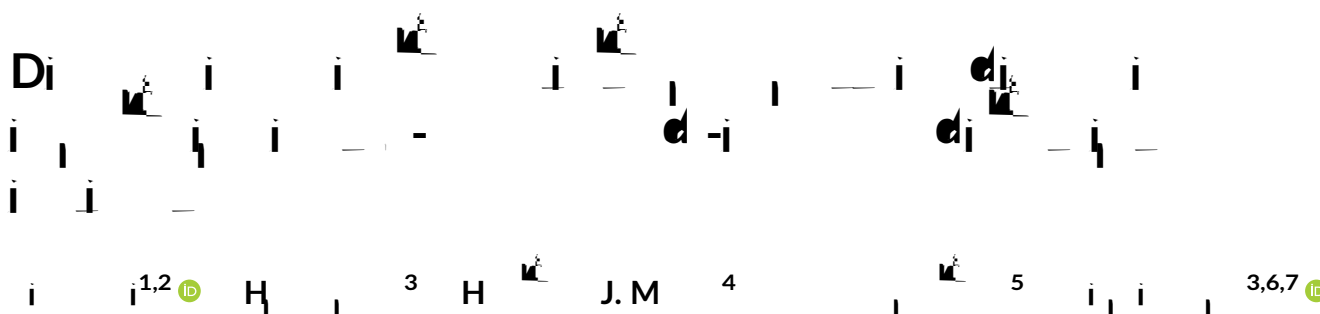


RESEARCH ARTICLE



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ABSTRACT

A crucial function of our goal-directed behavior is to select task-relevant targets among distractor stimuli, some of which may share properties with the target and thus compete for attentional selection. Here, by applying functional magnetic resonance imaging (fMRI) to a visual search task in which a target was embedded in an array of distractors that were homogeneous or heterogeneous along the task-relevant (orientation or form) and/or task-irrelevant (color) dimensions, we demonstrate that for both (orientation) feature search and (form) conjunction search, the fusiform gyrus is involved in processing the task-irrelevant color information, while the bilateral frontal eye fields (FEF), the cortex along the left intraparietal sulcus (IPS), and the left junction of intraparietal and transverse occipital sulci (IPTO) are involved in processing task-relevant distracting information, especially for target-absent trials. Moreover, in conjunction (but not in feature) search, activity in these frontoparietal regions is affected by stimulus heterogeneity along the task-irrelevant dimension: heterogeneity of the task-irrelevant information increases the activity in these regions only when the task-relevant information is homogeneous, not when it is heterogeneous. These findings suggest that differential neural mechanisms are involved in processing task-relevant and task-irrelevant dimensions of the searched-for objects. In addition, they show that the top-down task set plays a dominant role in determining whether or not task-irrelevant information can affect the processing of the task-relevant dimension in the frontoparietal regions.

KEYWORDS

conjunction search, feature search, fMRI, task-irrelevant, task-relevant, visual search

1 | INTRODUCTION

The human visual system is often confronted with many different objects at a time, but only some of the objects most relevant to the task at hand are selected for further processing. For example, when we search for a round building in a street, we need to ignore distracting buildings, which may vary in terms of shape (a task-relevant dimension) or color (a task-irrelevant dimension). Competition among

multiple stimuli is known to be resolved by attentional selection mechanisms that enhance the representation and processing efficiency of attended information (e.g., Moran & Desimone, 1985; Nakayama & Martini, 2011; Serences et al., 2005), and suppress the processing of unwanted information (e.g., Beck & Kastner, 2005; Friedman-Hill, Robertson, Ungerleider, & Desimone, 2003; Reeder, Olivers, & Pollmann, 2017; Shulman et al., 2010; Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007; Vossel, Weidner, Moos, & Fink,

2016). A network of frontoparietal areas, including posterior parietal cortex (PPC), intraparietal sulcus (IPS), frontal eye field (FEF), and supplementary motor area (SMA)/supplementary eye field (SEF), are thought to be important in biasing processing toward the top-down defined information and away from potentially distracting information in the visual field (Fairhall, Indovina, Driver, & Macaluso, 2009; Maximo, Neupane, Saxena, Joseph, & Kana, 2016; Reeder, Hanke, &

condition, the upright T target was placed among a mixture of differently oriented, non-upright Ts and Ls. Importantly, in both experiments, for the manipulation of the task-irrelevant dimension, the item colors were the same in the homogeneous conditions but different in the heterogeneous conditions. We chose color for the task-irrelevant dimension because, compared with other features, color is of higher perceptual saliency, and its variation is more likely to attract attention and affect performance for a task-relevant dimension (Theeuwes, 1991, 1992; Treisman, 1988; Wei & Zhou, 2006). Behaviorally, we expected heterogeneity along both the task-relevant dimension (Duncan & Humphreys, 1989, 1992; Wolfe et al., 1992) and the task-irrelevant dimension (Wei & Zhou, 2006) to affect search times; that is, RTs would be slower for heterogeneous compared to homogeneous conditions. Moreover, we expected the two dimensions to interact such that heterogeneity along the task-irrelevant color dimension would have a more prominent influence on RTs with homogeneous distractors in the task-relevant dimension (Wei & Zhou, 2006). At the neural level, we separately compared brain activity associated with detecting a target in heterogeneous versus homogeneous displays along the task-relevant and -irrelevant dimensions, on the assumption that heterogeneous displays involve stronger activations of frontoparietal attentional network regions (e.g., bilateral FEF, bilateral IPS, and SMA/SEF) compared to homogeneous displays. The distractors in heterogeneous displays consist of more variations of information along the task-relevant and -irrelevant dimensions, thus increasing the chance for some distractors to be falsely selected and/or falsely activate the target template (cf., Müller & Humphreys, 1993), and then to make greater demands on these frontoparietal regions in target selection. On the other hand, the ventral attentional areas, such as TPJ and posterior cingulate cortex (PCC), may be more related to homogeneous displays in allowing similar distractors to be segmented and rejected from the search in a group (Müller & Humphreys, 1993; Wilkinson et al., 2002). We expected these comparisons (and appropriate further contrasts) to reveal (a) possible differential brain mechanisms for processing distracting information along the two dimensions, as well as (b) a potential interaction between the two dimensions and modulation of the activation in these brain regions by the type of search.

2 | MATERIAL AND METHOD

2.1 | PARTICIPANTS

Seventeen right-handed undergraduate and graduate students participated in Experiment 1 (with an orientation search task), and another 15 in Experiment 2 (with a within-object conjunction search task). All of them had normal or corrected-to-normal vision, and participants with known color blindness or weakness were excluded in the recruiting procedure. None of the participants had a history of neurological or psychiatric disorders, and all gave written informed consent prior to the scanning. The study was approved by the Ethics Committee of the School of Psychological and Cognitive Sciences, Peking University. Three participants in Experiment 1 and one participant in Experiment 2 were excluded from data analysis due to excessive head movements (>3 mm) during fMRI scanning. The remaining participants were eight females and six males (age ranging

between 20 and 26 years) for Experiment 1, and seven females and seven males (between 21 and 28 years) for Experiment 2.

