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## The functional neuroanatomy of visual conjunction search: a parametric fMRI study

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### Abstract

Visual conjunction search is proposed to be a multicomponent process which involves scaling and successive shifts of attention in space as well as object identification. Here, we first mapped brain areas sustaining the proposed attentional subprocesses and then tested whether their activity was modulated by search load, i.e., the number of shifts, as predicted by serial search models. Search load was manipulated indirectly by precueing a varying number of locations at which relevant objects were shown. Multiple subregions within the intraparietal sulcus (IPS) and the prefrontal cortex were activated after cueing. Activity in the right posterior IPS was modulated by the distance of attention shifts and in the left posterior IPS by “zooming out” to cover a large region of the visual field. More anterior subregions of the left IPS responded to object identification irrespective of the need for serial scanning. Corresponding regions in the right IPS were modulated parametrically with respect to search load, along with the right temporoparietal junction. These results support a functional segregation of subregions of the IPS. The posterior regions participate in large-scale shifts and scaling of the attentional focus and the anterior regions in object identification and rapid serial shifts during search. The sustained activation in the frontal eye fields after cueing suggests a role in maintaining attention in the periphery. Together with the findings in early visual areas from this experiment (Müller et al., 2003) the current observations are best accounted for by hybrid models of visual conjunction search, where parallel processing in visual and temporoparietal regions and serial scanning controlled by the right IPS cooperate.

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### Introduction

Classical psychophysiology distinguishes two types of visual search (Treisman and Gelade, 1980; Nakayama and Silverman, 1986). When an object carries a unique and salient feature (like a red dot among green dots), it pops out and search time is independent of the number of other objects presented at the same time. In this case, search is proposed to be conducted in parallel without the need of attention. However, when an object is distinguishable from others only by the conjunction of two stimulus dimensions

(e.g., a red circle among red squares and green circles), search time typically increases as the number of objects presented becomes larger. Therefore, it has been proposed that visual conjunction search is conducted serially, by deploying attention to one object's location after the other. In the serial account, conjunction search is a multicomponent process that involves shifting of the attentional focus to an object's location, perceptual analysis of the object including feature binding and comparison with a memory template, and disengagement and reorienting of the focus in space. These processes are assumed to proceed until the last element is reached or the target is recognized.

Several researchers have suggested that an additional zooming process scales the size and resolution of the attentional focus. If, for example, likely locations for the target are known in advance, then attention is assumed to be scaled to

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cover solely the relevant region (Greenwood and Parasuraman, 1999; Luo et al., 2001; Müller et al., 2003). Moreover, during search, attention has to be adjusted with respect to the size of an object (Lamb and Yund, 1996) or it may grasp more than one object at a time (Grossberg et al., 1994). Attention during search therefore may operate like a “zoom lens” that is either narrowed or, at the expense of resolution, is distributed over a wide area (Eriksen and Yeh, 1985; Eriksen and St James, 1986; Castiello and Umiltà, 1990).

Other, contrasting models (Duncan and Humphreys, 1989; Desimone and Duncan, 1995) have challenged the above dichotomy between parallel and serial search by proposing that all kinds of search tasks can be accomplished by a parallel, competitive mechanism. In the case of conjunction search, this mechanism would simply be less efficient than with feature search but not qualitatively different.

Recent lesion, electrophysiological, transcranial magnetic stimulation, and imaging studies, however, have led to a revival of the notion of spatially serial search mechanisms (see Chelazzi, 1999, for a review). As serial models of conjunction search propose spatial shifts to be crucial during search, the same cortical areas should be activated in conjunction search and spatial orienting, but not during single feature search. Indeed, several studies reported this relation (Corbetta et al., 1995; Corbetta and Shulman, 1998; Donner et al., 2000a). Spatial orienting induced by a cue and conjunction search—but not simple feature search—activated regions in the posterior parietal cortex, namely, the anterior and posterior part of the intraparietal sulcus (IPS), the IPS junction with the transverse occipital sulcus (IPTO), and the frontal eye fields (FEF). Together, these studies suggest a strong overlap between cortical areas controlling eye movements/overt attention shifts and covert spatial orienting (Luck, 1994; Corbetta, 1998; Corbetta et al., 1998; Nobre et al., 2000; Perry and Zeki, 2000; Beauchamp et al., 2001; Gitelman et al., 2002).

However, whether the activation observed in the frontoparietal network during conjunction search indeed reflects serial scanning of object locations or other processes involved in the task remains unclear (Chelazzi, 1999). After all, even in serial models conjunction search involves several nonspatial processes, such as object identification, comparison of the attended object with the target object stored in working memory, decision making, and motor responses. Although Corbetta et al. (2000) and Hopfinger et al. (2000) reported that these processes predominantly activate other brain areas, such as motor areas, the temporal parietal junction (TPJ), occipital visual areas, and prefrontal cortex, they also observed parietal activation during target selection. Moreover, Wojciulik and Kanwisher (1999) have shown parietal activation in a number of attention tasks—whether they involved spatial processing or not. Donner et al. (2000b) reported activation in the AIPS and IPTO when a single object conjunction task was compared to an easy single object feature task. As the tasks were matched for spatial processing demands, the activation was proposed to

reflect nonspatial components of processing. Also, the proposed overlap between systems controlling eye movements and attention shifts may be limited: Serial scanning during conjunction search is proposed to take place at a rate of tens of milliseconds, thus exceeding by far the speed of saccadic eye movements (e.g., Treisman and Gelade, 1980; Saarinen and Julesz, 1991). In sum, there is still considerable uncertainty about which subprocesses are reflected by the cortical activation observed during conjunction search and whether the activation pattern is specific to this type of task.

Parametric manipulation of the cognitive function under investigation has proven valuable in distinguishing nonspecific task-related brain regions (like motor areas) from regions specifically computing the relevant process (Beauchamp et al., 2001; Culham et al., 2001). According to serial models, search-related activity in cortical areas controlling covert spatial orienting should closely mirror search load (i.e., set size) since the number of elements determines the number of attentional shifts. Chelazzi (1999) argued that parallel models, on the contrary, would not predict a parametric modulation in a specific brain region but rather in a wide range of cortical areas involved in visual processing.

Yet, varying set size by the number of elements presented introduces a potent confound of search load with physical properties (e.g., Leonards et al., 2000). To circumvent this problem, we followed the experimental design introduced by Eriksen and St James (1986) and varied search load indirectly by means of cues. The cues indicated the number of possible locations for the upcoming target, thereby determining the number of objects to sample during search. With this paradigm, Eriksen and St James observed search time functions equivalent to those obtained in conjunction tasks with varying set size, and pilot testing with our paradigm revealed the same line of results.

