not in the parietal or frontal regions correlated with subjects' search behavior, thus failing to substantiate a widespread claim for serial processing (question 2 in the Introduction section). Moreover, a frontal activation site in the SFS was specific for inefficient search, and was distinct from a frontal region (FEFs) usually thought to control visuospatial attention shifts, again arguing against serial processing in visual search (question 3 in the Introduction section).

## Serial Processing in Inefficient Search?

At first glance there seems to be little or no support for serial theories in our results. However, as pointed out by Wolfe (1996), activity in the parietal and frontal areas correlated with the number of attention shifts might be too subtle to distinguish from noise. This seems unlikely, since we observed clear correlation between number of items in inefficient search displays (asterisks in Figure 6b) or reaction times (triangles in right column of Figure 6b, see summary Figure 7) and activity changes in occipital regions COLS, R LOS, and TRIPS. An increase in extrastriate activity with search inefficiency fits well with single-cell studies in inferior temporal cortex (Chelazzi, Miller, Duncan, & Desimone, 1993) and studies demonstrating strong attention effects in the ventral extrastriate areas in both humans and monkeys (Brefczynski & DeYoe, 1999; DeWeerd, Peralta, Desimone, & Ungerleider, 1999; Kastner, DeWeerd, Desimone, & Ungerleider, 1998; Tootell et al., 1998; Vandenberghe et al., 1997, 2000; Heinze et al., 1994). In such studies, attention effects followed the topographic organization, and can be interpreted as implicating a parallel mechanism. Furthermore, similar regions in the monkey are known to be selective for orientation (Maunsell, Sclar, Nealey, & DePriest, 1991; Desimone & Schein, 1987) and for angles (Pasupathy & Connor, 1999). Finally, lesions in the human ventral regions, including COLS, have been reported to disrupt search (Humphreys, Riddoch, & Quinlan, 1985). Activity proportional to reaction times as observed here in the extrastriate regions could thus be easily interpreted as reflecting a parallel mechanism, wherein reaction times during visual search reflect not shifts of attention, but more global attentional/computational demands. Activity increases in the extrastriate regions such as COLS and R LOS might then be the physiological counterpart in humans of the slow competitive interactions postulated for parallel analysis in inefficient search on the basis of animal studies (Desimone & Duncan, 1995; Duncan, Ward, & Shapiro, 1994).

Nevertheless, the same increase in the extrastriate activity could also be interpreted as favoring serial processing, reflecting a high-speed, oculomotor-independent, redirection of attention (Efron, Yund, & Nichols, 1987; Bergen & Julesz, 1983; Treisman & Gelade, 1980). Evidence for such fast spatial shifts of attention operating in the extrastriate cortex during visual search has been presented in a recent study (Woodman & Luck, 1999), using the N2pc component of the event-related potential waveform as a marker for attention shifts between visual hemifields.

## The Role of the Parietal Cortex in Visual Search

The parietal cortex has been implicated in four major processes that play a role in visual search and object

selection: spatial and nonspatial attention (e.g. Wojciulik & Kanwisher, 1999; Culham et al., 1998; Husain, Shapiro, Martin, & Kennard, 1997; Corbetta et al., 1993; Pardo, Fox, & Raichle, 1991), visual working memory (e.g., Jonides et al., 1993), decision making (e.g., as in cognitive set shifting, Konishi et al., 1998), and feature binding (Friedman-Hill, Robertson, & Treisman, 1995). Activity in our main dorsal parietal site, DIPSM / DIPSL, did not correlate with reaction time and thus with increasing attentional demand, suggesting that parietal activity did not primarily reflect spatial shifts of attention during search. It could be argued that our results are consistent with a more restricted hypothesis that conjunction search is the only one of our three search types that requires spatial shifts of attention. However, the inefficiency of conjunction search can be explained in terms of noise levels as easily as any other type of inefficient search, and thus need not require more serial processing (Eckstein, 1998; see also McElree & Carrasco, 1999).

It is unlikely that the process reflected by the parietal activity is working memory used to keep track of visual field positions visited (Horowitz & Wolfe, 1998), since it should evoke activity modulations similar to those predicted for spatial shifts of attention.

