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Ab ac

A crucial functi of our goal-directe behavior is to select task-relevant targets among distractor stiuli, some of which may share propertis 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 taskirrelevant 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, & Pollmann, 2017; Shafritz, Gore, & Marois, 2002; Yantis et al., 2002).

Recent neuroimaging studies on visual search have demonstrated that these frontoparietal areas are more activated in inefficient feature search and conjunction search, relative to simple feature search. In conjunction search (e.g., searching for a blue circle among blue squares and yellow circles), the target shares one feature with half of the distractors and another feature with the other half. To find the target, observers need to focus on the relevant features while suppressing the distracting ones. Obviously, this type of search places greater demands on attentional selection than simple feature search, in which the target is defined by a single feature and may "pop out" among the distractors. In inefficient feature search, the distractors are either heterogeneous (e.g., Leonards, Sunaert, Hecke, & Orban, 2000), or they are visually similar to the target (e.g., Geringswald, Herbik, Hoffmann, & Pollmann, 2013; Nobre, Coull, Walsh, & Frith, 2003). In both conditions, there is an increased likelihood that a target-like distractor (falsely) activates the target template (Müller & Humphreys, 1993), thus making greater demands on attentional selection.

While studies have looked at the brain activation in these frontoparietal regions using different visual search tasks, there are only a handful of studies that examined the neural substrates of resolving interference from target-like distractors in visual search (Anderson et al., 2007; Maximo et al., 2016; Nobre et al., 2003; Wilkinson, Halligan, Henson, & Dolan, 2002). For example, varying the similarity between distractors and the target, Nobre et al. (2003; see also Anderson et al., 2007) observed increased activation in the superior parietal lobule when distractors were more similar to the target than when they were not. Wilkinson et al. (2002), on the other hand, found activation in both bilateral parietal cortex and temporal-parietal junction (TPJ) with different distractor types. They had participants search for an upright T among either differently oriented Ts (heterogeneous display) or identically oriented non-target Ts (homogeneous display). Behaviorally, participants took longer to find the target in heterogeneous than in homogeneous displays (see also Duncan & Humphreys, 1989, 1992; Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992). More importantly, activation in superior parietal cortex was more associated with heterogeneous displays, whereas activation in TPJ was more related to homogeneous displays. Moreover, Maximo et al. (2016) asked participants to search for the target letter L among fewer (easy search) or more (difficult search) differently oriented distractor Ts; they reported enhanced activation in FEF, IPS, and SMA in the latter as compared to the former search condition.

These studies, however, did not manipulate the relevance of distracting information to the top-down task set. If we take the above example of searching for a round building, then the shape of buildings is the task-relevant dimension, and their color is the task-irrelevant dimension. Previous behavioral studies have shown that, under certain circumstances, distracting information from a perceptually salient task-irrelevant dimension can interfere with the search process in the less salient, task-relevant dimension (Theeuwes, 1991, 1992; Wei & Zhou, 2006). Heterogeneity in the perceptually salient color dimen-

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 taskrelevant 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 con-



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 | MRI La a ac

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 leveldependent (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 $(256 \times 256 \text{ matrix})$. 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 | MRILaaaa

Data were analyzed with SPM8, Wellcome Department of Imaging Neuroscience, London (Friston et al., 1995), employing a randomeffects 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 betweenparticipants conjunction analyses across the two experiments (Friston, Penny, & Glaser, 2005; Price & Friston, 1997). The betweenparticipants contrasts were performed to identify differential activations between the two experiments for the interaction between the taskrelevant 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 betweenparticipants 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 | B a a

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 targetabsent trials (false alarms) in both experiments, suggestinr(2w91.3(a)-29tendencyge

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FIGURE 2 Behavioral results. RTs (msec) with standard errors in terms of the experimental conditions in Experiments 1 and 2. See abbreviations in the legends of Figure 1

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 task-relevant dimension was heterogeneous, heterogeneity along the irrelevant dimension had no impact on search RTs (759 vs. 744 ms), t(13) = 1.93, p > .05; in contrast, when the task-relevant dimension was homogeneous, heterogeneity in the task-irrelevant dimension prolonged the search RTs (766 vs. 703 ms), t(13) = 6.51, p < .001.

The error-rate ANOVA revealed a significant main effect of heterogeneity in the color dimension, F(1, 13) = 51.57, p < .05, and a significant main effect of target presence, F(1, 13) = 456.04, p < .005. Participants made more errors when the item colors were heterogeneous rather than homogeneous (9.6% vs. 6.8%). Also, more errors were produced on target-present than on -absent trials (misses vs. false alarms: 12.4% vs. 4.0%). No other effects reached significance.

