

# Involvement of the human frontal eye field and multiple parietal areas in covert visual selection during conjunction search

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## Abstract

Searching for a target object in a cluttered visual scene requires active visual attention if the target differs from distractors not by elementary visual features but rather by a feature conjunction. We used functional magnetic resonance imaging (fMRI) in human subjects to investigate the functional neuroanatomy of attentional mechanisms employed during conjunction search. In the experimental condition, subjects searched for a target defined by a conjunction of colour and orientation. In the baseline condition, subjects searched for a uniquely coloured target, regardless of its orientation. Eye movement recordings outside the scanner verified subjects' ability to maintain fixation during search. Reaction times indicated that the experimental condition was attentionally more demanding than the baseline condition. Differential activations between conditions were therefore ascribed to top-down modulation of neural activity. The frontal eye field, the ventral precentral sulcus and the following posterior parietal regions were consistently activated: (i) the postcentral sulcus; (ii) the posterior; and (iii) the anterior part of the intraparietal sulcus; and (iv) the junction of the intraparietal with the transverse occipital sulcus. Parietal regions were spatially distinct and displayed differential amplitudes of signal increase with a maximal amplitude in the posterior intraparietal sulcus. Less consistent activation was found in the lateral fusiform gyrus. These results suggest an involvement of the human frontal eye field in covert visual selection of potential targets during search. These results also provide evidence for a subdivision of posterior parietal cortex in multiple areas participating in covert visual selection, with a major contribution of the posterior intraparietal sulcus.

## Introduction

When we perceive a cluttered visual scene, the brain has to select currently relevant objects in order to use them for the control of our behaviour. If subjects search for a target that carries a unique visual feature (pop-out search), search time is independent of the number of distractors in an array. In contrast, if the target differs from distractors only in terms of a conjunction of elementary visual features (conjunction search), search time generally increases with the number of distractors (Treisman & Gelade, 1980). Many investigators explain this increase with a serial selection of object locations with rapid shifts of the attentional focus in conjunction search (Treisman, 1993; Posner & Dehaene, 1994; Wolfe, 1994). Others suggest that a limited-capacity parallel search process may account for the difficulty of conjunction search (Duncan & Humphreys, 1989; Desimone & Duncan, 1995). The aim of the present functional magnetic resonance imaging (fMRI) study was to investigate the functional neuroanatomy of selective mechanisms employed in conjunction search.

Based on lesion and functional imaging studies, a large-scale network for spatial attention in the human brain has been proposed. This network comprises the putative frontal eye fields (FEF) and the

posterior parietal cortex as the most critical cortical components (Mesulam, 1981; Posner & Petersen, 1990; Corbetta, 1998; Gitelman *et al.*, 1999).

The serial search model predicts an involvement of cortical areas controlling spatial shifts of attention in conjunction search. Using positron emission tomography (PET), Corbetta *et al.* (1995) found attentional modulation in the right superior parietal lobe during a conjunction search task. As the posterior parietal cortex comprises several distinct functional areas with substantial attentional modulation in macaque monkeys (Andersen & Gnadt, 1989; Colby & Goldberg, 1999), a similar parcellation should be expected for humans. Indeed, two distinct regions in the anterior and posterior part of the intraparietal sulcus (IPS) and one in the IPS junction with the transverse occipital sulcus (IPTO) have recently been found to be activated during a spatial attention-shifting task (Corbetta *et al.*, 1998, 2000). Therefore, we hypothesized that these distinct intraparietal subregions would also contribute to attentive search.

To date, a participation of the human FEF in covert visual selection during search has not been reported. However, single-unit recordings from this area in macaques demonstrated that neurons code the conspicuousness and behavioural significance of objects in their receptive fields (Schall & Bichot, 1998; Bichot & Schall, 1999). This property renders the FEF a likely source of neural signals guiding the attentional focus, overtly as well as covertly. Accordingly, we asked

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whether the human FEF would also be involved in the covert selective mechanisms of conjunction search, in addition to selecting visual targets by eye movements.

To address these questions, we measured regional changes in cerebral blood oxygenation while subjects alternately performed a demanding conjunction search task and a less demanding pop-out search task. Given identical sensory stimulation and motor response requirements in both tasks, signal changes should reflect neural activity related to attentional operations. We performed group analysis as well as single subjects' analysis and we used cortical surface reconstruction techniques to clarify the individual cortical topography of activations. Preliminary results have been published in abstract form (Donner *et al.*, 1999).

## Materials and methods

### Visual tasks

Visual search arrays were composed of four square clusters made up of coloured bars (Fig. 1). The orientation of the bars within a cluster was either vertical or horizontal, and bar colour was either yellow or blue. Clusters were embedded in an achromatic background texture and one cluster was located in each visual field quadrant. The clusters subtended  $7^\circ$  of visual angle and were located  $7^\circ$  off the fixation point, with their midpoints lying on the angle bisectors of the quadrants (Fig. 1).

To minimize the occurrence of exploratory eye movements, the search arrays were masked after a presentation time of 80 ms, which is below the peak latency of express saccades (Becker, 1989). Stimuli were presented by an adapted version of the RTGRAF software (Diesch, 1994). In the experimental condition (CONJUNCTION), subjects searched for one cluster of vertically orientated and yellow bars. In the baseline condition (POP-OUT), subjects searched for one cluster of yellow bars, regardless of their orientation. In both conditions, subjects were instructed to maintain fixation. Tasks were performed in a blocked design with eight trials per block. A visual cue, which was presented at the beginning of each task block, served as an instruction. Trials were contiguous within blocks. The target was presented randomly on 50% of the trials. Subjects used an MRI-compatible fibre optic two-button response-box for report. They were instructed to indicate the target's presence with the index finger and the target's absence with the middle finger of their dominant hand, respectively. Speed and accuracy were stressed and reaction times were recorded.