A more attractive alternative is the decision to select a target, a process that differs between search types. Conjunction search required the selection of one of four possible targets, while only one possible target was available for angle search, and two for feature search. Moreover, during feature and angle search, targets were consistently mapped and thus never used as distracters, while this was the case for conjunction search. Decision-making might involve several steps. TRIPS, in which activity reflected behavior, corresponds well to an area activated by various visual attention tasks as long as task-irrelevant distracters are used (Wojciulik & Kanwisher, 1999). This activation required no spatial shifts of attention, eye movement preparation, execution, nor suppression of eye movements to be activated. TRIPS, as an early dorsal stream component, might thus be important in assigning spatial (and nonspatial) tags to multiple potential targets (Pylyshyn, 1989). In a second step, region MIPS could then be activated to ascertain "the rule" of likely target candidates, since its activity levels varied with the number of possible targets ( $CVS > AVS \geq FVS$ ). Finally, DIPSM/DIPSL might be involved in the decision itself, selecting the target through communication with frontal area SFS keeping the targets on-line. The fourth process, the binding of specific features to certain locations, might, in addition to the "rule-finding," explain the DIPSA activation, which was specific to conjunction search. Friedman-Hill et al. (1995) described a patient with an anterior intraparietal sulcus lesion who was specifically deficient during conjunction search but not other types of inefficient search (but see Ashbridge, Cowey, & Wade, 1999).

## The Role of the Superior Frontal Sulcus in Visual Search

The frontal area SFS was the only region activated exclusively by inefficient search, irrespective of the conjunctions or angles that were searched for. Two observations argue against this region having a direct role in serial (spatial) attention processing. First, activity levels were not correlated with reaction time and thus with increasing demands on spatial attention, and second, this region was distinct from the FEFs known to be involved primarily in the control of classical spatial attention shifts (Rosen et al., 1999; Corbetta et al., 1998). If not specific for spatial attention, SFS activity might reflect working memory requirements for holding relevant structural information about possible target items on-line (Desimone & Duncan, 1995). Indeed, this SFS site has been repeatedly shown to be involved in working memory (Cornette et al., 1999; Cornette, Dupont, Bormans, Mortelmans, & Orban, 2000; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998), and to be distinct from the FEFs (Courtney et al., 1998). Alternatively, inefficient search-specific activity could be due to search termination processes. This issue will have to be clarified with an event-related paradigm, allowing separate analysis of target-present and target-absent trials.

## Search Strategy and Type of Spatial Attention Shifts

Tasks such as the Posner-like cueing paradigm (Rosen et al., 1999; Corbetta et al., 1998) or visual object enumeration (Sathian et al., 1999) require spatial shifts of attention in tight bound to oculomotor control, thus involving FEFs and the dorsal parietal cortex. The same might hold true for visual search covering large regions of the visual field or screening unfamiliar scenes. As the reader can see for himself by searching the targets in Figure 1, subjects presented with a visual search paradigm for the first time will most likely use spatial shifts of attention that are closely related to the oculomotor system to locate a particular object. However, new strategies evolve with experience, and experienced subjects, such as those in this study, no longer use oculomotor-related spatial shifts of attention. Subjects described their strategy as waiting for the target to show up. This change in strategy is probably due to training, not to instructions to maintain fixation. Indeed, training of inefficient visual search tasks under free viewing conditions revealed automatic decreases in saccades down to a total lack of saccades in some subjects (Sireteanu & Rettenbach, 1995). Visual processing thus seems to become decoupled from oculomotor processing in the interest of time (Wolfe & Alvarez, 1999), rendering inefficient search more efficient. We do not know, however, whether the subjects change their

attention-shifting mode from slow to fast or whether they stop using spatial shifts of attention all together.

## Conclusions

Attention effects in visual search are best reflected in activity modulations of the extrastriate areas COLS, LOS, and TRIPS. Moreover, the cortical network for visual search differs in two important ways from cortical networks so far known to be involved in visuospatial attention shifts. First, visual search does not involve the FEFs, and second, activity in the parietal cortex is not correlated with subjects' search behavior. We interpret these findings as support for object selection models based on parallel processing, unless an oculomotor-independent high-speed attentional searchlight were to operate in the extrastriate cortex.

## METHODS

### Subjects and Tasks

Twelve right-handed normal volunteers (seven females, five males), aged between 19 and 29 years (mean age  $24.3 \pm 3.45$ ) participated in two 1-hr training sessions and one or two MRI scanning sessions. All volunteers gave their informed written consent in accordance with the Declaration of Helsinki, and experiments were approved by the Ethical Committee of the K.U. Leuven Medical School. Subjects were tested with two different types of tasks: search tasks, and corresponding dimming control tasks.

