

Visual Feature and Conjunction Searches of Equal Difficulty Engage Only Partially Overlapping Frontoparietal Networks

Tobias H. Donner,* Andreas Kettermann,† Eugen Diesch,‡ Florian Ostendorf,*
Arno Villringer,* and Stephan A. Brandt*

*Department of Neurology, Charité, Humboldt-University, Berlin; †Institute for Psychology, Technical University, Berlin; and

‡Department of Clinical and Cognitive Neuroscience, Central Institute of Mental Health, Mannheim, Germany

Received January 16, 2001

According to a classical view of visual object recognition, targets are detected “preattentively” if they carry unique features, whereas attention has to be deployed serially to object locations for feature binding if the targets can be distinguished from distracters only in terms of their feature conjunctions. Consistent with this view, recent reports suggest a contribution of the posterior parietal cortex (PPC; one major region controlling spatial attention) to conjunction search as opposed to feature search. However, PPC engagement in conjunction search might also reflect feature-based attention or the difficulty of target selection. The present fMRI study compared regions and amplitudes of cortical activity reflecting the attention mechanisms of a conjunction and a feature search of equal difficulty performed during maintenance of fixation. Attention-related activity was assessed by comparing each hard feature and conjunction search with an easy feature search. Hard feature and conjunction search activated overlapping regions in multiple PPC areas and in the frontal eye field (FEF). Most consistent PPC overlaps were located in the anterior and posterior intraparietal sulcus (IPS). The response amplitude of posterior IPS did not differ between both search tasks. However, the IPS junction with the transverse occipital sulcus and the FEF responded at a higher amplitude during conjunction search. Moreover, regions of the prefrontal cortex and the PPC were activated only during either hard feature or conjunction search. These findings suggest that equally difficult visual searches for features and conjunctions are controlled by overlapping frontoparietal networks, but also that both search types involve specific mechanisms. © 2002 Elsevier Science

Key Words: attention; binding; posterior parietal cortex; frontal eye field; prefrontal cortex; fMRI; human.

INTRODUCTION

Current evidence indicates that the human brain employs mechanisms of selective attention for binding

distributed representations of elementary visual features (such as color and orientation; Felleman and Van Essen, 1991; Treisman, 1993) to coherent objects (Reynolds and Desimone, 1999; Treisman, 1996; Wolfe and Cave, 1999). For example, finding an object defined by a certain feature conjunction in an array of multiple objects appears to require sequential sampling of object locations by focal attention which is reflected by an increase of search time per additional object in the array (Treisman, 1993, 1996; Wolfe and Cave, 1999; but see Duncan and Humphreys, 1989). In contrast, earlier psychophysical results suggested that visual search for single features was accomplished without serial attention since search time was independent of the number of objects in the array (Treisman and Gelade, 1980).

However, subsequent studies revealed that search difficulty (as measured by the increase of search time per additional object) varies continuously between easy feature and hard conjunction tasks (Wolfe, 1998). The conscious identification of *any* search target may require attention, whether or not its features have to be combined (Chelazzi, 1999; Duncan and Humphreys, 1989; Nakayama and Josephs, 1998; Sagi and Julesz, 1986; Treisman 1993; Wolfe, 1994; but see Braun and Julesz, 1998). The attentional demands of a visual search may depend on the relative salience of distracters: Conjunction search might generally be demanding because distracters are similar to the target (Duncan and Humphreys, 1989). The difficulty of feature search can also be increased by the presence of salient distracters (Wolfe, 1994).

At the neural level, a large-scale network comprising the human posterior parietal cortex (PPC) and frontal eye field (FEF) seems to control selective attention by sending “bias-signals” to the early visual areas (Corbetta, 1998; Kastner *et al.*, 1999; Mesulam, 1990; Posner and Dehaene, 1994; Reynolds and Desimone, 1999). Evidence from neuroimaging and lesion studies in humans suggests that the PPC also contributes to visual feature binding (Corbetta and Shulman, 1998;

Robertson, 1998; Treisman, 1996): A PET study reported activation of the PPC during feature conjunction search, but not during easy visual searches for single features (Corbetta *et al.*, 1995). This result was corroborated by the impairment of conjunction search as opposed to easy feature search by transcranial magnetic stimulation (TMS) over the PPC (Ashbridge *et al.*, 1997) as well as uni- and bilateral PPC lesions (Arguin *et al.*, 1993; Robertson *et al.*, 1997). Moreover, patients with bilateral PPC lesions have also been reported to miscombine object features (Friedman-Hill *et al.*, 1995; Humphreys *et al.*, 2000; Robertson *et al.*, 1997).

On the other hand, there are at least two lines of evidence suggesting that the involvement of the PPC and FEF in visual search may not be binding-specific but rather reflect more general attentional mechanisms. First, the PPC and FEF have been shown to carry topographic representations of visual salience in macaque monkeys (Colby and Goldberg, 1999; Gottlieb *et al.*, 1998; Schall and Thompson, 1999; Bichot and Schall, 1999). If the difficulty of spatial target selection during search depends on the relative salience of distracters as represented in the PPC and FEF, then this difficulty should engage these areas irrespective of the necessity of feature binding. Second, visual search may involve nonspatial attention directed to the features of the target object represented in working memory (Duncan and Humphreys, 1989; Wolfe, 1994). Both neuroimaging in humans (Wojciulik and Kanwisher, 1999) and single-unit recordings in monkeys (Serenio and Maunsell, 1998) have revealed that the PPC subregions controlling spatial selection are also implicated in the selection of nonspatial features. Thus, the PPC might also be engaged in feature-based selection mechanisms during visual search in the absence of a binding problem.

The aim of the present fMRI study was to examine whether independent, identical, or overlapping frontoparietal networks are engaged in the attention mechanisms of *difficulty-matched* visual searches for features and conjunctions. Therefore, the regions and amplitudes of attention-related cortical activity during a covert conjunction search and a covert feature search of equal difficulty were compared. The feature search was rendered difficult by a low ratio of target-to-distracter salience. Exploratory eye movements were precluded by brief search array presentations. Attention-related activity was assessed by comparing the hard feature search and the conjunction search with an easy feature search in approximately identical search arrays.