### Data acquisition

In order to ensure that our modified version of the visual search paradigm produces the reported differential influence of distractor number between conjunction search and pop-out search, we measured reaction times in 14 subjects in a behavioural control study. In this study, set sizes of one and four bar clusters (ONE, FOUR) were used. If only one cluster was presented, it appeared randomly in one of the visual field quadrants. Another eight male subjects performed the four-cluster-array search tasks in the fMRI study. Their age ranged from 23 to 30 years. All subjects gave informed consent before participation in the study which was conducted in conformity with the Declaration of Helsinki.

Prior to fMRI, subjects trained the visual search tasks in the behavioural laboratory. After training, subjects performed the tasks, while eye movements were recorded in the horizontal axis with an infra-red oculography system (AMTEC, Weinheim, Germany) in an extra session. Subjects were subsequently scanned if they were able

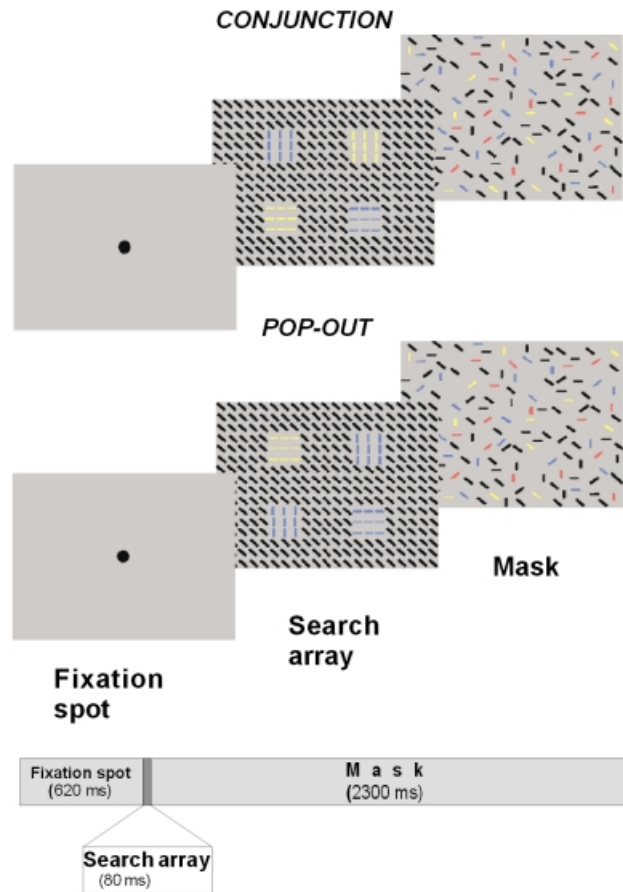


FIG. 1. Timing of stimuli in visual search tasks. Search arrays were masked after 80 ms. Exemplary 'target-present-trials' are shown for both conditions, conjunction and pop-out search. The target cluster consists of yellow and vertical bars in the conjunction condition (upper right quadrant) and yellow bars of either orientation in the pop-out condition (upper left quadrant). Subjects were instructed to indicate the absence or presence of the target by keypress. Conditions alternated after blocks of eight trials. This was indicated by a visual cue. Sensory stimulation parameters were approximately identical and motor responses were identical across both conditions.

to maintain gaze within  $2^\circ$  of the centre on more than 90% of the trials.

During functional imaging, subjects laid horizontally in a 1.5 Tesla MAGNETOM Vision magnetic resonance imaging system (Siemens Medical Systems, Erlangen, Germany) and fixated a back-projection screen (Dalite, Daplex) at a distance of 24 cm via a mirror. Both mirror and screen were mounted to the head-coil of the MRI scanner by purpose-built equipment. Stimuli were calculated on a personal computer and projected onto the screen by means of an liquid crystal display (LCD) projector (NEC 8000 G, Stuttgart, Germany), whose objective lens had been replaced by a purpose-made lens system of long focal length. The projector was situated in the same room as the scanner; the personal computer was situated outside the room. Subjects' heads were stabilized with a bite bar. We used a single-shot echoplanar (EPI) sequence [repetition time (TR)/echo time (TE)=3000/60 ms; flip angle (FA)= $90^\circ$ ; in-plane resolution= $4\text{ mm}^2$ ] optimized for the blood oxygenation level-dependent (BOLD) contrast. During each functional run, 132 volumes of 24 axial slices (slice thickness = 5 mm) spanning the cerebral cortex were collected. Each subject performed four runs. Structural three-dimensional data sets were acquired in the same session using a T1-weighted sagittal MP-RAGE-sequence [TR/TE=10/4 ms,

FA = 12°, inversion time (TI) = 100 ms, voxel size = 1 mm<sup>3</sup>. Additional T1-weighted three-dimensional data sets were recorded in extra sessions in five of the subjects with a sagittal FLASH sequence optimized for a high contrast between grey and white matter (TR/TE = 38/5 ms, FA = 30°, voxel size = 1 mm<sup>3</sup>).

When comparing conjunction and pop-out search, either the same four-cluster search arrays are presented in both conditions, the implication being that the number of targets varies across the conditions; or the number of targets is kept constant across conditions, implying that the physical stimulation parameters are not completely identical. We decided to proceed with the latter. Therefore, we conducted a control experiment to detect potential sensory effects in the differential activations. Here, subjects were instructed to fixate and passively view the same stimuli that were presented in the active tasks (CONJUNCTION, POP-OUT).

### Data analysis

Reaction times from the behavioural control study were entered into a three-way repeated measures ANOVA with the factors task (CONJUNCTION, POP-OUT), set size (ONE, FOUR) and target (PRESENT, ABSENT). Due to the hypothesized differential attentional demands it was predicted that reaction times are larger in CONJUNCTION than in POP-OUT and larger in FOUR than in ONE, respectively, and that the effect of set size is strongest within CONJUNCTION. Additionally, for set size FOUR, reaction times from the fMRI experiment were compared across conditions (CONJUNCTION, POP-OUT) using Wilcoxon's sign rank test.

