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Neural correlates of binding features within- or cross-dimensions in visual conjunction search: An fMRI study

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ABSTRACT

The fMRI technique was used to investigate the functional neuroanatomy of binding features within- or cross-dimension during visual conjunction search. Participants were asked to perform feature search (FS; e.g., search for a vertical bar among tilted bars), within-dimension search (WS; e.g., search for an upright T among non-target oriented Ts and Ls), cross-dimension search (CS; e.g., search for an orange vertical bar among blue vertical bars and orange tilted bars), and complex search combining within- and cross-dimension features (WCS; e.g., search for an orange upright T among orange leftward Ts and blue Ls). Reaction times (RTs) taken to decide whether a target was present or absent were faster in the FS than in the WS, CS, and WCS conditions, but did not differ between the latter three conditions. Neuroimaging results revealed a set of fronto-parietal regions, including frontal eye field and intraparietal sulcus, to be consistently activated in conjunction search (WS, CS, and WCS) relative to feature search, suggesting that these regions play a more prominent role in matching visual input against the target template in conjunction search. Furthermore, left occipito-temporal cortex was more activated in within-dimension conjunction search, and bilateral intraparietal sulci were more activated in cross-dimension conjunction search. This suggests that features from the same dimension are 'bound' at a higher stage of the ventral pathway by conjoining the inputs from lower-level neurons, whereas neurons along the intraparietal sulcus appear to be necessary for discerning the presence of cross-dimensional conjunctions.

Introduction

Visual search for feature conjunctions is typically much less efficient than search for simple features. In their classical Feature Integration Theory (FIT), Treisman and Gelade (1980) attempted to explain this by postulating a preattentive and an attentive processing stage. In the former, features are processed in parallel in feature maps, separately for stimulus dimensions such as color, orientation, curvature, etc. In the latter, conjunctions of features are analyzed by combining features from these separate feature maps — a process assumed to require attentional resources, thus leading to slow, inefficient search. While exceptions to this account have been described soon after its inception, the general notion of a parallel, preattentive feature analysis stage and a subsequent attentive analysis of feature conjunctions has prevailed in more recent models such as Guided Search (Cave and Wolfe, 1990; Wolfe, 1994).

Recent studies using functional magnetic resonance imaging (fMRI) have demonstrated that a large-scale brain network comprising the posterior parietal cortex (PPC), intraparietal sulcus (IPS), and frontal eye field (FEF) is involved in visual search (Arguin et al., 1993; Ashbridge et al., 1999; Corbetta et al., 1995; Coull et al., 2003; Donner et al., 2000, 2002, 2003; Gitelman et al., 2002; Leonards et al., 2000; Müller-Plath, 2008; Müller-Plath and Pollmann, 2003; Nobre et al. 2003; Rushworth et al., 2001; Sato et al., 2003; Wei et al., 2009; Wojciulik and Kanwisher, 1999; Wilkinson et al., 2002). A common question addressed in these studies is whether there are neural substrates specifically related to conjunction search, relative to feature search (Arguin et al., 1993; Corbetta et al., 1995; Coull et al., 2003; Friedman-Hill et al., 1995; Shafritz et al., 2002; Donner et al., 2000, 2002; Leonards et al., 2000; Nobre et al., 2003; Wojciulik and Kanwisher, 1999; Wilkinson et al., 2002). In almost all of these studies (with the exception of Wilkinson et al., 2002), the conjunction target was a combination of two features from two different dimensions; for example, the target was a red circle (containing dimensions of color and shape) presented among distractors of red squares and blue circles. However, there are also conjunction targets composed of two features from the same dimension (Duncan, 1987; Duncan and

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Humphreys, 1989); a well-known example is search for an upright T among differently oriented T's and L's (Duncan and Humphreys, 1989).

We reasoned that the neural substrates subserving search for cross-dimension conjunctions may be different from those for within-dimension conjunctions. Evidence in support of such a distinction comes from behavioral studies that demonstrated illusory conjunctions of color and form, but not of conjunctions within the form domain in normal observers (Cohen and Feintuch, 2002); intact binding of form features, but not color-form conjunctions in Balint's patients (Friedman-Hill et al., 1995; Humphreys, 2001; Humphreys et al., 2000); and a developmentally later onset of successful binding of color-form compared to within-form conjunctions in young children (Oakes et al., 2006). Importantly, patients with posterior parietal lesions showed deficits in conjoining color, size, and form features, but were unimpaired in search for form conjunctions in visual search (Humphreys et al., 2009).