To unconfound cue-related from target-related processing in an experiment with hemodynamic signals these two events had to be separated in time by several seconds. In the case of a single cued location, current models (Vandenberghe et al., 2001b; Corbetta et al., 2002) suggest the following sequence of subprocesses: first, attention is oriented, i.e., is shifted to the periphery, and scaled to cover the cued location, and then it is maintained there until the object appears. Finally, and without requiring further shifts of attention, the object at the cued location is identified and a response generated. With respect to the fMRI signal, these processes should manifest as a transient response to the cue (shifting), a sustained response after cueing and up to target appearance (maintenance), and a transient response to the search array (object identification). Therefore, for the single cue trials predictors were modeled that accounted for the three conceivable response time courses. This analysis served as a functional “localizer” intended to identify all those brain regions that can be functionally related to the various aspects of this task. The responses in these regions of interest (ROIs) were then submitted to a parametric

analysis across all trials, where search load as indexed by the number of cued locations was the crucial parameter.

This design enabled us to assess not only search as a function of cue number but also the orienting process induced by the cue itself, comprising attentional shifting and zooming. We assumed that when several locations were cued, attention “zoomed out” to form a large focus with a center closer to the fixation point than in single cue trials where attention would be shifted further to the periphery and focused on a small region (see Fig. 1B). This notion relies on previous reports showing that the attention focus adopts the form of an ellipsoid centered in the periphery while sparing the space between fixation and the attended region (Egley and Homa, 1984; Sagi and Julesz, 1986). With the demands on shifting/focusing and zooming varying systematically across conditions, parametric analysis of cue-related activity should reveal the neural correlates of these processes.

## Methods

### *Subjects*

Five healthy students (age 23 to 29 years) from the Humboldt University of Berlin with normal color vision and sufficient visual acuity served as subjects in the study conducted in conformity with the declaration of Helsinki. All subjects (three females, two males) were right-handed and were paid for their participation.

### *Experimental paradigm*

The experimental design is illustrated in Fig. 1. During the whole experiment, four small squares (visual angle,  $0.2^\circ$ , at  $0.5^\circ$  off the fixation point) and four black large squares ( $3^\circ$  of visual angle, at a radial distance of  $7.3^\circ$  from the fixation point) were presented in the upper hemifield on a light gray background. The upper hemifield was chosen with respect to our prior analysis of early visual areas as for area V4 only an upper hemifield representation has been identified. The large squares served as placeholders for the objects to facilitate the alignment and maintenance of attention. The search array consisted of simple two-dimensional geometric objects (circle, square, rhombus; size, approx.  $2.5^\circ$ ) in three different (blue, green, yellow) isoluminant colors, determined by adjusting the luminance of rapidly alternating color stripes until flickering was minimized. The blue circle was defined as the target. In every search array other blue objects and rings of another color were presented, so that correct answers indeed depended on the combination of features.

Each trial started with a fixation period of variable duration (0 to 2750 ms, step size 250 ms). Then one (the middle left), two (both left-sided), or all four of the central small squares turned dark, indicating the possible locations

for subsequent target presentation. Subjects were instructed to immediately shift attention to the specified region and to maintain it there without further shifting. For a given number of cues, we always cued the same locations to increase the amount of data that could be collected from a given retinotopic visual area. Prior studies (e.g., Vandenberghe et al., 2000, 2001b) had not found an impact of the side of presentation on activity in higher order areas, so that possible lateralization effects in such areas in the present study should not be attributable to the bias for left side presentation.

The cue squares remained dark during a variable period of time of 4, 7, or 10 s. Then, four objects were presented within the placeholder squares for 30 ms.<sup>1</sup> Subjects were instructed to search for the blue circle and to indicate its presence or absence by pressing one of two buttons of a response box as quickly and as accurately as possible. Only responses within a reaction time window of 2 s were recorded. The target was present in 50% of the trials. To avoid decision conflicts, no invalid cues were used, that is, either the target was presented within the cued region or it was not presented at all.

After responding, subjects continued to fixate the central cross passively for 10,320 to 13,070 ms, depending on the initial offset. As the delay between onset of the cue and search array varied unpredictably for the subjects, they had to maintain their attention focus on the cued location(s) during the whole cueing phase. Trials with different load (i.e., number of cues), cueing duration, and offset times as well as trials with and without a target were randomized. Each load condition was repeated 24 times within each of two scanning sessions. Each session lasted about 33 min; in between, subjects were allowed to rest for approximately 10 min.

### *Fixation control*

As subjects were required to maintain central fixation during the whole experiment, their fixation capabilities were tested in prior training sessions outside the scanner, where eye movements were recorded with an infrared video eye tracker system (SMI, Teltow, Germany). All subjects were able to perform the search task while maintaining fixation within  $2^\circ$  of the center in more than 99% of trials.

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<sup>1</sup> We used such a short target display time to reduce the subjects' tendency to move their eyes. As they knew that the target would be on for too short a time for even preparing a saccade they more readily constrained themselves to covert attention shifts. At the same time, without masking, afterimages could be searched by spatial attention shifts and since these were retinal as opposed to real-world images there was again no benefit from performing eye movements (the images would move in the same way). We believe that it was due to these factors that eye movement recordings during training showed very good suppression of overt attention shifting.

## FMRI procedure

FMRI data were acquired with a 1.5-T magnetic resonance imaging system (MAGNETOM Vision, Siemens, Erlangen, Germany). Subjects' heads were stabilized with a vacuum pillow in a standard head coil. Stimuli were back-projected onto a screen by an LCD projector (NEC 8000, Stuttgart, Germany). Subjects looked at the screen via a mirror and used a fiber optic two-button response box for report.

During each session, 667 volumes of 26 axial slices (3 mm thick, spanning the cerebral cortex) were collected using a gradient-echo echoplanar imaging sequence (TR, 3000 ms; TE, 51 ms; flip angle, 90°; in-plane resolution,  $3.28 \times 3.28$  mm). Structural three-dimensional data sets were acquired using a T1-weighted sagittal MP-RAGE sequence (TR, 10 ms; TE, 4 ms; flip angle, 12°; TI, 100 ms;  $265 \times 256$  matrix; 190 sagittal slices (thickness, 1 mm); voxel size,  $1 \text{ mm}^3$ ). Moreover, high-quality structural three-dimensional data sets of all subjects were recorded using a T1-weighted sagittal FLASH sequence (TR, 38 ms; TE, 5 ms, flip angle, 30°; TI, 100 ms;  $265 \times 256$  matrix; 190 sagittal slices; voxel size,  $1 \text{ mm}^3$ ).

