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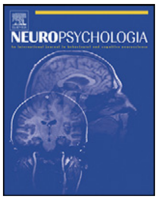

Note

Neural correlates of top-down letter processing

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ABSTRACT

This fMRI study investigated top-down letter processing with an illusory letter detection task. Participants responded whether one of a number of different possible letters was present in a very noisy image. After initial training that became increasingly difficult, they continued to detect letters even though the images consisted of pure noise, which eliminated contamination from strong bottom-up input. For illusory letter detection, greater fMRI activation was observed in several cortical regions. These regions included the precuneus, an area generally involved in top-down processing of objects, and the left superior parietal lobule, an area previously identified with the processing of valid letter and word stimuli. In addition, top-down letter detection also activated the left inferior frontal gyrus, an area that may be involved in the integration of general top-down processing and letter-specific bottom-up processing. These findings suggest that these regions may play a significant role in top-down as well as bottom-up processing of letters and words, and are likely to have reciprocal functional connections to more posterior regions in the word and letter processing network.

1. Introduction

The identification of separate letters in a visually presented word is foundational to an individual's success in reading and the inability to do so can lead to debilitating cognitive impairments such as dyslexia. To better understand this ability, there has been extensive research on the neural bases of word processing over the last two decades. The culmination of many neuroimaging studies have identified a distributed cortical network for visual word processing that ranges from the ventral occipitotemporal cortex (Cohen & Dehaene, 2004; Dehaene, Cohen, Sigman, & Vinckier, 2005; Dietz, Jones, Gareau, Zeffiro, & Eden, 2005; James & James, 2005) to the frontal cortex (Reinke, Fernandes, Schwindt, O'Craven, & Grady, 2008; for a review see Dien, 2009; Tan, Laird, Li, & Fox, 2005).

Current understanding of this word processing network has emphasized the feed-forward connections. Visual input is processed systematically starting with early stages of line detection in V1 and V2, leading to prelexical shape information extractions in V4, finally to the fusiform gyrus for integration of letter strings and word forms independent of location, size, and case (Dehaene et al., 2005; McCandliss, Cohen, & Dehaene, 2003). This last stage has been termed the 'visual word form area' (VWFA, Cohen & Dehaene, 2004; Cohen et al., 2002; McCandliss et al., 2003; but see Price & Devlin, 2003; Reinke et al., 2008, for other interpretations of this area). From the VWFA, information is further passed along to several language areas in the temporal, parietal, and frontal cortices, and, more specifically, the left middle temporal gyrus, left superior parietal lobule, and inferior frontal gyrus (Reinke et al., 2008; Tan et al., 2005). These areas are purportedly involved in grapheme-to-phoneme conversion and semantic decoding (see Jobard, Crivello, & Tzourio-Mazoyer, 2003 for a review).

Despite the success of this account in explaining neural processing of words, pure bottom-up word processing stands in opposition to classic behavioral phenomena, such as the 'word superiority effect' in which a letter is identified more rapidly in the context of a word (McClelland & Rumelhart, 1981). These behavioral results gave rise the 'interactive-activation' connectionist model in

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which letter identification arises from the interplay between top-down and bottom-up information. In keeping with this approach, researchers have speculated that frontal areas may play a role in the processing of letters and words and recent studies support this account. For instance, studies have shown the influence of task demands on both electrophysiological (Ruz & Nobre, 2008) and fMRI (Devlin, Rushworth, & Matthews, 2005) measures of word identification. However, these studies examined the interplay between top-down and bottom-up processing, rather than isolating top-down effects; in these studies, bottom-up input remained strong, providing unambiguous visual information about the presented word or letter. Thus, it is not clear whether the initial bottom-up input served to elicit subsequent top-down feedback, or whether top-down expectations might have played an important role regardless of bottom-up information. To the best of our knowledge, no studies have examined the neural activity of top-down letter processing in the absence of strong bottom-up input.

The current study isolated top-down components of letter detection by asking participants to indicate the presence or absence of a letter in different noise images when no letters were actually presented. The task was not detection of a particular letter, which would prompt a search for particular line segments, but rather to detect whether one of several different possible letters was presented. Over the last several years, this method has been successfully used to isolate top-down mechanisms of face detection (Li et al., 2009; Zhang et al., 2008). Application of this method to letter detection thus may also provide informative evidence about the neural mechanisms involved in the top-down processing of letters. By examining fMRI responses for the illusory detection of letters, we could reveal the neural regions involved in top-down letter processing without contamination from bottom-up information.

2. Methods

2.1. Participants

Twenty-four Chinese participants (twelve males, mean age = 21.2 years, SD = 2.6) with normal or corrected-to-normal vision participated in this study after giving their informed consent. All participants were familiar with the Roman alphabet through exposure to Pinyin, a phonetic form of the Chinese language introduced in the first grade of elementary school. This study was approved by the Human Research Protection Program of Tiantan Hospital, Beijing, China.