Imaging data were analysed using the Brainvoyager 3.7® software package (Max Planck Society, Germany; Goebel *et al.*, 1998). The three-dimensional anatomical data sets of each subject were transformed into Talairach space using a piecewise affine and continuous transformation for each of 12 predefined subvolumes (Talairach & Tournoux, 1988). The first four volumes of each functional run were discarded and only the following 128 volumes were used for further analysis. The two-dimensional slice time courses were converted into three-dimensional volume time courses by co-registration with the three-dimensional anatomical data sets from the same session and interpolation to the resolution of 1 mm<sup>3</sup>. Co-registration was based on the Siemens slice position parameters for the functional and anatomical measurements. The volume time courses were then transformed into Talairach space using the parameters specified for the anatomical data sets before. Volume time courses were spatially and temporally smoothed with a Gaussian kernel [full width at half maximum (FWHM) = 4/3 voxels/scan volumes] and linear drifts were removed. After z-transformation of the time courses, multiple regression analysis was performed to compute statistical maps for individual subjects and for the group average ( $n = 8$ ). The model contained an idealized reference function as predictor for the effect of interest. This reference function was generated by convolving a model of the haemodynamic impulse response (a gamma-function with  $\delta = 2.5$  and  $\tau = 1.25$ ) with a square-wave function representing the experimental protocol. Further predictors for the global mean of each run and for each subject were included. Both the group average and individual functional maps were rigorously thresholded at correlation coefficients corresponding to  $P < 10^{-5}$ .

We intended to localize precisely parietal activations with respect to IPS subregions, and to average and compare fMRI responses of these subregions and of the FEF. In order to generate surface-based representations of the individual sulcal and gyral pattern, the cortical surfaces were reconstructed on the basis of the high-quality three-dimensional data sets available for five subjects. This was achieved

by segmenting and tessellating the grey–white matter boundary and by inflating the resulting surface mesh (Linden *et al.*, 1999). Regions of interest (ROIs) could then be identified on the individual surface reconstruction. The identification of the FEF was guided by both a functional and an anatomical criterion in two subjects, and exclusively by the anatomical criterion in the remaining three subjects. The anatomical criterion was the location in the precentral sulcus, in the latitude of the caudal-most part of the superior frontal sulcus. This location is well supported by a series of oculomotor studies (see Paus, 1996 for a metaanalysis; Courtney *et al.*, 1998). The additional functional criterion was the location of the caudal-most portion of the frontal cortex that showed increased activity during a previous visually guided saccades study in which two of the subjects participated. The IPS representation on the surface reconstructions was divided into an anterior vertical limb (inferior postcentral sulcus), a horizontal ramus (IPS proper) and a posterior vertical limb (transverse occipital sulcus) according to Critchley (1953). The anterior and posterior part of the horizontal ramus (anterior IPS and posterior IPS) and the IPS junction with the transverse occipital sulcus (IPTO) were identified on the folded and inflated surface reconstructions. Significantly activated regions in these areas and in the FEF were marked on the cortical surfaces. Corresponding ROIs in the volume data sets were selected based on the surface marks. Although intraparietal activation peaks were clearly separated in all subjects (see Results), the surrounding regions were slightly confluent at the chosen threshold in two of the five subjects. In these cases, the threshold was raised until they were separated. Unsmoothed fMRI responses from the ROIs were averaged across voxels in each ROI, repetitions of task blocks, hemispheres and finally across the five subjects. Amplitudes of averaged time series from IPS regions were compared using a Friedman test.

## Results

### Behaviour

In the ANOVA of the reaction times from the behavioural control study, the main effects and two interactions attained significance (task,  $F_{1,13} = 111.67$ ,  $P < 0.01$ ; set size,  $F_{1,13} = 63.16$ ,  $P < 0.01$ ; target,  $F_{1,13} = 7.99$ ,  $P < 0.05$ ; task  $\times$  set size,  $F_{1,13} = 71.99$ ,  $P < 0.01$ ; task  $\times$  target,  $F_{1,13} = 45.25$ ,  $P < 0.01$ ). All other effects were not significant. Reaction times were significantly higher in CONJUNCTION and FOUR rather than POP-OUT and ONE, respectively, and the effect of set size was significantly stronger within CONJUNCTION. Together, these results are consistent with the hypothesis of higher attentional demands in the conjunction than in the pop-out search task.

All subjects participating in the fMRI study were able to maintain the direction of gaze within 2.0° of the centre on more than 93% of the trials in the eye movement recording session outside the scanner. Mean saccade rates were 1.74% in CONJUNCTION and 1.97% in POP-OUT. There was no significant difference in saccade rates between the conditions (Wilcoxon's  $T = 4$ ,  $P = 0.44$ ).

During fMRI, accuracy in task performance was high in both pop-out search (95.67%) and conjunction search (94.81%). Obviously, subjects could use the iconic image of the search array for accurate task performance. Mean reaction times were 597.73 ms (SD, 42.43) in CONJUNCTION and 509.95 ms (SD, 46.79) in POP-OUT. Reaction times were significantly higher in CONJUNCTION than in POP-OUT (Wilcoxon's  $T = 0$ ,  $P < 0.01$ ).

### Functional imaging

The comparison of passive viewing of the stimuli presented during the conjunction task and those presented during the pop-out task did

not yield differential activation in any cortical area, even if the threshold was lowered to a correlation coefficient corresponding to  $P < 0.01$ .