METHODS

Subjects

Eight male students from the Humboldt-University of Berlin without any history of neurological or psychi-

atric disorders served as subjects in the study, which was conducted in conformity with the declaration of Helsinki. Their age ranged from 23 to 30 years. Subjects were paid for their participation. Other than one subject (TD), all were naïve to the purpose of the experiment. Subjects had normal or corrected-to-normal visual acuity. In all cases, visual acuity was sufficient (refraction below -4 diopters) for the viewing distance of 20 cm in the fMRI scanner so that correcting lenses did not have to be employed. Subjects reported normal color vision, but were not tested in this respect.

Stimuli and Psychophysical Procedure

The visual search arrays presented were composed of four square clusters made up of colored bars (Fig. 1). The orientation of bars within a cluster was either vertical or horizontal; bar color was either yellow or blue. The clusters were embedded in a texture consisting of black diagonal bars on a light gray background. There was one cluster in each quadrant of the visual field. Each cluster subtended 7° of visual angle and was centered on an imaginary circle 7° off the fixation point. Subjects had to maintain central fixation during search. To minimize the occurrence of exploratory eye movements, the search arrays were presented for only 80 ms and subsequently masked.

The experimental condition ("Hard Feature") was a difficult search for a cluster of vertical bars among clusters of horizontal bars. One-half of the clusters were yellow, the other half were blue. The difficulty of this search task was established by a manipulation described below. The baseline condition ("Easy Feature") was a less demanding search for a cluster of yellow bars among clusters of blue bars. One-half of the clusters were vertical, the others were horizontal. Clusters were physically identical across conditions. Hard Feature was compared with Easy Feature in order to isolate cortical activity reflecting the selection mechanisms of visual search from cortical activity reflecting visual encoding of the search arrays as well as preparation and execution of the motor response. In a previous fMRI study, in which identical fMRI parameters were used and the same subjects were scanned, a "Conjunction" condition (search for a cluster of vertical and yellow bars; Fig. 1B) had been compared with the same Easy Feature condition (Donner *et al.*, 2000a). In the present study, we intended to compare the regions of activation found during Hard Feature and Conjunction within subjects in order to test whether the selection mechanisms of a difficult feature search engage the same or different cortical regions as those of a conjunction search. It is important to note that the difference between Hard Feature and Easy Feature as well as the difference between Conjunction and Easy Feature might reflect a combination of a number of different selection mechanisms employed during

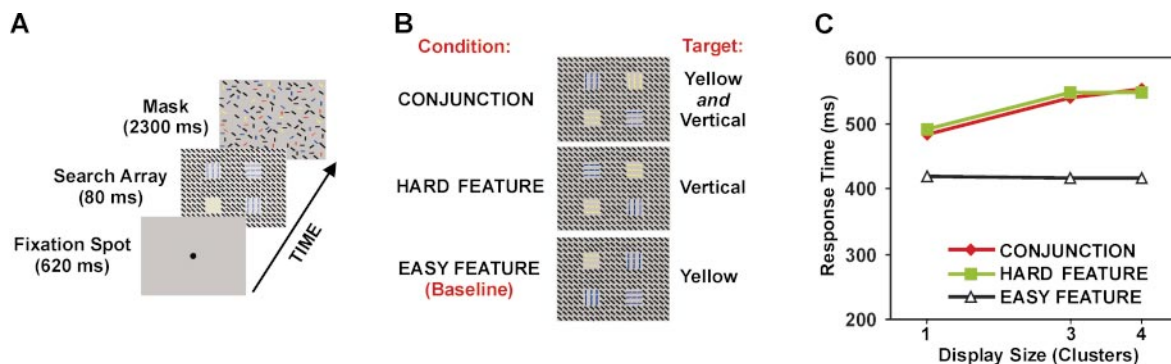


FIG. 1. Visual search tasks. (A) Sequence of stimuli. Each frame represents the display at a different time point of a trial. Search arrays were preceded by a fixation spot and masked after 80 ms. (B) Visual search conditions. Exemplary “target-present trials” are shown for the Hard Feature, Easy Feature, and Conjunction tasks. The target cluster consisted of vertical bars of either color in Hard Feature (lower right quadrant), yellow bars of either orientation in Easy Feature (upper left quadrant), and of yellow *and* vertical bars in Conjunction (upper right quadrant). Subjects were instructed to fixate and to indicate the absence or presence of the target. Due to the higher luminance of the yellow clusters, the ratio of target to distracter salience was lower in Hard Feature, rendering search more difficult than in Easy Feature. (C) Response time \times display size functions. Response times from the psychophysical control study are plotted as a function of display size for the three search conditions (Conjunction, Hard Feature, and Easy Feature).

search. In particular, it might reflect feature-based attention directed to the relevant orientation as well as serial shifts of spatial attention (Duncan and Humphreys, 1989; Treisman, 1993; Wolfe, 1994).

Using the same Easy Feature search condition as a baseline condition in both studies allowed us to also compare fMRI response amplitudes during Hard Feature and Conjunction. Thus it allowed us to investigate whether the selection mechanisms of a difficult feature search may activate the FEF and the PPC to the same degree as those of a conjunction search. Since we aimed to exclusively compare attention-related fMRI activity during Hard Feature and Conjunction we had to present clusters of bars in Hard Feature that were physically identical to those presented in Conjunction. In order to render Hard Feature more difficult than Easy Feature, the ratio of target and distracter salience had to be decreased in Hard Feature. Decreasing the ratio of target-to-distracter salience in Hard Feature while presenting identical clusters as in Conjunction could be accomplished by a modulation of the clusters’ luminance (Nothdurft, 1993): The yellow clusters had a higher luminance-derived salience (193 cd/m^2 ; background luminance 6.8 cd/m^2) than the blue clusters (14.3 cd/m^2). As a result, in Hard Feature one-half of the distracters were high salient (bright yellow), and one-half of the targets were low salient (dim blue). In contrast, all distracters were low salient (dim blue), and all targets were high salient (bright yellow) in Easy Feature.

