

# Encoding in the Visual Word Form Area: An fMRI Adaptation Study of Words versus Handwriting

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## Abstract

■ Written texts are not just words but complex multidimensional stimuli, including aspects such as case, font, and handwriting style, for example. Neuropsychological reports suggest that left fusiform lesions can impair the reading of text for word (lexical) content, being associated with alexia, whereas right-sided lesions may impair handwriting recognition. We used fMRI adaptation in 13 healthy participants to determine if repetition-suppression occurred for words but not handwriting in the left visual word form area (VWFA) and the reverse in the right fusiform gyrus.

Contrary to these expectations, we found adaptation for handwriting but not for words in both the left VWFA and the right VWFA homologue. A trend to adaptation for words but not handwriting was seen only in the left middle temporal gyrus. An analysis of anterior and posterior subdivisions of the left VWFA also failed to show any adaptation for words. We conclude that the right and the left fusiform gyri show similar patterns of adaptation for handwriting, consistent with a predominantly perceptual contribution to text processing. ■

## INTRODUCTION

Neuroimaging studies have demonstrated a network of cortical regions active during reading (Reinke, Fernandes, Schwindt, O'Craven, & Grady, 2008; Jobard, Crivello, & Tzourio-Mazoyer, 2003). One component in the left lateral fusiform gyrus has been named the visual word form area (VWFA), as it responds more to words than to other visual stimuli (McCandliss, Cohen, & Dehaene, 2003; Cohen et al., 2000). A critical contribution of this region to reading is also suggested by neuropsychological evidence. It has long been known that left occipital lesions can be associated with alexia without agraphia (Kleinschmidt & Cohen, 2006; Damasio & Damasio, 1983), and modern studies with fMRI and diffusion tensor imaging have shown that disconnection or destruction of the VWFA can impair reading (Epelbaum et al., 2008; Gaillard et al., 2006; Molko et al., 2002).

Although there is general agreement that words and word-like stimuli activate the VWFA, there remains considerable debate about its function, regarding both its relative selectivity for words and the type of encoding it performs in the reading process (Cohen & Dehaene, 2004; Price & Devlin, 2003, 2004). It is unlikely that the VWFA contains an orthographic lexicon because it responds as well if not more to “pseudowords”—pronounceable letter strings that obey the graphemic rules of a language—as to real words (Kronbichler et al., 2004, 2007; Mechelli, Gorno-Tempini, & Price,

2003; Fiez, Balota, Raichle, & Petersen, 1999). Rather, current models suggest that it performs some part of the perceptual analysis required to derive the “word-form” representations that serve as input to the grapheme-to-phoneme conversions and lexical-semantic associations that support the pronunciation and comprehension of written material (Dehaene, Cohen, Sigman, & Vinckier, 2005; Hillis et al., 2005; Jobard et al., 2003).

One common assertion about the VWFA's representations is that they are invariant for text properties that are irrelevant to letter or word processing. Thus, it has been stated that “...response characteristics of the VWFA suggest a relative insensitivity to variations in surface features of presented letters (i.e., letter case, font, size)” (McCandliss et al., 2003), and “...left midfusiform gyrus (‘VWFA’) is engaged in and perhaps specialized for ... computation of a font-, case- and location-independent representation of the string of graphemes” (Hillis et al., 2005). For example, the ability to recognize that “DRAG” is the same word as “drag” is a significant perceptual accomplishment, given the striking structural dissimilarities between the upper and the lower case versions of each letter, and “**drag**” and “*drag*” need to be perceived as the same word if they are to be read correctly. Such invariant representations are required visual inputs in connectionist models of the reading process (Dehaene et al., 2005).

Despite this claim, evidence for these invariant representations in the VWFA is still limited. Some have attempted to address this by using unusual orthographic constructs, such as alternating or mixed-case words (“DrAg”). The fact that the activation of the VWFA by such unusual stimuli is

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no different than that with uniform-case words in studies with fMRI (Polk & Farah, 2002) or PET (Mayall, Humphreys, Mechelli, Olson, & Price, 2001; Xu et al., 2001) has suggested to some that the VWFA encodes a case-invariant representation. However, because other studies show that the VWFA is also sensitive to single letters (James, James, Jobard, Wong, & Gauthier, 2005; Pernet, Celsis, & Demonet, 2005; Polk et al., 2002) and letter strings (Puce, Allison, Asgari, Gore, & McCarthy, 1996), sometimes to a degree equivalent to words (Vigneau, Jobard, Mazoyer, & Tzourio-Mazoyer, 2005; Joubert et al., 2004), one could argue that the same result with mixed-case letters would be obtained from representations in the VWFA of case-specific letters as it would from representations of case-invariant words.

As others have commented (Cohen & Dehaene, 2004; Jobard et al., 2003), more specific evidence regarding what properties of a complex stimulus like written text are being encoded in a particular region is likely to come from fMRI adaptation studies. This technique relies on the observation that BOLD signal decreases with repetition of a stimulus (Lin, 2007; Grill-Spector, Henson, & Martin, 2006; Krekberg, Boynton, & van Wezel, 2006; Grill-Spector & Malach, 2001). By changing one property of the stimulus at a time, one can determine which dimensions cause a decrement in BOLD signal when repeated, indicating that they are represented in that region, and which do not, indicating that they are irrelevant to the stimulus processing of that region. Studies have shown that repetition-suppression occurs for words even if the case is changed between the first and the second appearance of the word (Devlin, Jamison, Gonnerman, & Matthews, 2006; Devlin, Jamison, Matthews, & Gonnerman, 2004). However, there is still potential for some shared low-level structural properties between upper and lower case letters: What is needed is to show that repetition-suppression is no different when case is repeated than when it is not. Two studies have demonstrated that, although “case-specific priming” (meaning that changing case reduced repetition-suppression) was found in right lateral occipital cortex, “case-invariant priming” was found in the left fusiform gyrus (Dehaene et al., 2001, 2004).

Although the above results suggest that text representations in the VWFA may indeed be case invariant, little is known about whether these are also font invariant, as speculated elsewhere (Hillis et al., 2005; McCandliss et al., 2003). One study has examined fMRI adaptation for fonts (Gauthier et al., 2000). This study identified letter-selective (“letter area”) and face-selective areas (fusiform face area and occipital face area) in cortex and found that face-selective areas showed loss of repetition-suppression when identity was changed for faces, but not when font was changed for individual letters, whereas the letter area showed the reverse pattern and that this was true for areas in both the left and the right hemispheres. Although this result actually argues against font invariance, the Talairach coordinates ( $x, y, z = -53, -62, 3$ ) of their letter area, which was defined by a contrast of individual letters against faces,

are more lateral, posterior, and dorsal than the typical coordinates of the VWFA ( $x, y, z = -44, -58, -15$ ; Vigneau et al., 2005; Cohen et al., 2002) and slightly outside the VWFA boundary coordinates of ( $-50 < x < -30, -80 < y < -30, z < 0$ ) suggested in a review (Cohen et al., 2002).

The studies above underline the fact that texts, like faces, are complex stimuli with multiple dimensions. Seldom considered, though, is the fact that these other dimensions are not merely irrelevancies for reading but sources of information in themselves. Just as faces can be viewed not just to identify the person but also to determine emotional expression, age, attractiveness, and gender, so too text can be processed not just for reading but also for case, font, and handwriting. This creates parallels with models of face recognition that propose a segregation of information processing between identification of the face despite variations in expression, and interpretation of expressions that generalize across different individuals (Gobbini & Haxby, 2007; Haxby, Hoffman, & Gobbini, 2000). If different types of facial information may be processed in different anatomic structures, this may also be true of different types of information derived from text.

