Influence of lexical status and orthographic similarity on the multi-voxel response of the visual word form area

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ABSTRACT

Previous studies demonstrated that a region in the left fusiform gyrus, often referred to as the 'visual word form area' (VWFA), is responsive to written words, but the precise functional role of VWFA remains unclear. In the present study, we investigated the influence of orthographic similarity, and lexical factors on the multivoxel response patterns to written stimuli. Using high-resolution fMRI at 7 T, we compared the organization of visual word representations in VWFA to the organization in early visual cortex and a language region in the superior temporal gyrus. Sets of four letter words and pseudowords were presented, in which orthographic similarity was parametrically manipulated. We found that during a lexical decision task VWFA is responsive to the lexical status of a stimulus, but both real words and pseudowords were further processed in terms of orthographic similarity. In contrast, early visual cortex was only responsive to the visual aspects of the stimuli and in the left superior temporal gyrus there was an interaction between lexical status and orthography such that only real words were processed in terms of orthographic similarity. These findings indicate that VWFA represents the word/non-word status of letter strings as well as their orthographic similarity.

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Introduction

Reading is an important cognitive skill, trained by extensive experience with written words. A specific word is created by putting different letters in a particular order. Beyond this visual analysis, we also process the meaning associated with this specific combination of letters. The semantic content of a written word is largely independent of the visual appearance of a word: two words can differ in only one letter, but have a completely different meaning (e.g. 'flog' and 'flag'), while two other words that have a similar meaning can share not a single letter (e.g. 'flog' and 'beat'). In the present study, we made use of these characteristics to try to dissociate the influence of orthography, lexical factors and semantics on the neural response patterns to written words in different regions across the brain.

Learning to read causes a region in the left fusiform gyrus to become increasingly responsive to visual words (Ben-Shachar et al., 2011;

Olulade et al., 2013), often referred to as the 'visual word form area' (VWFA: Cohen and Dehaene, 2004). Dehaene et al. (2005) propose a hierarchy of local combination detectors that represent progressively larger word fragments (letters to bigrams to quadrigrams) along the ventral visual pathway. VWFA is presumed to serve an orthographic lexicon function (Bruno et al., 2008; Guo and Burgund, 2010; Kronbichler et al., 2004, 2007). However, there are two important questions about the functional role of VWFA. First, is VWFA restricted to lower-level representations, e.g. characters and sublexical letter combinations (Binder et al., 2006; Dehaene et al., 2002, 2005; Vinckier et al., 2007), or does VWFA contain neurons tuned to entire words (Glezer et al., 2009; Schurz et al., 2010)? Evidence for lower level representations is found, for example, in the sensitivity of VWFA to the degree of orthographic structure in a letter string, even when the letter sequences do not show a resemblance to words (Binder et al., 2006). In contrast, representations of whole words would predict a difference between the responses to real words and other non-word letter combinations. While some studies found a lower mean activation in VWFA when presenting real words compared with pseudowords or letter strings (Bruno et al., 2008; Kronbichler et al., 2004, 2007; Price et al., 1996; Woollams et al., 2010; Xu et al., 2001), others failed to find any difference in activity levels (Baker et al., 2007; Dehaene et al., 2002; Vinckier et al., 2007) or found a reverse effect (Cohen et al., 2002). However, in an fMRI adaptation study, Glezer et al. (2009) discovered a smaller release from adaptation after a one letter change for pseudowords compared to

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real words. Glezer et al. (2009) proposed that this difference was due to a difference in tuning selectivity for real words and pseudowords, with more selective tuning for words.

The second question is related to the functional specialization of VWFA: is this area specific to the processing of the 'visual word form', an abstract representation of the sequence of letters that composes a written string (Cohen et al., 2002; Dehaene et al., 2005; Dehaene and Cohen, 2011), or is it involved in the integration of visual information with higher level information such as semantics (Brunswick et al., 1999; Price and Devlin, 2003, 2011; Song et al., 2012; Xue et al., 2006)? Evidence for a role in representing higher level information is derived, for example, from the priming effect of semantically related pictures and words irrespective of the stimulus type in the left ventral occipito-temporal cortex (Kherif et al., 2011). However, multiple other studies did not find a modulation of the responses in VWFA based on the semantic content (e.g. Dehaene et al., 2002; Glezer et al., 2009). Thus, the extent to which higher level information is represented in VWFA is still a matter of debate. In contrast, in the domain of language, it is less controversial that an area in the superior temporal gyrus is involved in semantic processing (Haldgren et al., 2002; Pylkkänen and Marantz, 2003; Simos et al., 1997; Vartiainen et al., 2009).