Group average activations from the active tasks are shown in Fig. 2A. Mean locations in Talairach space and volumes are given in Table 1. A region in the dorsal precentral sulcus was bilaterally activated. This region's location corresponded to the human FEF due to the relation to anatomical landmarks and due to the peak coordinates in Talairach space. A more ventral region in the precentral sulcus was activated only in the left hemisphere at  $P < 10^{-5}$ . Lowering the threshold to a value corresponding to  $P < 10^{-4}$  revealed a corresponding activation in the right hemisphere. A large proportion of the posterior parietal cortex was activated. There were more activated voxels in the right than in the left hemisphere (5667 versus 1544 voxels). In this posterior parietal region, four distinct peaks of activation could be identified bilaterally: one in the postcentral sulcus, two in the horizontal IPS ramus and one in the IPS junction with the transverse occipital sulcus.

Cortical surface reconstructions with individual functional maps are shown in Fig. 2B and C. The FEF, ventral precentral sulcus, postcentral sulcus, posterior IPS and IPTO were bilaterally activated across all five subjects for whom surface reconstructions were obtained. Anterior IPS was bilaterally activated in four subjects. Activation peaks of IPS regions were spatially distinct across all five subjects; mean peak coordinates in the posterior–anterior direction are  $-45/-50$  (SD, 6/8) for anterior IPS,  $-67/-69$  (SD, 6/5) for posterior IPS and  $-75/-76$  (SD, 5/6) for IPTO (right/left hemisphere, respectively). Talairach coordinates of these regions demarcated in individual brains closely resembled those of peak activations in the group analysis. Interestingly, we also found the posterior part of the lateral fusiform gyrus to be activated in four subjects. Fusiform activation was bilateral in two subjects and restricted to the right hemisphere in the other two (mean peak coordinates  $x$ ,  $y$ ,  $z = 41/-48, -64/-64, -9/-7$ , SD = 4/6, 7/2, 9/3, respectively). Less consistent activations were found in the anterior cingulate ( $n = 3$ ), right BA 46/9 ( $n = 2$ ), putative supplementary eye field ( $n = 3$ ) and anterior insula ( $n = 3$ ).

Average responses of FEF, anterior and posterior IPS and IPTO are shown in Fig. 3. Modulation strength differed significantly between IPS regions (Friedman's  $\chi^2 = 12.0$ ,  $P < 0.01$ ) and was maximal in posterior IPS ( $P = 0.01$ , family-wise single comparisons).

## Discussion

During conjunction search, the fMRI signal increased bilaterally in the FEF, ventral precentral sulcus, postcentral sulcus, three distinct regions of the IPS (anterior and posterior IPS, and IPTO) and in the lateral fusiform gyrus. In the posterior parietal cortex, modulation strength was maximal in posterior IPS.

There was no differential activation during passive viewing of the stimuli. Thus, the signal increases cannot be attributed to the slight physical differences in retinal input. As manual responses were identical in both conditions and subjects were able to maintain the required direction of gaze, the signal increases are unlikely to be caused by differential motor output either. Hypothetically, differential activation could be caused by differences between the conjunction and pop-out task in working memory load or general arousal. However, these explanations seem unlikely. First, Luck & Vogel (1997) demonstrated that feature conjunctions consume the same amount of working memory capacity as single features. Second, a recent fMRI study of the parietal lobes revealed that IPTO, posterior IPS and anterior IPS were activated by tasks that demand visual

attention, but not by general task difficulty (Wojciulik & Kanwisher, 1999). Therefore, non-specific effects should not underlie the fMRI responses observed in these regions in the present experiment.

Instead, signal increases observed in the FEF and the IPS regions are explained best by top-down modulation of neural activity, reflecting the higher attentional demands of the conjunction search task. Activation of the right posterior parietal cortex is consistent with a previous PET study on conjunction search (Corbetta *et al.*, 1995). However, Corbetta *et al.* (1995) found no significant difference between conjunction and pop-out search in the left hemisphere. In the present study, all parietal regions were activated in both hemispheres; yet, the extent of parietal activations was smaller in the left than in the right hemisphere. Thus, we observed a parietal lateralization to the right hemisphere, which was quantitative rather than qualitative. This is in accordance with neuropsychological evidence from split-brain patients, showing that both hemispheres contain the necessary circuitry for visual search (Luck *et al.*, 1994). Moreover, surface reconstruction and analysis of individual subjects permitted more fine-grained mapping of multiple distinct parietal activations in our study. The activation site in the right superior parietal lobe observed by Corbetta *et al.* (1995) seems to correspond best to the right posterior IPS region. It would be interesting to know whether the observed signal changes reflect a qualitative (i.e. a difference between the involved neuronal populations) or a quantitative difference (i.e. a difference between the amount of activation of the very same neuronal populations) between the two search tasks. Psychophysical data on feature search suggest the latter (reviewed by Wolfe, 1994), and we are currently addressing this question in a new set of fMRI experiments.

Several functional imaging studies have also demonstrated activation of the precentral, postcentral and intraparietal sulcus by other tasks requiring spatial attention (Culham *et al.*, 1998; see Corbetta, 1998 for a recent review). In the following, possible attentional mechanisms controlled by the FEF and the IPS regions are discussed, and implications for neural models of visual search are outlined.

### *Participation of the human FEF in covert visual selection*

Top-down modulation in the human FEF has previously been found when subjects were explicitly instructed to covertly shift their attention across the visual field (Corbetta *et al.*, 1998; Gitelman *et al.*, 1999). In the case of visual search, serial spatial selection is presumably guided by the results of parallel feature analysis (Treisman, 1993; Wolfe, 1994). Neurons in the FEF are not feature selective in macaques (Goldberg & Segraves, 1989), and presumably this also applies with humans (Courtney & Ungerleider, 1997). However, the convergence of projections from macaque's occipito-ventral feature-selective areas to the FEF is suited to produce a topographically ordered map of visual salience in the FEF (Schall *et al.*, 1995; Schall & Bichot, 1998). Indeed, results from a single-unit recording experiment on conjunction search suggest that visual responses in the macaque's FEF represent the degree of similarity between objects within their receptive fields and a conjunctively defined target object (Bichot & Schall, 1999). This kind of representation may guide the attentional focus to candidate locations. As target distractor discriminability is lower in the conjunction task than in the pop-out task (Duncan & Humphreys, 1989), on average, more object locations might have to be selected in this condition (Wolfe, 1994) or attention might have to be focused on one location for a longer time (Chelazzi, 1999). This difference could underlie the observed differential activation.