Stimulus presentation was computer controlled by the ERTS software package (Berisoft, Frankfurt, Germany). The computer was triggered by a TTL signal from the scanner that was sent at the beginning of every slice scan. To allow for a better temporal resolution in recording the BOLD signal, a variable offset between trigger and stimulus presentation was used covering a range between 0 and 2750 ms in 250-ms steps. As the total length of a trial was determined by the number of triggers counted, the final fixation period in each trial varied in length depending on the initial offset, that is, the total length of a trial had constant values of 18, 21, or 24 s, depending on duration of the cueing period.

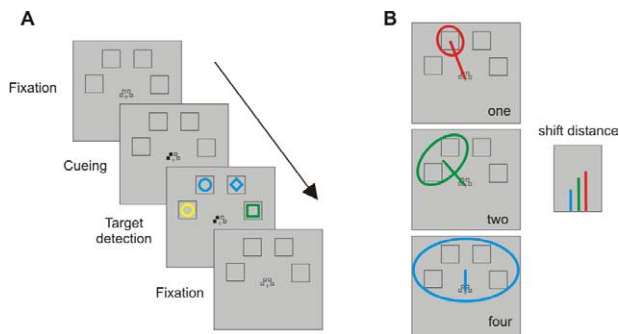


Fig. 1. (A) Schematic illustration of the experimental design. Cues were presented for 4 (not included in the analysis), 7, or 10 s and indicated the possible locations of the target (blue circle). One, two (as in this example), or four locations were cued determining the size of the attended region. (B) Assumed forms and locations of the attention foci in the task conditions are shown. Note the different distances between the foci's centers and the fixation mark.

## Data analysis

### Behavioral data

Mean reaction times for correct answers and errors (in percentages) were entered in separate one-way repeated measure ANOVAs with the factors “search load” and “trial type” (target present/target absent).<sup>2</sup> Degrees of freedom and *P* values are reported uncorrected as no violations of sphericity were detected by Mauchly tests.

### FMRI

FMRI data were analyzed with the Brainvoyager 2000 software (BrainInnovation, Maastricht, The Netherlands). Data from each subject were transformed into normalized stereotactic space (Talairach and Tournoux, 1988). To allow for steady-state magnetization, the first four scans of each functional run were discarded from analysis. After correction for slice scan time differences within a volume, functional volumes were coregistered with the three-dimensional structural data sets in order to generate volume time courses. Volume time courses were motion corrected by translating and rotating all remaining volumes with respect to the first volume using the Levenberg-Marquardt algorithm to find the least square fit, temporally high pass filtered at 240 s, and spatially smoothed with a 4-mm isotropic Gaussian kernel.

After *z* transformation, a fixed-effects general linear model (GLM) was employed to compute statistical maps for the group average. The model contained an idealized reference function as predictor of the effect of interest. This reference function was generated by convolving a model of the hemodynamic impulse response (a  $\gamma$  function with  $\delta = 2.5$  and  $\tau = 1.25$ ) with a square-wave function representing the experimental protocol (Boynton et al., 1996). Further predictors for the global mean of each run and for each subject were included. All effects were rigorously thresholded at correlation coefficients corresponding to  $P < 10^{-5}$ , uncorrected.

### ROI definition: analysis of search subprocesses

For identifying ROIs from the single cue trials, we defined predictors for transient responses to the cue and the search array by modeling hemodynamic responses to hypothetical events 100 ms in duration after the onset of the respective stimuli. Given the sluggishness of the BOLD response, these duration values did not need to reflect the exact time required for orienting or search but simply had to

<sup>2</sup> Note that we did not expect to find the usual search time difference between target present and absent trials under the single and double cue conditions. In the single cue trials only one item had to be checked anyway. With two cues, in some target absent trials both relevant objects shared a feature with the target object, in others only one, and in yet other trials no object shared a feature with the target. Thus, the average number of objects that had to be scanned because they shared a feature with the target was the same as that in target present trials.

account for the instantaneous and event-like nature of the two processes. As previous experimental work (Vandenberghe et al., 2001b; Corbetta et al., 2002) suggested that a spatial cue also evokes sustained activity, presumably related to maintaining attention in the periphery, a third predictor was defined to account for potential additional variance from tonic activations after cueing. Thus, the time span between the two events (cue and target) was convolved with hemodynamic response properties and modeled as a third condition (“late cueing”). We assumed that in trials with 7 to 10 s latency between cue and target and with only a single cued location, the processes of shifting and zooming of attention would be mostly reflected by the parameter estimates for the transient as opposed to the sustained response predictor.<sup>3</sup> This approach was motivated by the aim of modeling any conceivable type of signal change when defining the ROIs and thus not to miss any participating brain regions. Yet which type of response actually occurred was not a selection criterion, as the subsequent parametric analyses were performed across ROIs defined by any of these predictors.

Voxel clusters, activated during one of the three phases under the single cue condition (early, late cueing, search), were marked with different colors on reconstructed cortical surfaces derived from high-quality three-dimensional data sets by segmenting and tessellating the gray–white matter boundary and by inflating the resulting surface meshes (see www.brainvoyager.com). Only clusters of more than 50 mm<sup>2</sup> on the surface were marked. The group average data were projected onto one subject’s reconstructed cortical surface. Only data from the group average are reported here.

The following anatomical landmarks were used to identify brain regions of special interest on the reconstructed surface. The FEF was assumed to be located in the precentral sulcus, in the latitude of the caudalmost part of the superior frontal sulcus (Paus, 1996; Donner et al., 2000a). The IPS, which divides the parietal lobe into the superior parietal lobe (SPL) and the inferior parietal lobe (IPL), was subdivided into three parts (Duvernoy, 1999): the horizontal part adjacent to the inferior postcentral sulcus will be referred to as the AIPS and the descending part down to the latitude of the parieto-occipital sulcus as the PIPS. The continuation of the descending sulcus within the occipital cortex terminating at the junction with the transverse occipital sulcus (TO) will be referred to as the IPTO.

