

## Neural basis of interaction between target presence and display homogeneity in visual search: An fMRI study

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### ABSTRACT

The functional magnetic resonance imaging (fMRI) technique was used to investigate the functional neuroanatomy of the attention mechanisms employed in visual search with homogeneous or heterogeneous displays. Participants were asked to search for a vertically oriented bar among distractor bars with the same or different orientations, with half of the trials being target-present and the other half being target-absent. Behaviorally, RTs were slower for target-absent than for -present trials when the distractors were heterogeneous, but were faster for target-absent than for -present trials when the distractors were homogeneous. At the neural level, a widely distributed brain network was involved in this interaction. The bilateral frontal eye field, intraparietal sulcus, precentral gyrus and supplementary eye field may play a role in representing the target against distractors and further in detecting and responding to the presence of the target. The right superior frontal gyrus and the bilateral temporal–parietal junction may play a role in filtering distracting information in the search process.

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### Introduction

One frequent task for humans is to search a cluttered visual scene for a particular target, which could be an object defined by one feature or a conjunction of features. This search process is affected by the top-down task set and/or the context in which the target object is embedded. Recent studies using functional magnetic resonance imaging (fMRI) have demonstrated that a large-scale brain network comprising the posterior parietal cortex (PPC), intraparietal sulcus (IPS), and frontal eye field (FEF) is involved in visual search (Arguin et al., 1993; Ashbridge et al., 1999; Corbetta et al., 1995; Coull et al., 2003; Donner et al., 2000, 2002, 2003; Gitelman et al., 2002; Leonards et al., 2000; Nobre et al., 2003; Pollmann et al., 1998; Pollmann and Cramon, 2000; Rushworth et al., 2001; Sato et al., 2003; Wojciulik and Kanwisher, 1999; Wilkinson et al., 2002).

In the visual-search paradigm, the search display often contains a predefined target in half of the trials (target-present), and only distractors in the other half (target-absent). Observers are usually asked to make forced-choice responses as to whether the target is present or absent. Generally, the search reaction times (RTs) are found to be longer for target-absent than for -present trials, while the

difference between them is affected by the general task difficulty or search efficiency: the difference is larger for more demanding search tasks (e.g., Treisman, 1988; Treisman and Gelade, 1980; Duncan and Humphreys, 1989, 1992; Müller-Plath and Pollmann, 2003). Different cognitive mechanisms have been proposed for making correct target-present/absent decisions (Treisman and Gelade, 1980; Chun and Wolfe, 1996). The mechanism for making a target-present response seems straightforward: observers can respond positively as soon as they detect the target. In contrast, the mechanism leading to a target-absent response leaves scope for discussion.

Serial models of visual search (e.g., the Feature Integration Theory; Treisman and Gelade, 1980) propose that attention can process the identity of only one display item at a time. Consequently, establishing the presence of a target in the display will require the observer to examine, on average, only half of the items, if aided by an inhibitory ‘tagging’ mechanism which prevents already scanned items from being revisited (Niebur et al., 1993; Müller and von Mühlenen, 2000). On the other hand, establishing the absence of a target would require the observer to identify all the items in the display as distractors. In contrast, parallel theories of visual search (e.g., race models; Bundesen, 1987, 1993) assume that identity is computed in parallel for each item, and that an item’s identity becomes gradually more certain over the course of a trial. A response is initiated either when sufficient information confirms one item as the target, i.e., when the accumulated evidence for this item exceeds the “yes”-response

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threshold, or when none of the item identities activated in parallel reaches the threshold (Horowitz and Wolfe, 1998). A target-absent response can also be made as soon as the observer finds the display to be homogeneous (Chun and Wolfe, 1996).

Thus, the way the search display is composed may impact upon the strategy for deciding “target-absent”, leading to differential RT patterns for different types of search display. The computational SERR (SEArch via Recursive Rejection) model proposed by Humphreys and Müller (1993; Müller et al., 1994; for overviews, see Müller and Humphreys, 1993, and Müller et al., 1998) specifically predicts an interaction between display homogeneity/heterogeneity and the time required to determine whether a target is present versus absent. This model hypothesizes an architecture of spatially parallel visual coding mechanisms (Duncan and Humphreys, 1989, 1992), with a hierarchy of topographic maps corresponding to increasingly more complex features of visual form. Decisions as to whether a target is present or absent in a display can be made in either of two ways. First, activation within the match map, which receives the input from both the object units and a map of the location units, is summed and passed as input to temporary template units representing the target and distractors. The target is selected as soon as its template reaches the threshold in a competitive race amongst all other templates. The second procedure involves the recursive rejection of distractor groups. The template unit receiving the most activation on any iteration will be that whose match map exhibits the strongest grouping, which is likely to be a distractor template. Recursive rejection then operates by inhibiting the match map corresponding to the supra-threshold distractor template and by disabling the location units supported by the inhibited match map. The search then proceeds recursively over a reduced set of items and over a reduced region of field until either the target is detected or all distractor groups are rejected. The SERR model extended and specified the Attentional Engagement Theory (Duncan and Humphreys, 1989, 1992), which deals with how visual information is entered into visual short-term memory (VSTM) based on a parallel stage of perceptual segmentation and analysis. The template matching process in the SERR model corresponds to how selected information is entered into VSTM, where it may be processed by focused attention and used to guide report or action. Recursive rejection of distractor groups is based on the parallel perceptual segmentation and analysis. Grouped (homogeneous) nontargets do not compete individually for access to VSTM and focused attention, but can be coded and rejected altogether.

According to the SERR model, when observers search for a target amongst heterogeneous distractors, the search is terminated when the target template (as compared to templates for other items) reaches the threshold, in which case a target-present response is generated. But on target-absent trials, the search continues until the observers can reject all possible (groups of) distractor objects, leading to overall longer RTs for the target-absent compared to target-present responses. In contrast, when observers search for a target amongst homogeneous distractors, in the absence of a target, these distractors are grouped and rapidly activate the corresponding (distractor) template, whereupon they are rejected altogether, leading to shorter RTs for the target-absent compared to target-present responses. Such an interaction between display homogeneity and target presence has been confirmed in behavioral studies (e.g., Humphreys et al., 1989).