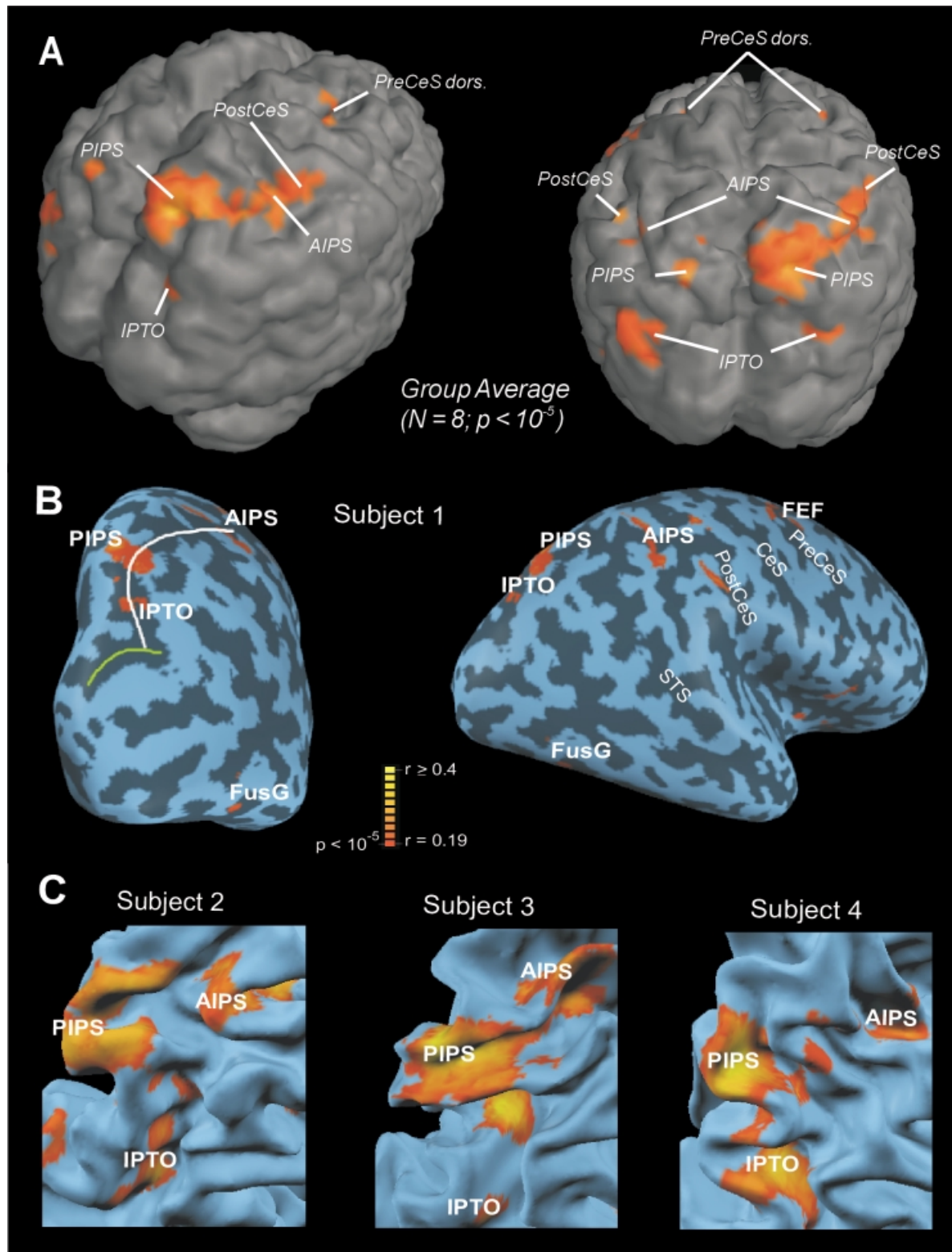


FIG. 2. (A) Group activation map, superimposed on one subject's rendered brain. Left, dorsolateral view; right, dorsoposterior view. Activations are produced by conjunction search, relative to pop-out search. Abbreviations: PreCeS, precentral sulcus; PostCeS, postcentral sulcus; AIPS, anterior intraparietal sulcus; PIPS, posterior intraparietal sulcus; IPTO, intraparietal transverse occipital. Posterior parietal activation is larger in the right than in the left hemisphere, but contains corresponding peaks in both hemispheres. (B) Posterior and lateral view of one subject's inflated right hemisphere. The individual functional map is superimposed. The white line marks the fundus of the intraparietal sulcus, the green line marks the fundus of the transverse occipital sulcus. Other sulci are labelled in white text: PreCeS, precentral sulcus; CeS, central sulcus; PostCeS, postcentral sulcus; STS, superior temporal sulcus; FusG, fusiform gyrus. See A for abbreviations of activation sites. (C) Sections of folded posterior parietal cortex of three further subjects with their individual activation patterns. Posterior IPS consistently extends to the convexity of the superior parietal lobulus. See A for abbreviations.

TABLE 1. Talairach coordinates of activated areas; group average ( $n=8$ )

Cortical region	Brodmann area (BA)		x	y	z	Volume (mm <sup>3</sup> )*
Frontal cortex						
FEF	6	Right	20	-9	49	456
	6	Left	-22	-10	50	191
Ventral PreCeS	6	Left	-37	-5	28	76
Parietal cortex						
PostCeS	5	Right	38	-47	48	924
	5	Left	-43	-50	52	471 <sup>†</sup>
Anterior IPS	7	Right	30	-56	48	3883 <sup>‡</sup>
	7	Left	-40	-56	52	
Posterior IPS	7	Right	13	-65	48	
	7	Left	-19	-77	50	
IPTO	19	Right	28	-68	27	860
	19	Left	-32	-74	21	706

Values are peak coordinates (mm in Talairach space). FEF, frontal eye field; PreCeS, precentral sulcus; PostCeS, postcentral sulcus; IPS, intraparietal sulcus; IPTO, junction of intraparietal and transverse occipital sulcus. \*Number of 1 mm<sup>3</sup> voxels. <sup>†</sup>Includes anterior IPS. <sup>‡</sup>Includes posterior IPS. (Volumes are given once for left PostCeS and anterior IPS, and for right anterior IPS and posterior IPS because these regions were tied together at  $P < 10^{-5}$ .)