<sup>3</sup> A more stringent assessment of these processes would have required us to introduce separate shift and maintenance trials (e.g., Vandenberghe et al., 2001b; Yantis et al., 2002), which was beyond the scope of the present study. Another approach would have been to run a deconvolution analysis (e.g., Glover, 1999) to separate the BOLD responses of events close in time. This, however, was not possible as presentation times were independent of the TR.

### Parametric analysis

The major goal of the present study was to assess which of the predefined ROIs showed load-dependent changes in the BOLD signal after cue onset and after onset of the search array. For all parametric approaches, a GLM analysis, fitted to the predefined voxels of the ROI analysis and corrected for serial autocorrelation, was calculated with separate predictors for each load level (i.e., number of cues) and each phase of the task (early, late cueing, and search). Then linear contrasts were calculated with the respective parameter estimates, which were weighted in three grades (−2 for cue one, −1 for cue two, 3 for cue four) to model the signal increase (Büchel et al., 2002). This analysis resulted in *t* statistics for each ROI. Because of strong *a priori* hypotheses introduced by restricting the analysis to predefined ROIs the threshold for these contrasts was set to  $P < 0.05$ .

Note that we weighted the predictors in the way above to secure that the contrast involved a parametric assessment of number of shifts. A contrast −3, 1, 2 could have led to positive results simply because the single cue condition was the only one to lack shifts. However, the chosen contrast involved a confound with side of presentation (i.e., left vs bilateral). Thus, whenever the left hemisphere was found to respond more strongly to bilateral (i.e., positive *t*) and the right to unilateral presentation (i.e., negative *t*) an additional contrast matching presentation sides (−3, 1, 2) was calculated.

## Results

### Behavior

The behavioral data are presented in Fig. 2. Subjects’ reaction times (RT) and error rates increased with the number of cued locations, i.e., search load ( $F(2,8) = 8.58$ ,  $P < 0.01$  for RT,  $F(2,8) = 4.99$ ,  $P < 0.04$  for errors). Thus, our paradigm yielded the typical set size  $\times$  search time function proposed to hallmark serial search. No main effect of trial type was observed ( $F(1,4) = 0.99$  for RT,  $F(1,4) = 1.28$  for errors). For reaction times there was an interaction search load  $\times$  trial type ( $F(2,8) = 4.8$ ,  $P < 0.05$ ). A pairwise comparison revealed a trend for faster responses in target present as opposed to target absent trials as expected in the four-cue condition only ( $P < 0.1$ , see footnote 1).

### fMRI

#### ROI definition in single cue trials

Fig. 3 presents cortical areas activated in transient and sustained response to the cue and in transient response to the search array in single cue trials. These different response types were observed in partially segregated and partially overlapping brain regions. The figure also depicts the time courses of the BOLD responses (10-s-delay trials) and the Talairach coordinates of the respective areas.

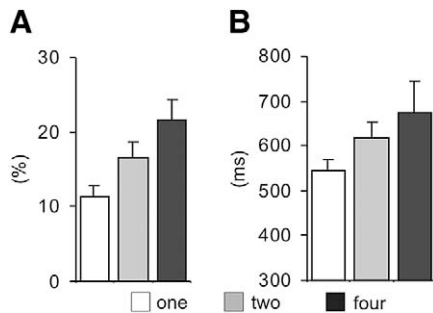


Fig. 2. Error rates (A) and reaction times (B) for correct answers. Both measures increased with the number of cued locations.

**Transient and sustained cue-related activation.** After the onset of the single cue, when subjects were supposed to shift their attentional focus to the periphery and scale it to cover the placeholder square, enhanced bilateral activity was observed in striate and extrastriate visual areas, along the lateral occipital sulcus (LOS), and in multiple subregions within and adjacent to the IPS. The latter were located in the IPTO, in the more inferior part of the PIPS, and at the junction of the PIPS and AIPS. Within the lateral frontal cortex two distinct regions were activated: the intersection of the upper precentral sulcus with the superior frontal sulcus (corresponding to the FEF) and the more ventral part of the precentral sulcus (vPreCeS, Beauchamp et al., 2001). On the medial surface (not shown), activations were seen in the superior frontal gyrus, in an area presumably corresponding to the supplementary eye field (SEF, see Merriam et al., 2001) and nearby presupplementary motor area (Talairach coordinates,  $-2, -6, 56$ ) and in the anterior cingulate gyrus (ACC, Talairach coordinates,  $-1, 10, 39$ ). The slope of the BOLD function in these frontal areas was shallower than that in the more posterior regions but continued to rise until onset of the search array, yielding a stronger correlation with the sustained than the transient response predictor. In LOS, the BOLD signal returned to near-baseline values shortly after cueing. In parietal areas also, the signal started to decline after about 7 s; therefore, in these areas the transient response predictor's contribution was larger than the sustained response predictor's.

**Transient search-related activation.** Parietal areas and the PreCeS showed a second peak after onset of the search array when the target object had to be identified (Fig. 3). In the left AIPS and nearby SPL this second increase yielded a significant response with the event-related "search" predictor.

Other regions with a significant signal increase related to object processing had remained silent during cueing, i.e., were driven exclusively by the processing of objects and generation of motor responses: several subregions of the right lateral prefrontal cortex (but not the FEF), in the vicinity of the left central sulcus (subjects used the right hand to respond), around the temporoparietal junction bi-

laterally (TPJ), the inferior parietal lobe bilaterally, and the medial occipital, i.e., visual, cortex.

#### Parametric analysis

Fig. 4 depicts the time course of the BOLD signal as a function of the number of cues (load). Different areas were modulated by load either in response to the cue or during search.

**Cueing.** The following of the areas identified above showed a linear increase in their transient responses to cueing as a function of the number of cues (Fig. 4): right and left LOS ( $t = 2.29, P < 0.02, t = 2.34, P < 0.02$ ), the left PIPS ( $t = 2.18, P < 0.03; t = 3.19, P < 0.01$ , for the presentation side controlled contrast), and the right vPreCeS ( $t = 2.28, P < 0.002$ ). A trend was observed in the right IPTO ( $t = 1.59, P < 0.1$ ). While we propose a functional behavior with a positive parametric modulation to reflect zooming, a negative relation could denote shifting or focusing in our experiment because under the single cue condition the spatial distance from fixation was largest and the attended region smallest. This latter behavior was observed in the right PIPS ( $t = -2.76, P < 0.006; t = -2.64, P < 0.009$ , for the presentation side controlled contrast).