While these data show a clear dissociation between within-dimension form conjunctions and cross-dimension conjunctions, the exact structure within parietal cortex supporting cross-domain binding remains unknown, due to lesion variability. Moreover, it remains unclear which neural structures support within-dimension binding in the form domain. Here, we used fMRI to directly investigate the differential neural substrates supporting cross-dimension (color-form) conjunctions and within-dimension (form) conjunctions.

We used four types of search tasks. The first one was simple feature search (FS): participants were asked to detect a vertically oriented bar among tilted distractor bars (Fig. 1). The second task was within-dimension search (WS); the target was an upright T among differently oriented T's and L's; that is, participants had to detect a specific conjunction of two features from the same dimension (i.e., a vertically and a horizontally oriented bar). The third task was cross-dimension search (CS): the target was, for example, an orange vertical bar presented among orange tilted bars and blue vertical bars; that is, participants had to find a specific conjunction of one feature from the color dimension and one feature from the orientation dimension. Finally, we created a fourth task that had not been investigated in previous behavioral or neuroimaging studies: a task requiring participants to search for a target which was a combination of within- and cross-dimension features (WCS), for example, an orange upright T among orange L's and blue T's; that is, participants had to find a specific conjunction of three features for the target, two from the orientation dimension and one from the color dimension.

Behaviorally, we hypothesized the search reaction times (RTs) to the target to be increasing as the target definition becomes more complex (involves more features): RTs would be the shortest in the FS condition and the longest in the WCS condition. At the neural level, we hypothesized that a set of fronto-parietal regions would be consistently activated in the CS, WS, and WCS conditions, relative to the FS condition. This would indicate a general neural basis for conjunction search. Moreover, as compared to the FS and CS conditions, the WS and WCS conditions, which involved within-dimension conjunctions, may show a specific neural signature in higher-level areas in ventral-occipitotemporal cortex for binding features from the same dimension. Conversely, as compared to the FS and WS conditions, the CS and WCS conditions, which required search for cross-dimension conjunctions, may involve activation of the cortex along the IPS for functioning along the lines of a master map of locations, as originally proposed by Treisman and Gelade (1980).

Method

Participants

Fourteen undergraduate and graduate students (8 females, aged between 20 and 26 years) participated in the experiment. All of them were right-handed and had normal or corrected-to-normal vision, and none had a history of neurological or psychiatric disorders. All the

paPchiaog26,297.4((Pekg)-293.4(inUnirseli.)-5J/F11TfT*02.6247TD[(FoDegnat32 search trials with 2 null trials were intermixed. A search trial lasted 2500 ms. At the start of a search trial, a white fixation cross, subtending 0.20° in visual angle, appeared at the center of the black screen for 400 ms, followed by a black screen for 100 ms. Then the fixation sign was presented again for another 500 ms, making the cross appear to flash briefly. This was to warn participants about the upcoming search display, which was presented for 500 ms. The search display consisted of a central fixation marker surrounded by 8 bar stimuli (each measuring 0.8° × 0.2°) or 8 T-shape stimuli (each subtending 0.8° × 0.8°). The stimuli were placed at 8 (randomly selected) positions on a virtual, cross-shaped grid, with a maximum eccentricity of 3° of visual angle (see Fig. 1 for block sequence and sample display). At the end of this 1500 ms, the fixation cross was presented for 1000 ms. For null trials, only the fixation sign was presented throughout the trial for 2500 ms. The 6 search and 2 null trials in each block were randomly ordered. After each trial, an additional presentation of the fixation sign, with the duration of either 0 ms (for one trial), 250 ms (two trials), 500 ms (two trials), 750 ms (two trials), or 1000 ms (one trial), was added for jittering between trials. Effectively, participants saw 6 search trials in each block, with variable intervals between trials. Participants were asked to search for the target and respond as quickly and accurately as possible upon the presentation of the search display. They were instructed to maintain eye fixation on the fixation cross in the display center throughout the whole experiment (see also Nobre et al., 2003; Soto et al., 2007). Before scanning, the observers were familiarized with the task and performed several practice blocks in which they were explicitly told to maintain fixation during the task.