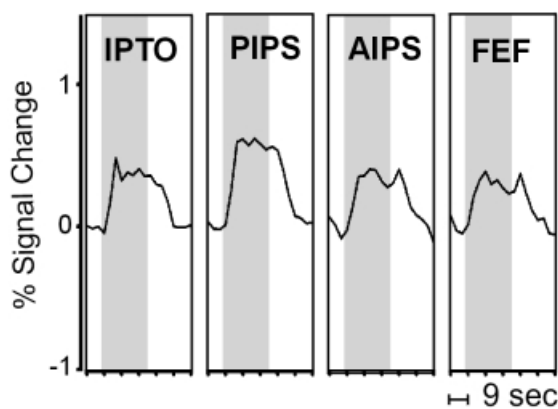


FIG. 3. Mean fMRI signal increases during blocks of conjunction search (grey bars), averaged across voxels in each region, repetitions of task blocks, hemispheres and subjects ( $n=5$ ). The signal intensity is normalized to the mean of the last three data points of pop-out search blocks (white). Changes in signal intensity reflect the switches between both visual search tasks. Regions of interest: FEF, frontal eye field; AIPS, anterior intraparietal sulcus; PIPS, posterior intraparietal sulcus; IPTO, intraparietal transverse occipital. Modulation amplitude is maximal in PIPS.

#### Subregions of the human posterior parietal cortex—spatial and non-spatial selection

In studies of covert attention shifts, distinct parietal regions in anterior and posterior IPS and IPTO were found to be activated (Corbetta *et al.*, 1998, 2000). According to our results, activation of these regions generalizes across diverse tasks requiring spatial selection and is significant for object recognition. The differential amplitudes of signal increase in anterior and posterior IPS and IPTO corroborate the notion of distinct functional areas. This is consistent with a large body of evidence demonstrating spatial processing and spatial attention in multiple areas of the macaque's posterior parietal cortex (Andersen & Gnadt, 1989; Colby & Goldberg, 1999). Posterior IPS activation consistently extended to the superior parietal lobe. The area might contain the human homologues of the macaque's areas LIP and 7a. This view is consistent with the hypothesis that human visuospatial areas are located more dorsal in parietal cortex than their counterparts in monkeys (Courtney & Ungerleider, 1997; Courtney *et al.*, 1998). Moreover, area 7a and LIP both receive substantial attentional modulation (Andersen & Gnadt, 1989). In LIP, a representation of visual salience similar to the one in the FEF has

been found (Gottlieb *et al.*, 1998). LIP is also strongly involved in oculomotor control (Andersen & Gnadt, 1989). Similarly, the human posterior IPS is consistently activated during saccadic eye movement tasks (reviewed by Corbetta *et al.*, 1998; Corbetta, 1998). A putative macaque homologue of anterior IPS is more difficult to identify. Its location resembles that of area AIP in the macaque. However, a homology seems unlikely from a functional perspective, because AIP is highly specialized for the control of grasping behaviour (Colby & Goldberg, 1999). Regarding IPTO, it has been suggested that the region corresponds to the human visual area 'V7', which was recently discovered by means of retinotopic mapping (Tootell *et al.*, 1998; Wojciulik & Kanwisher, 1999). A correspondence of IPTO and V7 is likely because of their common consistent location in the junction of the intraparietal and transverse occipital sulcus. V7 has a crude retinotopic organization, responds to a wide range of different stimuli, and receives strong modulation by spatial attention (Culham *et al.*, 1998; Tootell *et al.*, 1998). The putative macaque homologue, the dorsal parietal area (DP), has not been defined consensually (Tootell *et al.*, 1998). In humans, Wojciulik & Kanwisher (1999) found both spatial and non-spatial attention tasks producing overlapping activations in an anterior IPS region and in IPTO. Le *et al.* (1998) found activation of the superior parietal lobe also in the context of non-spatial attention shifts between shape and colour information. Lumer *et al.* (1998) demonstrated superior parietal involvement in the perceptual transitions of binocular rivalry. Non-spatial selection such as parallel top-down priming (Wolfe, 1994) or inhibition (Treisman, 1993) of feature processors and shifts between feature dimensions (Grossberg *et al.*, 1994) might well be employed during our conjunction search task. Activation of anterior IPS and IPTO in our study might reflect both spatial and non-spatial selective mechanisms, differing between the conjunction and pop-out search tasks. In contrast, the activation of posterior IPS during visual search might be specific to spatial selection mechanisms. The maximum signal amplitude we found in posterior IPS suggests a central role for this region in visual search. In addition to shifting the attentional focus, adjusting the spatial scale and holding the position of the focus might be crucial operations in conjunction search (Treisman, 1993; Chelazzi, 1999). We hypothesize that both are controlled by posterior IPS. The activation we found in the lateral fusiform gyrus might be an effect of this peripheral focusing and might be related to the increase of the N2-posterior-contralateral component of the event-related potential found during conjunction search (Luck *et al.*, 1997a). This interpretation accords with the finding that similar regions in the

posterior parietal cortex and fusiform gyrus are also activated during demanding discrimination tasks that require only sustained peripheral focusing and no spatial attention shifts (Vandenberghe *et al.*, 1996; Martinez *et al.*, 1999; Hopfinger *et al.*, 2000).