None of the signal time courses in the ROIs showed a parametric modulation of sustained responses after the cues.

**Search.** Of the areas activated during cue-related spatial orienting, only the right junction of the AIPS with the PIPS was modulated by search load ( $t = 2.12, P < 0.03$ ). Of the areas activated during object processing, only the right TPJ ( $t = 2.36, P < 0.02$ ) responded in this way. Signal intensity in all other areas—in particular the FEF ( $t = 0.73$ )—showed no linear relationship with search load. As only subportions of the FEF are supposed to take part in visual search (see Discussion for more details) small differences in individual topography might account for the absence of a parametric effect in the group analysis. However, single subject analyses did not reveal a load-related modulation in the FEF either.

#### Discussion

The main focus of this study was to identify brain regions that mediate the putative subprocesses of visual conjunction search and to assess which of these areas show activity modulations related to search load, i.e., the number of objects to search through. Search load was manipulated indirectly by means of cues that indicated in advance how many locations would be relevant for the task, i.e., could contain a target (Eriksen and St James, 1986). The behavioral results suggest that the top-down manipulation of search load employed here mimics the "classical" effect of manipulating set size (Palmer et al., 1993), as search times increased with the number of cued locations.

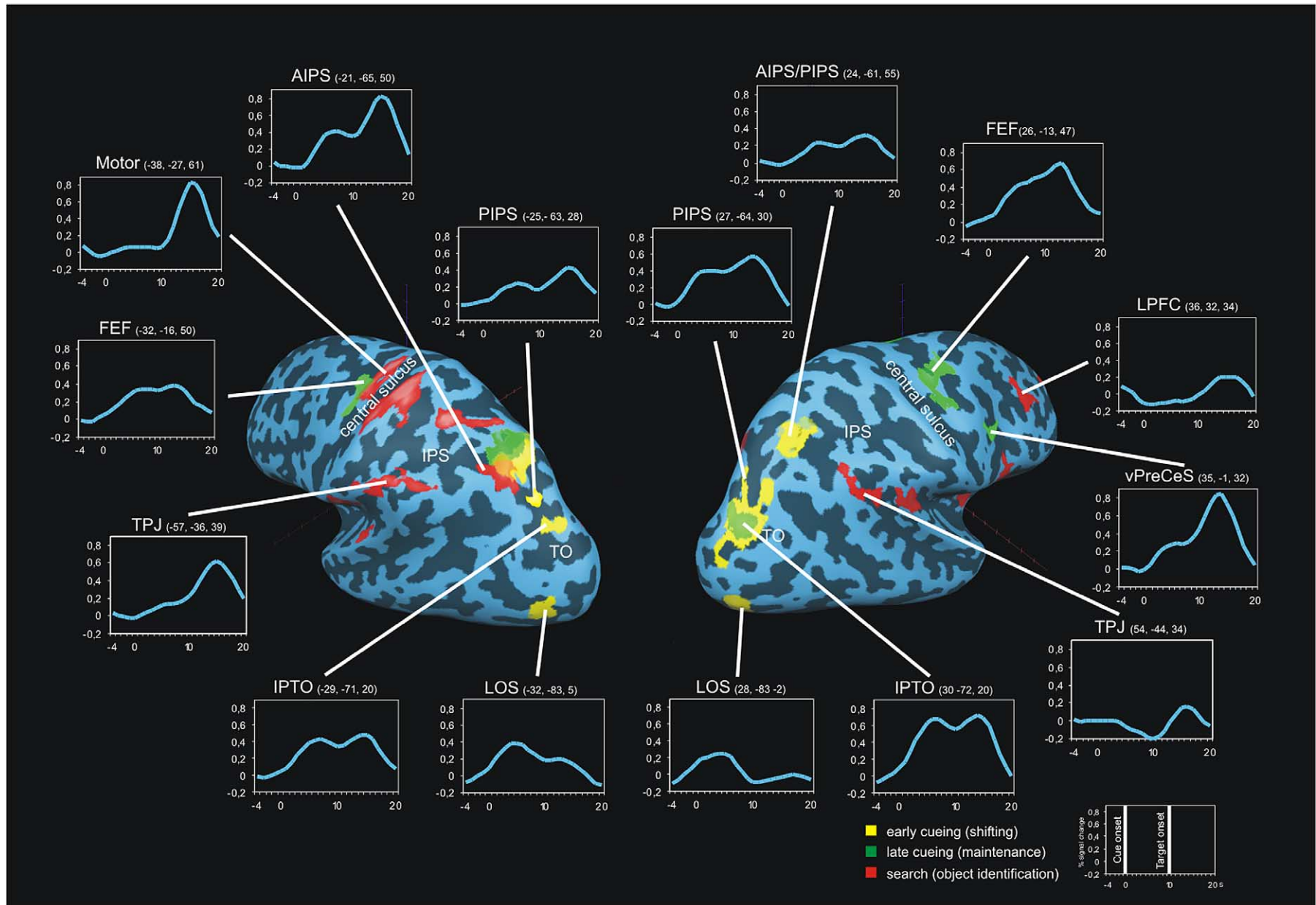


Fig. 3. Group average data of the single cue condition. Activated regions ( $P < 10^{-5}$ ) with corresponding BOLD time courses (10-s delay condition) and Talairach coordinates of the center of gravity of activated voxel clusters (x,y,z) are projected on the reconstructed and inflated cortex of one subject. Colors indicate in which trial phase activation was most pronounced.