In the present study, we parametrically manipulated the orthographic similarity of four letter real words and pseudowords: stimuli could differ by 1, 2, 3 or all letters. Further, to try and dissociate the influence of orthography and semantics on the response patterns, stimuli with no orthographic overlap were semantically related. The organization of these visual word representations was investigated in VWFA and compared to the organization in the early visual cortex region and the superior temporal gyrus. Data were analyzed using multivariate analysis techniques. These relatively recent methods (e.g. Haxby et al., 2001; Norman et al., 2006) combine the information of the responses across voxels. With these methods, we can investigate the internal organization of the visual word representations based on the pattern of information within each region. This internal organization might be missed with univariate analyses in which each voxel is treated as a separate entity (Mahmoudi et al., 2012) and in which the integration of information across voxels assumes that nearby voxels contain the same signal (e.g., through averaging across all voxels in an ROI). For example, Nestor et al. (2013) showed that VWFA can discriminate between real words and equally complex false-font controls when multivariate mapping was applied, while no difference in mean activation was found. If an area is responsive to the lexical status, a difference between the response patterns of the real words and the pseudowords should emerge. Responsiveness to the orthographic structure of the stimuli would be shown by a difference in similarity between stimuli that have no, a few or all letters in common. We hypothesized that areas that strongly represent orthography will show a linear effect of the numbers of letters difference on the similarity of the response patterns. Finally, if semantics are represented within an area, the response patterns of the semantically related stimuli should be more similar compared to response patterns of semantically unrelated words.

Method

Participants

21 native English speakers with normal or corrected-to-normal vision participated in this study as paid volunteers. All reported being right-handed. Data from five participants were excluded, three due to technical problems during scanning and two because the participants did not perform the tasks as instructed (less than 50% correct responses in total or no responses during multiple runs). The protocol for the experiments was approved by the National Institutes of Health Institutional Review Board (Protocol 93-M-0170, NCT00001360). Participants signed an informed consent at the start of the imaging session.

Stimuli

Stimuli included two sets of five real words (RWs) and two sets of five pseudowords (PWs) (Fig. 1). In each set of real words, every next word differed in only one letter with the previous word. The position of the substituted letter across words was varied over the two sets. The first and last word within each set did not have any letters in common, but were semantically related i.e. synonyms. No close semantic relationship existed between the remaining stimuli or between words of the different sets. Two sets of pseudowords were created, consisting of pronounceable non-existing words and one uncommon word (frequency: 1 per million) unknown to all participants except one (in which case the data for this stimulus were not included in the analyses). PW sets matched the RW sets in a number of criteria. For each RW set, a PW set was created using the same vowels, in order to control for phonology between the two different lexical categories as much as possible. The position of the substituted letter across words also remained the same for matching RW and PW sets. Finally, RW and PW sets were matched for summated bigram ($t(18) = .916$, $p = .372$) and trigram ($t(18) = 1.364$, $p = .190$) frequency. Stimulus matching information on psycholinguistic factors is summarized in Table 1.

Apparatus

Imaging data were acquired using a 7 T Siemens scanner in the functional MRI facility at NIH. Functional images were acquired using a 32-channel head coil with an in-plane resolution of 1.6×1.6 mm and 49 1.6 mm slices (0.16 mm inter-slice gap, repetition time (TR) = 2 s, echo time (TE) = 25 ms, matrix size = 120×120, field of view (FOV) = 192 mm). Slices were oriented approximately parallel to the base of the temporal lobe and extended throughout the temporal lobe and part of the frontal and parietal lobes. Each functional run consisted of 200 T2*-weighted echoplanar images (EPIs). In addition we collected a standard high-resolution T1-weighted MPRAGE anatomical scan for each participant (192 slices). For more information on the characteristics of high field scanning, we refer to Norris (2003), Ohlman and Yacoub (2011) and Ugurbil et al. (2005); or to Lee et al. (2013) which is based on the same 7 T scanner. Stimuli were presented using Psychtoolbox 3 (Brainard, 1997) via an LCD projector that

Fig. 1. Real word and pseudoword stimulus sets.