Stimulus presentation was controlled by a personal computer running an adapted version of the RTGRAF software (Diesch, 1994). Stimuli were projected onto a back-projection screen by means of an LCD projector (NEC 8000 G; Stuttgart, Germany). Lying in the magnet, subjects fixated the screen via a mirror. Subjects

used a fiber-optic two-button response box for report. In both conditions, 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. Speed and accuracy of response were stressed and subjects were instructed to maintain central fixation during the whole experiment. Response times and correctness of response were recorded. Conditions were performed in alternating blocks of 24 s duration consisting of eight trials. One run consisted of 8 blocks of each condition (16 blocks in total). A visual cue instructed subjects at the beginning of each task block to switch from one search condition to the other. Trials were contiguous within blocks. Each subject performed four runs.

We intended to exclude a contamination of attention-related differential fMRI activity with potential oculomotor and sensory effects due to a difference in saccade rates and due to the slight difference between the arrangement of clusters in both conditions (Fig. 1). Therefore, eye movement recordings with an infrared oculography system (AMTech, Weinheim, Germany) during Conjunction, Hard Feature, and Easy Feature as well as fMRI recordings during passive viewing of the stimuli were performed in extra sessions prior to the main experiment. In the passive viewing experiments, the same stimuli presented in the blocks of the active search experiments (Hard Feature vs Easy Feature; Conjunction vs Easy Feature) were presented in the same block-wise fashion. Here, subjects were instructed to observe the stimuli passively while maintaining central fixation.

In order to obtain a psychophysical measure for the difficulty of the Hard Feature, Easy Feature, and Conjunction search conditions the slopes of functions relating response time to display size (i.e., the number of

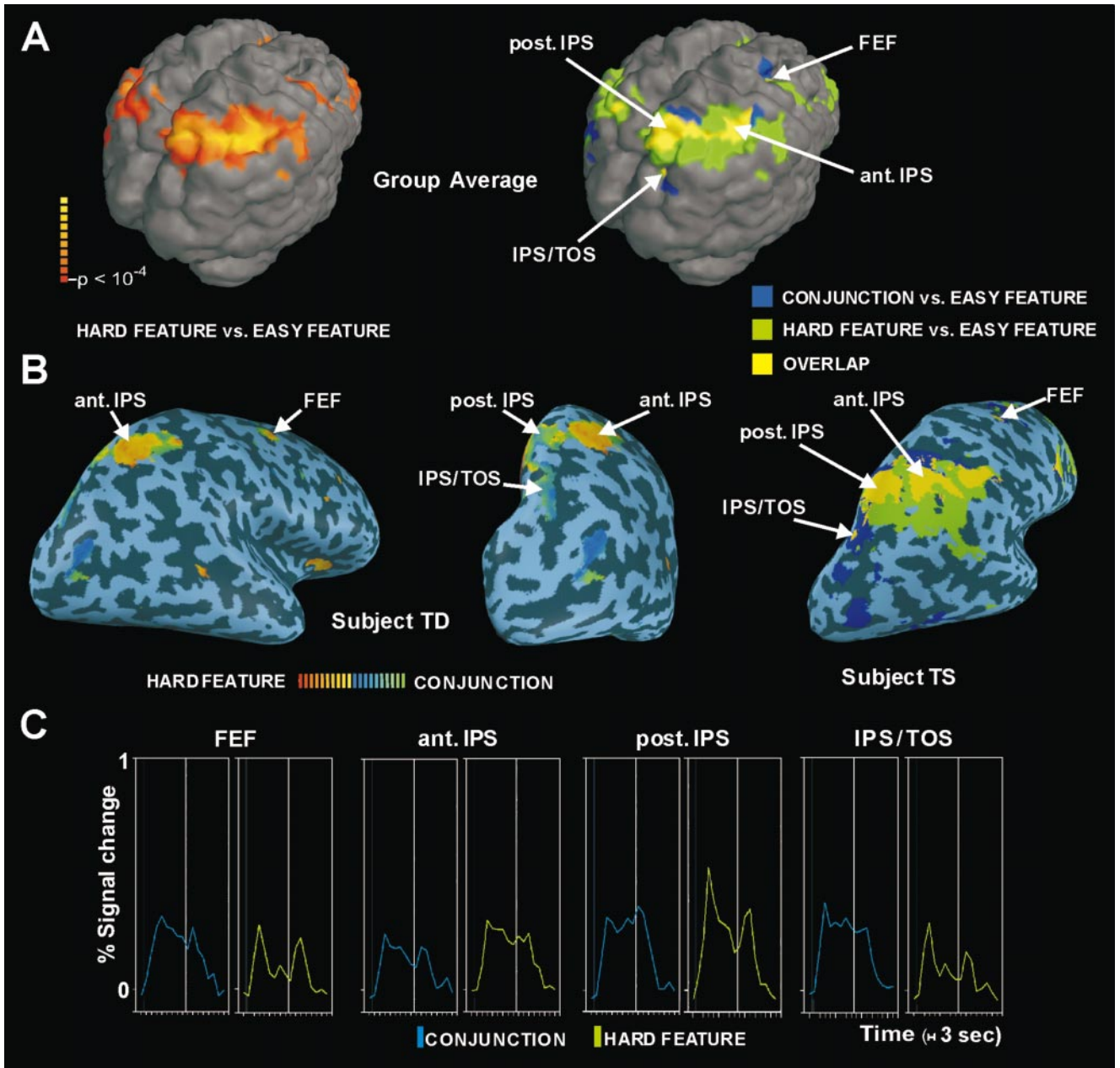


FIG. 2. Activation patterns during Hard Feature and Conjunction. (A) Group activation maps, superimposed on one subject's rendered brain (dorsolateral view). Left: Activation pattern produced by difficult Hard Feature relative to easy Easy Feature. Right: Overlay of activation produced by Hard Feature and Conjunction. Abbreviations: ant. IPS, anterior intraparietal sulcus; post. IPS, posterior intraparietal sulcus; IPS/TOS, junction of the intraparietal and the transverse occipital sulcus. (B) Individual activation maps, superimposed on inflated right hemispheres. Left: Contrast between modulation strength during Hard Feature and Conjunction in subject TD (lateral and posterior view). Right: Overlay of activation produced by Hard Feature and Conjunction in subject TS (dorsolateral view). (C) Mean time courses of the unsmoothed and normalized fMRI signal during blocks of Conjunction (green) and blocks of Hard Feature (blue). Regions of interest are the regions of consistent activation during Conjunction. Signal intensity is normalized to the mean of Easy Feature. The beginning of the baseline (Easy Feature) period block is indicated by a white vertical line.

clusters in the display) had to be determined (Wolfe, 1998). Therefore, we performed a psychophysical control study in 14 subjects: Response times were measured as a function of display size using one, three, and four clusters (One, Three, Four). In all conditions, the clusters appeared randomly in the visual field quadrants.