In the neuropsychological literature, there is anecdotal support for a dissociation between processing text for reading versus for handwriting identification. One prosopagnosic patient (KD) with a right posterior cerebral artery infarct had trouble recognizing handwriting although she was not alexic, whereas patient MT with a left-sided lesion had pure alexia but no difficulty recognizing handwriting (Rentschler, Treutwein, & Landis, 1994; Landis & Regard, 1988; Campbell, Landis, & Regard, 1986), mirroring an older observation that two alexic patients could still recognize handwriting (Alajouanine, Lhermitte, & de Ribaucourt-Ducarne, 1960). Although these observations have never been formally tested, they raise the possibility that written text may be processed by both hemispheres but in a complementary fashion. Indeed, just as faces activate not only the fusiform face area (FFA) in the right hemisphere but a minor analogous location in the left fusiform gyrus, so too words activate not only the VWFA on the left side but a homologous region on the right (Cohen et al., 2002).

If right and left lesions can affect the ability to recognize the word versus the ability to recognize the handwriting of text in a dissociable fashion, this suggests that the anatomic structures or networks supporting these two processes differ and may involve a hemispheric specialization. We examined this possibility by conducting an fMRI adaptation experiment using repetition-suppression and an ROI approach to identify both handwriting-sensitive and word-sensitive activation in the left VWFA, a right VWFA homologue, and the right FFA. Based on the neuropsychological suggestions of dissociation (Rentschler et al., 1994; Landis & Regard, 1988; Campbell et al., 1986; Alajouanine et al., 1960) and the fMRI adaptation experiments showing case-invariant priming for words in the left VWFA (Dehaene et al., 2001, 2004), we hypothesized that we would find repetition-suppression for words but not handwriting in

the left VWFA and repetition-suppression for handwriting but not words in either the right VWFA homologue or the right FFA.

## METHODS

### Participants

Thirteen healthy people with mean age of 26.5 years (range = 22 to 35 years), five women and eight men, all right-handed, participated in the experiment. All had normal or corrected-to-normal acuity and were literate in English but not Korean. The protocol was approved by the institutional review boards of the University of British Columbia and the Vancouver General Hospital. All participants gave informed consent, and the experiment was conducted in agreement with the principles embedded in the Declaration of Helsinki.

### Stimuli

We selected 10 words (Figure 1) from word databases (Marchand & Friedman, 2005; Coltheart, 1981), chosen to maximize both linguistic and perceptual differences between stimuli. Thus, each word had a different number of letters, ranging from 2 to 11, with examples of both high- and low-frequency words, concrete and abstract words, regular and irregular words, and of different parts of speech (nouns, verbs, modifiers, and functors).

WORD	CONTROL	HANDWRITING
island	go	go
island	but	but
island	plum	plum
island	early	early
island	island	island
island	because	because
island	ambulate	ambulate
island	orchestra	orchestra
island	vigorously	vigorously
island	maintenance	maintenance

**Figure 1.** Examples of stimuli used in the study. Each block contains 10 stimuli shown sequentially. In the control condition, each stimulus is a different word in a different handwriting. In the handwriting condition, each word is a different one, but the handwriting is the same. In the word condition, a single word is shown repeatedly but always in different handwriting.

For script, we chose to use samples of human handwriting rather than font type because the anecdotal neuropsychological reports of text style involved handwriting. We had 16 individuals ranging in age from 8 to 49 years, with different educational and ethnic backgrounds, write each of the 10 words. We then had a panel of 10 participants compare these handwritten lists to identify which handwriting samples were most similar to one or more samples in the set. The six samples most frequently identified as sharing similarities to other samples were removed, leaving us with a set of 10 handwriting styles that, like the words, were chosen to maximize differences. The end result was a matrix of 100 stimuli, 10 words each written in 10 different handwriting styles. All words were legible to all participants.

### Protocol

All scans were acquired in a 3.0-T Philips scanner. Stimuli were presented using Presentation 9.81 software and rear-projected onto a mirror mounted on the head coil. Whole-brain anatomical scans were acquired using a T1-weighted EPI sequence, consisting of 170 axial slices of 1-mm thickness (1-mm gap) with an in-plane resolution of  $1 \times 1$  mm (field of view = 256). T2-weighted functional scans (repetition time = 2 sec; echo time = 30 msec) were acquired using an interleaved ascending EPI sequence, consisting of 36 axial slices of 3-mm thickness (1-mm gap) with an in-plane resolution of  $1.875 \times 1.875$  mm (field of view = 240). The first volume of each functional scan was discarded to allow for scanner equilibration.

We first performed two functional localizer runs. The first functional localizer was designed to identify word- and/or letter-selective regions of cortex. We note that currently there is no agreement on the optimum localizer for the VWFA, particularly regarding the control condition (Cohen & Dehaene, 2004). Thus, words have been contrasted with a rest condition with either no visual stimulus (Reinke et al., 2008) or a repetition of the masks also used in the word condition (Dehaene et al., 2004), with dot patterns (Reinke et al., 2008) or checkerboards (Cohen et al., 2002), with non-word letter strings (James et al., 2005; Polk & Farah, 2002), faces (Gauthier et al., 2000), digits (Polk et al., 2002), line drawings of objects (Baker et al., 2007), or geometric shapes (Tagamets, Novick, Chalmers, & Friedman, 2000). We reasoned that a reasonable control for the low-level properties of text would be text from another language. Written texts share an emphasis on two-tone contrasts, on line form rather than surface, with approximately similar variations in curvature, orientation, and length of segments. Studies have also shown that activation in the VWFA is greater for a language text for which a participant is literate than for one that they cannot read (Baker et al., 2007). For this reason, we chose to contrast English with Korean words in our English-literate but Korean-illiterate participants, similar to the contrast made between letter strings and Chinese

characters used in other studies (Baker et al., 2007; James et al., 2005).

The second functional localizer identified face-selective ROIs. Participants viewed static photographs of nonliving objects (e.g., television, basketball) and faces (neutral and expressive) presented in separate blocks (Saxe, Brett, & Kanwisher, 2006; Kanwisher, McDermott, & Chun, 1997).

In both functional localizers, participants performed an irrelevant “one-back task,” pressing a button if an image was identical to the previous one—that is, if the same word in the same handwriting was seen twice in a row, a task that was easily performed by all subjects. Fixation blocks, which consisted of a cross in the center of an otherwise blank screen, were alternated with image blocks, all blocks lasting 12 sec. Six image blocks of each image category were presented in a counterbalanced order. Each image block consisted of 15 images (12 novel and 3 repeated), all sized to a standard width of 400 pixels and presented at screen center for 500 msec, with an inter-stimulus interval of 300 msec. The face localizer consisted of 224 functional volumes, and the word localizer consisted of 144 functional volumes.

Following the localizer scan, participants underwent the experimental scan. Three different types of blocks were constructed, with each block containing 10 stimuli. In a “control” block, each of the 10 stimuli was a different word in a different handwriting; thus, no words or handwriting styles were repeated within the block. In a “word” block, the 10 stimuli were all the same word but each in a different handwriting. In a “handwriting” block, the 10 stimuli were all in the same handwriting but each a different word. There were 10 blocks for each of the three conditions, so that each of the 100 stimuli was seen once in each type of block; thus, stimulus presentation was balanced across all conditions. As with the functional localizer runs, participants performed a “one-back task.” The experimental scan consisted of 360 functional volumes.

## Analysis

All MRI data were analyzed using BrainVoyager QX Version 1.8 ([www.brainvoyager.com](http://www.brainvoyager.com)). Anatomical scans were not preprocessed. Preprocessing of functional scans consisted of corrections for slice scan time acquisition, head motion (trilinear interpolation), and temporal filtering with a high-pass filter to remove frequencies less than three cycles/time course. For each participant, functional scans were individually coregistered to their respective anatomical scan, using the first retained functional volume to generate the coregistration matrix.