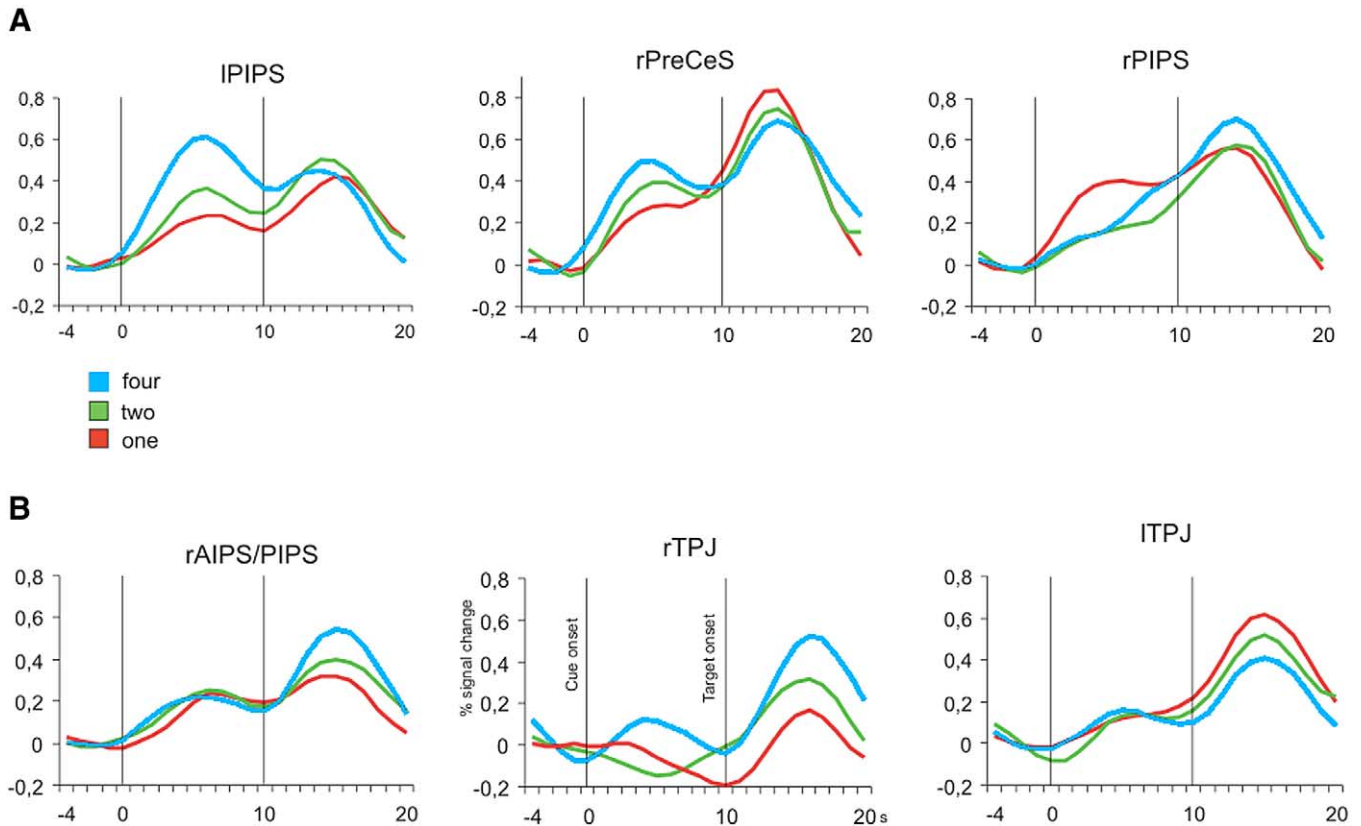


Fig. 4. Time courses in ROIs that were parametrically modulated by the number of cues either after cue onset (A) or during search (B). Note that area rPIPS showed an inverse correlation, i.e., was activated most under the single cue condition. The same seems to apply for the ITPJ; however, in this area the effect failed to reach significance.

### Identifying subprocesses of search

#### Spatial orienting

In accordance with several previous studies (Corbetta et al., 1993, 1995, 2000; Nobre et al., 1997, 2000; Corbetta, 1998; Corbetta and Shulman, 1998; Gitelman et al., 1999; Hopfinger et al., 2000) we found signal increases after a single spatial cue in multiple visual areas, including the vicinity of the LOS, in subregions of and near the IPS (IPTO, PIPS, PIPS/AIPS junction), and in the lateral prefrontal cortex (vPreCeS, FEF). A signal increase was also observed in the medial frontal cortex (pre-SMA, SEF, ACC). Activity in these latter areas has been found in numerous attention demanding studies and a general role in anticipation of a task, motivation/arousal, and performance monitoring has been proposed (Duncan and Owen, 2000; Stuphorn et al., 2000; Critchley et al., 2002; Schall et al., 2002). Activity in posterior parietal and frontal areas was more pronounced in the right hemisphere. Although the latter is confounded by the fact that under the single cue condition subjects always had to shift attention to the left, there is overwhelming evidence from previous studies for right hemispheric specialization in spatial processing (Nobre et al., 1997; Coull and Nobre, 1998; Gitelman et al., 1999; Corbetta et al., 2000; Vandenberghe et al., 2001b;

Gitelman et al., 2002; Müller and Knight, 2002). Moreover, in previous fMRI studies that controlled for the directions of attention shifts, no correlation was observed between the direction of shift and laterality of parietal activation (Corbetta et al., 2000; Hopfinger et al., 2000; Vandenberghe et al., 2001a, 2001b).

As reported elsewhere (Müller et al., 2003) the signal increase in early visual cortex occurred in subregions of areas V1 to V4 that were retinotopically mapped to the cued location(s). Unlike these early visual areas, activity in the LOS started to decline during the cueing period. A transient signal increase in the same area in response to a foveally presented cue has been reported before and was interpreted to reflect encoding of the cue (Corbetta et al., 2000; Hopfinger et al., 2000). The fact that the LOS was more activated by the centrally presented small cue than by the peripherally presented large objects might be related to the proposed eccentricity biased organization of object areas (Levy et al., 2001; Hasson et al., 2002; Malach et al., 2002), where objects demanding high resolution are associated with a center biased representation in lateral aspects of the occipitotemporal cortex. Note, however, that the respective area of this model is located somewhat anterior to the lateral occipital region described in our and previous studies (Dupont et al., 1997; Mendola et al., 1999; Corbetta et al., 2000).

Compared to that in the posterior parietal brain areas the



signal increase in frontal areas was slower and continued until the search array was presented. In parietal regions, on the other hand, after about 7 s the signal started to decline and showed a second increase with onset of the search array. This double-peak pattern was most pronounced in the most posterior region IPTO. In spite of the poor time resolution of the BOLD signal and potential differences in the hemodynamic response across different brain areas, one might speculate that these variations in response latencies arise from functional differences between posterior parietal and frontal areas. This notion is further supported by the finding that only activity in the right PIPS was modulated with respect to the supposed distance of attention shifts. Thus, together with earlier findings by Vandenberghe et al. (2001b) and Yantis et al. (2002), the current data support the idea that posterior parietal and frontal areas contribute preferentially to spatial shifting and maintaining, respectively.