However, to date, no brain imaging study has been conducted to examine the neural basis of this interaction, limiting our understanding of the attention mechanisms involved in visual search. Indeed, previous fMRI studies, which have focused mainly on whether there are specific brain mechanisms for conjunction as compared to feature search, have typically collapsed the data across target-present and -absent trials in comparing the different search tasks (Coull et al., 2003; Donner et al., 2000, 2002, 2003; Leonard et al., 2000; Nobre et al., 2003; Wilkinson et al., 2002; Wojciulik and Kanwisher, 1999). As a result, it is unclear to what extent the findings

concerning the activated brain regions in different tasks are affected by this procedure. An event-related potential (ERP) study (Schubö et al., 2004) directly compared brain responses to target-present vs. -absent trials in “pop-out” search and found that the amplitude of an ERP component, the N2p, was increased for target-absent (relative to -present) trials when the search display contained more than 45 homogeneous items. A follow-up study (Schubö et al., 2007) demonstrated further that the degree of distractor homogeneity modulates the differential N2p amplitude between target-absent and target-present trials in visual search. A recent fMRI study (Wilkinson et al., 2002) also found that distractor homogeneity influences brain activity associated with within-object (form) conjunction search (Duncan, 1987): When observers had to search for an upright T amongst either differently (orthogonally) oriented (heterogeneous displays) or identically oriented non-target Ts (homogeneous displays), the superior parietal lobule was activated with heterogeneous displays, whereas the temporal–parietal junction (TPJ) was activated with homogeneous displays, but they did not examine how these related brain areas would be affected by target-presence. Therefore, it is reasonable to hypothesize that there might be differential brain networks dealing with the different strategies of making “yes” vs. “no” responses to either heterogeneous or homogeneous search displays.

In the present study, we used a feature search task to investigate the neural basis of the possible interaction between top-down controlled target search and display composition. While the distractors could be either homogenous or heterogeneous, the target could be present or absent in a display. At the behavioral level, we expected to replicate the interaction between target presence and display homogeneity (Humphreys et al., 1989; Müller and Humphreys, 1993). At the neural level, we hypothesized that the dorsal frontoparietal brain network (Corbetta and Shulman, 2002) is involved in providing top-down signals biasing the search process and target template matching, whereas TPJ and other ventral brain regions (Corbetta and Shulman, 2002) may play a role in analyzing the bottom-up coded stimuli, especially when the distractors are forming a homogeneous group, which can be rejected altogether.

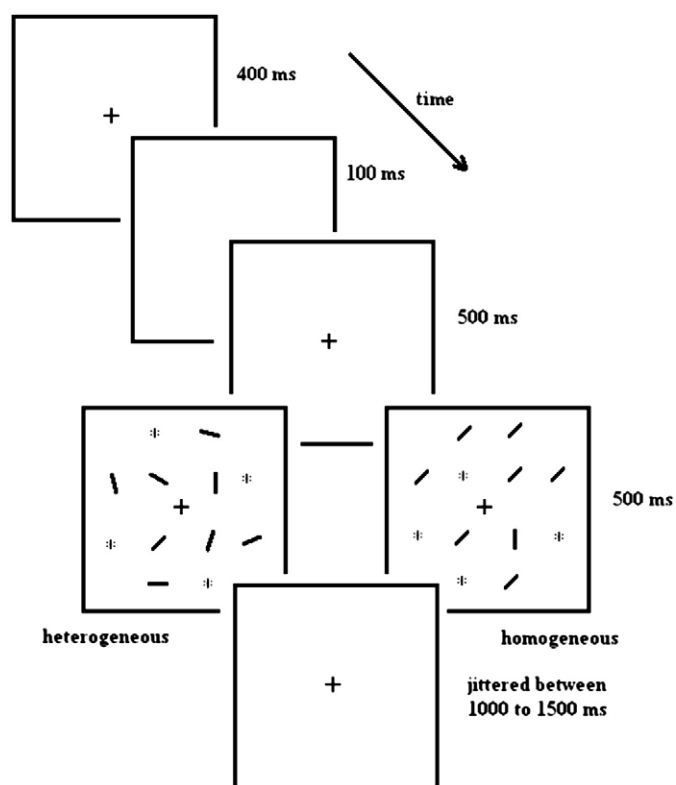
## Materials and methods

### Participants

Sixteen undergraduate and graduate students (8 female, aged between 20 and 26 years) participated in the experiment. All of them were right-handed and had normal or corrected-to-normal vision, and none of them had a history of neurological or psychiatric disorders. All participants gave written informed consent before the scanning. This study was approved by the Academic Committee of the Department of Psychology, Peking University.

### Stimuli and experimental paradigm

Participants were required to search for a vertically oriented bar in the search display. A 2×2 within-participant design was used for this fast event-related fMRI experiment. The first factor was homogeneity of the distractor features along the task-relevant dimension (orientation): the distractors were either oriented in the same way (homogeneous display) or oriented in different directions (heterogeneous display). Each of the distractor orientations within heterogeneous displays was equally often to the orientation in homogenous displays. The second factor was target presence: the target was present in half of the trials and absent in the other half. With two response buttons under the participant's right index finger and middle finger, half of the participants were instructed to respond “target-present” with their index finger and “target-absent” with middle finger, and vice versa for the other half.



**Fig. 1.** An example trial sequence with a target present in a heterogeneous or homogeneous search display. Stars (not shown in the real search display) in the display examples here are the remaining 4 positions after 8 were randomly selected from the total 12 possible positions for search items to be displayed.

Stimuli were presented through an LCD projector onto a rear projection screen located behind the participant's head. Participants viewed the screen through an angled mirror on the head-coil. Presentation of the stimuli and recording of the responses were controlled by the Presentation software (<http://nbs.neuro-bs.com/>). At the start of each trial, a white fixation cross, measuring  $0.20^\circ$  of visual angle, appeared at the center of the black screen for 1000 ms. A black screen of 100 ms was inserted 400 ms after the onset of the fixation sign, so that the cross appeared to flash briefly. This was to warn participants about the upcoming search display, which was presented for 500 ms. The search display consisted of a central fixation marker surrounded by 8 bar stimuli (each measuring  $0.8 \times 0.2^\circ$  in visual angle). The stimuli were placed at 8 (randomly selected) positions on a virtual, cross-shaped grid, with a maximum eccentricity of  $3^\circ$  of visual angle (see Fig. 1 for trial sequence and sample display).

Each experimental condition consisted of 48 trials, intermixed with 48 null trials on which only the fixation cross was presented. The four experimental conditions and null trials were randomized in one continuous scanning session of 12 min and 7.5 s. Only the fixation sign was displayed during the first 7.5 s for participants to become accustomed to the scanning noise and for the MR signal to reach a steady state. All participants completed a training session of 10 min before the scanning.

#### Data acquisition

A 3T Siemens Trio system with a standard head coil at the MRI Center for Brain Research in Beijing Normal University was used to obtain T2\*-weighted echo-planar images (EPI) with blood oxygenation level-dependent (BOLD) contrast (matrix size:  $64 \times 64$ , pixel size:  $3.4 \times 3.4$  mm). Twenty-four transversal slices oriented parallel to anterior and posterior commissures of 4 mm thickness that covered the whole brain were acquired sequentially in ascending order with a

1 mm gap (TR=1.5 s, TE=30 ms, FOV=220 mm, flip angle= $90^\circ$ ). The first five volumes were discarded to allow for T1 equilibration effects. Images were spatially realigned to the sixth volume for head movement correction, interpolated in time (temporal realignment to the middle slice for slice acquisition order correction), and normalized to a standard EPI template (Montreal Neurological Institute template provided by Statistical Parametric Mapping [SPM], see below) with resample of  $2 \times 2 \times 2$  mm<sup>3</sup> voxels. Data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to accommodate inter-subject anatomical variability.