2.2 | DESIGN AND STIMULI

Participants were required to search for a vertically oriented bar in Experiment 1 and for an upright T in Experiment 2. For both search tasks, a $2 \times 2 \times 2$ within-participant design was used (see the right panel of Figure 1 for exemplar stimuli). The first factor was the heterogeneity of the feature values in the task-irrelevant (color) dimension: the color of the display items was either identical (ir_hom) or variable (ir_het), randomly selected from red, orange, purple, deeppink, green, blue, cyan, and indigo. The second factor was the heterogeneity of the distractor features in the task-relevant dimension (bar orientation in Experiment 1, randomly selected from 0°, 22.5°, 45°, and 67.5° away from the horizontal orientation; the composition of horizontal and vertical bars to make non-target T and L shapes in Experiment 2): the distractors were either homogeneous (re_hom) or heterogeneous (re_het). The third factor was target presence: a target was present in half the trials and absent in the other half. With two response buttons under the participants' right index and middle finger, half of them were instructed to respond with their index finger to indicate "target-present" and the middle finger to indicate "target-absent," and vice versa for the other half. Participants were told that the stimuli's color was entirely task-irrelevant and should therefore be ignored.

The 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 stimuli and recording of responses were controlled by Presentation software (<http://nbs.neuro-bs.com/>). At the start of each trial, a white fixation cross, measuring 0.20° of visual angle, appeared at the center of the black screen for 1,000 ms. A black screen of 100 ms was inserted 400 ms after the onset of the fixation marker, 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 eight items, each measuring $0.8^\circ \times 0.2^\circ$, that were randomly presented on each trial at the 12 locations surrounding the fixation cross at an eccentricity of 1.4° (the inner one) and 3° (the outer one) of visual angle. In the target-present trials, one of the eight items was the target. In the target-absent trials, all of the items presented were distractors. The locations of these items were randomly selected in each trial. After the search display, the fixation cross was presented in the center of the screen for 1,000, 1,100, 1,200, 1,300, 1,400, or 1,500 ms, with a mean of 1,250 ms (see the left panel of Figure 1).

Each experimental condition consisted of 48 trials, intermixed with a total of 48 null trials in which only the fixation cross was presented. The eight experimental conditions and null trials were randomized in one continuous scanning session. In order to accustom participants to the scanning noise and to allow for the MR signal to reach a steady state, only the fixation point was displayed during the first 7.5 s. Participants were asked to search for the target and respond as quickly and accurately as possible upon presentation of the search display. They were instructed to maintain eye fixation on the cross in the display center throughout the whole experiment (see also Nobre et al., 2003; Soto, Humphreys, & Rotshtein, 2007). Before scanning, the observers were

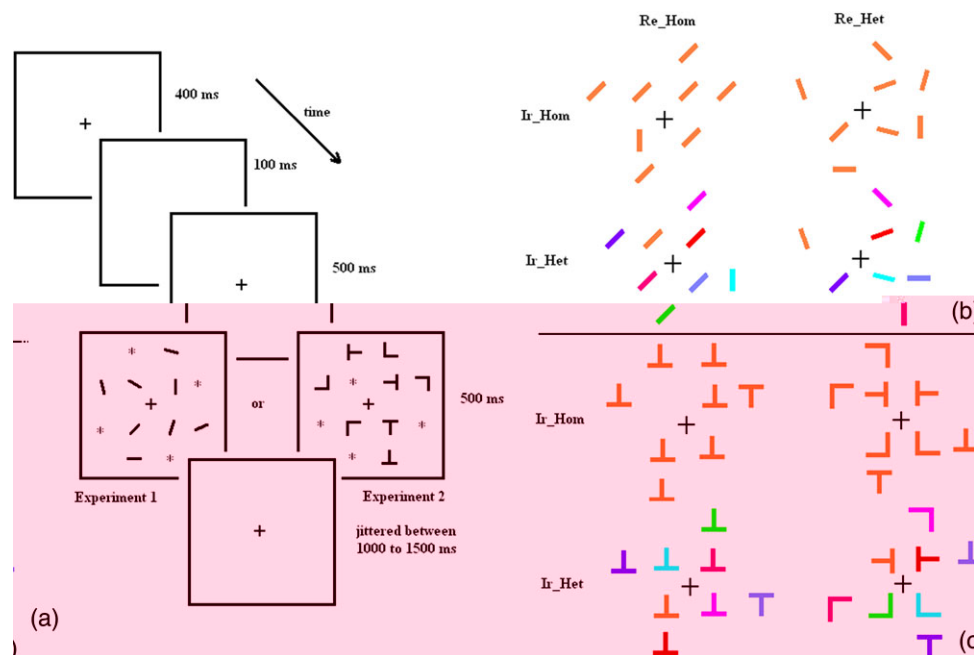


FIGURE 1 (a) Example of trial sequence and exemplar display with target-present in Experiment 1 or Experiment 2. Stars (not shown in the real search display) in the display examples here are the remaining four positions after eight were randomly selected from the total 12 possible positions for search items to be displayed. The four experimental conditions of target-present trials in Experiment 1 (b) and in Experiment 2 (c) in terms of variations along the task-relevant and task-irrelevant conditions. Re_hom = relevant dimension has homogeneous distractors, Re_het = relevant dimension has heterogeneous distractors; Ir_hom = irrelevant dimension has homogeneous colors; and Ir_het = irrelevant dimension has heterogeneous colors [Color figure can be viewed at wileyonlinelibrary.com]

familiarized with the task and performed several practice blocks in which they were explicitly told to maintain fixation during the task. All participants completed a training section of 10 min outside the scanner.

2.3 | Materials and Procedure

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: 64×64 , pixel size: 3.4×3.4 mm. Twenty-four transversal slices of 4 mm thickness, oriented parallel to the anterior and posterior commissures, were acquired sequentially in ascending order with a 1 mm gap (TR = 1.5 s, TE = 30 ms, FOV = 220 mm, flip angle = 90°). The slices enabled whole-brain coverage. High-resolution anatomic images were obtained using a standard 3D T1-weighted sequence with 0.9×0.9 mm in plane resolution and 1.3 mm slice thickness (256×256 matrix). The total of 880 volumes of EPI images were obtained with the first five volumes discarded to allow for T1 equilibration effects. Images were spatially realigned to the sixth volume for head movement correction, coregistered with the anatomical 3D image. The functional images were then normalized by applying the transforming matrix obtained through normalizing anatomical scans to a standard T1 template (Montreal Neurological Institute template provided by Statistical Parametric Mapping [SPM], see below), and by using the “unified-segmentation” function in SPM8 (see below) with a resampling of $2 \times 2 \times 2$ mm³ voxels. The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to accommodate inter-subject anatomical variability.

