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The right temporo-parietal junction contributes to visual feature binding

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ABSTRACT

We investigated the neural basis of conjoined processing of color and spatial frequency with functional magnetic resonance imaging (fMRI). A multivariate classification algorithm was trained to differentiate between either isolated color or spatial frequency differences, or between conjoint differences in both feature dimensions. All displays were presented in a singleton search task, avoiding confounds between conjunctive feature processing and search difficulty that arose in previous studies contrasting single feature and conjunction search tasks. Based on patient studies, we expected the right temporo-parietal junction (TPJ) to be involved in conjunctive feature processing. This hypothesis was confirmed in that only conjoined color and spatial frequency differences, but not isolated feature differences could be classified above chance level in this area. Furthermore, we could show that the accuracy of a classification of differences in both feature dimensions was superadditive compared to the classification accuracies of isolated color or spatial frequency differences within the right TPJ. These data provide evidence for the processing of feature conjunctions, here color and spatial frequency, in the right TPJ.
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Introduction

Visual search in a cluttered scene is easy if the target is distinct in a basic visual feature like color or form, e.g. a red apple among green apples. In contrast, detection of a target that is distinct only by a combination of features, like a red apple among green apples and red pears, is often much more difficult. According to visual search models (Chan and Hayward, 2009; Treisman and Gelade, 1980; Wolfe et al., 1989), attentive processes are needed to conjoin (or "bind") feature values from different visual dimensions at a given location in space to determine their presence within an object, e.g. to determine if a particular apple-shaped object is red or green.

Parietal cortex appears to play a central role in visual feature binding. Transcranial magnetic stimulation studies showed that the efficiency of feature binding could be modulated by TMS over parietal sites. In early TMS-studies, single-pulse stimulation over right, but not left, parietal cortex slowed visual conjunction search performance (Ashbridge et al., 1997; Walsh, Ashbridge and Cowey, 1998). In these early studies, no exact localization of the stimulation site was available, but the stimulation occurred in the vicinity of electrode location P4 of the 10–20 EEG-system. More recently, Esterman et al. (2007) reported an attenuation of binding errors after 1 Hz repetitive TMS over right intraparietal sulcus (IPS), at the junction of the horizontal and ascending segments. No such effect was observed after stimulation of the left IPS or the IPS at the junction with the transverse occipital sulcus bilaterally.

Selective deficits in conjunction search were observed after posterior parietal lesions. Patient R.M., who suffered from a feature-binding deficit, had a large bilateral lesion affecting the cortex along the descending segments of the intraparietal sulcus, reaching laterally into the TPJ, the cortex along the ascending segments of the STS (Friedman-Hill et al., 1995). Patient G.K., who suffered from impaired binding of shape with surface details, had a large bilateral (right-dominant) lesion affecting the right occipito-parietal region, the right temporo-parietal region and the left temporo-parietal region (Humphreys et al., 2000). Humphreys et al (2009) studied a group of six patients with parietal lesions extending from the anterior part of the superior parietal lobule down to the inferior parietal cortex including the TPJ.

Functional magnetic resonance imaging (fMRI) studies have compared single feature search and conjunction search to investigate the neural substrate of feature binding. Donner et al. (2002) reported increased activation for conjunction search in anterior and posterior locations along the IPS. Binding-related activation along the IPS was also observed by Nobre et al. (2003). Two further studies reported IPS- and superior parietal activation due to feature binding (Shafritz et al., 2002; Wei et al., 2011). The comparison of conjunction with feature search led to difficulties in separating feature binding from task difficulty, which is typically higher in conjunction search (We refer to Baumgartner et al., 2013, for a more detailed discussion). Studies which succeeded in equalizing search difficulty for single feature and conjunction search ran into other difficulties, e.g. very small, hard to

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perceive feature differences in difficult single feature search (Donner et al., 2002) or sequential subset searches in easy conjunction search tasks (Nobre et al., 2003). In a recent study we circumvented this problem by comparing multi-voxel activation patterns elicited by single or conjunct feature differences in search displays in a common singleton search task. In this task, again used in the present study, participants have to indicate the presence or absence of a stimulus with a unique combination of feature values from the feature dimensions color and spatial frequency (Fig. 1). This task forces the participants to attend to both stimulus dimensions, because the singleton target can vary from trial to trial. Apart from that, it serves only to define a common task setting for stimulus arrays with different local feature combinations that we use to analyze conjoint feature processing via MVPA. For instance, there is no reason that response times or accuracies for correct rejection of target presence should differ between e.g. stimulus C1, C2 or C4 of Fig. 1c. The task is always the same and there is no a priori reason why target rejection should be more difficult for one of these stimuli or another. The situation is different, however, when we analyze the fMRI activation with a classifier. Comparing stimuli C1 and C2, only color differs at any given location in the display (resp. only spatial frequency differs when we compare C1 with C3). In contrast, discriminating the activation pattern elicited by C1 and C4 may rely on a difference in color as well as spatial frequency processing, because both vary at any given location. Therefore, a higher classification accuracy for a C1 vs. C4 than a C1 vs. C2 or C3 comparison may be due to true conjunctive processing of color and spatial frequency, but it may as well be due to the additive effect of unimodal neural ensembles processing color and space. Such unimodal ensembles could easily be contained within a single voxel of our fMRI measurements. However, if the classification accuracy for joint color and spatial frequency differences surpasses this additive effect, then we can speak of conjoined processing. Note that it is impossible to look at the additive effect of spatial frequency and color differences on behavioral measures — this would only make sense if participants had to search for a fixed target that differed in one or two dimensions from the respective comparison stimulus, but not in singleton search. We intentionally used singleton search to decouple task difficulty effects from the classification of single versus double feature changes.