#### fMRI data analysis

Data were analyzed by using Statistical Parametric Mapping software SPM2, Wellcome Department of Imaging Neuroscience, London (Friston et al., 1995), employing a random-effects model. At the first level, four event types were defined, including: target-absent trials for heterogeneous displays (Het\_ab), target-present trials for heterogeneous displays (Het\_pre), target-absent trials for homogeneous displays (Hom\_ab), and target-present trials for homogeneous displays (Hom\_pre). The event type was time-locked to the onset of the search display by a canonical synthetic hemodynamic response function (HRF). Additionally, all error trials were included as an extra regressor of no interest. The obtained contrast images of the first-level analysis were entered into a second level random-effects group analysis. The activations will be reported at a family-wise error (FWE) corrected threshold of  $p < 0.05$ .

Moreover, to examine in detail how the activated brain areas were modulated by display homogeneity and target-presence, we carried out a region-of-interest (ROI) analysis by extracting beta values from the peak voxels in the activated brain areas (see Table 2 for exact locations).

## Results

### Behavior

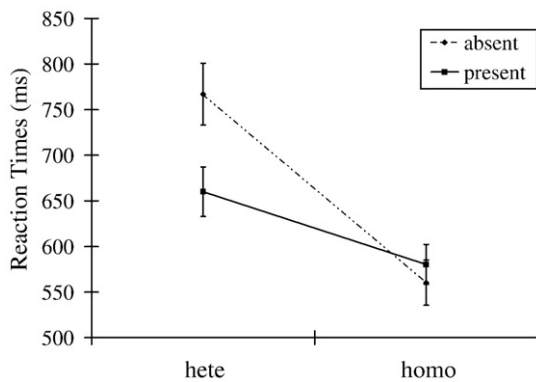
Mean reaction times (RTs) and response error rates were calculated for each of the participants. As can be seen in Table 1, the error rates were higher for target-present (target misses) than for target-absent trials (false alarm), suggesting that participants tended to terminate the search prematurely and therefore miss the target. To correct for the potential speed-accuracy tradeoffs, we carried out a “kill-the-twin” procedure (Eriksen, 1988; Grice et al., 1977). The logic is that if participants have a tendency to respond “no” in a fast guess manner, thus generating faster correct-rejection RTs on target-absent trials and target-miss errors on -present trials, then eliminating correct-rejection trials whose RTs are “twins” of target-miss RTs would correct the mean RT estimate for the correct-rejection trials. Similarly, if participants have a tendency to respond “yes” in a fast-guess manner, thus generating faster correct-hit RTs on target-present trials and false-alarms on -absent trials, then eliminating correct-hit trials whose RTs are the “twins” of false-alarm RTs would correct the mean RT estimate for the correct-hit trials. In the present analysis, twins of error RTs were computed by searching for an RT in correct-

**Table 1**

Mean reaction times (ms), standard deviations, and error percentages (%) as a function of display homogeneity and target presence

|       | Heterogeneous |                | Homogeneous   |                |
|-------|---------------|----------------|---------------|----------------|
|       | Target-absent | Target-present | Target-absent | Target-present |
| RT    | 770 (767)     | 661 (660)      | 560 (560)     | 580 (580)      |
| SD    | 139 (136)     | 109 (109)      | 99 (99)       | 87 (87)        |
| % Err | 7.6           | 12.9           | 1.2           | 4.3            |

RTs and standard deviations prior to removing error “twins” are reported in parentheses.



**Fig. 2.** Behavioral results (ms) with standard errors in terms of the experimental conditions. Hete = heterogeneous display, and homo = homogeneous display.

rejection or correct-hit trials which corresponded to an error RT (within a range of  $\pm 3$  ms) on target-miss or false-alarm trials, respectively. These “twins” RTs were then removed from the “correct” data set. This procedure was carried out separately for heterogeneous and homogeneous displays for each participant, which led to the elimination of 2.0% of the data in total. As can be seen from Table 1, RT performance did not change as a result of removing the error “twins”, indicating that the RT data were largely undistorted by possible speed-accuracy tradeoffs.

The remaining data were then trimmed by deleting outlier RTs that were more than three standard deviations above or below the mean in each experimental condition (1.2% of the data in total). A 2 (homogeneous vs. heterogeneous)  $\times$  2 (target absent vs. present) analysis of variance (ANOVA) was then conducted, which revealed both main effects to be significant: display homogeneity,  $F(1, 15)=102.79$ ,  $p<.001$ , and target presence,  $F(1, 15)=11.41$ ,  $p<.005$ . RTs were slower to heterogeneous than to homogeneous display (714 vs. 570 ms), and

**Table 2**

Activated brain regions in the homogeneity and the interaction contrasts, with FEW correction of  $p<.05$

| Anatomical regions                           | L/R | BA     | No. of voxels | Z score | Cluster peak (X, Y, Z) |
|--|-----|--------|---------------|---------|------------------------|
| <b>(A) Heterogeneous vs. homogeneous</b>     |     |        |               |         |                        |
| FEF  | L   | 6      | 315           | 7.06    | -30, -4, 46            |
|  | R   | 6      | 451           | 6.90    | 28, 2, 48              |
| IPS  | L   | 7, 40  | 1458          | 6.43    | -18, -56, 45           |
|  | R   | 7, 40  | 697           | 6.62    | 32, -48, 58            |
| Precentral gyrus                             | L   | 6, 44  | 342           | 6.40    | 50, 11, 29             |
|  | R   | 6, 44  | 46            | 5.25    | -42, 3, 29             |
| SEF  | L/R | 6      | 745           | 6.77    | 6, 20, 41              |
| Anterior insular                             | L   | 47     | 296           | 6.66    | 32, 23, -1             |
|  | R   | 47     | 222           | 5.88    | -28, 23, -5            |
| Occipital gyrus                              | L   | 18, 19 | 80            | 5.53    | 38, -85, 13            |
|  | R   | 18, 19 | 75            | 5.26    | -44, -80, 1            |
| Cerebellum                                   | L   | /      | 206           | 6.44    | -4, -73, -17           |
|  | R   | /      | 97            | 6.27    | 10, -73, -18           |
| <b>(B) Interaction: positive beta values</b> |     |        |               |         |                        |
| FEF  | L   | 6      | 85            | 5.44    | -26, -1, 50            |
|  | R   | 6      | 99            | 5.17    | 32, -5, 52             |
| IPS  | L   | 7, 40  | 428           | 5.73    | -30, -46, 45           |
|  | R   | 7, 40  | 744           | 5.93    | 22, -59, 56            |
| Precentral gyrus                             | L   | 6, 44  | 58            | 5.18    | -42, 5, 29             |
|  | R   | 6, 44  | 277           | 5.74    | 48, 7, 27              |
| SEF  | L/R | 6      | 77            | 5.22    | 6, 16, 45              |
| <b>(C) Interaction: negative beta values</b> |     |        |               |         |                        |
| SFG  | R   | 9      | 103           | 5.52    | 22, 45, 42             |
| TPJ  | L   | 39     | 491           | 5.85    | -42, -76, 35           |
|  | R   | 39     | 353           | 5.61    | 46, -57, 29            |