For the functional localizers, the time course was analyzed using a single-participant general linear model. For the word-localizer data, English words (ENG) and Korean words (KOR) were used as predictors, with an analysis of  $ENG > KOR$  overlaid on the whole brain. For the face-localizer data, object (O), neutral (NF), and expres-

sive (EF) faces were used as predictors, and an analysis of  $NF + EF > 2*O$  was overlaid on the whole brain. Significance was set at a false discovery rate of  $q < .05$ , corrected for multiple comparisons. Within each participant, we attempted to define several ROIs. For faces, contiguous clusters of  $>10$  voxels located on the lateral portion of the right midfusiform gyrus were designated as the FFA. For words, contiguous clusters of  $>10$  voxels located on the lateral portion of the left midfusiform gyrus were designated as the VWFA and a similar region in the right midfusiform gyrus as the right VWFA homologue. In addition to these three a priori ROI, we also noted highly word-activated regions in the left middle temporal gyrus (MTG), right MTG, and left inferior frontal gyrus (IFG): Because of the large extent of activation in these regions, we used a more conservative threshold (one-tailed Bonferroni-corrected  $p < .05$ ) to localize these regions in all participants. For the adaptation experiment, we performed an ROI analysis on the areas localized above, contrasting the percent change in BOLD signal in the control condition versus each of the two experimental conditions (word and handwriting).

## RESULTS

### Functional Localization

In our 13 participants, the functional localizer contrasting English with Korean text identified a left VWFA in 12, a right VWFA homologue in 6, a left MTG in 13, a right MTG in 7, and a left IFG in 12 (Table 1). The face localizer found a right FFA in 12 participants and a left FFA homologue in 11.

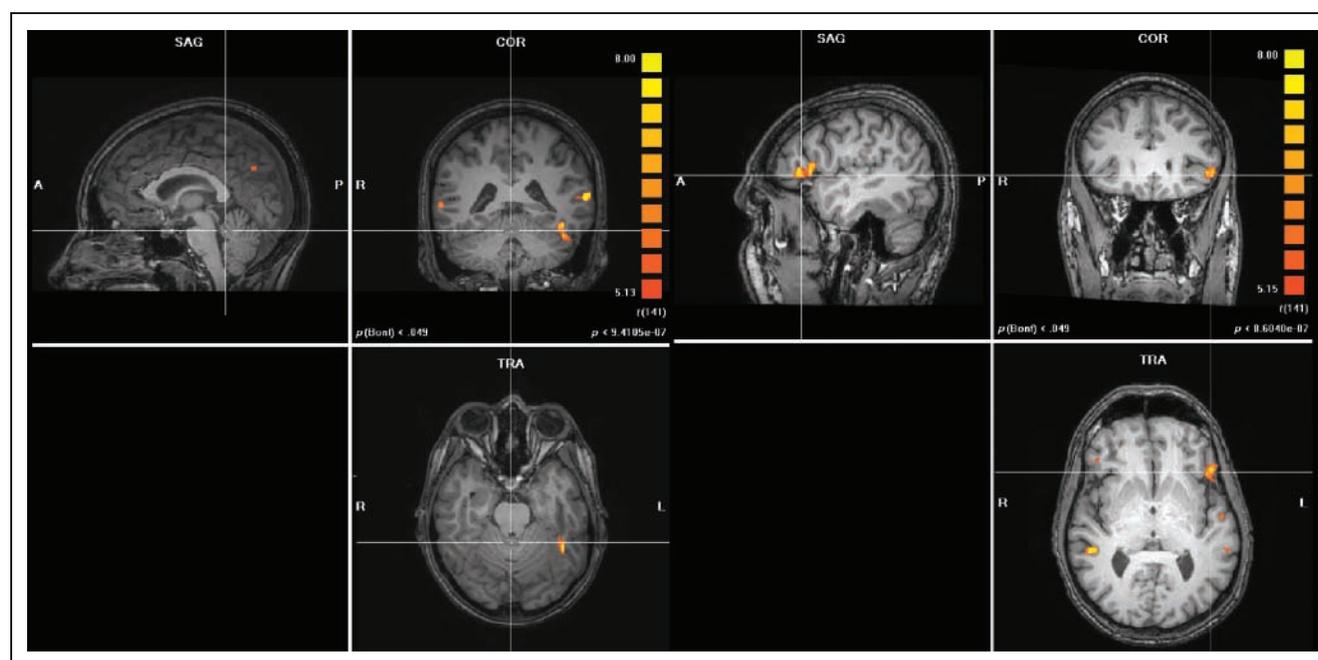
The mean Talairach coordinates of the peak of activation in the left fusiform gyrus were ( $x, y, z = -41, -43, -21$ ; Table 1, Figure 2), which places our VWFA slightly anterior to the usual location cited ( $x, y, z = -43, -53, -13$ ; Callan, Callan, & Masaki, 2005; Vigneau et al., 2005; McCandliss et al., 2003). Nevertheless, our VWFA falls within the bounding coordinates of ( $x, y, z = -50$  to  $-30, -80$  to  $-30, <0$ ) established in a review (Cohen et al., 2002). Our slightly anterior location may reflect the use of Korean script as a baseline rather than the fixation condition, shapes, or dot patterns of prior studies. A study that contrasted letters with digits or Chinese characters produced a similar anterior localization of ( $x, y, z = -42, -37, -3$ ; James et al., 2005), as has one study contrasting words with letter strings ( $x, y, z = -42, -38, -16$ ; Büchel, Price, & Friston, 1998). Studies showing several word-selective foci in the left fusiform gyrus have generally found  $y$  coordinates similar to ours for their most anterior focus; for example,  $y = -42$  (Price et al., 2003),  $y = -40$  (Vinckier et al., 2007),  $y = -48$  (Dehaene et al., 2004), and  $y = -50$  (Kronbichler et al., 2004). Finally, a meta-analysis of word-selective regions located its left inferior temporal gyral cluster at ( $x, y, z = -48, -41, -16$ ; Jobard et al., 2003).

**Table 1.** Mean Coordinates of ROI

	No. Subjects	Talairach Coordinates			Mean No. Voxels	Mean Peak <i>t</i> Value
		<i>x</i>	<i>y</i>	<i>z</i>		
Left VWFA	12	-41	-43	-21	989	6.83
Right VWFA	6	44	-43	-22	338	4.93
Right FFA	12	37	-49	-20	1026	9.13
Left FFA	11	-34	-43	-18	173	4.74
Left MTG	13	-57	-48	5	454	8.86
Right MTG	7	56	-41	4	239	8.20
Left IFG	12	-44	19	14	294	7.74
Left anterior VWFA	11	-40	-38	-17	785	7.03
Left posterior VWFA	11	-43	-51	-21	751	6.40

Although less attention has been paid to the location of the right VWFA homologue, it is generally in a mirror-symmetric location to the VWFA, with similar *y* and *z* Talairach coordinates (Cohen et al., 2003; Dehaene et al., 2001; Price, Wise, & Frackowiak, 1996). The location of our right VWFA homologue is consistent with this. Likewise, the mean coordinates of our right FFA are similar to those reported in the first fMRI study of this region (*x*, *y*, *z* = 40, -55, -10; Kanwisher et al., 1997) and in the adaptation study of faces and words mentioned above (*x*, *y*, *z* = 35, -49, -8; Gauthier et al., 2000).

The peak of activation for our left MTG region (Table 1, Figure 2) is nearly identical to the coordinates (*x*, *y*, *z* = -56, -50, 6) of a region designated posterior superior temporal in another study (Mechelli et al., 2003) and similar to a word-selective region variously labeled as MTG (Vigneau et al., 2005; Devlin et al., 2004; Kronbichler et al., 2004; Cohen et al., 2000), middle/superior temporal junction (Price et al., 1996), and inferior/MTG (Tagamets et al., 2000). It approximates the left posterior MTG cluster (*x*, *y*, *z* = -49, -54, 13) in the meta-analysis of word-selective regions (Jobard et al., 2003).