#### Search Task

Examples of the stimuli subjects observed are shown in Figure 1. While maintaining fixation, subjects were tested with FVS (Figure 1a left column) for orientation or luminance differences, and CVS (Figure 1a right column) for contrast polarity and orientation in experiment 1. Three of the twelve subjects were additionally tested with CVS and AVS (Figure 1b left column) with  $90^\circ$  angles in experiment 2.

For FVS, we used displays containing white and black line elements tilted for  $+45^\circ$  or  $-45^\circ$  as distracters. There were two different classes of targets depending on whether the feature was orientation or luminance. Orientation targets were defined by white or black line elements with an orientation of  $+5^\circ$ ,  $-5^\circ$ ,  $+95^\circ$ , or  $+85^\circ$ , whereas luminance targets were represented by gray line elements tilted  $+45^\circ$  or  $-45^\circ$  with a luminance contrast relative to the gray background of about  $+15\%$  or  $-15\%$ . During CVS, subjects searched for targets that consisted of (a) white lines ( $+45^\circ$ ) among black lines of  $+45^\circ$  and white lines of  $-45^\circ$ , (b) white lines ( $-45^\circ$ ) among black lines of  $-45^\circ$  and white lines of  $+45^\circ$ , (c) black lines ( $+45^\circ$ ) among white lines of  $+45^\circ$  and black

lines of  $-45^\circ$ , or (d) black lines ( $-45^\circ$ ) among white lines of  $-45^\circ$  and black lines of  $+45^\circ$ . Note that the relatively unusual design of the FVS condition of embedding the target in two distracter types that are identical to those of the conjunction search led to identical displays for target-absent conditions for FVS and CVS. Subjects' search behavior thus depended exclusively on the searched targets.

During conjunction search, the target was not consistently mapped. The target in one trial could be distracter in the following trial, forcing subjects to re-identify the target in every trial by comparing the presented items. We used this design to prevent subjects from ignoring one type of distracters (e.g., in the case of a white target ignoring all black elements), that might have allowed them to perform an inefficient conjunction search like an efficient feature search. During angle search, targets with an included angle of  $90^\circ$  and random orientation were presented among two types of randomly oriented distracters with included angles of  $40^\circ$  and  $140^\circ$ , respectively. In half of the trials white elements were presented, in the other half black elements. For all three search types, white and black elements had similar luminance contrasts (approximately 40%) relative to the gray background, as controlled in the scanner by flicker photometry. The stimulus display subtended a visual angle of  $13.5^\circ \times 13.5^\circ$ , and single line elements measured  $0.92^\circ \times 0.35^\circ$ . The number of items in the display varied between 1, 8, 16, and 24 items during training and were presented in random order, whereas 8 and 24 elements were presented blockwise during scanning. Targets were present in 50% of the trials. Independently of the target's presence or absence, the fixation cross dimmed within the first 400 msec in 50% of the trials. Subjects made a two-alternative-forced choice, pressing as quickly as possible one pushbutton during search when a target was present, the other when absent. After the response, stimuli immediately disappeared from the screen, leaving the fixation cross on the uniform gray background.

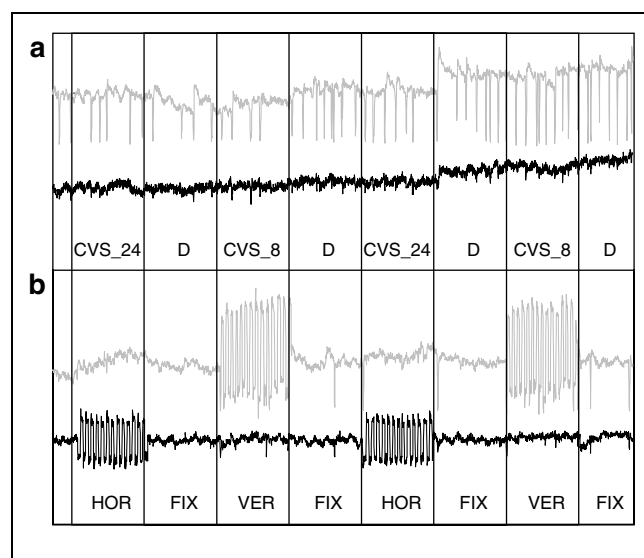
#### Control Tasks

In control tasks, we used displays identical to those during search, but this time subjects indicated by pressing the left or right push-button whether or not the central fixation cross had dimmed (D, dimming). The visibility of the dimming was individually adjusted to a performance level of 90 to 95% correct, equating difficulty levels for search and dimming. Each of the three tested search tasks had its corresponding control task.