3.1.2 | E 🎽 2

The RT ANOVA again revealed all three main effects to be significant: heterogeneity in the irrelevant color dimension (ir_het vs. ir_hom: 802 vs. 759 ms), F(1, 13) = 35.94, p < .001, heterogeneity in the taskrelevant dimension (re_het vs. re_hom: 846 vs. 716 ms), F(1, 13) = 82.92, p < .001, and target presence (target-absent vs. -present: 847 vs. 715 ms), F(1, 13) = 48.40, p < .001. Moreover, heterogeneity in the task-relevant dimension interacted with heterogeneity in the task-irrelevant dimension, F(1, 13) = 45.61, p < .001, and with target presence, F(1, 13) = 60.59, p < .001. The interaction between task-irrelevant dimension and target presence was also significant, F(1, 13) = 6.28, p < .05, although the three-way interaction was not, F(1, 13) = 1.50, p > .1. As illustrated in Figure 2, the interaction between heterogeneity in the task-relevant dimension and heterogeneity in the task-irrelevant dimension was significant for both targetabsent and -present trials, F(1, 13) = 101.69, p < .001, and F(1, 13) = 15.63, p < .005, respectively. Heterogeneity along the taskirrelevant (color) dimension affected RTs only when the distractors in the task-relevant dimension were homogeneous.

The error-rate ANOVA also revealed significant main effects of heterogeneity in the task-irrelevant dimension, F(1, 13) = 21.83,

p < .001, heterogeneity in the task-relevant dimension, F(1, 13) = 65.15, p < .001, and target presence, F(1, 13) = 58.51, p < .001. Participants made more errors when the item colors were different rather than the same (9.3%vs. 5.5%). More errors were made when the distractors were heterogeneous as compared to homogeneous in the task-relevant dimension (9.3%vs. 5.5%), and more errors on target-present than on -absent trials (misses vs. false alams: 13.1% vs. 1.7%). The interaction between target presence and heterogeneity along the task-irrelevant dimension was significant, F(1, 13) = 17.36, p < .005, as was the interaction between target presence and heterogeneity in the task-relevant dimension, F(1, 13) = 6.95, p < .05. These interactions indicated that the heterogeneity along the task-relevant or -irrelevant dimensions gave rise to increased rates of target-miss errors, but not false-alarm errors.

To be consistent with previous imaging studies on visual search (Donner et al., 2000, 2002; Donner, Kettermann, Diesch, Villringer, & Brandt, 2003; Maximo et al., 2016; Nobre et al., 2003; Wilkinson et al., 2002), target-absent and target-present trials were collapsed first in examining brain activations for the main effects of heterogeneity in the task-relevant and -irrelevant dimensions. The main effect of the task-irrelevant dimension, ir_het (re_het + re_hom) > ir_hom (re_het + re_hom), yielded activation in the posterior part of the right fusiform gyrus in Experiment 1, and the anterior part of the left fusiform gyrus in Experiment 2 (see Table 2 and Figure 3).

The conjunction analysis of this contrast across the two experiments did not reveal any common activation. The reversed contrast, ir_hom (re_het + re_hom) > ir_het (re_het + re_hom), did not disclose any activation in either of the experiments.

As can be seen from Table 2, separate analysis for each experiment revealed overlapping brain regions responsive to heterogeneity along the task-relevant dimension (orientation in Experiment 1 and form conjunction in Experiment 2). The between-experiment conjunction

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TABLE 2 Brain areas activated in the effects of the task-irrelevant dimension and the task-relevant dimension across target present and target absent trials and, separately, for target-absent trials