**Figure 2.** Example of ROIs in a single subject. Regions with significantly greater activity during English than Korean word viewing are shown ( $q < .05$ , Bonferroni corrected). Right hemisphere is on the left side of each image. The left set of coronal, axial, and sagittal images shows the left VWFA in the inferior fusiform gyrus as well as the left and right MTG in the coronal slice. The right set of images shows the left IFG at the center of the crosshairs. Posteriorly, the right MTG is also visible on the axial slice.

Our left IFG region is located in the region of the left IFG (triangular part) cluster, whose mean coordinates across 17 studies are  $x, y, z = -44, 23, 17$  (Jobard et al., 2003).

Thus, we consider that our localizations of VWFA, its right VWFA homologue, FFA, MTG, and IFG are comparable to those in previous reports.

### Adaptation Experiment

Our strategy was first to establish a baseline measure of activity without repetition-suppression, using control blocks in which neither word nor handwriting were repeated (Figure 1). We next kept one dimension (handwriting or word) constant while continuing to vary the other and then reversed this treatment of the dimensions. Any decrease in activity when a particular dimension was held constant, relative to the activity in the control condition when the dimension varied, would suggest a sensitivity of the ROI to that dimension.

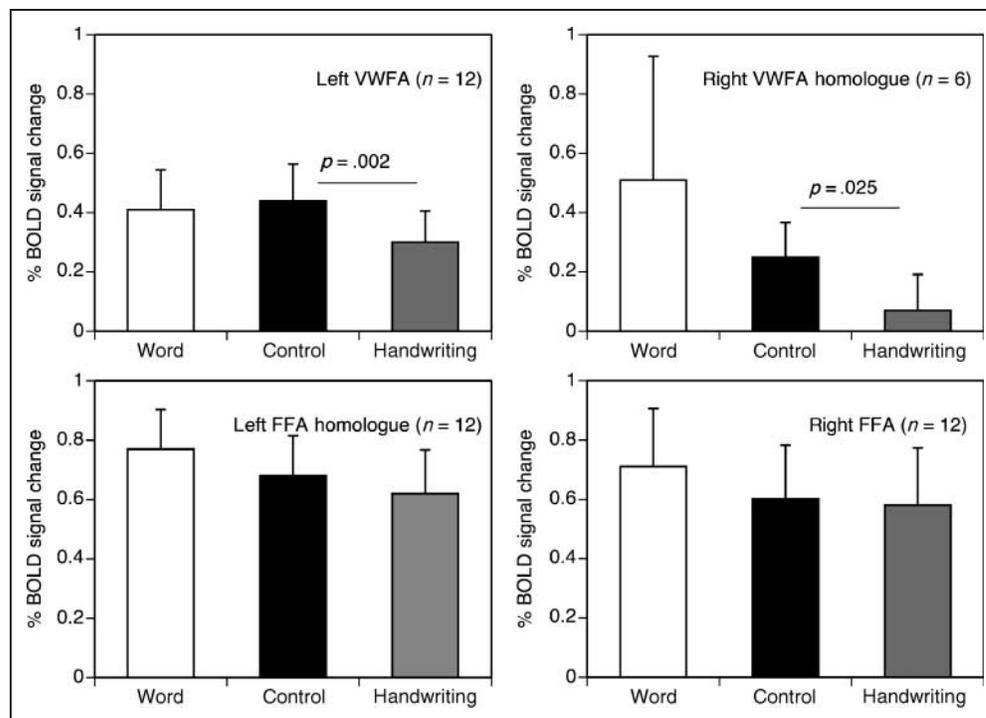
The left VWFA (Figure 2) showed significant repetition-suppression for the handwriting condition compared with the control condition, mean difference  $\pm SE = 0.13 \pm 0.04$ ,  $t(11) = 3.93$ ,  $p = .002$ , one-tailed, but not for the contrast between word and control conditions, mean  $\pm SE = 0.02 \pm 0.07$ ,  $t(11) = 0.95$ ,  $p = .36$  (Figure 3). The right VWFA homologue also showed repetition-suppression for handwriting, mean  $\pm SE = 0.16 \pm 0.07$ ,  $t(5) = 3.18$ ,  $p = .026$ , but not for words.<sup>1</sup> Neither the right FFA nor a left FFA homologue showed significant repetition-suppression for either words or handwriting.

The lack of repetition-suppression for words in the left VWFA was surprising. This led us first to consider whether our hypothesis-driven ROI approach may have missed word adaptation in adjacent regions of the fusiform gyrus that may have word responsivity but not identified by our highly selective localizer contrast between English and Korean, a “telescopic error” (Saxe et al., 2006). To address this possibility, we transformed each individual’s data into Talairach space (Talairach & Tournoux, 1988) and performed a random-effect voxel-based whole-brain analysis (one-tailed Bonferroni correction of  $p < .05$ , clusters  $>10$  voxels). The contrast between the word and the control conditions of the experimental run did not reveal any significant word adaptation clusters in the fusiform or occipital regions of the right or left hemispheres.

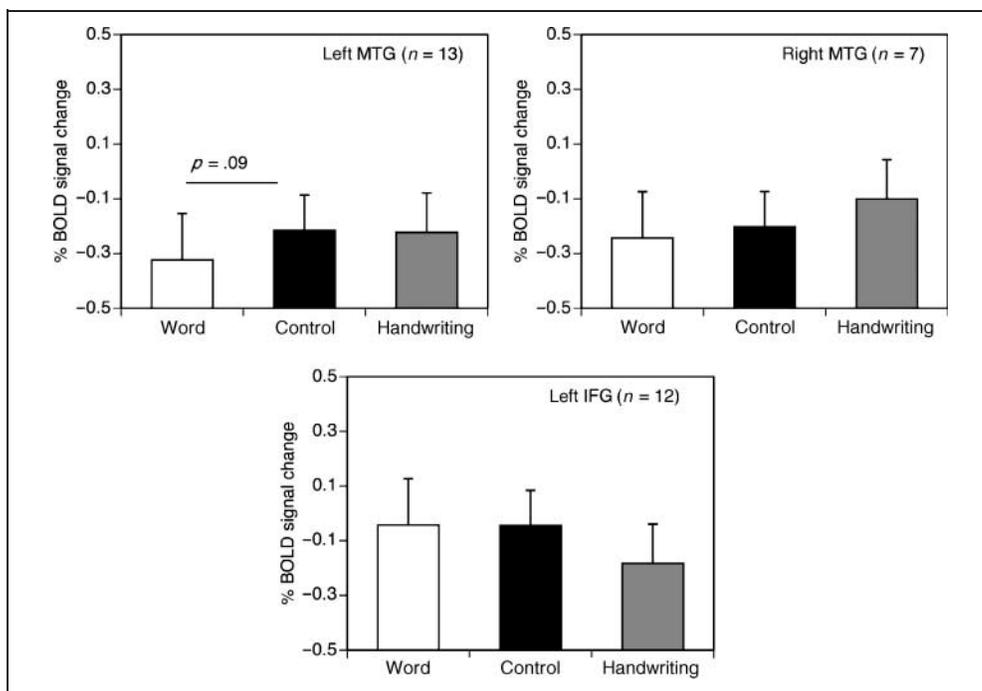
Second, we then asked whether word adaptation could be found in other strongly activated components of the reading network visible in our subjects. In the left MTG (Figure 2), we did find a trend to repetition-suppression for words, mean  $\pm SE = 0.11 \pm 0.07$ ,  $t(12) = 1.84$ ,  $p = .09$ , but not for handwriting (Figure 4). Neither the right MTG nor the left IFG showed repetition-suppression for words or handwriting.