2.4 | Materials and Procedure

Data were analyzed with SPM8, Wellcome Department of Imaging Neuroscience, London (Friston et al., 1995), employing a random-effects model. At the first level, eight event types were defined. The eight event types represent all combinations of (a) the heterogeneity of the task-irrelevant dimension, (b) the heterogeneity of the task-relevant dimension, and (c) the target presence. The event type was time-locked to the onset of the search display by a canonical synthetic hemodynamic response function (HRF) implemented in SPM8. Additionally, all error trials (including excluded outliers and “twin data,” see “Results” section) were included as an extra regressor of no interest in the design matrix. For each participant, simple main effects for each of the eight experimental conditions were computed by applying appropriate baseline contrasts, that is, the experimental conditions versus the implicit baseline (null trials). The obtained event-type images of all participants were entered into the flexible factorial design with the standard implementation in SPM8 (including an additional factor modeling the participant mean) for calculating the main effects of the task-relevant and -irrelevant dimensions, the simple main effects of the two dimensions separately for target-present and target-absent trials (see “Results” section), and the interaction effects between the two dimensions in both experiments. The group activations are reported at a family-wise error (FWE) corrected threshold of $p < .05$.

Moreover, we examined certain contrasts for individual participants, with the obtained contrast images of the first-level analysis in the two experiments entered into a second-level two-sample *t* test for performing between-participants comparisons and for between-participants conjunction analyses across the two experiments (Friston,

Penny, & Glaser, 2005; Price & Friston, 1997). The between-participants contrasts were performed to identify differential activations between the two experiments for the interaction between the task-relevant and task-irrelevant dimensions. The conjunction analysis was carried out to locate the common brain activations related to the main effects of task-irrelevant/task-relevant heterogeneous information across the two experiments, with the "conjunction null" hypothesis being tested (Nichols, Brett, Andersson, Wager, & Poline, 2005). Although this between-participants conjunction analysis may not be typical, it can be justified since we normalized the functional images of different groups of participants in Experiments 1 and 2 to the same standard template in SPM8, so the activation locations for the same contrasts should be comparable between experiments. The between-participants effects were thresholded with $p < .001$, uncorrected at voxel level, and with $p < .05$ corrected at cluster level, following previous studies (e.g., Kim, Johnson, Cilles, & Gold, 2011; Weissman, Mangun, & Woldorff, 2002). The same analyses with FWE correction ($p < .05$) would produce a null effect. Note, this conjunction analysis was conducted to identify brain regions that allow us to carry out detailed region-of-interest (ROI) analyses and to illustrate how the activations in these brain areas were modulated by display heterogeneity along the two dimensions and target-presence in each experiment. The ROI analyses were done by extracting beta values within a sphere centered at the peak voxel and with a radius of 5 mm at the activated brain areas in the conjunction analysis. Correlation analyses were then performed for each ROI. Here, each participant's mean behavioral RT in each experimental condition was taken as one data point, so the mean beta value for each condition. Partial correlations were performed by controlling for the variations along the task-irrelevant dimension, the task-relevant dimension, and target-presence.

3 | Results

3.1 | Behavioral results

Mean reaction times (RTs) and response error rates were calculated for each of the participants. As shown in Table 1, the error rates were

higher for target-present trials (target misses) than for the target-absent trials (false alarms) in both experiments, suggesting a tendency toward "no-target" responses. To correct for potential speed-accuracy trade-offs, we carried out a "kill-the-twin" procedure (Eriksen, 1988; Grice, Nullmeyer, & Spiker, 1977). Twins of error RTs were computed by searching for an RT in correct-rejection or correct-hit trials which corresponded to an error RT (within a range of 3 ms) on target-miss or false-alarm trials, respectively. These "twins" RTs were then removed from the "correct" data set. This procedure, which was carried out separately for different displays for each participant, led to the elimination of 2.7% of the data points for orientation search, and 3.0% for conjunction search. The remaining data were then processed further by the elimination of outlier RTs more than three standard deviations above or below individuals' mean in each experimental condition (0.9% of the remaining data points for orientation search, 0.7% for conjunction search). RTs in the various experimental conditions with and without error correction are shown in Table 1 and Figure 2. As can be seen, RT performance did not change as a result of removing the error "twins"; that is, the patterns of RT effects were largely undistorted by potential speed-accuracy trade-offs.

After eliminating the error twin RTs and deleting outliers, RT's were entered into a 2 (heterogeneous vs. homogeneous along the task-irrelevant dimension) \times 2 (heterogeneous vs. homogeneous along the task-relevant dimension) \times 2 (target absent vs. present) analysis of variance (ANOVA).

3.1.1 | Experiment 1

The RT ANOVA revealed all three main effects to be significant: heterogeneity in the task-irrelevant color dimension, with longer RTs in the *ir_het* versus the *ir_hom* condition (796 vs. 779 ms), $F(1, 13) = 34.14$, $p < .001$; heterogeneity in the orientation dimension, with longer RTs in *re_het* versus the *re_hom* condition (848 vs. 727 ms), $F(1, 13) = 91.27$, $p < .001$; and target presence, with longer RTs on target-absent than on target-present trials (824 vs. 750 ms), $F(1, 13) = 80.10$, $p < .001$. Moreover, heterogeneity in the orientation dimension interacted with heterogeneity in the color dimension, $F(1, 13) = 30.42$, $p < .001$, and with target presence, $F(1, 13) = 77.68$, $p < .001$. The three-way interaction was also significant,

TABLE 1 Mean reaction times (ms), standard deviations, and percentages of errors (%) as a function of cue validity and stimulus type

| Experiment | Task-relevant dimension | | Heterogeneous | | Homogeneous | |
|--------------|-------------------------|----------------|---------------|-----------|-------------|-----------|
| | Target-absent | Target-present | RT | Error | RT | Error |
| Experiment 1 | Task-relevant dimension | Target-absent | RT | 933 (930) | 725 (725) | 926 (924) |
| | | | SD | 152 (152) | 137 (137) | 143 (143) |
| | | | Error | 7.3 | 1.8 | 6.4 |
| | Task-relevant dimension | Target-present | RT | 759 (758) | 766 (766) | 774 (771) |
| | | | SD | 141 (140) | 131 (131) | 139 (138) |
| | | | Error | 11.8 | 17.6 | 9.4 |
| Experiment 2 | Task-relevant dimension | Target-absent | RT | 955 (952) | 794 (794) | 956 (954) |
| | | | SD | 188 (186) | 139 (139) | 169 (170) |
| | | | Error | 2.2 | 0.6 | 3.3 |
| | Task-relevant dimension | Target-present | RT | 730 (732) | 731 (731) | 742 (743) |
| | | | SD | 118 (120) | 123 (123) | 120 (122) |
| | | | Error | 19.2 | 15.2 | 12.5 |

Note. The reaction times and standard deviations without removing the "twins" data are reported in parentheses.