During the two daily training sessions, subjects performed a total of 14 experimental time series, seven for feature search (or angle search) and seven for conjunction search, randomly interleaved. A time series consisted of 4 blocks with 16 search trials each, interleaved with 4 blocks of 8 dimming control trials each. Visual

indicators at the beginning of each block informed subjects whether they had to perform search or dimming tasks. The high number of training trials (448 search trials and 224 dimming trials) allowed us to eliminate all eventual interference between search tasks that might have resulted from the fact that target-absent conditions for FVS and CVS were based on identical stimulus displays. Moreover, the permanent control of eye movements ensured that all subjects had performed the search consistently without saccades.

Eight different time-series were presented in a scanning session, in which feature search (or angle search) and conjunction search series were interleaved. Within one time series, all trials were of the same search type but differed in the number of elements: trials with 8 or 24 elements were presented in blocks of 36 sec each. Search blocks were interleaved with equally long blocks of the dimming control task, in which displays similar to those presented in the preceding search blocks and with identical temporal stimulus characteristics. Therefore, the subject's mean reaction time during the preceding search block was used as stimulus presentation time for the following dimming trials. Intertrial intervals (onset-onset) were fixed at 5 sec for both search and dimming trials. Subjects' reaction times and error rates were recorded. Contrasting neuronal activations during search with those during dimming allowed us to isolate search-specific from search-nonspecific processes such as early visual information processing, motor preparation, or motor execution.



**Figure 8.** Eye movement recordings of one subject during scanning. Recording during (a) conjunction search (CVS) and its corresponding dimming control condition (D). CVS24, CVS8 = conjunction search for 24 and 8 elements, respectively. (b) The 5° horizontal (HOR) and vertical (VER) saccades, alternated with fixation (FIX). Black recording lines correspond to horizontal eye movements, gray lines to vertical. Example with an unusually high number of eye blinks during conjunction search.

Fixation was continuously controlled and recorded, using an MR-compatible eye movement tracking system (Ober2) with a reliable resolution during scanning of about 1° (see Sinaert et al., 1999). We counted every eye movement with an initial velocity of more than 20°/sec as a saccade (Zuber, Stark, & Cook, 1965).

To identify the oculomotor cortical network (experiment 3), 6 of the 12 subjects were scanned for an additional two time series during which they performed saccades. Time series consisted of 36-sec periods of self-induced horizontal and vertical 5° saccades (performed in separate blocks, following verbal instructions, with a mean of  $1.4 \pm 0.4$  horizontal and  $1.4 \pm 0.3$  vertical saccades per second), separated by equally long periods of steady fixation. Throughout the time series, subjects viewed a visual display, consisting of four peripheral (2.5° eccentricity) points and one central fixation point, which helped them to achieve reliable saccadic amplitudes. Self-induced saccades were chosen to match presumed internally generated attention shifts during inefficient search. Figure 8 shows eye movement recordings of one subject while performing conjunction search (Figure 8a), and the oculomotor task (Figure 8b) during scanning.

### Imaging and Data Analysis

Imaging was performed by a 1.5-T Siemens Vision MR Imager fitted with a standard head coil. Eight series of 80 brain scans (32 axial slices; FOV =  $192 \times 192$  mm; matrix =  $64 \times 64$  pixels; slice thickness = 4 mm; slice gap = 13%; flip angle = 90°) were acquired using a gradient-echo echo-planar imaging (GE-EPI) sequence with a repetition time of 3.6 sec, and an echo time of 40 msec. Functional images were co-aligned with a high-resolution anatomical scan taken in the same session (3D-MPRAGE). Images were transformed into Talairach space (Talairach & Tournoux, 1988) and smoothed (effective smoothing for group: ~12 mm). Activation sites were identified by means of multiple regression analysis of the time series of MR signal intensities in every voxel and eight covariates of interest (four different search conditions—two search types times two array sizes—and their corresponding D-conditions), using SPM96 (Friston et al., 1995). Covariates of no interest were used to factor out variances due to between-run changes in mean intensity, to low frequency signal components, and to the visual indicators, informing subjects about the task in the following block. Statistical significance of activated regions was assessed by using both a spatial extent threshold,  $p < .05$ , and a height threshold,  $Z > 4.5$ , corresponding to a  $p \leq .05$  corrected for multiple comparisons. Group data for experiment 1 were analyzed using the random effects model implemented in SPM96 to make inferences on population levels, resulting in activation sites common to all subjects. For the remaining experiments, group analyses were based on the fixed effects model.

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The data reported in this experiment have been deposited in National fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2000-1114K.

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