The cue not only signaled subjects to shift attention to the periphery but was also supposed to induce zooming, for attention to cover a small, medium, or large region in the periphery. Areas LOS, left PIPS, and right vPreCeS showed a modulation in response to the cue(s) that correlated positively with the number of cues, a trend was also observed in the right IPTO. The fact that this analysis was confounded by the physical properties of the cues (the overall contrast change was stronger when more cues turned dark) can hardly account for the effects observed. The representation of the fovea within the contrast-sensitive early visual areas showed no variations across conditions; thus it is rather unlikely that the effects in higher areas, known to be largely contrast invariant (Avidan et al., 2002), were caused by the small physical differences in the cues across conditions. Other explanations may relate the cue-related modulation to varying levels of arousal/effort or to different strategies in deploying spatial attention. For example, subjects might have continuously shifted attention between locations when more than one location was cued. This strategy, too, would have led to the observed negative correlation between level of activity in visual areas and load, however, due to reduced “dwell” times on a given location. Differences in both arousal and strategy should have emerged during the late cueing period as well. For this period, our analysis did not reveal significant modulations in parietal and frontal areas. With all the caution necessary in interpreting an absent effect, this suggests that subjects indeed—and as intended—shifted and zoomed their attentional focus immediately after the cue but then “locked” it onto the relevant region.

We are not aware of any previous study specifically addressing the neural generators of zooming.<sup>4</sup> However,

switching between perceptual levels, i.e., from local to global, may be understood as a zooming problem as well. Fink et al. (1997) showed that activity in the left parietal cortex correlated with the frequency of shifts subjects had to perform between local and global aspects of their stimuli (large letters made of small letters). Employing similar stimuli, Weissman et al. (2002) presented cues that indicated to their subjects in advance whether global or local aspects would be relevant. It can be assumed that a global cue induced attention to zoom out, whereas a local cue induced focusing on a small spot of the visual field. Their results are consistent with the proposed left/right dichotomy for controlling zooming and shifting/focusing of attention, insofar as the global cue activated predominantly the left and the local cue the right hemisphere.

### *Object identification*

Under the single-cue condition, attention was expected to remain locked onto the cued location. Therefore, enhanced activity after onset of the search array was expected in brain areas involved in object identification and response generation. As these nonspatial processes were not relevant prior to array onset, these brain areas should have remained “silent” during the preceding cueing epoch. The BOLD responses in the TPJs and nearby inferior parietal lobe, around the left central sulcus, the insulae, and the right lateral PFC corresponded to this pattern. Apart from the TPJ, these areas have been implemented in motor response generation, working memory, and decision making, i.e., processes expected to be part of the visual search task (Hadland et al., 2001; Schall, 2001; Manes et al., 2002; Müller et al., 2002).

However, parietal regions that already had been active during cueing also tended to show a second signal increase during search. This increase was pronounced and surpassed the maximal activity during cueing considerably in the left AIPS and nearby SPL. Both Wojciulik and Kanwisher (1999) and Donner et al. (2000b) reported left parietal activation in conjunction tasks as opposed to feature detection tasks, although in their experiments spatial shifts were irrelevant as they employed single object displays. Schubotz and von Cramon (2001) reported stronger activation in the left AIPS during anticipation of object properties as opposed to location. Donner et al. (2000b), therefore, suggested that the left parietal cortex is involved in feature-based attention during search and Wojciulik and Kanwisher (1999) that it mediates feature binding. These processes were necessary even under the single cue condition in our experiment, presumably explaining the strong signal increase in left parietal areas.

### *Parametric assessment of visual search*

Of the areas mentioned above only the right IPS (at the junction between the AIPS and PIPS) and the right TPJ showed parametric modulation as a function of search load.

<sup>4</sup> Note that Luo et al. (2001) recorded ERPs in response to cues of varying size that indicated to their subjects the region they later had to search through for a target. However, the authors refrained from commenting on the cue-related zooming effects due to a confound with the physical appearance of the cues.

On the other hand, in response to the cue, the left IPS was modulated by the number of cues. This lateralization pattern within the IPS indicates that although both cues and conjunction search evoked deployment of spatial attention, they brought out different subcomponents of this process. With several cues, attention, under the control of the left IPS, likely zoomed out first, whereas later, during search, several serial shifts of focused attention were induced by the right IPS. The assumption that the right parietal activations during search were driven by rapid attention shifts rather than by some other nonspecific processes correlating with search load, such as arousal or decision making, is underscored by the observed predominantly right parietal response to the single spatial cue. This conclusion is in accord with search models involving a spatially serial component (Treisman and Gelade, 1980; Grossberg et al., 1994; Wolfe, 1994; Woodman and Luck, 1999, 2003) and has also been reached by the authors of previous studies, where activation of posterior parietal and prefrontal areas during conjunction search was attributed to serial scanning (Corbetta et al., 1995; Donner et al., 2000a).

However, other studies cast doubt on the notion that posterior parietal activation is a unique signature of spatial attention shifts and suspected a more general role in selective attention (Vandenberghe et al., 1997; Wojciulik and Kanwisher, 1999; Coull et al., 2000; Donner et al., 2000b; Leonards et al., 2000). The current data might contribute to resolving this discrepancy. According to our results, only a small subregion of the posterior parietal attention system, the right middle part of the IPS, reveals properties in accord with a generator of rapid attention shifts during search. Conversely, the left AIPS seems more involved in the integration of features, and the left PIPS is a candidate “zooming center.” Together, these results support a fine-grained functional specialization within the IPS (Culham and Kanwisher, 2001). Some of the subprocesses considered here are probably involved in any attention task, which might explain why parietal involvement generalizes across a wide variety of attention requiring tasks (Wojciulik and Kanwisher, 1999).

As with the parietal cortex, the functional role of the TPJ has provoked considerable controversy (Ro et al., 1998; Downar et al., 2002; Wilkinson et al., 2002). Here, we observed a strong bilateral signal increase in the TPJ with onset of the search array, which on the right side correlated with search load. Corbetta et al. (2000) reported a similar signal increase in the rTPJ during target selection. In their study, the BOLD response was more pronounced when the target appeared at an unexpected location. In accordance with earlier patient reports (Posner et al., 1984; Morrow and Ratcliff, 1988), Corbetta and colleagues (2000) assumed that the rTPJ is involved in disengagement and reorientation of attention. As serial scanning during search also involves these processes, the load effect in the rTPJ might reflect the frequency of disengaging and reorienting processes. However, reorienting during search is rather a voluntary (endogenous), top-down-driven process, contrasting with the automatic stimulus-driven (exogenous) response of the rTPJ to targets at unexpected locations (Corbetta and Shulman, 1998; Friedrich et al., 1998; Corbetta et al., 2000, see, however, Rosen et al., 1999). Thus, reorienting is an unlikely explanation for load-dependent responses in the right TPJ here.