#### *Activation of the frontoparietal attention network and neural models of visual search*

Desimone & Duncan (1995; see also Duncan *et al.*, 1997; Desimone, 1998) proposed that in visual search, a template of the searched-for object held in working memory is used to send a top-down signal to those neurons in the occipitovernal pathway that selectively respond to the features of this object. This top-down signal may bias competition between visual objects towards the representation of the object most similar to the template. Prefrontal cortex is suggested to be the source of this signal. In the strong form of this 'biased competition model', the outlined parallel mechanism is proposed to be sufficient for visual search performance without any need for sequential attention shifts or sustained peripheral focusing. Non-spatial features of visual objects are known to be primarily processed outside of the parietal cortex and the FEF (Courtney & Ungerleider, 1997; Tootell *et al.*, 1996; Tanaka, 1997). Therefore, the stronger activation of the FEF and the IPS during conjunction search than during pop-out search can hardly be accounted for by the pure version of the biased competition model. It could be objected that activation of these areas during visual search may be without functional relevance. However, this is contradicted by the finding that transcranial magnetic stimulation over the parietal cortex disrupts performance during a conjunction search as opposed to a pop-out search (Ashbridge *et al.*, 1997). On the other hand, strong physiological evidence supports the tenets that object representations compete for processing in the occipitotemporal pathway by means of mutual suppression, and that this competition can be resolved by top-down bias (Chelazzi *et al.*, 1993; Luck *et al.*, 1997b; Kastner *et al.*, 1999). During visual search, these parallel competitive mechanisms might nevertheless work in concert with focal processing (Wolfe, 1994), the latter controlled by the frontoparietal attention network and prolonged during a demanding visual conjunction analysis (Chelazzi, 1999).

The human FEF participates in covert visual selection employed during conjunction search. This is in accordance with findings from non-human primates performing a similar task. Thus, the role of human FEF in visuomotor integration is not confined to overt selection of visual target objects by means of saccadic eye movements. Multiple posterior parietal regions are also involved in covert visual selection during conjunction search. Furthermore, the maximal modulation in posterior IPS suggests a central contribution of this region to the control of the attentional focus.

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#### Abbreviations

BOLD, blood oxygenation level dependent; DP, dorsal parietal visual area; EPI, echoplanar imaging; FA, flip angle; FEF, frontal eye field; fMRI, functional magnetic resonance imaging; FWHM, full width at half maximum; IPS, intraparietal sulcus; IPTO, junction of intraparietal and transverse occipital sulcus; LCD, liquid crystal display; PET, positron emission tomography; ROI, region of interest; TE, echo time; TI, inversion time; TR, repetition time.

#### References

- Andersen, R.A. & Gnadt, J.W. (1989) Posterior parietal cortex. In Wurtz, R.H. & Goldberg, M.E. (eds), *Neurobiology of Saccadic Eye Movements*. Elsevier Science, Amsterdam, pp. 315–335.
- Ashbridge, E., Walsh, V. & Cowey, A. (1997) Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia*, **35**, 1121–1131.
- Becker, W. (1989) Metrics. In Wurtz, R.H. & Goldberg, M.E. (eds), *Neurobiology of Saccadic Eye Movements*. Elsevier Science, Amsterdam, pp. 13–61.
- Bichot, N.P. & Schall, J.D. (1999) Effects of similarity and history on neural mechanisms of visual selection. *Nature Neurosci.*, **2**, 549–554.
- Chelazzi, L., Miller, E.K., Duncan, J. & Desimone, R. (1993) A neural basis for visual search in inferior temporal cortex. *Nature*, **363**, 345–347.
- Chelazzi, L. (1999) Serial attention mechanisms in visual search: a critical look at the evidence. *Psychol. Res.*, **62**, 195–219.
- Colby, C.L. & Goldberg, M.E. (1999) Space and attention in parietal cortex. *Annu. Rev. Neurosci.*, **22**, 319–349.
- Corbetta, M., Shulman, G.L., Miezin, F.M. & Petersen, S.E. (1995) Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, **270**, 802–805.
- Corbetta, M. (1998) Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? *Proc. Nat. Acad. Sci. USA*, **95**, 831–838.
- Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, A.Z., Linenweber, M.R., Petersen, S.E., Raichle, M.E., Van Essen, D.C. & Shulman, G.L. (1998) A common network of functional areas for attention and eye movements. *Neuron*, **21**, 761–773.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P. & Shulman, G.L. (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neurosci.*, **3**, 292–297.
- Courtney, S.M. & Ungerleider, L.G. (1997) What fMRI has taught us about human vision. *Curr. Opin. Neurobiol.*, **7**, 554–561.
- 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.
- Critchley, M. (1953) *The Parietal Lobes*. Arnold, London.
- Culham, J.C., Brandt, S.A., Cavanagh, P., Kanwisher, N.G., Dale, A.M. & Tootell, R.B. (1998) Cortical fMRI activation produced by attentive tracking of moving targets. *J. Neurophysiol.*, **80**, 2657–2670.
- Desimone, R. & Duncan, J. (1995) Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.*, **18**, 193–222.
- Desimone, R. (1998) Visual attention mediated by biased competition in extrastriate visual cortex. *Phil. Trans. R. Soc. Lond.*, **B 353**, 1245–1255.
- Diesch, E. (1994) A high resolution color graphic display four channel software tachistoscope. *Behav. Res. Meth. Instr. Comp.*, **26**, 331–335.
- Donner, T., Kettermann, A., Diesch, E., Goebel, R., Villringer, A. & Brandt, S.A. (1999) fMRI-activity related to visual feature integration. *Neuroimage*, **9** (Suppl. 6), 868.
- Duncan, J. & Humphreys, G.W. (1989) Visual search and stimulus similarity. *Psychol. Rev.*, **96**, 433–458.
- Duncan, J., Humphreys, G.W. & Ward, R. (1997) Competitive brain activity in visual attention. *Curr. Opin. Neurobiol.*, **7**, 255–261.
- Gitelman, D.R., Nobre, A.C., Parrish, T.B., LaBar, K.S., Kim, Y.H., Meyer, J.R. & Mesulam, M.M. (1999) A large-scale distributed network for covert spatial attention. *Brain*, **122**, 1093–1106.
- Goebel, R., Khorram-Sefat, D., Muckli, L., Hacker, H. & Singer, W. (1998) The constructive nature of vision: direct evidence from fMRI studies of apparent motion and motion imagery. *Eur. J. Neurosci.*, **10**, 1563–1573.
- Goldberg, M.E. & Segraves, M.A. (1989) The visual and frontal cortices. In Wurtz, R.H. & Goldberg, M.E. (eds), *Neurobiology of Saccadic Eye Movements*. Elsevier Science, Amsterdam, pp. 283–313.
- Gottlieb, J.P., Kusunoki, M. & Golberg, M.E. (1998) The representation of visual salience in monkey parietal cortex. *Nature*, **391**, 481–484.
- Grossberg, S., Mingolla, E. & Ross, W.D. (1994) A neural theory of attentive visual search: interactions of boundary, surface, spatial, and object representations. *Psychol. Rev.*, **101**, 470–489.
- Hopfinger, J.B., Buonocore, M.H. & Mangun, G.R. (2000) The neural mechanisms of top-down attentional control. *Nature Neurosci.*, **3**, 284–291.
- Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R. & Ungerleider, L.G. (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, **22**, 751–761.
- Le, T.H., Pardo, J.V. & Hu, X. (1998) 4 T-fMRI study of nonspatial shifting of selective attention: cerebellar and parietal contributions. *J. Neurophysiol.*, **79**, 1535–1548.