FMRI Procedure

MRI was performed using a 1.5-T Magnetom Vision magnetic resonance imaging system (Siemens Medical Systems, Erlangen, Germany). Subjects' heads were stabilized with a bite bar. We used an echo-planar

sequence optimized for the blood oxygenation level-dependent contrast (TR/TE = 3000/60 ms; FA 90°; in-plane resolution 4 mm²) in all experiments. Four functional runs were performed in all experiments. During each functional run, 128 volumes of 24 axial slices (5 mm thickness, spanning the cerebral cortex) were collected. 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°; TI = 100 ms; voxel size 1 mm³).

Data Analysis

Response times from the psychophysical control study were entered into a three-way repeated-measures ANOVA with the factors task (Conjunction, Hard Feature, Easy Feature), display size (One, Three, Four), and target (Present, Absent). Regression analysis was used to fit linear response time \times display size functions for the three different search tasks (Conjunction, Hard Feature, Easy Feature). The slopes of these functions were compared by means of a one-way repeated-measures ANOVA.

Response times from the fMRI-experiments (display size Four only) were compared across conditions (Hard Feature, Easy Feature) using Wilcoxon's sign rank test. Within Hard Feature, response times were compared between trials with (bright) yellow targets and trials with (dim) blue targets using Wilcoxon's sign rank test. Response times were then Z transformed for each run in order to compare performance during Hard Feature and Conjunction in a way that accords with the fMRI data analysis (see below). Z scores for Hard Feature and Conjunction were analyzed using a t test.

fMRI data were analyzed using the BrainVoyager 3.7 software package (Max Planck Society, Germany; Goebel *et al.*, 1998). All data from each subject were transformed into Talairach space (Talairach and Tournoux, 1988). Functional volumes were coregistered with the three-dimensional structural data sets in order to generate volume-time courses. Volume-time courses were spatially and temporally smoothed with a Gaussian kernel (FWHM 4 mm/9 s) and Z transformed. Multiple regression analysis was performed to compute statistical maps. Predictors for Hard Feature and Conjunction were specified. Predictors were generated by convolving a square-wave function representing the time course of experimental conditions with a γ function ($\delta = 2.5$; $\tau = 1.25$ s⁻¹) modeling the hemodynamic impulse response (Boynton *et al.*, 1996; Cohen, 1997). Further predictors for each run and each subject were included. Activation patterns were analyzed independently for the group average and for five of the eight subjects for whom cortical surface reconstructions had been generated (Donner *et al.*, 2000a). These surface reconstructions allowed for a precise localization of activated regions with respect to previously mapped

individual functional areas and with respect to individual anatomical landmarks. Activation maps for Hard Feature relative to Easy Feature and for Conjunction relative to Easy Feature were computed and thresholded at $P < 10^{-4}$ (uncorrected for multiple comparisons). Additional maps for the contrast between Hard Feature and Conjunction were computed. We identified regions of overlap (ROOs) between regions activated during Hard Feature and Conjunction: both maps were overlaid, yielding green for voxels activated during Hard Feature only, blue for voxels activated during Conjunction only, and yellow for ROO voxels activated in both conditions.

In order to compare the mean fMRI responses of individual areas during Hard Feature and Conjunction, those areas consistently activated during Conjunction across subjects were selected as regions of interests (ROIs): the FEF, the anterior and the posterior part of the intraparietal sulcus (IPS), and the IPS junction with the transverse occipital sulcus (TOS). ROIs were marked on the cortical surfaces for each of the five subjects; unsmoothed fMRI time courses of each ROI were averaged across voxels, repetitions of blocks of each condition (Hard Feature, Conjunction), hemispheres, and the five subjects. The amplitudes were normalized to the mean of Easy Feature. Finally, normalized response amplitudes of Hard Feature and Conjunction (with 6-s delay for hemodynamics) were compared for each ROI using Wilcoxon's sign rank test.

RESULTS

Psychophysical Results

Response times from the psychophysical control study are plotted as a function of display size for the search conditions Conjunction, Hard Feature, and Easy Feature in Fig. 1C. Conjunction and Hard Feature each yielded response time \times display size functions with positive slopes of 23.8 and 20.1 ms/cluster, respectively. Easy Feature yielded a flat function with a slope of -0.7 ms/cluster. The differences between slopes produced by the search tasks were significant according to ANOVA ($P < 0.01$). Single comparisons revealed a higher slope of Conjunction and Hard Feature compared to Easy Feature ($P < 0.01$) and no difference between the slopes of Conjunction and Hard Feature ($P = 0.39$).

This pattern of results was also reflected by a three-way ANOVA of the response times: The main effects of task and display size, as well as the interaction of task and display size, attained significance [task, $F(2, 26) = 69.2$, $P < 0.01$; display size, $F(2, 26) = 39.9$, $P < 0.01$; task \times display size, $F(4, 52) = 20.1$, $P < 0.01$]. Moreover, the main effect of target and the interaction of task and target, as well as the interaction of task, display size, and target, attained significance [target,

$F(1, 13) = 53.7, P < 0.01$; task \times target: $F(2, 26) = 11.6, P < 0.01$; task \times display size \times target, $F(4, 52) = 4.73, P < 0.01$]. Taken together, the psychophysical results suggest equally high difficulty of Conjunction and Hard Feature, as well as low difficulty of Easy Feature.

During the fMRI experiments (display size Four only), accuracy in task performance was high in both Easy Feature (95.83%) and Hard Feature (95.31%). Mean response times were 535.84 ms in Hard Feature and 442.87 ms in Easy Feature. Response times were significantly longer in Hard Feature than in Easy Feature (Wilcoxon's $T = 0, P < 0.01$). Within Hard Feature, (bright) yellow vertical targets were found significantly faster than the (dim) blue vertical targets (Wilcoxon's $T = 0, P < 0.01$), supporting the hypothesized salience effect of luminance. Z scores of response times were 0.44 in Hard Feature and 0.42 in Conjunction. There was no significant difference between the Z transformed response times from Hard Feature and Conjunction [$t(31) = 0.471, P = 0.641$].