Based on patient data (Robertson et al., 1988; Robertson and Lamb, 1991; Hellige, 1993), the TPJ has also been linked to selective processing of local (left TPJ) vs global (right TPJ) stimulus aspects. Moreover, the right TPJ was found to be selectively activated when elements of an array could be grouped (Wilkinson et al., 2002), which might reflect a certain aspect of global processing. Nakayama and Joseph (1998, see also Luo et al., 2001) noted that visual search might operate at different spatial scales involving a compromise between the size of the area to be sampled and resolution. Thus, TPJ modulation might be caused by variations in the sampling scale or the perceptual level, where activation on the right reflects a more global (coarse) and activation on the left a more local (detailed) processing mode. The global mode, involving grouping, might have been employed when all objects of the array were relevant and the local mode when only one object was relevant. The first would have driven the right TPJ and the latter the left TPJ. The load effect within the right TPJ is consistent with this idea; for the left TPJ visual inspection indeed suggests a stronger activation with a single cue but this effect failed to reach significance. Note that the functions ascribed to the TPJs here differ from the zooming/focusing processes which we have related to the IPS above: while the latter occur in response to symbolic spatial cues, activity in the TPJ seems to be bound to the presence of objects and reflects the processing of either their local or global features, i.e., presents the outcome of the preceding zooming/focusing processes. These differences in functional specialization may explain the opposed lateralization patterns, with respect to cue number, across areas IPS and TPJ.

The question arises why other brain regions that have been associated with conjunction search, in particular the FEF (Donner et al., 2000a, see, however, Leonards et al., 2000), were not modulated as a function of search load in our study. Such a modulation could have been expected based on single-cell recordings demonstrating that a subpopulation of FEF neurons—different from those controlling saccades—takes part in target selection during search (see Schall, 2002, for a review). A higher search load should hence increase the duration of the target selection process in this subportion of the FEF, thereby evoking a more pronounced BOLD response in trials with multiple cues. It is, however, conceivable that the expected load-related differences in *duration* of neural activity (where the mean *level* of activity remains constant) were too subtle for fMRI to depict, especially as only a subportion of the FEF is expected to behave this way. This is in line with others' failing to observe parametric FEF modulation by attentional load

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(Culham et al., 2001). Our results suggest that a major function of the FEF, in accord with its role in exerting eye movements, consists in controlling large-scale shifts and maintenance of attention in the periphery (Sweeney et al., 1996; Corbetta et al., 1998; Gitelman et al., 1999; Vandenberghe et al., 2001a, 2001b). This is underscored by the fact that a strong activation in the FEF was observed during single object search where no serial scanning was necessary. In this condition, maintaining of attention in the periphery guaranteed that no irrelevant information from elsewhere hampered target identification.

#### *Implications for models of visual conjunction search*

We have so far argued that the observed correlation of activity in the right IPS with search load supports serial search models, where the number of shifts is determined by the number of relevant elements in a set. According to Chelazzi (1999) a specific activation of this area can hardly be accounted for by parallel models like the biased competition model. A central tenet of these models is that there is no such thing as an attentional center. Instead the neural circuitry responsible for selecting a relevant object among others is proposed to be distributed across most of the visually responsive structures.

However, our previous analysis of activity in retinotopic visual areas (Müller et al., 2003) is hardly compatible with classical serial models. Neither is the assumption of zooming and a global processing/coarse sampling mode during search under high-load conditions. In classical serial models, search requires attention to be focused on a single object location for feature binding. To take advantage of a cue, attention should therefore be focused on one single location in expectation of a search array. This effect should occur irrespective of the number of cued locations as (globally) distributing attention over the whole array would lead to misidentification of objects due to binding errors. Once the array appears and after the object at the selected location has been processed attention should be shifted and focused on another cued location. If subjects had operated that way, then top-down-driven modulation of visual areas preceding the search array should have shown enhancement in retinotopic representations of only one of the locations across *all* conditions. Instead, with more than one cued location, additional visual subregions were activated, and this was presumably not caused by shifting the attentional focus during cueing within or between trials. This neural response pattern corresponds to activity distribution models implemented in the zoom lens analogy (LaBerge, 1983; Eriksen and St James, 1986; LaBerge et al., 1997). Taken together, the activity observed in early visual areas therefore supports a parallel processing mode.

Only hybrid models, which propose coexisting parallel and serial mechanisms for search, seem suitable to accommodate the findings in both visual and frontoparietal areas. For example, some researchers have suggested that the

attentional focus, albeit moving serially, can encompass more than one item at a time and that these items are processed in parallel (Treisman, 1982; Gilmore et al., 1985; Humphreys and Müller, 1993; Grossberg et al., 1994). The guided search model by Wolfe and collaborators (Wolfe et al., 1989; Wolfe, 1994, 1998) proposes that parallel extracted feature information is represented in topographically organized maps that guide focal attention to the location of a likely target. The feature maps, computed by specialized visual areas, are under top-down control so that attention is guided preferentially to objects that share a common feature with the target. Spatial cueing in this model can be assumed to induce another top-down bias based on *location* reflected in the enhanced activity in retinotopic areas representing the cued location(s).

#### **Conclusion**

Our findings suggest that the cognitive operations which are recruited during visual conjunction search are implemented in segregated but partially overlapping neural structures. Beyond mapping of these regions of interest our approach involved a parametric modulation of search load that enabled us to characterize and differentiate localized functional response properties across different brain regions. Left and right posterior parietal areas control shifting and scaling of attention to a relevant visual field region and induce preactivation of visual areas retinotopically mapped to this region (see also Hopf et al., 2000). Preactivation of visual areas boosts parallel feature extraction for objects presented within this region and the rTPJ supports grouping of these objects (presuming that the latter is—in contrast to earlier theories—under attentional control (Roelfsema et al., 2000; Kim and Cave, 2001)). Attention shifts are biased to objects at the cued locations, which share features with the target and which are not grouped together. These findings, together with the previously reported activation pattern in visual areas in the same task, are most consistent with hybrid models of visual search where parallel and serial processes coexist and temporally overlap. In sum, the parametric approach to visual search has proven to be a powerful instrument in separating process-specific activity and should be employed in further experiments on selective attention.

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