$F(1, 13) = 12.55, p < .005$. As can be seen from Figure 2, heterogeneity in the orientation dimension did not interact with heterogeneity in the color dimension for target-absent trials, $F(1, 13) < 1$, but did interact for target-present trials, $F(1, 13) = 27.21, p < .001$. Further pairwise comparisons for target-present trials showed that when the

analysis of the main effect of heterogeneity in the task-relevant dimension, $re_het - (ir_het + ir_hom) > re_hom - (ir_het + ir_hom)$, showed that the bilateral FEFs, left anterior part of IPS, and left junction of intraparietal and transverse occipital sulci (IPTO) were both activated in the two experiments (see Table 3).

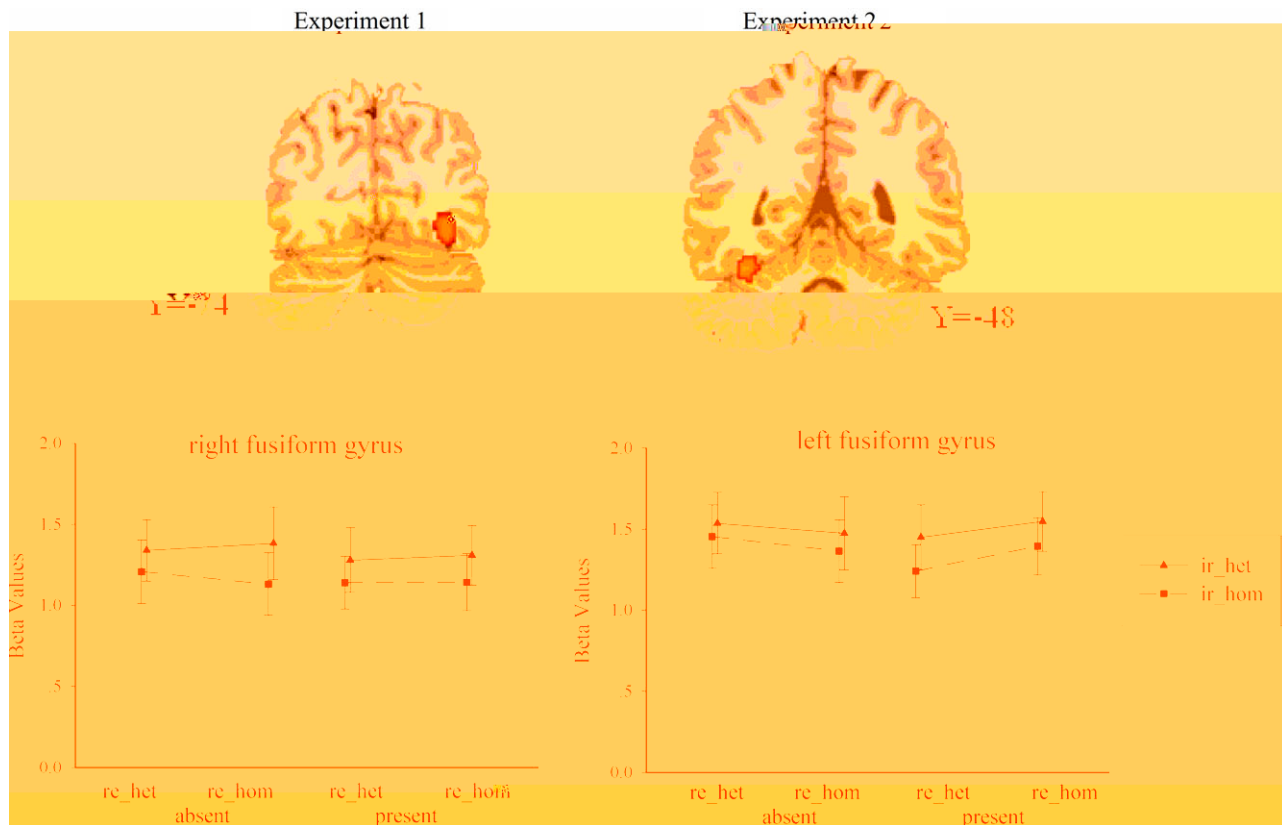


FIGURE 3 The brain activations related to processing task-irrelevant heterogeneous information (ir_het vs. ir_hom) in Experiments 1 and 2, and the extracted beta values from these two regions [Color figure can be viewed at wileyonlinelibrary.com]

for target-absent trials exhibited an activation pattern very similar to that when target-absent and target-present trials were collapsed (see Table 2), the same contrasts calculated for target-present trials failed to reveal activations at the same threshold, with the exception of the contrast Re_Hom versus Re_Het for target-present trials in Experiment 1 which revealed significant activation in the right anterior cingulate cortex (centered at 9/41/4, BA 39, $Z = 5.81$, voxel number = 46).

3.2.4 | Interaction analysis

An interaction analysis, $re_hom (ir_het - ir_hom) > re_het (ir_het - ir_hom)$, was conducted for each experiment in order to uncover the neural correlates of the differential effects of heterogeneity in the

task-irrelevant dimension when the task-relevant dimension consisted of homogeneous or heterogeneous distractors. This analysis revealed activations in bilateral frontal eye fields, intraparietal sulci, and left anterior insula with FWE correction of $p < .05$ in conjunction search (see Table 4), but no activation in orientation search. Separate analyses for target-absent and target-present trials in conjunction search revealed similar pattern of activation for target-absent trials in conjunction search (see Table 4), but no activation in target-present trials.

Moreover, two-sample t tests over the obtained contrast images of the interaction between the task-relevant and -irrelevant dimensions revealed that left FEF (centered at $-26/-2/42$, BA 6, $Z = 4.20$, voxel number = 86) and left IPS (centered at $-20/-70/48$, BA

TABLE 3 Brain areas activated in the conjunction analysis of re_het versus re_hom across two experiments (upper panel) and the brain areas in the same conjunction analysis for target-absent trials across two experiments (lower panel)

| A | BA | x | y | z | Z- | Cluster size |
|--|----|-----|-----|----|------|--------------|
| <i>Conjunction analysis</i> | | | | | | |
| Left IPS | 7 | -28 | -48 | 44 | 3.87 | 68 |
| Left IPTO | 7 | -20 | -70 | 40 | 3.63 | 139 |
| Left FEF | 6 | -24 | 0 | 48 | 3.75 | 115 |
| Right FEF | 6 | 28 | 0 | 46 | 3.61 | 22 |
| <i>Conjunction analysis for target-absent trials</i> | | | | | | |
| Left IPS | 7 | -30 | -42 | 44 | 5.21 | 46 |
| Left IPTO | 7 | -22 | -70 | 38 | 5.26 | 64 |
| Left FEF | 6 | -28 | -2 | 52 | 4.80 | 4 |
| Right FEF | 6 | 30 | 0 | 48 | 4.95 | 11 |

Note. Coordinates (x, y, z) correspond to the MNI (Montreal Neurological Institute) space.