Subjects' ability to maintain stable fixation during search was verified for Easy Feature and Conjunction previously (Donner *et al.*, 2000a) and was additionally tested in two subjects for Hard Feature prior to fMRI. Subjects made saccades larger than 1° of visual angle in less than 3% of the trials. Furthermore, no significant differences in the number of saccades were observed between both conditions.

FMRI Results

The comparison of passive viewing of the stimuli presented during Hard Feature, Easy Feature, and Conjunction did not yield differential activation in any cortical area at a liberal threshold of $P < 0.01$ (uncorrected) in control experiments. Thus, differential activation between the active conditions should reflect active performance of the search tasks rather than the small differences in retinal stimulation.

The activation patterns during covert visual search are illustrated in Fig. 2. In Fig. 2A, the group average activation pattern between Hard Feature and Easy Feature is shown on the left and the overlay of activation patterns during Hard Feature and Conjunction, each compared to Easy Feature, is shown on the right. The Talairach coordinates of the yellow ROOs are given in Table 1. ROOs were bilaterally present in the dorsal and ventral part of the precentral sulcus, the postcentral sulcus, the anterior and posterior part of the IPS, and the IPS/TOS junction. The dorsal precentral sulcus ROO (in the junction with the superior frontal sulcus) was located in the putative human FEF (Corbetta, 1998; Paus, 1996). However, we also found large regions selectively activated during either Hard Feature or Conjunction. They were located in the prefrontal cortex (BA 46/9) and adjacent to the ROOs in the precentral sulcus and the IPS.

TABLE 1

Talairach Coordinates of Overlapping Activation in Hard Feature and Conjunction: Group Average ($N = 8$)

Cortical region	Brodman area (BA)		x	y	z
Frontal cortex FEF	6	R	23	-11	49
	6	L	-26	-8	48
	6	L	-53	-4	39
PreCeS ventr.	6	L	-37	-5	28
Parietal cortex	5	R	38	-47	48
		L	-43	-50	52
Ant. IPS	7	R	30	-56	48
	7	L	-40	-56	52
Post. IPS	7	R	13	-65	48
		L	-18	-71	46
IPS/TOS	19	R	22	-71	27
		L	-32	-74	21

Note. Values are Talairach coordinates of the centers of mass of overlap regions. R, right; L, left; FEF, frontal eye field; PreCeS, precentral sulcus; PostCeS, postcentral sulcus; IPS, intraparietal sulcus; IPS/TOS, junction of intraparietal and transverse occipital sulcus.

Figure 2B shows the contrast between Hard Feature and Conjunction in subject TD (left) and the overlay of activation patterns during Hard Feature and Conjunction in subject TS (right). Modulation strengths were similar in both conditions for most voxels in the activated areas. In parts of anterior and posterior IPS, modulation strengths were even higher during Hard Feature than during Conjunction. Of the five subjects studied with surface reconstruction techniques, four displayed ROOs in the FEF and in anterior and posterior IPS. Three subjects displayed ROOs in postcentral sulcus and two in IPS/TOS. In accordance with the group results, regions in the prefrontal cortex (BA 46/9) and regions adjacent to the ROOs in the precentral sulcus and the IPS were selectively activated during either Hard Feature or Conjunction as illustrated for subject TS in Fig. 2B. The normalized average fMRI time courses during Hard Feature and Conjunction of the ROIs in FEF, anterior and posterior IPS, and IPS/TOS are plotted in Fig. 2C.

The normalized response amplitudes of the FEF, anterior and posterior IPS, and IPS/TOS during Hard Feature and Conjunction are displayed in Fig. 3. In anterior IPS the amplitude of activation was higher in Hard Feature rather than in Conjunction (Wilcoxon's $T = 0, P < 0.01$). Conversely, in the FEF and IPS/TOS, the activation was higher in Conjunction (FEF, Wilcoxon's $T = 1, P < 0.05$; IPS/TOS, Wilcoxon's $T = 0, P < 0.01$). There was no significant difference in posterior IPS (Wilcoxon's $T = 9, P = 0.25$). The different patterns of response amplitudes of the parietal subregions suggest that these regions might be distinct functional areas.

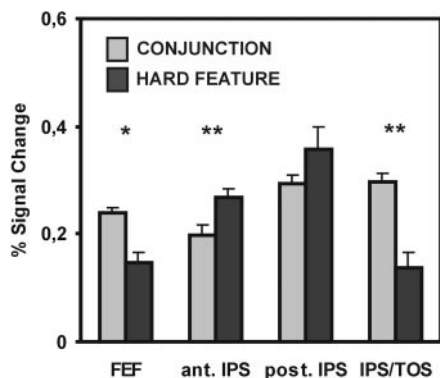


FIG. 3. fMRI responses during Hard Feature and Conjunction. Normalized and averaged response amplitudes of the regions in FEF, anterior and posterior IPS, and IPS/TOS of significant activation during Conjunction are noted for Conjunction and Hard Feature. Error bars represent standard error. Significant differences between Conjunction and Hard Feature are indicated by "*" for $P < 0.05$ and by "**" for $P < 0.01$.

DISCUSSION

We recorded differential cortical activation during a hard feature search (yielding an increase of response time per additional object in the array) and an easy feature search (yielding no increase of response time per additional object). We compared activation during the hard feature search with activation during search for a feature conjunction recorded in the same subjects. At the behavioral level, the hard feature and conjunction search were indistinguishable as determined by the identical increase in their response time \times display size functions. Consistent overlap of cortical activity during hard feature and conjunction search was found in the FEF and in anterior and posterior IPS. Regions activated only during hard feature search or during conjunction search were consistently found in the prefrontal cortex and adjacent to the overlaps in the FEF and the IPS. Posterior IPS responded at equal amplitudes during hard feature and conjunction search. Anterior IPS responded at a higher amplitude during hard feature search and the FEF and IPS/TOS responded at a higher amplitude during conjunction search.