- Linden, D.E.J., Prvulovic, D., Formisano, E., Völlinger, M., Zanella, F.E., Goebel, R. & Dierks, T. (1999) The functional neuroanatomy of target detection: an fMRI study of visual and auditory oddball tasks. *Cereb. Cortex*, **9**, 815–823.
- Luck, S.J., Hillyard, S.A., Marguin, G.R. & Gazzaniga, M.S. (1994) Independent attentional scanning in the separated hemispheres of split-brain patients. *J. Cognit. Neurosci.*, **6**, 84–91.
- Luck, S.J., Girelli, M., McDermott, M.T. & Ford, M.A. (1997a) Bridging the gap between monkey neurophysiology and human perception: an ambiguity resolution theory of visual selective attention. *Cognit. Psychol.*, **33**, 64–87.
- Luck, S.J., Chelazzi, L., Hillyard, S.A. & Desimone, R. (1997b) Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.*, **77**, 24–42.
- Luck, S.J. & Vogel, E.V. (1997) The capacity of visual working memory for features and conjunctions. *Nature*, **390**, 279–281.
- Lumer, E.D., Friston, K.J. & Rees, G. (1998) Neural correlates of perceptual rivalry in the human brain. *Science*, **280**, 1930–1934.
- Martinez, A., Anllo-Vento, L., Sereno, M.I., Frank, L.R., Buxton, R.B., Dubowitz, D.J., Wong, E.C., Hinrichs, H., Heinze, H.J. & Hillyard, S.A. (1999) Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neurosci.*, **2**, 364–369.
- Mesulam, M.M. (1981) A cortical network for directed attention and unilateral neglect. *Ann. Neurol.*, **10**, 309–315.
- Paus, T. (1996) Location and function of the human frontal eye field: a selective review. *Neuropsychologia*, **34**, 475–483.
- Posner, M.I. & Petersen, S.E. (1990) The attention system of the human brain. *Annu. Rev. Neurosci.*, **13**, 25–42.
- Posner, M.I. & Dehaene, S. (1994) Attentional networks. *Trends Neurosci.*, **17**, 75–79.
- Schall, J.D., Morel, A., King, D.J. & Bullier, J. (1995) Topography of cortical afferents to frontal eye field in macaque: functional convergence and segregation of processing streams. *J. Neurosci.*, **15**, 4464–4487.
- Schall, J.D. & Bichot, N.P. (1998) Neural correlates of visual and motor decision processes. *Curr. Opin. Neurobiol.*, **8**, 211–217.
- Talairach, J. & Tournoux, P. (1988) *Co-Planar Stereotactic Atlas of the Human Brain*. Thieme, New York.
- Tanaka, K. (1997) Mechanisms of visual object recognition: monkey and human studies. *Curr. Opin. Neurobiol.*, **7**, 523–529.
- Tootell, R.B.H., Dale, A.M., Sereno, M.I. & Malach, R. (1996) New images from human visual cortex. *Trends Neurosci.*, **19**, 481–489.
- Tootell, R.B.H., Hadjikhani, N., Hall, E.K., Marrett, S., Vanduffel, W., Vaughan, J.T. & Dale, A.M. (1998) The retinotopy of visual spatial attention. *Neuron*, **21**, 1409–1422.
- Treisman, A.M. (1993) The perception of features and objects. In Baddeley, A. & Weiskrantz, L. (eds), *Attention: Selection, Awareness, and Control*. Clarendon Press, Oxford, pp. 5–35.
- Treisman, A.M. & Gelade, G. (1980) A feature-integration theory of attention. *Cognit. Psychol.*, **12**, 97–136.
- Vandenberghe, R., Dupont, P., De Bruyn, B., Bormans, G., Mortelmans, L. & Orban, G.A. (1996) The influence of stimulus location on the brain activation pattern in detection and orientation discrimination. *Brain*, **119**, 1263–1276.
- Wojculik, E. & Kanwisher, N. (1999) The generality of parietal involvement in visual attention. *Neuron*, **23**, 747–764.
- Wolfe, J. (1994) Guided search 2.0. A revised model of visual search. *Psychonomic Bull. Rev.*, **1**, 202–228.