TABLE 4 Brain areas activated in the interaction between the heterogeneity along the task-relevant and -irrelevant dimensions (upper panel) and this interaction effects for target-absent trials (lower panel) in Experiment 2

| A | BA | x | y | z | Z | |
|---------------------------|------|-----|-----|----|------|-----|
| <i>Interaction</i> | | | | | | |
| Left FEF | 6 | -26 | -2 | 46 | 6.79 | 310 |
| Left inferior FEF | 6 | -44 | 2 | 34 | 5.22 | 47 |
| Right FEF | 6 | 30 | -4 | 48 | 5.29 | 27 |
| Left IPS | 7 | -22 | -68 | 40 | 6.36 | 889 |
| Right IPS | 7 | 26 | -54 | 48 | 6.71 | 465 |
| Left anterior insular | 47 | -32 | 20 | 12 | 5.02 | 12 |
| <i>Interaction_absent</i> | | | | | | |
| Left FEF | 6 | -28 | -4 | 48 | 4.42 | 272 |
| Right FEF | 6 | 30 | -4 | 48 | 5.82 | 73 |
| SMA | 6 | -8 | 12 | 56 | 4.89 | 382 |
| Left IPS | 7 | -22 | -56 | 40 | 5.36 | 679 |
| Right IPS | 7 | 22 | -60 | 50 | 4.57 | 637 |
| Right IPTO | 7/18 | 24 | -70 | 22 | 3.92 | 94 |
| Left occipital gyrus | 19 | -52 | -68 | -8 | 3.97 | 86 |
| Left anterior insular | 47 | -32 | 20 | 12 | 5.81 | 24 |

Note. The same interaction effects for target-present trials revealed no activation. Activations are reported with FWE correction of $p < .05$. Coordinates (x, y, z) correspond to the MNI (Montreal Neurological Institute) space.

7, $Z = 4.33$, voxel number = 88) were more highly activated for this interaction in conjunction search relative to feature search. These differential effects were again significant for target-absent trials, with activation in left FEF (centered at $-30/-6/48$, BA 6, $Z = 4.65$, voxel number = 161), left IPS (centered at $-22/-68/50$, BA 7, $Z = 4.40$, voxel number = 205), and right IPS (centered at $26/-68/50$, BA 7, $Z = 4.37$, voxel number = 109), but not for target-present trials.

3.2.5 | Interaction of heterogeneity in the task-relevant and -irrelevant dimensions

The bilateral FEFs, left IPS, and left IPTO were activated in both separate analysis for individual experiments and the conjunction analysis of heterogeneous versus homogeneous distractors in the task-relevant dimension across experiments, demonstrating that these frontoparietal regions are both involved in feature and conjunction search with heterogeneous, task-relevant distractors. To further examine how these effects were modulated by variations in the task-irrelevant dimension and target presence, beta values were extracted from these regions. These beta values, which are illustrated in Figure 4, were then entered into a 2 (heterogeneous vs. homogeneous along the task-irrelevant color dimension) \times 2 (heterogeneous vs. homogeneous along the task-relevant orientation dimension) \times 2 (target absent vs. present) ANOVA. As can be seen from Figure 4, in Experiment 1, all four regions showed a significant interaction between heterogeneity in the task-relevant dimension and target-presence ($p < .005$ for all regions). For target-absent trials, the beta values were higher when distractors were heterogeneous than when they were homogeneous in the task-relevant dimension. For target-present trials, by contrast, the beta values were comparable whether distractors were heterogeneous or homogeneous in the task-relevant dimension. This pattern is consistent with the whole-brain analyses conducted separately for target-absent and target-present trials in the current study, as well as with our previous findings that it is mainly on

the target-absent trials that displays with heterogeneous versus homogeneous distractors along the task-relevant dimension elicited differential involvement of these frontoparietal regions (Wei et al., 2009). Importantly, heterogeneity along the task-irrelevant and along the task-relevant dimension did not interact with each other.

In Experiment 2, the four regions also showed a significant interaction between heterogeneity in the task-relevant dimension and target-presence ($p < .001$ for all regions). Consistent with the results in Experiment 1 and Wei et al. (2009), the beta values were higher for displays with heterogeneous distractors than for displays with homogeneous distractors in the task-relevant dimension on target-absent trials. These differences, however, disappeared on target-present trials. Importantly, unlike Experiment 1, the heterogeneities in the task-irrelevant and -relevant dimensions interacted with each other ($p < .005$ for all regions): when distractors were homogeneous in the task-relevant dimension, variation of the task-irrelevant color information increased the activation levels of these regions; when distractors were heterogeneous in the task-relevant dimension, variation of the task-irrelevant color information had no effect upon the activations in these regions. This interaction pattern was consistent with the pattern in the behavioral data.

We then performed partial correlation analyses for each experiment, over participants and for each of the four regions (bilateral FEFs, left IPS, and left IPTO), between the mean beta values of each experimental condition and the mean RTs in the respective condition after controlling the variations along the task-irrelevant dimension, the task-relevant dimension, and target-presence. Partial correlation showed that, for Experiment 1, there were uncorrected correlations between behavioral RTs and the left FEF activation, $r = .19$, $p = .043$, the left IPS, $r = .19$, $p = .042$, and left IPTO, $r = .32$, $p = .001$, but not between RTs and right FEF, $r = .16$, $p = .1$. However, only the correlation between RTs and left IPTO was significant after FDR corrections for multiple comparisons (Benjamini & Hochberg, 1995). The pattern was similar for

Experiment 2: there were correlations for left FEF, $r = .38, p < .001$, left IPS, $r = .43, p < .001$, and left IPTO, $r = .52, p < .001$, but not for right FEF, $r = .10, p > .1$. The correlations for the former three regions

than when they were the same color. This activation was not modulated by heterogeneity along the task-relevant dimension (i.e., orientation or form conjunction). It may thus be taken to reflect automatic processing of the task-irrelevant color information, which interferes with search in the task-relevant orientation or shape dimension, as evidenced by slower RTs in the heterogeneous conditions. At the present, it is not clear whether the stronger activation in the fusiform areas for heterogeneous displays reflects more active processing of color information and/or an attempt to suppress the variation of the color information when color is task-irrelevant.