Coordinates (x, y, z) correspond to the Talairach atlas. L = left hemisphere, R = right hemisphere, BA = Brodmann area, FEF = frontal eye field, SEF = supplementary eye field, IPS = intraparietal sulcus, TPJ = temporal-parietal junction, SFG = superior frontal gyrus.

overall slower to target-absent than to target-present trials (664 vs. 620 ms). As can be seen from Fig. 2, more importantly, the interaction between homogeneity and target presence was significant,  $F(1, 15) = 52.89$ ,  $p<.001$ . Pairwise comparisons showed that RTs were slower to target-absent than to -present trials with heterogeneous displays (770 vs. 661 ms),  $t(15)=5.38$ ,  $p<.001$ , but were faster to target-absent than to -present trials with homogenous displays (560 vs. 580 ms),  $t(15)=2.13$ ,  $p=.05$ . Moreover, the RT difference between heterogeneous and homogeneous displays for target-absent trials (770 vs. 560 ms) was larger than that for target-present trials (661 vs. 580 ms),  $t(15)=7.44$ ,  $p<.001$ .

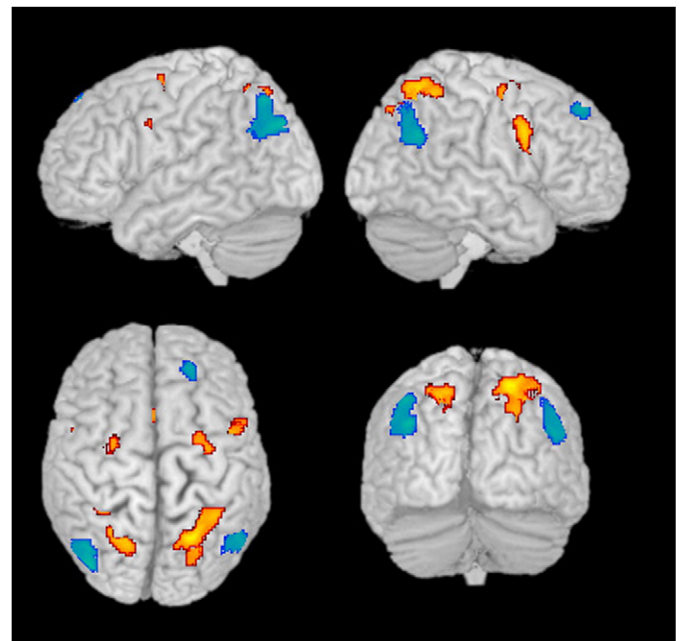
An ANOVA on the error rates revealed also the significant main effects of display homogeneity,  $F(1, 15)=68.71$ ,  $p<.001$ , and of target presence,  $F(1, 15)=10.91$ ,  $p=.005$ . Participants made more errors with heterogeneous than with homogeneous displays (10.2% vs. 2.7%) and more errors on target-present than on -absent trials (8.6% vs. 4.3%). No interaction was found between the two factors,  $F(1, 15)<1$ .

### Imaging

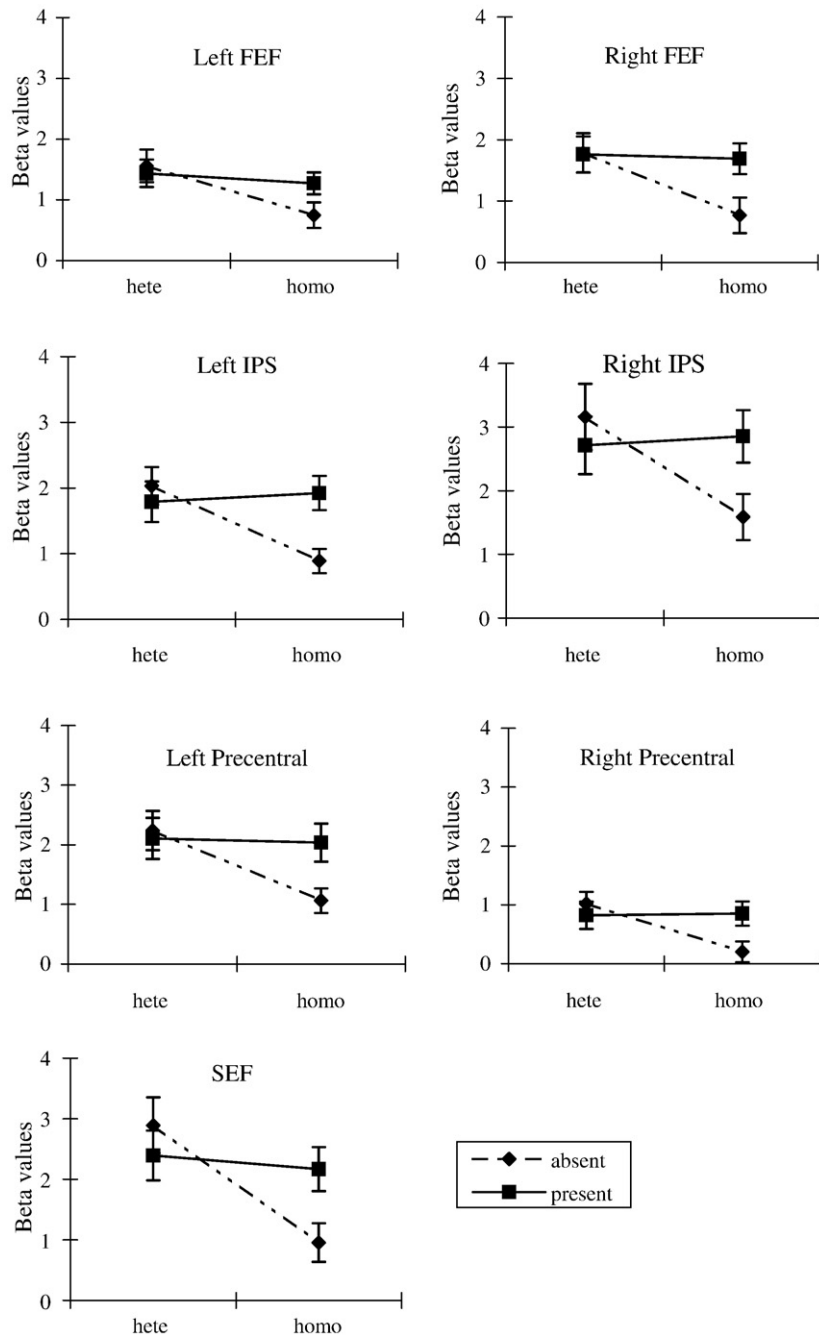
In accordance with the analyses of the behavioral data, the main effects of display homogeneity [(Het\_ab+Het\_pre) vs. (Hom\_ab+Hom\_pre)] and of target presence [(Het\_ab+Hom\_ab) vs. (Het\_pre+Hom\_pre)] and the interaction between them [(Het\_ab-Het\_pre) vs. (Hom\_ab-Hom\_pre)] were computed in the whole-brain analysis. While the contrast between target-absent and -present trials did not show any activation in either direction, the contrast between heterogeneous and homogeneous displays revealed a set of brain regions (Table 2 and Fig. 3). The beta values for the peak activations in these regions were extracted for the four experimental conditions and are depicted in terms of whether the regions showed positive (Fig. 4) or negative (Fig. 5) signal change.