Data acquisition

A 3T Siemens Trio system with a standard head coil at the MRI Center for Brain Research in Beijing Normal University was used to are shown in Table 2 and Fig. 3. As compared to the FS condition, the WS, CS, and WCS conditions activated similar brain areas in frontal and parietal lobes.

In order to determine the neural substrates of binding features from the same dimension, we performed a conjunction analysis (Friston et al., 2005; Price and Friston, 1997) between contrasts of WCS vs. CS and WS vs. FS. If this within-dimension search requires specific neural substrates for accomplishing the task, it should be consistently activated whenever there is a need to bind two features from the same dimension, that is, the horizontally and the vertically oriented bar. Based on a conservative conjunction null hypothesis (Friston et al., 2005; Nichols et al., 2005) implemented in SPM 5, we set the threshold of $p<0.001$, uncorrected, in combination with an extent threshold of 20 voxels (see also, for example, Kim et al., 2011; Weissman et al., 2002). Results revealed activations in the left fusiform gyrus (see Table 3 and Fig. 4).

The same logic was applied to the conjunction analysis of WCS vs. WS and CS vs. FS, which revealed the neural substrates involved in binding features from different dimensions, that is, color with orientation in the CS condition or color with T-shape in the WCS condition. This contrast revealed activations in bilateral superior parietal cortex and bilateral IPTO (junction of intraparietal and transverse occipital sulcus; uncorrected $p<.001$ in combination with an extent threshold of 20 voxels; see also Table 3 and Fig. 4).

Discussion

By asking participants to perform four types of visual search, we found that RTs for discerning target presence were faster in the FS condition (feature search) than in the WS (within-dimenu17Phis search) conditions, while RTs in the latter three conditions did not differ statistically from each other. Neuroimaging results found a set of fronto-parietal regions, including frontal eye fields and intraparietal sulci, were consistently activated in conjunction search (WS, CS, and WCS) relative to feature search, suggesting that these areas play a more prominent role in matching visual input against the target template represented in these areas in conjunction search than in feature search. Moreover, left fusiform were more activated in within-dimension conjunction search, whereas bilateral intraparietal sulci and IPTO were more activated in cross-dimension conjunction search, suggesting that differential neural correlates are involved in binding features from the same and, respectively, different dimensions.

The general activation of frontal eye field and intraparietal sulcus across different types of conjunction searches suggests that these areas are responsible for representing the target against distractors and for target template matching. Previous studies have found overlap of activation in these areas for conjunction search and difficult feature search (Donner et al., 2002, 2003; Leonards et al., 2000; Wei et al., 2009), indicating a common target representation or selection mechanism engaged in different types of visual search. For example, Donner et al. (2003) reported that the anterior IPS and IPTO were activated in conjunction search, relative to feature search, in the absence of distractors (i.e., with only the target being presented), demonstrating that target template matching or target selection is more demanding in conjunction search than in feature search. In both within- and cross-dimension search, the more features by which the target is (potentially) defined, the greater the likelihood that the target shares features with the distractors. This suggests that distractors having more features in common with the target would be more likely to falsely activate the target template. This would lead to false alarms and a need for rechecking (e.g., Humphreys and Müller, 1993), the latter resulting in heavier demands on target selection and thus the involvement of FEF and IPS (see also Wei et al., 2009).

Moreover, the present data, along with behavioral (Cohen and Feintuch, 2002) and neuropsychological evidence (Humphreys, 2001; Humphreys et al., 2009), indicate that fundamentally different mechanisms may underlie the binding of features of the same visual dimension compared with feature binding across different dimensions. From V1 via V4 to IT, the complexity of stimuli optimally activating the respective neurons increases (Tanaka, 1996). Thus, neurons at a higher processing stage appear to process the combined input of neurons with simpler response characteristics at lower stages. While this has been well investigated for single dimensions (e.g., form), there is, to our knowledge, less evidence for such computations across dimensions (such as color and orientation). It may thus be that nearby features from the same dimension (such as the bars forming a T) can be bound together without recourse to parietal cortex, just by combining the inputs of lower-level neurons at a higher stage of the ventral pathway.