The observed activations during feature and conjunction search most likely reflect covert selective attention. Of course, the slightly different search arrays should elicit slightly different neuronal responses in visual areas. However, these differences should be expected primarily in the occipitotemporal areas of the visual system where the response properties are suited to discriminate different arrangements of orientations and colors in the visual field; these differences should elicit smaller or no differential responses in the occipitoparietal areas primarily performing spatial computations and in the FEF (Courtney *et al.*, 1997; Felleman and Van Essen, 1991; Tootell *et al.*, 1998). The fMRI

activations produced by the active search tasks were largely restricted to these parietal areas and the FEF. Moreover, possible differences in neuronal responses during both conditions were too small to be measured as fMRI responses during passive viewing of the same stimuli that had been presented during the active search tasks. Therefore, the differential fMRI responses of posterior parietal areas and the FEF during active search should not be contaminated by sensory activation of parietal and FEF neurons.

Saccadic eye movements are also unlikely to account for the recorded differential activations. First, eye movements were monitored and found to be negligible during an oculographic control experiment. More importantly, there was no difference in the frequency of saccades between both conditions. Second, if saccades had varied systematically between both conditions, then robust differential activations should have been detected in early visual cortex due to differences in retinal slip (Brandt *et al.*, 1999). We found no such differential activation in early visual cortex. Third, we are not aware of any studies suggesting that small eye movements subserving gaze stabilization (e.g., microsaccades) during fixation vary with the attentional demands of visual tasks.

Finally, the activation should not be related to non-selective modulatory mechanisms (such as arousal) induced by the difference in difficulty of both feature search tasks, since IPS/TOS and anterior and posterior IPS are activated by difficult tasks that demand selective visual attention, but not by task difficulty in non-visual domains (Wojciulik and Kanwisher, 1999).

If the activation patterns during feature and conjunction search in the present study indeed reflect selective attention, then the present results imply that the contribution of human cortical regions located in the FEF and IPS to the attention mechanisms of visual search is not restricted to tasks posing a feature binding problem for the visual system. Instead, overlapping frontoparietal networks are engaged, partly to the same degree, by feature and conjunction search, provided that the search tasks are matched in difficulty. This might imply that the different search tasks share neural control mechanisms. On the other hand, the results also indicate that difficult feature and conjunction searches, which are indistinguishable by their behavioral signatures, may still produce different magnitudes of activation in the FEF and certain IPS subregions. In addition, they may produce a large degree of regionally distinct activations in prefrontal cortex as well as in PPC regions adjacent to the IPS. These observations imply that the different search tasks may also involve specific neural mechanisms, one of which might be related to feature binding.

Leonards *et al.* (2000) also reported activations during a feature search task at parietal locations similar to those of the overlaps in the present study. However,

their feature search task was very easy and correspondingly, they recorded weaker responses in these regions during the feature task compared to a more demanding conjunction search task. Moreover, they found no activity in the FEF. In contrast to the findings of Leonards *et al.* (2000) and our present findings, several lesion, brain imaging, and TMS studies argue against an involvement of the PPC (and the FEF) in feature search. Using PET, Corbetta *et al.* (1995) found an increase in cerebral blood flow in the right PPC during a conjunction search, but no such activation during easy feature search tasks in any area controlling visuospatial attention. By interference with performance, single-pulse TMS over the PPC ensured the functional significance of PPC activation for conjunction search as opposed to an easy feature search task (Ashbridge *et al.*, 1997). Uni- and bilateral lesions of the PPC impaired conjunction search performance but had no effect on search performance in easy feature tasks (Arguin *et al.*, 1993; Robertson *et al.*, 1997). The discrepancy between the two lines of evidence might be related to the nature of the FEF and PPC contributions to covert spatial and nonspatial visual selection. Possible ways to reconcile the findings are discussed below.

Representation of Saliency, Feature Binding, and Visuomotor Areas

The employment of attention in feature search has been demonstrated in several psychophysical studies (Joseph *et al.*, 1997; Nothdurft, 1999; Sagi and Julesz, 1985). However, in easy feature search tasks such as those used in the PET study of Corbetta *et al.* (1995) and the TMS study of Ashbridge *et al.* (1997), the high-saliency target might induce high stimulus-driven activity yielding a strong “bottom-up bias” in the occipitotemporal stream (Chelazzi, 1999; Reynolds and Desimone, 1999) which might be sufficient for immediate target selection (Nothdurft, 1999; Wolfe, 1994). Therefore, additional spatial bias signals from the PPC and the FEF might not be necessary for guiding attention to the target.

By contrast, if targets have a sufficiently low saliency compared to distracters, feature search can be as difficult as conjunction search (Duncan and Humphreys, 1989; Wolfe, 1994). This was the case in the present experiment because the hard feature and conjunction search yielded identical slopes of the response time \times display size functions as well as identical absolute response times. We hypothesize that the difficulty of hard feature search was caused by a lower ratio of target-to-distracter saliency compared to the easy feature task due to the saliency effect of luminance in orientation search (see Material and Methods; Nothdurft, 1993). Parts of the anterior and posterior IPS and of the FEF displayed robust activation during both

the hard feature and the conjunction task of our study, perhaps because they may be critical for the selection of low-saliency targets regardless of whether their features need to be conjoined.

Results from single-unit recordings implicate that the macaque’s lateral intraparietal area (LIP) and FEF contain topographic “saliency maps” on which objects are coded for both their conspicuousness and behavioral relevance (Bichot and Schall, 1999; Colby and Goldberg, 1999; Gottlieb *et al.*, 1998; Schall and Thompson, 1999). The putative homologues of the macaque’s FEF in the human precentral sulcus (Corbetta, 1998; Paus, 1996) and of the macaque’s LIP in the human IPS (Corbetta, 1998) might also carry representations of saliency. If search is difficult because of similar saliency of target and distracter locations, selection of the target location might operate on the saliency representations in the human IPS subregions and the FEF. These areas might send spatially selective signals to the corresponding location in retinotopic visual areas, thereby biasing the occipitotemporal stream toward representation of the target (Kastner *et al.*, 1999).

On the other hand, the higher response amplitudes of IPS/TOS and the FEF during the conjunction search as well as the selective activation of other parts of the PPC and the precentral sulcus during the conjunction search might imply that in fact, binding-specific neural mechanisms exist within these visuomotor areas. In particular, the role of these mechanisms might be either to bind visual features or to route integrated neural representations to structures responsible for conscious report. This interpretation is consistent with the results of previous fMRI studies of tasks requiring visual feature binding, but lacking the requirement of spatial selection (Perry and Zeki, 2000; Wojciulik and Kanwisher, 1999): These studies demonstrated an involvement of PPC regions located in the superior parietal lobule and closely resembling the regions of selective activation found during the conjunction search in the present study.