#### Regions with positive signal change

As shown in Fig. 3, the interactions in this set of regions, including bilateral frontal eye field (FEF), intraparietal sulcus (IPS), precentral gyri, and supplementary eye field (SEF), were caused mainly by lower beta values for target-absent compared to target-present trials when



**Fig. 3.** Regions showing a significant interaction between display homogeneity and target presence. The red colored areas indicate those with positive signal changes, the blue colored areas those with negative changes.



**Fig. 4.** The positive beta values in the four experimental conditions for bilateral intraparietal sulcus (IPS), frontal eye field (FEF), precentral gyri, and supplementary eye field (SEF). Hete = heterogeneous display, and homo = homogeneous display.

the display was homogeneous ( $p < .001$  for all the regions), but comparable or larger beta values for target-absent and -present trials for heterogeneous display (for right IPS and SEF, the beta values were larger for target-absent trials,  $p < .05$ ). Moreover, while beta values showed little change for target-present trials as a function of homogeneity ( $p < .05$  for left FEF, but  $p > .1$  for all the other regions), they were significantly decreased for target-absent trials when displays were homogeneous ( $p < .001$  for all the regions).

*Regions with negative signal change*

Both bilateral temporal parietal junctions (TPJ) and a region in right superior frontal gyrus (SFG) showed negative signal changes. As shown in Fig. 4, interactions were caused mainly by the more negative beta values for target-absent compared to target-present trials when

the display was heterogeneous ( $p < .005$  for bilateral TPJ and  $p < .05$  for right SFG) and less negative values for target-absent relative to target-present trials when the display was homogeneous ( $p < .05$  for left TPJ and  $p < .005$  for right TPJ and SFG). On the other hand, while beta values showed little change for target-present trials over homogeneity ( $p > .1$  for all the three regions), for target-absent trials, they were less negative when the displays were homogeneous and more negative when the displays were heterogeneous ( $p < .001$  for all the three regions).

**Discussion**

The behavioral findings in the present experiment replicated previous studies (e.g., Humphreys et al., 1989; Müller and Humphreys,

1993), with a significant interaction between display homogeneity and target presence. RTs were faster for target-absent than for -present displays when the distractors were homogeneous; in contrast, RTs were slower for target-absent than for -present displays when the distractors were heterogeneous. The speed with which a target was detected depended not only on how much it differed from the surrounding distractor items, but also on the homogeneity among the distractors. According to the SERR model (e.g., Humphreys and Müller, 1993), the processing system evaluates the homogeneity of the display, which allows for faster rejection of distractor groups in the case of homogeneous distractors.

At the neural level, the present experiment revealed a set of brain regions sensitive to display homogeneity. More importantly, it demonstrated that bilateral FEF, IPS, precentral gyrus, and SEF were also involved in the interaction between display homogeneity and target presence, with positive activations in these regions. In addition, SFG and TPJ showed a significant interaction, but with negative signal changes. Furthermore, the patterns of estimated activations in these regions were generally parallel to the pattern of the RT interaction, with little difference in signal strength between homogeneity conditions for target-present trials and larger increases from homogeneous to heterogeneous displays for target-absent trials. In the following paragraphs, we discuss these brain activations in relation to the cognitive processes in visual search.

#### Target representation and identification

The activated dorsal brain areas, including bilateral FEF, IPS, precentral gyrus, as well as SEF, showed consistent activation patterns, with roughly equivalent activations for the heterogeneous target-present and -absent trials as well as homogeneous target-present trials (Fig. 4). In these conditions, target template matching is necessary for making proper responses. In contrast, a “no” response can be quickly made to a homogeneous target-absent display; the absence of any visual irregularity permits all display items to be rejected together, with no need for template matching of the target. Therefore, it is likely that the activated dorsal brain regions are responsible for template matching in visual target selection.

Concerning the specific role of IPS and FEF in visual search, previous studies have found overlap of activation in these areas for conjunction search and difficult feature search (Donner et al. 2002, 2003; Leonards et al. 2000), suggesting a common target representation or selection mechanism engaged in different types of visual search. For example, Donner et al. (2003) reported that the anterior IPS and IPTO (junction of intraparietal and transverse occipital sulcus) were activated in conjunction search, relative to feature search, in the absence of distractors (i.e., with only the target being presented), demonstrating that target template matching or target selection is more demanding in the conjunction search task than in the feature search task. A single-unit recording study using a conjunction search task suggested that the macaque's FEF represents the degree of similarity of objects within their receptive fields with a conjunctively defined target object (Bichot and Schall, 1999). Moreover, the FEF may even encode the similarity between distractors and the absent target (Sato et al., 2003): responses to distractors are delayed when the distractors resemble the target. This suggests that a target-like distractor has some chance of falsely activating the target template – which (in terms of SERR) would lead to false alarms and a need for rechecking.

Although the RTs were much faster for the target-present than for the -absent trials with heterogeneous displays, the beta values in the imaging data were similar for target-absent and -present trials for all regions (except right IPS and SEF). In contrast, for homogeneous displays, while the RT difference between target-present and -absent trials was relatively small, the beta values for the two types of trials were significantly different. Given that the task difficulty is generally assumed to be reflected by RT, these differential patterns of the RT data and imaging data demonstrate that the dorsal brain regions were immune to the influence of task difficulty but were related to template matching processes *per se*.