Third, given the relatively large size of the word-selective activation in the fusiform gyrus, we considered whether adaptation to word identity in a subregion might have been obscured by averaging over the entire region through a false “assumption of homogeneity” (Friston, Rotshtein, Geng, Sterzer, & Henson, 2006; Saxe et al., 2006). As noted, there are studies that find multiple rather than single word-selective regions in the left fusiform gyrus (Vinckier et al., 2007; Dehaene et al., 2004; Kronbichler et al., 2004; Price

**Figure 3.** Results of fMRI adaptation experiment, for left VWFA, right VWFA homologue, right FFA, and left FFA homologue. In each graph, the control condition (black bars) is shown compared with the word condition (white bars) and the handwriting condition (gray bars). Error bars indicate one standard error. For both the right and the left VWFA, there is a significant reduction in activity in the handwriting condition.



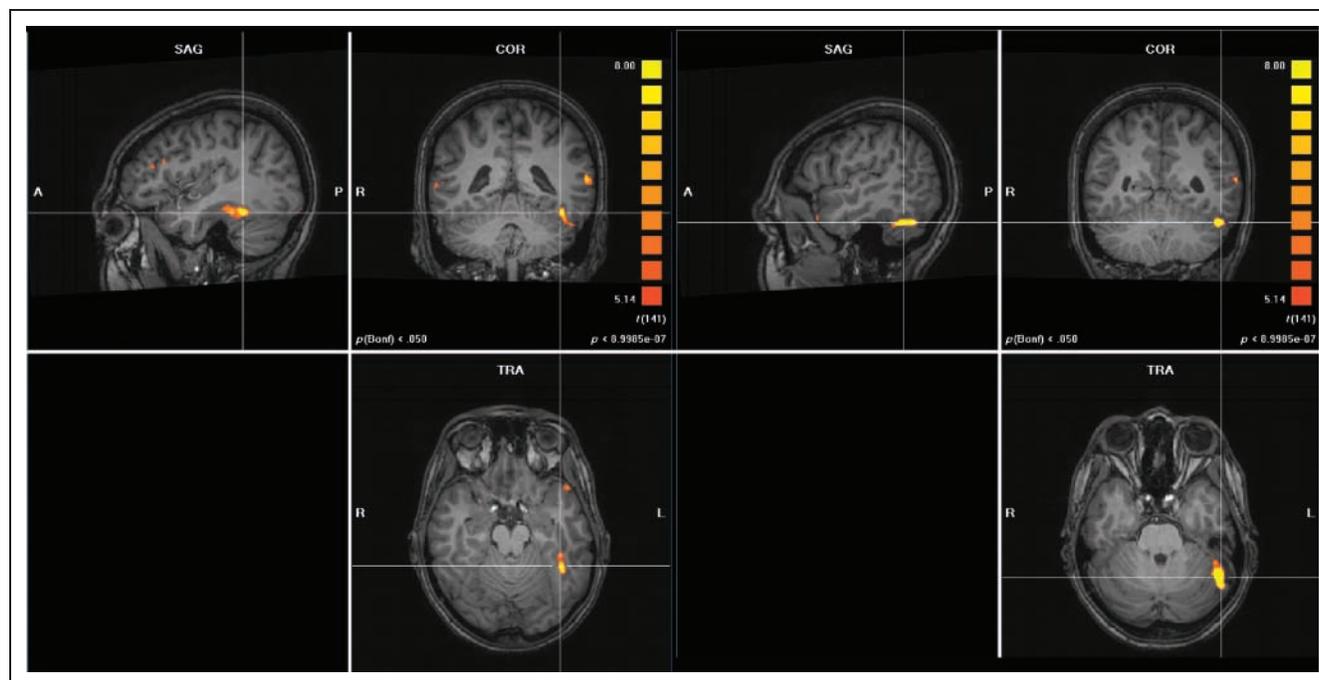
**Figure 4.** Results of fMRI adaptation experiment for left MTG, right MTG, and left IFG. Conventions as in Figure 3. The left MTG shows a trend to reduction in activity in the word condition.



et al., 2003). Another report has suggested that, rather than discrete regions, the fusiform gyrus may contain a posterior-to-anterior hierarchical gradient of increasing word selectivity, from letters to bigrams, quadrigrams, and words (Vinckier et al., 2007). Therefore, we performed

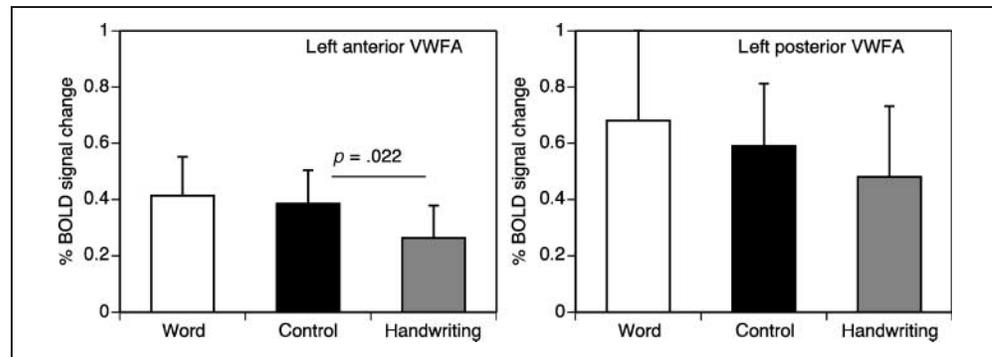
another analysis to determine whether word or handwriting adaptation might be present in smaller components of the VWFA.

We reanalyzed the data from functional localizer, searching within the proposed boundaries for the VWFA (Cohen



**Figure 5.** Example of anterior (left set of images) and posterior (right set of images) components of the VWFA from the same subject. Regions with significantly greater activity during English than Korean word viewing are shown ( $q < .05$ , Bonferroni corrected).

**Figure 6.** Results of fMRI adaptation experiment for left anterior and left posterior VWFA. Conventions as in Figure 3. The left anterior VWFA shows a significant reduction in activity in the handwriting condition.



et al., 2002) for multiple discrete foci of word selectivity. We identified in 11 participants at least two distinct peaks to indicate posterior and anterior VWFA components in the left fusiform gyrus (Table 1, Figure 5). The anterior VWFA continued to show significant repetition–suppression for handwriting, mean  $\pm$  SE = 0.12  $\pm$  0.05,  $t(10) = 2.72$ ,  $p = .022$  (Figure 6). The posterior VWFA did not show significant repetition–suppression for handwriting, due mainly to increased variability across participants, mean  $\pm$  SE = 0.11  $\pm$  0.11,  $t(10) = 1.45$ ,  $p = .18$ . Neither the anterior nor the posterior VWFA showed repetition–suppression for words.

## DISCUSSION

Based on neuropsychological anecdotes (Rentschler et al., 1994; Landis & Regard, 1988; Campbell et al., 1986; Alajouanine et al., 1960) and fMRI adaptation experiments that varied the case of letters (Dehaene et al., 2001, 2004), we hypothesized that we would find repetition–suppression for words but not handwriting in the left VWFA and for handwriting but not words in its right hemispheric homologue. Instead, we found repetition–suppression for handwriting in both the left VWFA and the right VWFA homologue. A trend to repetition–suppression for words was found only in the left MTG. This raises questions about whether abstract letter or word identities—abstract because they generalize across differences in font, case, and size—emerge at the level of the fusiform gyrus or in other areas of the network activated by reading, such as the MTG. It also suggests that the VWFA has greater representation of the stylistic aspects of writing than considered in current models, consistent with one study of font adaptation in letter perception (Gauthier et al., 2000).