Feature-Based Selection by Prefrontal and Posterior Parietal Cortex

Alternatively, the present results may be accounted for in terms of nonspatial selection mechanisms. Neurons in the macaque’s prefrontal cortex and LIP show responses reflecting attention directed to objects or simple shapes (Serenio and Maunsell, 1998; Ungerleider *et al.*, 1998). Human prefrontal cortex and IPS subregions display fMRI activation that can be explained by nonspatial attention directed toward shape features (Donner *et al.*, 2000b; Ungerleider *et al.*, 1998; Wojciulik and Kanwisher, 1999). It is conceivable that the overlapping PPC activations during hard feature and during conjunction search reflect feature-based

selection of vertically oriented items (Duncan and Humphreys, 1989; Wolfe, 1994). On the other hand, this working-memory-driven attention mechanism might also underlie the selective activation of prefrontal areas during the hard feature task (Ungerleider *et al.*, 1998), since this mechanism may have been engaged even more strongly during the hard feature search task than during the conjunction task: in the latter, subjects may have tended to employ the “bottom-up” mechanism of grouping the salient, yellow clusters (Grossberg *et al.*, 1994) and then detecting the presence of an orientation difference within this group.

The overlaps of PPC activations may also reflect nonspatial attention shifts between feature dimensions: In both the hard feature and the conjunction search tasks, subjects may have first selected the subset of yellow clusters and then shifted their attention to the orientation dimension in order to inspect the yellow subset for vertical bars (Grossberg *et al.*, 1994). Shifting attention between nonspatial feature dimensions has also been found to engage the PPC (Le *et al.*, 1998).

Finally, the overlapping PPC activations might be due to the relevance of different spatial frequencies in both hard searches and the easy feature search (see Fig. 1). Switching between spatial frequencies and/or levels of perceptual hierarchy has also been proposed to engage the PPC (Rafal and Robertson, 1995; Fink *et al.*, 1996). However, these studies suggest that attention shifts between different spatial frequencies are controlled by the temporoparietal junction. Maintaining tonic attention on the global level of visual stimuli was reported to activate the right lingual gyrus; maintaining tonic attention on the local level activated the left inferior occipital cortex (Fink *et al.*, 1996). In contrast, we found the IPS and adjacent regions to be differentially activated.

In summary, the current study demonstrates that difficulty-matched visual searches for features and conjunctions engage overlapping cortical regions located in the FEF and in the IPS. Thus, the contributions of these visuomotor regions to the covert selection mechanisms of visual search do not presuppose the necessity to conjoin object features. Rather, it might be more generally determined by the difficulty of spatially serial selection and/or by the engagement of feature-based selection. However, the study also demonstrates that feature and conjunction searches with identical behavioral signatures may produce different degrees of activation of the FEF and IPS subregions and may even engage distinct regions of the prefrontal cortex and the PPC. Taken together, our present findings suggest that conjunction search as well as difficult feature search are controlled by only partially overlapping frontoparietal networks. Further studies should compare the degrees to which feature binding, spatial selection based on saliency, and feature-based selection engage each component of these networks.

ACKNOWLEDGMENTS

This work was supported by the Deutsche Forschungsgemeinschaft, Grants GRK 423 to T. H. Donner and EI-207/2 to S. A. Brandt. We thank Jody Culham, Gabriel Curio, Andreas Lueschow, Christoph Ploner, Sein Schmidt, and two anonymous reviewers for their comments on the manuscript.

REFERENCES

- Ashbridge, E., Walsh, V., and Cowey, A. 1997. Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia* **35**: 1121–1131.
- Arguin, M., Joanette, Y., and Cavanagh, P. 1993. Visual search for features and conjunction targets with an attention deficit. *J. Cognit. Neurosci.* **5**: 436–452.
- Bichot, N. P., and Schall, J. D. 1999. Effects of similarity and history on neural mechanisms of visual selection. *Nat. Neurosci.* **2**: 549–554.
- Boynton, G. M., Engel, S. A., Glover, G. H., and Heeger, D. J. 1996. Linear system analysis of functional magnetic resonance imaging in human V1. *J. Neurosci.* **16**: 4207–4221.
- Brandt, S. A., Takahashni, T., Reppas, J. B., Wenzel, R., Villringer, A., Dale, A. M., and Tootell, R. B. H. 1999. Sensory and motor components of smooth pursuit eye movements in extrastriate cortex: An fMRI study. In *Current Oculomotor Research* (W. Becker, H. Deubel, and T. Mergner, Eds.), pp. 213–222. Plenum, New York.
- Braun, J., and Julesz, B. 1998. Withdrawing attention at little or no cost. *Percept. Psychophys.* **60**: 1–23.
- Chelazzi, L. 1999. Serial attention mechanisms in visual search: A critical look at the evidence. *Psychol. Res.* **62**: 195–219.
- Cohen, M. S. 1997. Parametric analysis of fMRI data using linear systems methods. *NeuroImage* **6**: 93–103.
- Colby, C. L., and Goldberg, M. E. 1999. Space and attention in parietal cortex. *Annu. Rev. Neurosci.* **22**: 319–349.
- Corbetta, M. 1998. Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proc. Natl. Acad. Sci. USA* **95**: 831–838.
- Corbetta, M., Shulman, G. L., Miezin, F. M., and Petersen, S. E. 1995. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* **270**: 802–805.
- Corbetta, M., and Shulman, G. L. 1998. Human cortical mechanisms of visual attention during orienting and search. *Philos. Trans R. Soc. London B* **353**: 1353–1362.
- Courtney, S. M., and Ungerleider, L. G. 1997. What fMRI has taught us about human vision. *Curr. Opin. Neurobiol.* **7**: 554–561.
- Diesch, E. 1994. A high resolution color graphic display four channel software tachistoscope. *Behav. Res. Methods Instrum. Comput.* **26**: 331–335.
- Donner, T., Kettermann, A., Diesch, E., Ostendorf, F., Villringer, A., and Brandt, S. A. 2000a. Involvement of the human frontal eye field and multiple parietal areas in covert visual selection during conjunction search. *Eur. J. Neurosci.* **12**: 3407–3414.
- Donner, T., Kettermann, A., Diesch, E., Villringer, A., and Brandt, S. A. 2000b. Visual search in arrays with single and multiple objects: Differences and overlap of activation in the human attention system. *NeuroImage* **11**: 942.
- Duncan, J., and Humphreys, G. W. 1989. Visual search and stimulus similarity. *Psychol. Rev.* **96**: 433–458.
- Felleman, D. J., and Van Essen, D. C. 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex* **1**: 1–47.
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiack, R. S. J., and Dolan, R. J. 1996. Where in the brain does visual attention select the forest and the trees? *Nature* **382**: 626–628.