This raises the question why the amount of template matching in the first three conditions (Hom\_pre, Het\_ab, Het\_pre) did not affect the level of activation in these regions. Along the lines of SERR, on heterogeneous trials, several possible groups of items may be conceived as competing to activate their templates, whereupon groups of distractor items are rejected recursively once their templates reach threshold. This would lead to stronger activation for

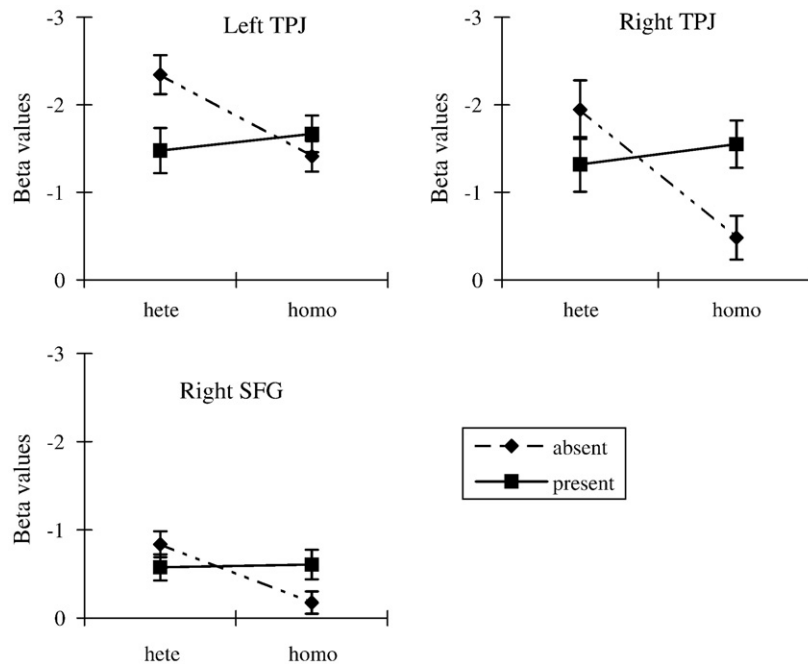


Fig. 5. The negative beta values in the four experimental conditions for bilateral temporal-parietal junction (TPJ) and right superior frontal gyrus (SFG). Note that the values on Y-axis are negative. Hete = heterogeneous display, and homo = homogeneous display.

heterogeneous compared to homogeneous target-present trials, which was found only in left FEF, but not in the other areas such as bilateral IPS, precentral gyri and right FEF. As discussed above, activity in these later areas may reflect increased demands on template matching for target selection, as with conjunction relative to feature targets (e.g., Donner et al., 2003). However, in the present experiment, the target was always a vertical bar (i.e., a feature target), minimizing differences in target template matching between homogeneous and heterogeneous displays. Indeed, as reported earlier, a main effect of display heterogeneity was evident in bilateral IPS, FEF, and precentral gyri, but this effect was mainly due to lower activation for homogeneous target-absent trials compared to the other three (Hom\_pre, Het\_ab, and Het\_pre) conditions, as revealed by the ROI data. Thus, although the largest RT difference was between the Het\_ab and Het\_pre conditions, the dorsal brain areas showed no or little difference in activation between these two conditions. Activations in these areas may reflect the demand for target template matching, but not the amount of template matching. As we will argue later, there are other brain areas that are responsible for distractor rejection before template matching accumulates evidence for the presence of a target.

An alternative role of IPS (and also FEF) is perhaps that they provide an intermediate, topographic saliency representation of the visual display that signals the conspicuity of the various display objects, rather than the mere presence of their physical properties at particular locations (Gottlieb, 2007). However, in the present study, if the IPS and FEF activations represent the saliency signal of the target, this activation should be stronger for target-present trials with homogeneous displays (where the target is of a higher saliency as compared to the distractors, which do not differ amongst each other) than for trials with heterogeneous displays (where the target is nearer in saliency to the distractors, which differ amongst each other). However, as can be seen in Fig. 3, the Hom\_pre and the Het\_pre conditions did not differ significantly, at variance with the suggestion that the activation level of the bilateral IPS directly represents the saliency value of the target. On the other hand, to maintain the candidacy of IPS as representing a saliency map of the search display, one might assume that IPS is activated either when the target is of a higher saliency (in homogeneous displays) or when processing effort is required to make the target salient (in heterogeneous displays). Indeed, the SERR model actually predicts a gradual rise in target saliency as an increasing number of distractor groups are rejected from the search. Future experiments with an appropriate design will have to dissociate these possibilities.

#### *Distractor filtering and rejection*

Another set of brain areas, including bilateral TPJ and the right SFG, showed an consistent interaction pattern which differs from that for the first set (see Fig. 5): they exhibited negative beta values that were more negative for target-absent compared to -present trials with heterogeneous displays and less negative for target-absent relative to -present with homogeneous displays. In functional terms, these areas do not simply reflect the general task difficulty or search efficiency. As reported above, the beta values in TPJ did not show a main effect of homogeneity (in contrast to the RTs which were overall slower for heterogeneous than for homogeneous displays), arguing against a simple relationship between search difficulty and the magnitude of signal change in this region.

There are two potential accounts of BOLD signal decreases in fMRI. One account assumes that the total metabolism of the brain is approximately constant over a wide range of mental and motor activities (Raichle and Gusnard, 2002, for different opinion, see Tomasi et al. 2006). An increase of rCBF (regional Cerebral Blood Flow) in one active brain region needs to “borrow” or “steal” blood from neighboring regions, leading to signal decreases in the borrowed regions. If this account stands for the present data, then we would

have observed signal increases in brain regions around bilateral TPJ and right SFG in conditions in which the latter regions show negative signal change. Although we did observe such positive change for right IPS which is close to right TPJ, we did not observe similar increases for left TPJ and right SFG. The second account suggests these signal decreases reflect an inhibition of neural activity related to cognitive processes. Deactivation of these brain areas during rapid visual information processing (e.g., Marois et al., 2004; Shulman, 1997), for instance, is associated with the need for focusing attention on tasks at hand. Clearly, in this account the decrease of the BOLD signal is a result of direct neural inhibition rather than a pure blood stealing (see also Shulman et al., 2003). Our results are in favor of the second account, suggesting that the deactivation of bilateral TPJ and right SFG may reflect the need for filtering distracting information during visual search.

The temporal parietal junction (TPJ), a region encompassing the supramarginal gyrus, the caudal parts of the superior temporal gyrus, and the dorsal-rostral parts of the occipital gyrus (Downar et al., 2002), has been reported to deactivate during attention-demanding visual search tasks, relative to baseline conditions (Marois et al., 2004; Shulman, 1997; Shulman et al., 2003, 2007; Tomasi et al., 2006; see also Gusnard and Raichle, 2001). For example, in a task in which participants had to search for a target embedded in a series of non-targets presented in an RSVP (rapid serial visual presentation) stream, Shulman et al. (2007) observed TPJ activation when the target appeared in the early part of the stream, but deactivation when it appeared in the middle or late parts. They proposed that the deactivation reflects the filtering of irrelevant inputs from TPJ, preventing unimportant objects from being attended. There is a filter that determines the range of stimuli that the TPJ will respond to, and the dorsal frontoparietal regions may be involved in setting up this filter (Shulman et al., 2003, 2007). Before the target appears in the RSVP stream, TPJ is deactivated to focus on the current task. When a proper item meets the current task setting for the target, it passes through the filter, and increases TPJ activity (see also Serences et al., 2005).