2.2. Stimuli and procedure

Pure noise stimuli (Fig. 1c) were created by additively combining Gaussian blobs of different sizes at random locations. Each pure noise image was only used once, either alone or in combination with a letter image. Detection images that contained a letter were created by subtracting a blurred version of a chosen letter (a, s, c, e, m, n, o, r, or u) from a noise image. Because the letters were light against a black background (intensity 0), this meant that the background was unchanged after subtraction, which left the noise image undisturbed in those regions, whereas the regions where the letter existed were made darker. Easily detected letters (Fig. 1a) or hard to detect letters (Fig. 1b) were created by subtracting the letter at 60% or 35% of its full value. Checkerboard-images (Fig. 1d) were additionally used to calculate participant's baseline hemodynamic response.

The experiment consisted of two parts: an initial training period where actual letters were presented on 50% of trials, and a testing period where only noise images were presented. Participants were scanned only during the testing period. The training session consisted of six blocks, each of which included 20 detection images and 8 checkerboard-images. The first two blocks contained an equal number of easy to detect (Fig. 1a) and pure noise (Fig. 1c) stimuli. The next two blocks contained an equal number of hard to detect (Fig. 1b) and pure noise stimuli. Trials in the last two training blocks used pure noise stimuli on all detection trials. Participants were instructed that half of the detection images would contain letters and the other half would not and that the detection task would become progressively more difficult. They were instructed to press one button on a response device with their left or right index finger when they detected a letter or a second button with their opposite index finger when they did not detect a letter. Whether the detection finger was left or right was counterbalanced across-subjects. Participants were instructed not to respond to the checkerboard-images. Each trial started with a 200 ms fixation crosshair followed by either the detection image or checkerboard image for 600 ms. Participants' responses were collected during a blank screen presented for 1200 ms after each trial. The aim of the training session was to teach participants the nature of the experiment, and to motivate them to attempt to detect letters even in pure noise images.

Four testing sessions followed the training blocks, with each consisting of 40 checkerboard-images and 120 pure noise trials presented in random order. The task instructions were the same as for the training session and participants were instructed that half the images contained letters.

2.3. Functional MRI data acquisition and analysis

Structural and functional MRI data were collected using a 3.0 T MR imaging system (Siemens Trio, Germany) at Tiantan Hospital. fMRI was collected using a single shot, $T2^*$-weighted gradient-echo planar imaging (EPI) sequence (TR/TE = 2000/30 ms; 32 slices; 4 mm thickness; matrix = 64 × 64) covering the whole brain with a resolution of 3.75 mm × 3.75 mm. High-resolution anatomical scans were acquired with a three-dimensional enhanced fast gradient-echo sequence, recording 256 axial images with a thickness of 1 mm and a resolution of 1 mm × 1 mm.

Spatial preprocessing and statistical mapping were performed with SPM5 software (http://www.fil.ion.ucl.ac.uk/spm/, Friston et al., 1995). The first three scans of each testing session were excluded for signal saturation. After slice-timing correction, spatial realignment and normalization to the MNI152 template (Montreal Neurological Institute), the scans of all sessions were resampled into 2 mm × 2 mm × 2 mm voxels, and then spatially smoothed with an isotropic 6 mm full-width-half-maximal (FWHM) Gaussian kernel. The time series of each session was high-pass filtered (high-pass filter = 128 s) to remove low frequency noise such as with scanner drift (Friston et al., 1995).

Trials from the testing session were classified according to whether participants did or did not detect a letter, resulting in two regressors convolved with a proptypical hemodynamic response function (HRF) to produce the letter response and no-letter response conditions. For each participant, scans of all testing sessions were combined and analyzed using a general linear model (GLM). Movement parameters were added in the GLM as additional regressors to account for residual head motion. After participant-specific parameter estimates were computed, a conventional whole-brain analysis was performed at the group level using random effect analysis to contrast letter response and no-letter response thresholds at $p = 0.05$, FWE corrected and cluster ≥ 5.

3. Results

Participants detected letters on 34.6% (SD 19.0%) of the 480 pure noise detection trials. There was no significant difference in response time between letter responses and no-letter responses (letter response: mean = 760.81 ms, SD = 183.78 ms; no-letter response: mean = 741.31 ms, SD = 175.13 ms; $t(23) = 1.422$, $p = 0.169$).

A conventional whole-brain analysis identified a distributed network showing more activation for letter responses than for no-letter responses with a threshold of $p < 0.05$ (FWE corrected) and cluster ≥ 5 (Table 1). This network included the left inferior frontal gyrus (IFG, Fig. 2a), the left superior parietal lobules (SPL, Fig. 2b), the right precuneus (Fig. 2c), the right middle occipital gyrus (MOG, Fig. 2d), and the right middle temporal gyrus (MTG, Fig. 2e). In contrast, the reverse comparison did not identify significant activation anywhere in the brain (Table 1).

Table 1
Activation differences between letter response trials and no-letter response trials ($p < 0.05$ FWE corrected, cluster ≥ 5).

Brain regions	Hemisphere	Cluster voxels	Talarac coordinates			Z
			x	y	z	
Letter response minus no-letter response						
Inferior frontal gyrus	Left	55	−48	5	26	5.41
Superior parietal lobules	Left	15	−34	−50	50	5.29
Middle temporal gyrus	Right	5	40	−75	20	5.22
Precuneus	Right	6	20	−56	51	5.2
Middle occipital gyrus	Right	32	51	−61	−7	5.85
No-letter response minus letter response						
No results						