- Friedman-Hill, S. R., Robertson, L. C., and Treisman, A. 1995. Parietal contributions to visual feature binding: Evidence from a patient with bilateral lesions. *Science* **269**: 853–855.
- Goebel, R., Khorrám-Sefat, D., Muckli, L., Hacker, H., and 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.
- Gottlieb, J. P., Kusunoki, M., and Golberg, M. E. 1998. The representation of visual salience in monkey parietal cortex. *Nature* **391**: 481–484.
- Grossberg, S., Mingolla, E., and Ross, W. D. 1994. A neural theory of attentive visual search: Interactions of boundary, surface, spatial, and object representations. *Psychol. Rev.* **101**: 470–489.
- Humphreys, G. W., Cinel, C., Wolfe, J., Olson, A., and Klempen, N. 2000. Fractionating the binding process: Neuropsychological evidence distinguishing binding of form from binding of surface features. *Vision Res.* **40**: 1569–1596.
- Joseph, J. S., Chun, M. M., and Nakayama, K. 1997. Attentional requirements in a “preattentive” feature search task. *Nature* **387**: 805–807.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., and 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., and Hu, X. 1998. 4T-fMRI study of nonspatial shifting of selective attention: Cerebellar and parietal contributions. *J. Neurophysiol.* **79**: 1535–1548.
- Leonards, U., Sunaert, S., Van Hecke, P., and Orban, G. A. 2000. Attention mechanisms in visual search—An fMRI study. *J. Cognit. Neurosci.* **12**: 61–75.
- Mesulam, M. M. 1990. Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Ann. Neurol.* **28**: 597–613.
- Nakayama, K., and Joseph, J. S. 1998. Attention, pattern recognition, and pop-out in visual search. In *The Attentive Brain* (R. Parasuraman, Ed.), pp. 278–298. MIT Press, Cambridge, MA.
- Nothdurft, H. C. 1993. Saliency effects across dimensions in visual search. *Vision Res.* **33**: 839–844.
- Nothdurft, H. C. 1999. Focal attention in visual search. *Vision Res.* **39**: 2305–2310.
- Paus, T. 1996. Location and function of the human frontal eye field: A selective review. *Neuropsychologia* **34**: 475–483.
- Perry, R. J., and Zeki, S. 2000. Integrating motion and colour within the visual brain: An fMRI approach to the binding problem. *Soc. Neurosci. Abstr.* **26**: 669.
- Posner, M. I., and Dehaene, S. 1994. Attentional networks. *Trends Neurosci.* **17**: 75–79.
- Rafal, R. D., and Robertson, L. C. 1995. The neurology of attention. In *The Cognitive Neurosciences* (M. S. Gazzaniga, Ed.), pp. 625–648. MIT Press, Cambridge, MA.
- Reynolds, J. H., and Desimone, R. 1999. The role of neural mechanisms of attention in solving the binding problem. *Neuron* **24**: 19–29.
- Robertson, L. C. 1998. Visuospatial attention and parietal function: Their role in object perception. In *The Attentive Brain* (R. Parasuraman, Ed.), pp. 257–278. MIT Press, Cambridge, MA.
- Robertson, L. C., Treisman, A., Friedman-Hill, S. R., and Grabowecy, M. 1997. The interaction of spatial and object pathways: Evidence from Balint’s syndrome. *J. Cognit. Neurosci.* **9**: 295–317.
- Sagi, D., and Julesz, B. 1985. “Where” and “what” in vision. *Science* **228**: 1217–1219.
- Schall, J. D., and Thompson, K. G. 1999. Neural selection and control of visually guided eye movements. *Annu. Rev. Neurosci.* **22**: 2431–2459.
- Sereno, A. B., and Maunsell, J. H. R. 1998. Shape selectivity in primate lateral intraparietal cortex. *Nature* **395**: 500–503.
- Talairach, J., and Tournoux, P. 1988. *Co-planar Stereotactic Atlas of the Human Brain*. Thieme, New York.
- Tootell, R. B. H., Hadjikhani, N. K., Mendola, J. D., Marrett, S., and Dale, A. 1998. From retinotopy to cognition: fMRI in human visual cortex. *Trends Cognit. Sci.* **2**: 174–183.
- Treisman, A. M. 1993. The perception of features and objects. In *Attention: Selection, Awareness, and Control* (A. Baddeley and L. Weiskrantz, Eds.), pp. 5–35. Clarendon, Oxford.
- Treisman, A. M. 1996. The binding problem. *Curr. Opin. Neurobiol.* **6**: 171–178.
- Treisman, A. M., and Gelade, G. 1980. A feature-integration theory of attention. *Cognit. Psychol.* **12**: 97–136.
- Ungerleider, L. G., Courtney, A. M., and Haxby, J. V. 1998. A neural system for visual working memory. *Proc. Natl. Acad. Sci. USA* **95**: 883–890.
- Wojciulik, E., and Kanwisher, N. 1999. The generality of parietal involvement in visual attention. *Neuron* **23**: 747–764.
- Wolfe, J. M. 1994. Guided search 2.0. A revised model of visual search. *Psychonom. Bull. Rev.* **1**: 202–228.
- Wolfe, J. M. 1998. Visual search. In *Attention* (H. Pashler, Ed.), pp. 13–73. Psychology Press, East Sussex.
- Wolfe, J. M., and Cave K. 1999. The psychophysical evidence for a binding problem in human vision. *Neuron* **24**: 11–17.