Adapting the above proposal to the conditions of the present study, we suggest that TPJ, together with the right superior frontal gyrus, might be involved in rejecting groups of distractors and maintaining inhibition of their locations to prevent them from interfering with target template matching. The key argument is: the greater the need to shield the gathering of target evidence from distractor interference, the more negative the activation. This argument is supported by the pattern of effects for both the homogeneous and the heterogeneous displays. Specifically, with homogeneous displays, there is less need for shielding on target-absent compared to -present trials. According to SERR, on target-absent trials, the homogeneous group of distractors would rapidly activate its template, enabling the one-step rejection of all display locations – indicative of the absence of any irregularity in the display – and the issuing of a fast target-absent response. In contrast, on target-present trials, the rejected distractor locations would have to be suppressed, so as to prevent interference with the evidence accumulation by the target template. Consequently, TPJ activity would show less suppression on homogeneous target-absent compared to target-present trials.

Conversely, with heterogeneous displays, relatively less shielding is required on target-present than on target-absent trials. According to SERR, if a target is not found in the first-pass process, the system cannot be certain that there is none. The reason is that the target may be falsely grouped with a set of distractors and be rejected, leading to a target miss error. To reduce such errors to an acceptable level, rechecking is required. Thus, for heterogeneous target-present trials, inhibition of distractor locations can be immediately terminated once the target template reaches threshold, upon which a target-present response can be made. But on target-absent trials, the system needs to continue searching (rechecking) to achieve certainty that no target is

present, and this involves ongoing suppression of distractor groups. This would induce more negative activations for target-absent than for -present trials (see Fig. 4).

While Shulman et al. (2007) demonstrated that TPJ may decrease or increase its activity across a series of temporal events, the current study suggests that bilateral TPJ and the right SFG can also operate spatially in a similar way in visual search (which is, of course, also a temporally extended process). As discussed above, TPJ might be involved in inhibiting distractor locations so as to enable the target to pass through ‘the filter’. The earlier the target passes through the filter (as with target-present trials compared with target-absent trials in heterogeneous displays), the smaller the TPJ deactivation. Extending the ‘circuit breaker’ view of TPJ which assumes that TPJ reduces its deactivation when the search process encounters a target or an item with target-defined features (Shulman et al., 2003, 2007; see also Serences et al., 2005), results for the present homogeneous displays suggest that the earlier a response can be made and the current task can be terminated, the smaller the TPJ deactivation, even if there is no target at all that passes through the filter and the response is ‘no target’.

In line with this filtering hypothesis, Shulman et al. (2007) also suggested that, in their RSVP paradigm, the mean magnitude of the deactivation in right TPJ was significantly larger on trials on which the subsequent target was detected rather than missed, reflecting more efficient filtering. Since there were too few (target miss and false-alarm) errors in the present experiment to permit such a comparison (and error trials were excluded from analysis), it remains to be examined in future work whether target miss errors would also be related to ineffective filtering by TPJ in visual search for a target in space rather than time. Furthermore, Wilkinson et al. (2002) also reported TPJ activation in a within-object conjunction search task with homogeneous (as compared to heterogeneous) distractors and suggested that right TPJ is sensitive to similarity-based visual grouping (as with homogeneous displays). But they did not report an ROI analysis to examine whether TPJ shows more positive activation for homogeneous compared to heterogeneous displays, which would have supported their grouping account. However, in the light of the present findings, it is possible that the activation for homogeneous, as contrasted with heterogeneous, displays was actually caused by the lesser degree of negative (or de-)activation with homogeneous displays, arguing in favor of the distractor suppression hypothesis advanced above.

In sum, while TPJ activity may very well be associated with the function of broad information gathering from the environment (Raichle et al., 2001), this activity may be inhibited during goal-driven, attention-demanding processing to prevent irrelevant sources of information from interfering with task performance. Consistent with this, TPJ has been reported to be increasingly suppressed as the visual short-term memory load increased (Todd et al., 2005).

## Conclusion

By asking the participants to search for a vertically orientated bar among distracting bars with homogenous or heterogeneous orientations, the present study revealed an interaction between display homogeneity and target presence at both the behavioral and the neural level. The search RT for deciding whether a target was present or absent varied with the way the search display was constructed, suggesting a top-down controlled target search process interacting with bottom-up coded stimulus properties. At the neural level, a distributed set of brain areas was involved in this interaction. The bilateral frontal eye field, intraparietal sulcus, precentral gyri and supplementary eye field may play a role in focusing attention for target template matching. The right superior frontal gyrus and the bilateral temporal-parietal junction may play a role in filtering and rejecting distracting information in the search process.