An interesting finding with regard to the processing of color information was that the activation locus was more anterior in the fusiform gyrus for conjunction search (on the left hemisphere) than for orientation search (on the right hemisphere; see Figure 3). According to Bartels and Zeki (2000), the human color center in the brain consists of two subdivisions, a posterior one (V4) and an anterior one (V4_α). While the functional specializations of the two subdivisions are still under investigation, Zeki and Marini (1998) reported that the anterior subdivision is more activated to the “correctly” colored objects (e.g., red strawberries) than to the unconventionally colored objects (e.g., violet strawberries), while the posterior subdivision shows the reverse pattern. It is possible that only the anterior center processes color information to a higher order, for example, analyzing its relations with other attributes of the same object. In the current study, the differential activations in the posterior and anterior parts of the fusiform gyrus for feature and conjunction search may reflect different levels of color information processing in the two tasks. Further studies are required to test this suggestion and to investigate why the right fusiform gyrus was more activated in orientation search, whereas the left fusiform gyrus was more activated in conjunction search.

4.2 |

In both feature and conjunction search, heterogeneous distractors along the task-relevant dimension engaged activation of frontoparietal regions including bilateral FEF, the left IPS, and IPTO. These regions have been reported for different types of attentional selection, such as biasing attention to a feature dimension (Le, Pardo, & Hu, 1998; Liu, Slotnick, Serences, & Yantis, 2003), encoding behavioral relevance (Assad, 2003; Culham & Kanwisher, 2001; Liu, Bengson, Huang, Mangun, & Ding, 2016; Silk, Bellgrove, Wrafter, Mattingley, & Cunningham, 2010), and top-down filtering of distractors (Friedman-Hill et al., 2003). These regions may work together in effectively setting the top-down attentional bias to the task-relevant dimension, including selection of the top-down defined target among distractors and rejection of distracting information (Ellison et al., 2014; Lane, Smith, Schenk, & Ellison, 2012).

There are two reasons why these frontoparietal regions became more activated when the distractors along the task-relevant dimension were heterogeneous rather than homogeneous. The first is that the distractors in heterogeneous displays consisted of differently oriented bars in orientation search, and different form conjunctions of the T- and L-types in conjunction search. There was, thus, a greater chance for some distractors to falsely activate the target template (i.e., the accumulator for target-present evidence; Müller &

Humphreys, 1993), and then to require these regions to differentiate the target from the confounding distractors. Single-unit recording studies suggest that visual responses in the macaque's FEF are significantly enhanced when the to-be-searched items include distractors that resemble the target than when the distractors are greatly different from the target (Bichot & Schall, 1999; Sato, Watanabe, Thompson, & Schall, 2003). Moreover, when target-like distractors happen to falsely activate the target template, or attract focal attention, the necessary distractor rejection and re-checking processes would involve a higher incidence of attention shifts under heterogeneous (vs. homogeneous) distractor condition (Geng & Mangun, 2009; Shulman et al., 2003). The current results suggest that such attentional re-sampling processes are particularly manifested on target-absent trials: on target-absent trials on which search cannot be terminated early (compared with target-present trials), there would be a higher incidence of false attention allocations and thus a greater need for re-checking to establish that there is actually no target present in the display. By contrast, on target-present trials, when the target can be selected and identified relatively more rapidly, variations along the task-relevant dimension would involve fewer extra demands of attentional (re-)selection in these frontoparietal regions, making the corresponding activations harder to discern. Previous neuroimaging studies (Donner et al., 2000, 2002, 2003; Maximo et al., 2016; Nobre et al., 2003; Wilkinson et al., 2002; but see Wei et al., 2009) typically collapsed the target-absent and target-present trials in examining for differential neural mechanisms involved in different types of visual search (e.g., conjunction vs. feature search, difficult vs. easy search), leaving the issue of the extent to which the reported activations were driven by target-absent versus target-present trials unaddressed.

A related reason for this frontoparietal region activation may be that distractors in heterogeneous displays possess higher saliency than distractors in homogeneous displays. Moreover, these frontoparietal regions play a role in biasing processing toward the top-down defined information and in preventing salient distractors from interfering with target search (Chun & Marois, 2002; Friedman-Hill et al., 2003; Madden et al., 2014; Marois, Chun, & Gore, 2000). The saliency value of a distractor, signaling the extent to which it differs from other items in its vicinity, would be higher in heterogeneous displays than in homogeneous displays (Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Wei, Lü, Müller, & Zhou, 2008; Zhaoping & May, 2007). Accordingly, suppressing or rejecting heterogeneous distractors would require greater involvement of these frontoparietal regions, especially on target-absent trials. In addition, the correlation analysis revealed a more prominent role of left (as compared to right) frontoparietal regions—including left IPTO in Experiment 1, and left FEF, left IPS, and left IPTO in Experiment 2—in selecting the task-relevant information in the presence of other, task-irrelevant distracting information during visual search processes. This is consistent with recent studies demonstrating the asymmetrical role of left and right posterior parietal cortex (PPC) in biasing salience-based selection (Mevorach, Humphreys, & Shalev, 2006; Mevorach, Shalev, Allen, & Humphreys, 2009). Mevorach et al. (2006) showed that repetitive transcranial magnetic stimulation (rTMS) to the left PPC, but not right PPC, affects the ability to direct attention away from salient stimuli. Thus, our results would suggest that the left PPC plays a special role in selecting

the task-relevant information in the presence of other salient, but task-irrelevant information.

The behavioral interaction between the task-relevant and task-irrelevant dimensions observed in both feature and conjunction search is consistent with the "perceptual-load theory" of visual selection (Lavie, 2005; Lavie & Tsal, 1994). According to this theory, attentional resources are limited, and the perceptual load imposed by the processing of relevant information determines the extent to which irrelevant distracting information is processed. For the current study, when the distractors are heterogeneous in the task-relevant dimension, attentional resources should be largely used up in searching for the target, while the task-irrelevant color information should receive little processing, with little effect of color heterogeneity (see also Xu, 2010). By contrast, when the distractors are homogeneous in the task-relevant dimension, there would be spare attentional resources to be diverted to process the color information, which in turn would interfere with target search when the distractors are heterogeneously colored (see also Wei & Zhou, 2006).