As with all fMRI data, caution is required in the interpretation of our results. First, the absence of repetition–suppression for words cannot be taken as definitive evidence that a style-invariant abstract word or letter representation is not encoded in the VWFA. Hypothetical alternative explanations for lack of repetition–suppression include a protocol suboptimal for the specific time course of word adaptation, the presence of a mixture of enhanced and

suppressed responses within a region, or a processing of additional stimulus dimensions that masks the adaptation effect (Krekelberg et al., 2006). Although handwriting might have been such an additional dimension, both our control and word conditions contained the same variations in handwriting; hence, any processing related to handwriting should be equivalent in the two conditions. Also against some of these caveats is the fact that we did observe at least a trend to repetition–suppression for words in the left MTG. Last, another possible explanation of lack of effect is averaging across two subregions, only one of which may show repetition–suppression for the dimension being repeated; however, our analysis of anterior and posterior components of the VWFA still did not reveal any word adaptation.

Second, the fact that repetition–suppression for handwriting was obtained in both the left VWFA and the right VWFA homologue does not necessarily indicate that these regions are critical for encoding this dimension of written text. Adaptation effects may be “inherited” from earlier areas in the visual pathway where the true encoding is occurring (Krekelberg et al., 2006) or represent top–down modulation of activity from higher areas. Our analysis of the left MTG and IFG shows at least that adaptation to handwriting is not reflected generically across the word-processing network. However, we cannot exclude the first possibility that handwriting adaptation occurs in earlier components of the visual pathway.

Thus, although our results suggest the intriguing possibility that both the left VWFA and its right hemispheric homologue share sensitivity to handwriting but not words, converging evidence from lesion data is needed to clarify the contribution of these regions to the processing of written text. Evidence to support a role for the VWFA in word processing is suggested by cases of alexia following damage to or disconnection of the VWFA (Epelbaum et al., 2008; Gaillard et al., 2006; Molko et al., 2002), although these cannot distinguish between the VWFA being the site of abstract letter and word representation versus the VWFA performing a font- and word-sensitive analysis that provides perceptual data to higher regions that derive abstract representations. As yet, there are no equivalent lesion studies on the ability to recognize font or handwriting.

## Function of the VWFA

The role of the VWFA in text processing remains controversial (Cohen & Dehaene, 2004; Price & Devlin, 2003, 2004). A prominent model proposes that it is involved in “prelexical processing,” the processing of text components or “grapheme sequences” that are assembled into words (Dehaene et al., 2005; Hillis et al., 2005; McCandliss et al., 2003). Sensitivity to graphemes rather than words is suggested by the fact that the VWFA responds as well to pronounceable pseudowords as to real words (Cohen et al., 2002), if not more (Kronbichler et al., 2004, 2007; Fiez et al., 1999). In support, some studies find better responses to pseudowords, which contain grapheme sequences that obey orthographic constraints, than to random consonant strings, which do not (Cohen et al., 2002; Xu et al., 2001). However, others have shown equal responsivity to words and letter strings that violate orthographic rules (Vigneau et al., 2005; Joubert et al., 2004), and an fMRI adaptation study showed repetition–suppression for words but not pseudowords, against a prelexical representation of graphemes (Devlin et al., 2006).

Letter, grapheme, or word processing suggest an abstraction from the proximal visual stimulus that generalizes across different styles. Two fMRI adaptation studies have reported case invariance of letter and word processing in the left VWFA (Dehaene et al., 2001, 2004). Against this are an fMRI adaptation study that showed sensitivity of repetition–suppression to font type (Gauthier et al., 2000) and an fMRI study showing increased activity when words are presented in atypical alternating case (Kronbichler et al., 2009), both of which indicate a sensitivity of the VWFA to the visual properties of text, not just abstract letter identity. Indeed, others have argued for a model in which, rather than containing prelexical representations, the VWFA “transiently instantiates a representation of a visual stimulus that interfaces between its invariant visual characteristics (e.g., form) and higher order properties of that stimulus” and that it is “primarily driven by visual information but that this can be influenced by nonvisual factors” (Devlin et al., 2006). In this model, abstract letter and word representations emerge from the interaction of visual information encoded in the VWFA with linguistic processing in other components of a reading network, including the MTG, the angular gyrus, and the IFG, among others (Price & Devlin, 2003).

Although our results cannot settle this debate, they clearly indicate a sensitivity of the VWFA to the stylistic properties of text. Sensitivity to handwriting or font does not necessarily imply that the VWFA is discriminating handwriting or font instead of words, however. Tuning for font or handwriting is an integral part of deciphering the word content of text by experts (Gauthier, Wong, Hayward, & Cheung, 2006), and it may be that the handwriting sensitivity of the VWFA is a marker of its participation in the

translation of the proximal stimulus into an abstract letter representation. If so, it places the VWFA at a more perceptual level of analysis than a linguistic one, which is not inconsistent with the opinions of others (Kronbichler et al., 2009; Devlin et al., 2006; McCandliss et al., 2003; Price & Devlin, 2003).

## Right versus Left Word-selective Areas

Just as face processing shows a dominant FFA in the right occipital cortex and minor activation in a similar location on the left (Kanwisher et al., 1997), we replicate the mirror result previously reported for written text that the area activated on the right is smaller, less significant, and seen in fewer participants than that on the left (Cohen et al., 2002). A lower degree of word specificity in the right fusiform gyrus is also reflected in other observations. First, activity on the right is similar for words, symbols, digits, and checkerboard stimuli, whereas that on the left is greater for words and/or abstract symbols than for the other visual categories (Reinke et al., 2008; Cohen et al., 2003). Second, the asymmetry favoring left over right fusiform activity is greater during the reading of words than during the reading of nonwords (Vigneau et al., 2005). Third, a posterior-to-anterior gradient of increasing specificity for words in the fusiform gyrus is more pronounced on the left than the right (Vinckier et al., 2007).

All of these results suggest greater specialization for words on the left. What is not clear is whether the text processing in the right VWFA homologue is simply a less selective version of that on the left or a qualitatively different type of information extraction. An fMRI adaptation study pointing to the latter found that repetition–suppression was independent of case in the left VWFA but not in the right fusiform gyrus (Dehaene et al., 2004), implying that abstract letter representations emerge only in the left VWFA. This parallels work on object perception that has shown repetition–suppression in the left fusiform gyrus regardless of whether the same or a different exemplar of an object is repeated but repetition–suppression in the right fusiform gyrus only when the same exemplar is repeated (Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Koutstaal et al., 2001).

We did not find a qualitative difference between the left and the right fusiform gyri in our study: Both right and left word-selective areas showed repetition–suppression for handwriting but not words. However, caution is necessary before concluding that both areas show similar repetition–suppression effects because, as with most VWFA studies, fewer right VWFA homologues were localized than left VWFA regions. Although we did find a statistically significant repetition–suppression for handwriting in both the right and the left fusiform regions, the fact that the data for the right VWFA homologue derive from half as many subjects as the left VWFA data creates a statistical inequality that imparts less confidence in the findings for the right

VWFA homologue. Furthermore, similarities in repetition–suppression effects for handwriting do not exclude the possibilities (a) that differences might be found with other dimensions of text or (b) that the right and left fusiform gyri are both processing handwriting but for different purposes and as parts of different networks.