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## References

- Arguin, M., Joanette, Y., Cavanagh, P., 1993. Visual search for feature and conjunction targets with an attention deficit. *J. Cogn. Neurosci.* 5, 5436–5452.
- Ashbridge, E., Cowey, A., Wade, D., 1999. Does parietal cortex contribute to feature binding? *Neuropsychologia* 37, 999–1004.
- Bichot, N.P., Schall, J.D., 1999. Effects of similarity and history on neural mechanisms of visual selection. *Nat. Neurosci.* 2, 549–554.
- Bundesden, C., 1987. Visual attention: race models for selection from multielement displays. *Psychol. Res.* 49, 113–121.
- Bundesden, C., 1993. The relationship between independent race models and Luce's choice axiom. *J. Math. Psychol.* 37, 446–471.
- Chun, M.M., Wolfe, J.M., 1996. Just say no: how are visual searches terminated when there is no target present? *Cogn. Psychol.* 30, 39–78.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 215–229.
- Corbetta, M., Shulman, G.L., Miezin, F.M., Petersen, S.E., 1995. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* 270, 802–805.
- Coull, J.T., Walsh, V., Frith, C.D., Nobre, A.C., 2003. Distinct neural substrates for visual search amongst spatial versus temporal distractors. *Cogn. Brain Res.* 17, 368–379.
- Donner, T.H., Kettermann, A., Diesch, E., Ostendorf, F., Villringer, A., Brandt, S.A., 2000. 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.H., Kettermann, A., Diesch, E., Ostendorf, F., Villringer, A., Brandt, S.A., 2002. Visual feature and conjunction searches of equal difficulty engage only partially overlapping frontoparietal networks. *NeuroImage* 15, 16–25.
- Donner, T.H., Kettermann, A., Diesch, E., Villringer, A., Brandt, S.A., 2003. Parietal activation during visual search in the absence of multiple distractors. *NeuroReport* 14, 2257–2261.
- Downar, J., Crawley, A.P., Mikulis, D.J., Davis, K.D., 2002. A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. *J. Neurophysiol.* 87, 615–620.
- Duncan, J., 1987. Attention and reading: wholes and parts in shape recognition. A tutorial review. In: Coltheart, M. (Ed.), *Attention and Performance XII: The Psychology of Reading*. Lawrence Erlbaum Associates, London, pp. 39–61.
- Duncan, J., Humphreys, G.W., 1989. Visual-search and stimulus similarity. *Psychol. Rev.* 96, 433–458.
- Duncan, J., Humphreys, G.W., 1992. Beyond the search surface: visual search and attentional engagement. *J. Exp. Psychol. Hum. Percept. Perform.* 18, 578–588.
- Eriksen, C.W., 1988. A source of error in attempts to distinguish coactivation from separate activation in the perception of redundant targets. *Percept. Psychophys.* 44, 191–193.
- Friston, K., Holmes, A.P., Poline, J.B., Grasby, P.J., Williams, S.C., Frackowiak, R.S., Turner, R., 1995. Analysis of fMRI time series revisited. *NeuroImage* 2, 45–53.
- Gusnard, D.A., Raichle, M.E., 2001. Searching for a baseline: functional imaging and the resting human brain. *Nat. Rev. Neurosci.* 2, 685–694.
- Gottlieb, J., 2007. From thought to action: the parietal cortex as a bridge between perception, action, and cognition. *Neuron* 53, 9–16.
- Gitelman, D.R., Parrish, T.B., Friston, K.J., Mesulam, M.M., 2002. Functional anatomy of visual search: regional segregations within the frontal eye fields and effective connectivity of the superior colliculus. *NeuroImage* 15, 970–982.
- Grice, G.R., Nullmeyer, R., Spiker, V.A., 1977. Application of variable criterion theory to choice reaction time. *Percept. Psychophys.* 22, 431–449.
- Horowitz, T.S., Wolfe, J.M., 1998. Visual search has no memory. *Nature* 394, 575–577.
- Humphreys, G.W., Müller, H.J., 1993. SEArch via recursive rejection (SERR): a connectionist model of visual search. *Cogn. Psychol.* 25, 43–110.
- Humphreys, G.W., Quinlan, P.T., Riddoch, M.J., 1989. Grouping processes in visual search: effects with single- and combined-feature targets. *J. Exp. Psychol. Gen.* 118, 258–279.
- Leonards, U., Sunaert, S., Hecke, P.V., Orban, G.A., 2000. Attention mechanisms in visual search – an fMRI study. *J. Cogn. Neurosci.* 12, 61–75.
- Marois, R., Yi, D.J., Chun, M.M., 2004. The neural fate of consciously perceived and missed events in the attentional blink. *Neuron* 41, 465–472.
- Müller, H.J., Humphreys, G.W., 1993. A connectionist model of visual search for simple form conjunctions. In: Brogan, D., Gale, A., Carr, K. (Eds.), *Visual Search 2*. Taylor and Francis, London, pp. 61–71.
- Müller, H.J., von Mühlen, A., 2000. Probing distractor inhibition in visual search: inhibition of return. *J. Exp. Psychol. Hum. Percept. Perform.* 26, 1591–1605.
- Müller, H.J., Humphreys, G.W., Donnelly, N., 1994. SEArch via Recursive Rejection (SERR): visual search for single and dual form-conjunction targets. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 235–258.



- Müller, H.J., Humphreys, G.W., Olson, A.C., 1998. SEArch via Recursive Rejection (SERR). In: Wright, R.D. (Ed.), *Visual Attention*. Vancouver Studies in Cognitive Science, Vol. 8. Oxford University Press, New York, pp. 389–416.
- Müller-Plath, G., Pollmann, S., 2003. Determining subprocesses of visual feature search with reaction time models. *Psychol. Res.* 67, 80–105.
- Niebur, E., Koch, C., Rosin, C., 1993. An oscillation-based model for the neuronal basis of attention. *Vis. Res.* 18, 2789–2802.
- Nobre, A.C., Coull, J.T., Walsh, V., Frith, C.D., 2003. Brain activations during visual search: contributions of search efficiency versus feature binding. *NeuroImage* 18, 91–103.
- Pollmann, S., Cramon, D.Y., 2000. Object working memory and visuospatial processing: functional neuroanatomy analyzed by event-related fMRI. *Exp. Brain Res.* 133, 12–22.
- Pollmann, S., Wiggins, C.J., Norris, D.N., von Cramon, D.Y., Schubert, T., 1998. Use of short inter-trial intervals in single-trial experiments: a 3T-fMRI-study. *NeuroImage* 8, 327–339.
- Raichle, M.E., Gusnard, D.A., 2002. Appraising the brain's energy budget. *Proc. Natl. Acad. Sci.* 99 (16), 10237–10239.
- Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. *Proc. Natl. Acad. Sci.* 98, 676–682.
- Rushworth, M.F.S., Paus, T., Sipila, P.K., 2001. Attention systems and the organization of the human parietal cortex. *J. Neurosci.* 21, 5262–5271.
- Sato, T.R., Watanabe, K., Thompson, K.G., Schall, J.D., 2003. Effect of target-distractor similarity on FEF visual selection in the absence of the target. *Exp. Brain Res.* 151, 356–363.
- Schubö, A., Schröger, E., Meinecke, C., 2004. Texture segmentation and visual search for pop-out targets. An ERP study. *Cogn. Brain Res.* 21, 317–334.
- Schubö, A., Wykowska, A., Müller, H.J., 2007. Detecting pop-out targets in contexts of varying homogeneity: investigating homogeneity coding with event-related brain potentials. *Brain Res.* 1138, 136–147.
- Serences, J.T., Shomstein, S., Leber, A.B., Golay, X., Egeth, H.E., Yantis, S., 2005. Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychol. Sci.* 16, 114–122.
- Shulman, G.L., 1997. Common blood flow changes across visual tasks: II. decreases in cerebral cortex. *J. Cogn. Neurosci.* 9, 648–663.
- Shulman, G.L., McAvoy, M.P., Cowan, M.C., Astafiev, S.V., Tansy, A.P., d'Avossa, G., Corbetta, M., 2003. Quantitative analysis of attention and detection signals during visual search. *J. Neurophysiol.* 90, 3384–3397.
- Shulman, G.L., Astafiev, S.V., McAvoy, M.P., d'Avossa, G., Corbetta, M., 2007. Right TPJ deactivation during visual search: functional significance and support for a filter hypothesis. *Cereb. Cortex* 17, 2625–2633.
- Todd, J.J., Fougny, D., Marois, R., 2005. Visual short-term memory load suppresses temporo-parietal junction activity and induces inattention blindness. *Psychol. Sci.* 16, 965–972.
- Tomasi, D., Ernst, T., Caparelli, E.C., Chang, L., 2006. Common deactivation patterns during working memory and visual attention tasks: an intra-subject fMRI study at 4 Tesla. *Hum. Brain Mapp.* 27, 694–705.
- Treisman, A.M., 1988. Features and objects: the fourteenth Bartlett memorial lecture. *Q. J. Exp. Psychol.* 40, 201–237.
- Treisman, A.M., Gelade, G., 1980. Feature-integration theory of attention. *Cogn. Psychol.* 12, 97–136.
- Wilkinson, D.T., Halligan, P.W., Henson, R.N.A., Dolan, R.J., 2002. The effects of inter-distracter similarity on search processes in superior parietal cortex. *NeuroImage* 15, 611–619.
- Wojciulik, E., Kanwisher, N., 1999. The generality of parietal involvement in visual attention. *Neuron* 23, 747–764.