In a recent fMRI study, Xu (2010) asked participants to view a display containing one, two, or six colored sample shapes and then, later, to judge whether a test color matched one of the sample colors. The shapes of the sample items were either the same or different. Activation in lateral occipital cortex (LOC) signaled an interaction between task-relevant color encoding load and the task-irrelevant shape variations. Also, the processing of task-irrelevant features of sample items depended on the encoding demands of the task-relevant feature. However, the activation in IPS was affected only by the task-relevant color encoding load, not by the task-irrelevant shape variations. The latter finding is consistent with the current Experiment 1, in which the involvement of bilateral FEF, left IPS, and IPTO showed no interaction between the task-relevant and task-irrelevant dimensions. We believe that the similarity in findings between the two studies is attributable to the fact that both Xu's (2010) experiment and the present Experiment 1 used a task in which participants were responding to a target defined in terms of a single feature dimension (color in Xu, 2010, orientation in the current Experiment 1). Taken together, the two studies suggest that activation in IPS for the task-relevant dimension is not affected by whether it is more or less salient than the task-irrelevant dimension, at least for tasks defined by a single feature dimension.

However, when the target is defined in terms of feature combinations, as in the current Experiment 2, activations in frontoparietal regions may exhibit an interaction between the task-relevant and -irrelevant dimensions. As demonstrated by Experiment 2, when there is a high-load task-relevant dimension, activations in these regions may be unaffected by task-irrelevant heterogeneity; however, when the task-relevant dimension imposes a low load, activations in these regions may increase in response to the heterogeneous task-irrelevant dimension. This pattern of activation suggests a role of these regions, including bilateral FEF, left IPS, and IPTO, in setting up the top-down search mode or attentional control setting.

Previous studies (e.g., Eimer & Kiss, 2008; Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994) demonstrated that involuntary attention shifts (i.e., attentional capture) are contingent upon the relationship between the properties of the eliciting event and the top-down defined task mode. In the current conjunction

search for an upright T, observers had to integrate the horizontal bar with the vertical bar. This conjunction search mode may be extended to the task-irrelevant dimension, such that the color information is also automatically bound into the object representation. Given that the frontoparietal regions might be involved in binding different features for conjunction search (Arguin, Jeanette, & Cavanagh, 1993; Corbetta, Shulman, Miezin, & Petersen, 1995; Coull, Walsh, Frith, & Nobre, 2003; Shafritz et al., 2002), it is then conceivable that in searching for the target, these regions are more involved in binding, or suppressing the binding, of color information in the heterogeneous condition than in the homogeneous condition. By contrast, in feature search, observers need to adopt a narrow set focusing on the target-defining feature (i.e., without involving a conjunction process), so that the processing of the task-irrelevant color information does not affect the level of activation in these frontoparietal regions. It would be of theoretical interest to test whether the IPS activation exhibits an interaction between the task-relevant and task-irrelevant dimensions when participants are asked to encode feature conjunctions under different load conditions, while the heterogeneity along the task-irrelevant dimension is manipulated, as in Xu (2010). Further, as the current study did not involve conditions in which color was task-relevant, it would be of interests to see whether variation in the shape dimension (a less salient task-irrelevant information) would affect activations in these frontoparietal regions when target detection requires color combination.

In summary, the present study found that processing distracting information along task-relevant and task-irrelevant dimensions involves differential brain mechanisms and that the top-down task set plays a dominant role in determining whether task-irrelevant color information can affect the processing of the task-relevant dimension (orientation, form) in frontoparietal cortex.

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CONFLICT OF INTEREST

All authors declare no conflict of interests.

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EFFECTS

- Anderson, E. J., Mannan, S. K., Husain, M., Rees, G., Sumner, P., Mort, D. J., & Kennard, C. (2007). Involvement of prefrontal cortex in visual search. *Experimental Brain Research*, 180(2), 289–302.
- Arguin, M., Jeanette, Y., & Cavanagh, P. (1993). Visual search for features and conjunction targets with an attention deficit. *Journal of Cognitive Neuroscience*, 5, 436–452.
- Assad, J. A. (2003). Neural coding of behavioral relevance in parietal cortex. *Current Opinion in Neurobiology*, 13, 194–197.
- Bartels, A., & Zeki, S. (2000). The architecture of the colour centre in the human visual brain: New results and a review. *European Journal of Neuroscience*, 12, 172–193.
- Beck, D. M., & Kastner, S. (2005). Stimulus context modulates competition in human extrastriate cortex. *Nature Neuroscience*, 8, 1110–1116.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society*, 57(1), 289–300.
- Bichot, N. P., & Schall, J. D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature Neuroscience*, 2, 549–554.
- Chun, M. M., & Marois, R. (2002). The dark side of visual attention. *Current Opinion in Neurobiology*, 12, 184–189.
- 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. *Cognitive Brain Research*, 17, 368–379.
- Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Current Opinion in Neurobiology*, 11, 157–163.
- 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. *European Journal of Neuroscience*, 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.
- Duncan, J. (1987). Attention and reading: Wholes and parts in shape recognition: A tutorial review. In M. Coltheart (Ed.), *Attention and performance XII: The psychology of reading* (pp. 39–61). London, England: Lawrence Erlbaum Associates.
- Duncan, J., & Humphreys, G. W. (1989). Visual-search and stimulus similarity. *Psychological Review*, 96, 433–458.
- Duncan, J., & Humphreys, G. W. (1992). Beyond the search surface: Visual search and attentional engagement. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 578–588.
- Eimer, M., & Grubert, A. (2014). The gradual emergence of spatially selective target processing in visual search: From feature-specific to object-based attentional control. *Journal of Experimental Psychology Human Perception & Performance*, 40(5), 1819–1831.
- Eimer, M., & Kiss, M. (2008). Involuntary attentional capture is determined by task set: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, 20, 1423–1433.
- Ellison, A., Ball, K. L., Moseley, P., Dowsett, J., Smith, D. T., Weis, S., & Lane, A. R. (2014). Functional interaction between right parietal and bilateral frontal cortices during visual search tasks revealed using functional magnetic imaging and transcranial direct current stimulation. *PLoS One*, 9(4), e93767.
- Eriksen, C. W. (1988). A source of error in attempts to distinguish coactivation from separate activation in the perception of redundant targets. *Perception & Psychophysics*, 44, 191–193.
- Fairhall, S. L., Indovina, I., Driver, J., & Macaluso, E. (2009). The brain network underlying serial visual search: Comparing overt and covert spatial orienting, for activations and for effective connectivity. *Cerebral Cortex*, 19(12), 2946–2958.
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 1030–1044.
- Folk, C. L., Remington, R. W., & Wright, J. H. (1994). The structure of attentional control: Contingent attentional capture by apparent motion abrupt onset and color. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 317–329.
- Friedman-Hill, S. R., Robertson, L. C., Ungerleider, L. G., & Desimone, R. (2003). Posterior parietal cortex and the filtering of distractors. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 4263–4268.
- Friston, K. J., 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.
- Friston, K. J., Penny, W. D., & Glaser, D. E. (2005). Conjunction revisited. *NeuroImage*, 25, 661–667.
- Geng, J. J., & Mangun, G. R. (2009). Anterior intraparietal sulcus is sensitive to bottom-up attention driven by stimulus salience. *Journal of Cognitive Neuroscience*, 218, 1584–1601.
- Geringswald, F., Herbig, A., Hoffmann, M. B., & Pollmann, S. (2013). Contextual cueing impairment in patients with age-related macular degeneration. *Journal of Vision*, 13(3), 1–18.
- Grice, G. R., Nullmeyer, R., & Spiker, V. A. (1977). Application of variable criterion theory to choice reaction time. *Perception & Psychophysics*, 22, 431–449.
- Kim, C., Johnson, N. F., Cilles, S. E., & Gold, B. T. (2011). Common and distinct mechanisms of cognitive flexibility in prefrontal cortex. *Journal of Neuroscience*, 31, 4771–4779.
- Kiss, M., Grubert, A., & Eimer, M. (2013). Top-down task sets for combined features: Behavioral and electrophysiological evidence for two stages in attentional object selection. *Attention Perception & Psychophysics*, 75(2), 216–228.
- Lane, A. R., Smith, D. T., Schenk, T., & Ellison, A. (2012). The involvement of posterior parietal cortex and frontal eye fields in spatially primed visual search. *Brain Stimulation*, 5(1), 11–17.
- Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, 9, 75–82.
- Lavie, N., & Tsai, Y. (1994). Perceptual load as a major determinant of the locus of selection in visual attention. *Perception & Psychophysics*, 56, 183–197.
- Le, T. H., Pardo, J. V., & Hu, X. (1998). 4 T-fMRI study of non-spatial shifting of selective attention: Cerebellar and parietal contributions. *Journal of Neurophysiology*, 79, 1535–1548.
- Leonards, U., Sanaert, S., Hecke, P. V., & Orban, G. A. (2000). Attention mechanisms in visual search—An fMRI study. *Journal of Cognitive Neuroscience*, 12, 61–75.
- Liu, T., Slotnick, S., Serences, J., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral Cortex*, 13, 1334–1343.
- Liu, Y., Bengson, J., Huang, H., Mangun, G. R., & Ding, M. (2016). Top-down modulation of neural activity in anticipatory visual attention: Control mechanisms revealed by simultaneous EEG-fMRI. *Cerebral Cortex*, 26, 517–529.
- Madden, D. J., Parks, E. L., Davis, S. W., Diaz, M. T., Potter, G. G., Chou, Y., ... Cabeza, R. (2014). Age mediation of frontoparietal activation during visual feature search. *NeuroImage*, 102, 262–274.
- Marois, R., Chun, M. M., & Gore, J. C. (2000). Neural correlates of the attentional blink. *Neuron*, 28, 299–308.
- Maximo, J. O., Neupane, A., Saxena, N., Joseph, R. M., & Kana, R. K. (2016). Task-dependent changes in frontal-parietal activation and connectivity during visual search. *Brain Connectivity*, 6(4), 335–344.
- Mevorach, C., Humphreys, G. W., & Shalev, L. (2006). Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience*, 9, 740–742.
- Mevorach, C., Shalev, L., Allen, H. A., & Humphreys, G. W. (2009). The left intraparietal sulcus modulates the selection of low salient stimuli. *Journal of Cognitive Neuroscience*, 21, 303–315.
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in extrastriate cortex. *Science*, 229, 782–784.
- Müller, H. J., & Humphreys, G. W. (1993). A connectionist model of visual search for simple form conjunctions. In D. Brogan, A. Gale, & K. Carr