Ca/aa ^k ca	E 🌬	1					E 🏴	2				
	BA	х	y	z	Z-value	Voxel no.	BA	x	y	Z	Z-value	Voxel no.
Ir_Het versus Ir_Hom												
Right fusiform gyrus	19	34	-74	-8	5.74	101						
Left fusiform gyrus							19/37	-38	-48	-24	5.43	26
(Ir_Het vs. Ir_Hom)_absent												
Right fusiform gyrus	19	33	-73	-8	5.33	17						
Left middle occipital gyrus							19/37	-27	-85	16	4.93	8
Re_Het versus Re_Hom												
Left IPS	7	-24	-58	50	7.14	548	7	-26	-48	46	6.05	278
Right IPS	7	24	-52	42	5.6	182						
Left FEF	6	-38	-2	46	7.1	410	6	-30	-8	44	5.95	90
Right FEF	6	34	-2	50	5.85	59	6	24	-2	46	5.33	12
SMA/SEF	32	-8	24	36	5.69	25						
Left IPTO	19	-26	-78	22	5.87	74	19	-28	-80	18	6.05	102
Right IPTO	19	30	-76	22	5.21	21						
Left MOL middle occipital lobe							19	-48	-82	2	5.68	25
Left anterior insula							47	-30	28	0	5.10	13
Right anterior insula							47	34	24	6	4.90	2
(Re_Het vs. Re_Hom)_absent												
Left IPS	7	-24	-58	49	5.46	700	7	-24	-61	52	7.02	250
Right IPS	7	24	-61	49	7.78	502	7	24	-58	49	5.19	34
Left FEF	6	-39	-4	52	6.94	370	6	-30	-4	49	7.55	130
Right FEF	6	33	-1	52	7.31	59	6	27	-4	46	6.86	54
SMA/SEF	32	12	24	40	7.31	254	32	6	11	55	6.72	99
Left precentral gyrus							6/44	-42	2	31	6.12	37
Left anterior insula	47	-30	26	4	7.26	55						
Right anterior insula	47	30	26	1	6.01	48						
Vermis	/	-3	-73	-26	7.23	156						
Re_Hom versus Re_Het												
Left TPJ	48/40	-48	-48	36	5.23	89						
Right TPJ	48/39	48	-50	36	6.01	208						
Right MFG	46	36	26	38	5.81	84						
Right PCC	7	8	-50	38	5.19	119						
Right ITG							37	64	-46	12	5.81	152
(Re_Hom vs. Re_Het)_absent												
Left TPJ	48/40	-48	-55	49	6.69	251						
Right TPJ	48/39	45	-67	46	7.04	423	39	42	-55	28	5.61	58
Right PCC	7	9	-31	40	5.50	76						
Right ITG	37	63	-52	-2	5.48	59	37	57	-49	-5	5.65	15

Note. Activations are reported with FWE correction of p < .05. Coordinates (x, y, z) correspond to the MNI (Montreal Neurological Institute) space. BA: Brodmann's area; IPS: intraparietal sulcus; FEF: frontal eye field; IPTO: junction of intraparietal and transverse occipital sulci; SMA: supplementary motor area; SEF: supplementary eye field; TPJ: temporal-parietal junction; MFG: middle frontal gyrus; PCC: posterior cingulate cortex; ITG: inferior temporal gyrus.

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). 39, Z = 3.42, voxel number = 36), p < .001, uncorrected, consistent with a similar contrast in Wilkinson et al. (2002) and Wei, Müller, Pollmann, and Zhou (2009) with manipulation in only one dimension.

The conjunction analysis of the reversed contrast, re_hom (ir_het + ir_hom) > re_het (ir_het + ir_hom), revealed activations in the right superior frontal gyrus (centered at 34/20/42, BA 9, Z = 3.76, voxel number = 45), left TPJ (centered at -50/-46/48, BA 39, Z = 3.45, voxel number = 8), and right TPJ (centered at 42/-50/34, BA

3.2.3 | T c a - c

Since behavioral data revealed that the heterogeneity in the taskrelevant dimension and/or the heterogeneity in the task-irrelevant dimension interacted with target presence in both experiments, the effects of the task-irrelevant and -relevant dimensions were separately calculated for target-present and target-absent trials. While the effects



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 | T ac a a

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 a 🖡 ca	ВА	x	у	z	Z-a	V .				
Conjunction analysis										
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				
Conjunction analysis for target-absent trials										
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.

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 | R - - (ROI) a a

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 ta8121sin61ti61expertimen27605)3diimenTheseRes1(45)-6107(we451t)-272(bo453t)12nvol

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4 | DISCUSSION

The present study employed feature and conjunction search tasks, together with an orthogonal manipulation of heterogeneity in the task-relevant and task-irrelevant dimensions. In doing so, we found evidence for differential neural substrates involved in the processing of distracting information across the two selected dimensions, and for the differential involvement of frontoparietal regions in different types of visual search. The behavioral results replicated previous findings (Wei & Zhou, 2006), namely, that heterogeneity in both the task-relevant and task-irrelevant dimensions impacts search RTs, and that task-irrelevant heterogeneous color information affects search RTs only when distractors are homogeneous in the task-relevant dimension. At the neural level, the imaging results showed that processing the task-irrelevant distracting information engages fusiform areas related to color processing, and that processing the task-relevant

distractors activates frontoparietal regions, including bilateral FEF, left IPS, and IPTO, in both feature and conjunctioncu.2.6(ors)-348.ioreover, these frontoparietal regions are involved in the interaction between task-relevant and task-irrelevant dimensions in conjunction u.2.6(,)]TJT[(but)-25

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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 | P c a - a /

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, & Cunnington, 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 resampling 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 rechecking 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 taskirrelevant 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 targetdefining 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 taskirrelevant 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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