Our previous data was obtained at high magnetic field strength in order to optimize spatial resolution (Baumgartner et al., 2013). This forced us to limit data acquisition to a limited region. In the light of the – particularly imaging – studies on feature binding we previously focused on the dorsal part of parietal cortex, including the superior parietal lobules and the cortex along the IPS. In the right anterior superior parietal lobule (aSPL), we found an increase in classification accuracy for conjoined feature differences that exceeded the summation of the accuracies for single feature classifications. However, the lesions leading to binding deficits range from the aSPL down into the inferior parietal lobule and the temporo-parietal junction (TPJ), mostly in the right hemisphere (Friedman-Hill et al., 1995; Humphreys et al., 2000, 2009).

Moreover, the TPJ is involved in crossmodal feature binding. It shows a superadditive enhanced fMRI-activation to congruent visual and auditory object and speech cues compared to unimodal stimulation (Beauchamp et al., 2004; Calvert, Campbell & Brammer, 2000). In addition, the posterior ascending segment of the superior temporal sulcus (STS) has been found to support the integration of visual form and motion (Beauchamp et al., 2003; Puce et al., 2003). This has led to the hypothesis that the TPJ, particularly the cortex along the posterior STS, serves to integrate features both within and across modalities (Beauchamp et al., 2004). Therefore, in the present study, we used the same singleton search paradigm and multivariate analysis strategy as in our previous study (Baumgartner et al., 2013), but at conventional spatial resolution, to achieve whole brain coverage. Our aim was to investigate if the TPJ contained representations of visual feature conjunctions in addition to the right aSPL. We particularly expected this for the right TPJ, primarily because of the finding of lateralized right TMS-modulation of feature binding (Ashbridge et al., 1997; Esterman et al., 2007).

Methods

Participants

Fifteen right-handed subjects (6 male, 25.27 ± 1.06 years) participated in the experiments. Subjects had normal or corrected to normal vision, and no known history of neurological disorders. The

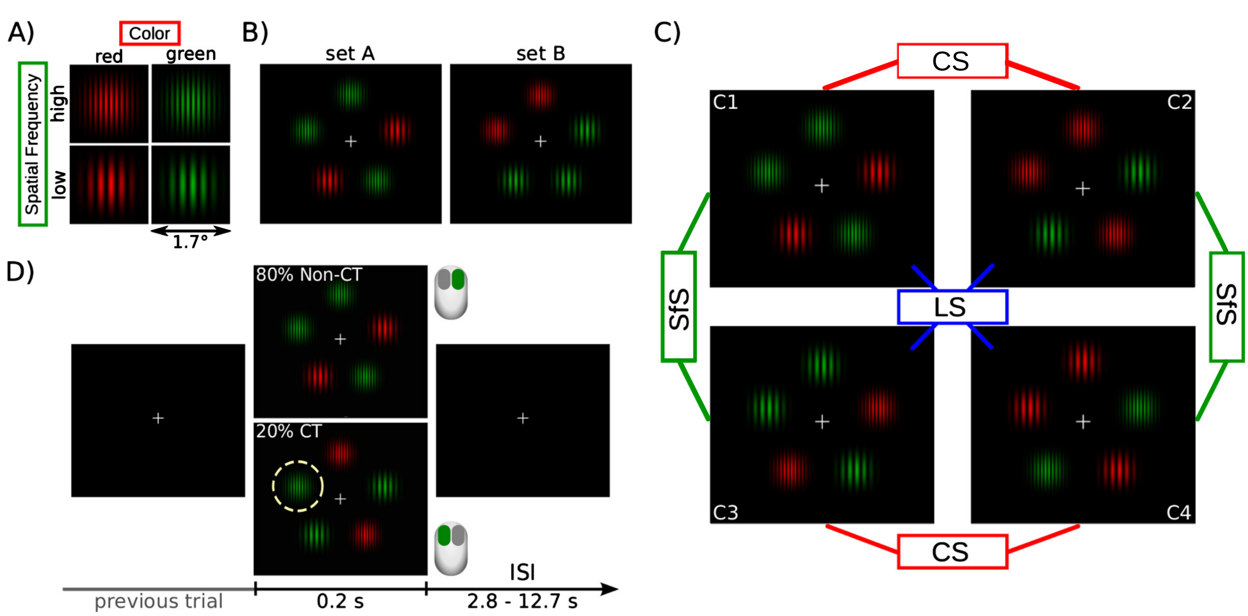

Fig. 1. Task design. A) Gabor patches were defined by two possible colors and spatial frequencies. B) Example configurations of the Gabor stimuli for Sets A and B. C) For each display set, displays were paired in a way that allowed, at each stimulus location, the classification of isolated differences in color (CS, red), spatial frequency (SfS, green), or of a conjoined difference in both feature dimensions (LS, blue). D) Example task outline. Only 20% of the trials contained a singleton conjunction target, i.e. a Gabor patch with a unique combination of color and spatial frequency. Subjects had to indicate the presence versus absence of a target by left or right button press, respectively. Subsequent display presentations were separated from each other by a variable inter-stimulus-interval (ISI).

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