- (Eds.), *Visual search* (Vol. 2, pp. 61–71). London, England: Taylor and Francis.
- Nakayama, K., & Martini, P. (2011). Situating visual search. *Vision Research*, 51(13), 1526–1537.
- Nako, R., Grubert, A., & Eimer, M. (2016). Category-based guidance of spatial attention during visual search for feature conjunctions. *Journal of Experimental Psychology Human Perception & Performance*, 42(10), 1571–1586.
- Nichols, T. E., Brett, M., Andersson, J., Wager, T., & Poline, J. B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage*, 25, 653–660.
- 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.
- Price, C. J., & Friston, K. J. (1997). Cognitive conjunction: A new approach to brain activation experiments. *NeuroImage*, 5, 261–270.
- Rangelov, D., Müller, H. J., & Zehetleitner, M. (2013). Visual search for feature singletons: Multiple mechanisms produce sequence effects in visual search. *Journal of Vision*, 13(3), 22 1–16.
- Reeder, R., Olivers, C. N. L., & Pollmann, S. (2017). Cortical evidence for negative search templates. *Visual Cognition*, 25(1–3), 278–290. <https://doi.org/10.1080/13506285.2017.1339755>
- Reeder, R. R., Hanke, M., & Pollmann, S. (2017). Task relevance modulates the cortical representation of feature conjunctions in the target template. *Scientific Reports*, 7(1), 4514.
- 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. *Experimental Brain Research*, 151, 356–363.
- 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. *Psychological Science*, 16, 114–122.
- Shafritz, K. M., Gore, J. C., & Marois, R. (2002). The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 10917–10922.
- 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. *Cerebral Cortex*, 17, 2625–2633.
- 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. *Journal of Neurophysiology*, 90, 3384–3397.
- Shulman, G. L., Pope, D. L. W., Astafiev, S. V., McAvoy, M. P., Snyder, A. Z., & Corbetta, M. (2010). Right hemisphere dominance during spatial selective attention and target detection occurs outside the dorsal frontoparietal network. *Journal of Neuroscience*, 30(10), 3640–3651.
- Silk, T. J., Bellgrove, M. A., Wrafter, P., Mattingley, J. B., & Cunnington, R. (2010). Spatial working memory and spatial attention rely on common neural processes in the intraparietal sulcus. *NeuroImage*, 53(2), 718–724.
- Sillito, A. M., Grieve, K. L., Jones, H. E., Cudeiro, J., & Davis, J. (1995). Visual cortical mechanisms detecting focal orientation discontinuities. *Nature*, 378, 492–496.
- Soto, D., Humphreys, G. W., & Rotshtein, P. (2007). Dissociating the neural mechanisms of memory-based guidance of visual selection. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 17186–17191.
- Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception & Psychophysics*, 50, 184–193.
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, 51, 599–606.
- Treisman, A. (1988). Features and objects: The fourteenth Bartlett memorial lecture. *Quarterly Journal of Experimental Psychology*, 40, 201–237.
- Vossel, S., Weidner, R., Moos, K., & Fink, G. R. (2016). Individual attentional selection capacities are reflected in interhemispheric connectivity of the parietal cortex. *NeuroImage*, 129, 148–158.
- Wei, P., Lü, J., Müller, H. J., & Zhou, X. (2008). Searching for two feature singletons in the visual scene: The localized attentional interference effect. *Experimental Brain Research*, 185, 175–188.

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