However, the same may not be possible for features of different dimensions, even though they share the same location in the visual field (e.g., a vertical bar in orange color). One possibility for the involvement of posterior parietal regions in cross-conjunctions is that these areas play a role in integrating visual features from different dimensions for visual search. As pointed out by Nobre et al. (2003), posterior parietal areas are situated at the end of the dorsal visual processing stream, in which perception is coordinated for action (Goodale and Milner, 1992; Snyder et al., 2000) along multiple spatial frameworks (Andersen, 1997; Colby and Duhamel, 1996; Snyder et al., 1998). They receive input from many specialized areas that analyze features in visual as well as in other modalities (Gottlieb, 2007). The posterior parietal cortex is thus in a position to bridge, coordinate, or bias activity across different specialized visual areas involved in selective perception during visual search. Another possible reason for the IPS involvement in -509(One)-515.3(poss3IPS)-.3(p5sual)-253.3(se3495.

increasing the number of distractors having another color (e.g., blue) does not (Kaptein et al., 1994; Braithwaite et al., 2005; Geyer et al., 2010). This indicates that in finding a conjunction of two features from two different dimensions, participants may group the distractors by one target feature (e.g., red) to constrain their search process and to search for the target among this group (effectively reducing a conjunction search to a feature search). However, this strategy cannot be applied to within-dimension conjunction search as it is impossible to separate the display by any specific feature. Thus, the more pronounced activations along the IPS may suggest that these areas are important in sending top-down attentional bias signals to items sharing the (color) feature with the target.

One may question the reliability of the finding that specific neural substrates are subserving different types of conjunction search, as feature and conjunction searches involve different levels of task difficulty (as evidenced by RT differences in the present study). Previous studies have attempted to match task difficulty between feature and conjunction search (e.g., Donner et al., 2002; Nobre et al., 2003) for the purpose of revealing specific neutral substrates of conjunction search. For example, Donner et al. (2002) used fMRI to measure common and, respectively, specific brain activity for color–form conjunction search and for an equally difficult feature search, relative to an easy feature-search baseline. Although several areas were found to be activated in both the conjunction and the hard feature search tasks (e.g., in posterior regions of the intraparietal sulcus), other areas showed greater activity in one task than in the other, suggesting the recruitment of distinct processes for the two tasks. However, making the feature search harder can introduce other confounding factors, such as participants using serial scanning of the display for hard feature search (see Humphreys et al., 2009, for discussion), thus leading to parietal activation. This activation would be indistinguishable from the activation for binding process in conjunction search. In the current experiment, although the task difficulty was not matched for feature and conjunction search, it was probably matched for different types of conjunction search, as demonstrated by the comparable search RTs. Although the activation differences for the CS, WS, and WCS conditions, relative to the FS condition, might involve not only the binding processes but also general cognitive processes related to the task difficulty (e.g., attentional devotion), activation differences between the three conjunction search tasks should not be contaminated by task difficulty. With the factorial manipulation of cross-dimension and within-dimension binding and using the conjunction analysis method (Price and Friston, 1997), we can generally rule out explanations relying on task difficulty. For example, for the conjunction analysis between contrasts of WCS vs. WS and CS vs. FS, the resulting brain activation in bilateral IPS and IPTO cannot be simply attributed to the differential difficulty between the CS and FS conditions, but rather to cognitive processes underlying cross-dimension binding that were consistently involved in both the contrast WCS vs. WS and the contrast CS vs. FS.

Finally, Feature Integration Theory (Treisman, 1998; Treisman and Gelade, 1980) proposed that feature binding is mediated by spatial attention, through which the various features belonging to one object at the focally attended location are linked together. This is characterized as assuming a single binding process, irrespective of the nature of features. However, the present results, together with neuropsychological evidence (Humphreys, 2001; Humphreys et al., 2000, 2009), suggest that binding of form elements operates within the ventral pathway, while binding of form with surface properties such as color is modulated by the parietal cortex. Such differentiations should be integrated into future theories of visual search.

Conclusion

By asking participants to perform four types of visual search, feature search (FS), within-dimension conjunction search (WS), cross-dimension conjunction search (CS), and a combination of within- and cross-dimension conjunction search (WCS), we showed that a set of fronto-parietal regions, including frontal eye fields and intraparietal sulcus, was consistently activated in conjunction search (WS, CS, and WCS) relative to feature search, suggesting that these areas may play a more prominent role in representing the target against distractors in conjunction search than in feature search. Moreover, there might be a neural 'master map' in posterior parietal cortex that subserves the binding of individual features coded in distinct feature maps by common location. However, it appears to be needed only for cross-dimension conjunctions, such as of color and form, whereas within-dimension conjunctions, of form, can be processed within the ventral occipito-temporal object processing stream.

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