How can we reconcile these data with neuropsychological observations? Pure alexia or peripheral alexia does appear to result almost exclusively from left hemispheric lesions in right-handed patients (Kleinschmidt & Cohen, 2006; Black & Behrmann, 1994). Whether this is attributable to loss of abstract letter identification can be questioned: Alexia can vary in severity from slowed reading speed (Coslett, Saffran, Greenbaum, & Schwartz, 1993; Bub, Black, & Howell, 1989) to global alexia affecting musical notation and other symbols as well (Beverdort & Heilman, 1998; Horikoshi et al., 1997; Binder & Mohr, 1992). Furthermore, as others have remarked (Reinke et al., 2008; Price & Devlin, 2003), the lesions in alexia do not always affect the VWFA but sometimes other regions such as the underlying white matter, splenium, or MTG (Erdem & Kansu, 1995; Henderson, Friedman, Teng, & Weiner, 1985; Vincent, Sadowsky, Saunders, & Reeves, 1977; Greenblatt, 1973). Reading involves a network of regions (Reinke et al., 2008; Jobard et al., 2003; Price & Devlin, 2003; Tagamets et al., 2000), of which the VWFA is merely one node. Although some hypothesize that damage to the VWFA may directly affect abstract letter representations, it is also possible that such damage affects critical inputs of style-dependent perceptual representations from the VWFA to other left-sided regions in the network, and that it is at these levels or in interactions with these levels that abstract word identity emerges.

Our suggestion that the VWFA operates at a more perceptual level of analysis is also consistent with observations indicating that at least some cases of alexia following left occipito-temporal lesions are linked to dysfunction at a perceptual stage of encoding (Farah & Wallace, 1991). A detailed literature review concluded that almost all alexic patients show problems with letter misidentification and concluded that “the fundamental impairment is one of visual processing, arising relatively early and preventing the derivation of an adequate orthographic representation” (Behrmann, Plaut, & Nelson, 1998). In some accounts, this deficit is specific to orthography and letter identification (Arguin & Bub, 1993), in others it is a more general perceptual dysfunction that can also affect recognition of digits, complex objects, and visual patterns (Ingles & Eskes, 2008; Behrmann, Nelson, & Sekuler, 1998; Rentschler et al., 1994; Farah & Wallace, 1991), although the reading impairment may be its most dramatic and severe manifestation. Supporting a fundamental perceptual deficit in alexia are observations that the reading of many alexic patients is adversely affected by the surface properties of the text: They have more trouble with script than print (Warrington & Shallice, 1980), with words that contain letters highly similar to other letters—the letter confus-

ability effect (Fiset, Arguin, Bub, Humphreys, & Riddoch, 2005), and show a multiplicative interaction between word length and perceptual degradation of text (Farah & Wallace, 1991).

### Role of the Left MTG

Although we did not find adaptation for words in the VWFA, we did find a trend for this in the left MTG. Numerous studies have shown that the left superior temporal gyrus and MTG are part of a reading network (Jobard et al., 2003), and functional connectivity studies during reading show positive correlations between the VWFA, the hippocampus, the lateral temporal, and the pFC of the left hemisphere (Reinke et al., 2008). A meta-analysis (Jobard et al., 2003) has concluded that the superior temporal gyrus is involved in grapheme-to-phoneme conversion, and the posterior MTG has a role in lexical-semantic associations. Indeed, a PET study proposed that this region may be the site of the written lexicon (Howard et al., 1992), and an fMRI adaptation study showed that although the left fusiform cortex shows priming for words with similar forms independent of meaning (e.g., corn—corner), the left MTG shows priming for words with similar meaning independent of form (e.g., idea—notion; Devlin et al., 2004). Also, learning the meaning of unfamiliar Asian phonograms resulted in greater integration of the left angular and superior temporal gyri on functional connectivity analysis (Callan et al., 2005).

Thus, there is considerable evidence for involvement of regions in and around the MTG in deriving both sound and semantics from the written word, processes that require the recognition of abstract letter identity. Hence, a trend to repetition–suppression for words but not handwriting in the MTG is not surprising. One interpretation of this result is that the emergence of an abstract text representation does not occur until the MTG, at the same hierarchical level that processes word meaning and sound conversion. However, caution is required: Adaptation for words in the MTG could be inherited from a lower hierarchical level such as the VWFA, and lack of adaptation for words in the VWFA cannot exclude the possibility that abstract letter identity is encoded in the VWFA but obscured by additional processes (Krekelberg et al., 2006). The result also deserves caution as the left MTG findings were only at the level of a trend and require verification in further studies.

In summary, we find the same repetition–suppression for handwriting but not words in both the left VWFA and the right VWFA homologue, indicating that these regions are sensitive to the style of text. Whether this indicates a role for these regions in handwriting recognition or a use of handwriting data to facilitate expert text processing for reading requires neuropsychological investigation. Nevertheless, the data support proposals that the role for the VWFA in reading is perceptual rather than linguistic. A trend to repetition–suppression for words but

not handwriting was seen in the left MTG rather than the VWFA, suggesting the emergence of abstract letter representations at least at the level of the MTG.

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## Note

1. The fact that we localized more left VWFA regions than right VWFA homologues creates a statistical imbalance. Nevertheless, when the analysis is repeated on the left VWFA of only the six subjects with a right VWFA homologue, the result is the same, with a significant difference between handwriting and control conditions ( $p = .013$ ) but not between word and control conditions.

## REFERENCES

- Alajouanine, T., Lhermitte, F., & de Ribaucourt-Ducarne, B. (1960). Les alexies agnosiques et aphasiques. In *Les grandes activités du lobe occipital* (pp. 235–260). Paris: Masson.
- Arguin, M., & Bub, D. N. (1993). Single-character processing in a case of pure alexia. *Neuropsychologia*, *31*, 435–458.
- Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *104*, 9087–9092.
- Behrmann, M., Nelson, J., & Sekuler, E. B. (1998). Visual complexity in letter-by-letter reading: “Pure” alexia is not pure. *Neuropsychologia*, *36*, 1115–1132.
- Behrmann, M., Plaut, D. C., & Nelson, J. (1998). A literature review and new data supporting an interactive account of letter-by-letter reading. *Cognitive Neuropsychology*, *15*, 7–51.
- Beverdors, D., & Heilman, K. (1998). Progressive ventral posterior cortical degeneration presenting as alexia for music and words. *Neurology*, *50*, 657–659.
- Binder, J., & Mohr, J. (1992). The topography of callosal reading pathways. A case control analysis. *Brain*, *115*, 1807–1826.
- Black, S., & Behrmann, M. (1994). Localization in alexia. In *Localization and neuroimaging in neuropsychology* edited by Andrew Kertesz (pp. 331–376). New York: Academic Press.
- Bub, D., Black, S., & Howell, J. (1989). Word recognition and orthographic context effects in a letter-by-letter reader. *Brain and Language*, *36*, 357–376.
- Büchel, C., Price, C., & Friston, K. (1998). A multimodal language region in the ventral visual pathway. *Nature*, *394*, 274–277.
- Callan, A. M., Callan, D. E., & Masaki, S. (2005). When meaningless symbols become letters: Neural activity change in learning new phonograms. *Neuroimage*, *28*, 553–562.
- Campbell, R., Landis, T., & Regard, M. (1986). Face recognition and lipreading. A neurological dissociation. *Brain*, *109*, 509–521.
- Cohen, L., & Dehaene, S. (2004). Specialization within the ventral stream: The case for the visual word form area. *Neuroimage*, *22*, 466–476.
- Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M. A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*, *123*, 291–307.
- Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain*, *125*, 1054–1069.
- Cohen, L., Martinaud, O., Lemer, C., Lehericy, S., Samson, Y., Obadia, M., et al. (2003). Visual word recognition in the left and right hemispheres: Anatomical and functional correlates of peripheral alexias. *Cerebral Cortex*, *13*, 1313–1333.
- Coltheart, M. (1981). The MRC psycholinguistic database. *Quarterly Journal of Experimental Psychology*, *33A*, 497–505.
- Coslett, H., Saffran, E., Greenbaum, S., & Schwartz, H. (1993). Reading in pure alexia. *Brain*, *116*, 21–37.
- Damasio, A., & Damasio, H. (1983). The anatomic basis of pure alexia. *Neurology*, *33*, 1573–1583.
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, *9*, 335–341.
- Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J. B., Le Bihan, D., et al. (2004). Letter binding and invariant recognition of masked words: Behavioral and neuroimaging evidence. *Psychological Science*, *15*, 307–313.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, *4*, 752–758.
- Devlin, J. T., Jamison, H. L., Gonnerman, L. M., & Matthews, P. M. (2006). The role of the posterior fusiform gyrus in reading. *Journal of Cognitive Neuroscience*, *18*, 911–922.
- Devlin, J. T., Jamison, H. L., Matthews, P. M., & Gonnerman, L. M. (2004). Morphology and the internal structure of words. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 14984–14988.
- Epelbaum, S., Pinel, P., Gaillard, R., Delmaire, C., Perrin, M., Dupont, S., et al. (2008). Pure alexia as a disconnection syndrome: New diffusion imaging evidence for an old concept. *Cortex*, *44*, 962–974.
- Erdem, S., & Kansu, T. (1995). Alexia without either agraphia or hemianopia in temporal lobe lesion due to herpes simplex encephalitis. *Journal of Neuro-ophthalmology*, *15*, 102–104.
- Farah, M. J., & Wallace, M. A. (1991). Pure alexia as a visual impairment: A reconsideration. *Cognitive Neuropsychology*, *8*, 313–334.
- Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (1999). Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. *Neuron*, *24*, 205–218.
- Fiset, D., Arguin, M., Bub, D., Humphreys, G. W., & Riddoch, M. J. (2005). How to make the word-length effect disappear

- in letter-by-letter dyslexia: Implications for an account of the disorder. *Psychological Science*, *16*, 535–541.
- Friston, K. J., Rotshtein, P., Geng, J. J., Sterzer, P., & Henson, R. N. (2006). A critique of functional localisers. *Neuroimage*, *30*, 1077–1087.
- Gaillard, R., Naccache, L., Pinel, P., Clemenceau, S., Volle, E., Hasboun, D., et al. (2006). Direct intracranial, fMRI, and lesion evidence for the causal role of left inferotemporal cortex in reading. *Neuron*, *50*, 191–204.
- Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform “face area” is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, *12*, 495–504.
- Gauthier, I., Wong, A. C., Hayward, W. G., & Cheung, O. S. (2006). Font tuning associated with expertise in letter perception. *Perception*, *35*, 541–559.
- Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia*, *45*, 32–41.
- Greenblatt, S. (1973). Alexia without agraphia or hemianopia. *Brain*, *96*, 307–316.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*, 14–23.
- Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*, 293–321.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.
- Henderson, V., Friedman, R., Teng, E., & Weiner, J. (1985). Left hemisphere pathways in reading: Inferences from pure alexia without hemianopia. *Neurology*, *35*, 962–968.
- Hillis, A. E., Newhart, M., Heidler, J., Barker, P., Herskovits, E., & Degaonkar, M. (2005). The roles of the “visual word form area” in reading. *Neuroimage*, *24*, 548–559.
- Horikoshi, T., Asari, Y., Watanabe, A., Nagaseki, Y., Nukui, H., Sasaki, H., et al. (1997). Music alexia in a patient with mild pure alexia: Disturbed visual perception of non-verbal meaningful figures. *Cortex*, *33*, 187–194.
- Howard, D., Patterson, K., Wise, R., Brown, W. D., Friston, K., Weiller, C., et al. (1992). The cortical localization of the lexicons. Positron emission tomography evidence. *Brain*, *115*, 1769–1782.
- Ingles, J. L., & Eskes, G. A. (2008). A comparison of letter and digit processing in letter-by-letter reading. *Journal of the International Neuropsychological Society*, *14*, 164–173.
- James, K. H., James, T. W., Jobard, G., Wong, A. C., & Gauthier, I. (2005). Letter processing in the visual system: Different activation patterns for single letters and strings. *Cognitive, Affective & Behavioral Neuroscience*, *5*, 452–466.
- Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: A metanalysis of 35 neuroimaging studies. *Neuroimage*, *20*, 693–712.
- Joubert, S., Beauregard, M., Walter, N., Bourgouin, P., Beaudoin, G., Leroux, J. M., et al. (2004). Neural correlates of lexical and sublexical processes in reading. *Brain and Language*, *89*, 9–20.
- Kanwisher, N., McDermott, J., & Chun, M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Kleinschmidt, A., & Cohen, L. (2006). The neural bases of prosopagnosia and pure alexia: Recent insights from functional neuroimaging. *Current Opinion in Neurology*, *19*, 386–391.
- Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: Functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, *39*, 184–199.
- Krekelberg, B., Boynton, G. M., & van Wezel, R. J. (2006). Adaptation: From single cells to BOLD signals. *Trends in Neurosciences*, *29*, 250–256.
- Kronbichler, M., Bergmann, J., Hutzler, F., Staffen, W., Mair, A., Ladurner, G., et al. (2007). Taxi vs. taksi: On orthographic word recognition in the left ventral occipitotemporal cortex. *Journal of Cognitive Neuroscience*, *19*, 1584–1594.
- Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., & Ladurner, G. (2004). The visual word form area and the frequency with which words are encountered: Evidence from a parametric fMRI study. *Neuroimage*, *21*, 946–953.
- Kronbichler, M., Klackl, J., Richlan, F., Schurz, M., Staffen, W., Ladurner, G., et al. (2009). On the functional neuroanatomy of visual word processing: Effects of case and letter deviance. *Journal of Cognitive Neuroscience*, *21*, 1–8.
- Landis, T., & Regard, M. (1988). Hemianopsia and agnosia. *Klinische Monatsblätter für Augenheilkunde*, *192*, 525–528.
- Lin, Z. (2007). fMRI adaptation: Stimulus specific or processing load specific? *Journal of Neuroscience*, *27*, 11453–11454.
- Marchand, Y., & Friedman, R. B. (2005). Impaired oral reading in two atypical dyslexics: A comparison with a computational lexical-analogy model. *Brain and Language*, *93*, 255–266.
- Mayall, K., Humphreys, G. W., Mechelli, A., Olson, A., & Price, C. J. (2001). The effects of case mixing on word recognition: Evidence from a PET study. *Journal of Cognitive Neuroscience*, *13*, 844–853.
- McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, *7*, 293–299.
- Mechelli, A., Gorno-Tempini, M. L., & Price, C. J. (2003). Neuroimaging studies of word and pseudoword reading: Consistencies, inconsistencies, and limitations. *Journal of Cognitive Neuroscience*, *15*, 260–271.
- Molko, N., Cohen, L., Mangin, J. F., Chochon, F., Lehericy, S., Le Bihan, D., et al. (2002). Visualizing the neural bases of a disconnection syndrome with diffusion tensor imaging. *Journal of Cognitive Neuroscience*, *14*, 629–636.
- Pernet, C., Celsis, P., & Demonet, J. F. (2005). Selective response to letter categorization within the left fusiform gyrus. *Neuroimage*, *28*, 738–744.
- Polk, T. A., & Farah, M. J. (2002). Functional MRI evidence for an abstract, not perceptual, word-form area. *Journal of Experimental Psychology: General*, *131*, 65–72.
- Polk, T. A., Stallcup, M., Aguirre, G. K., Alsop, D. C., D’Esposito, M., Detre, J. A., et al. (2002). Neural specialization for letter recognition. *Journal of Cognitive Neuroscience*, *14*, 145–159.
- Price, C. J., & Devlin, J. T. (2003). The myth of the visual word form area. *Neuroimage*, *19*, 473–481.
- Price, C. J., & Devlin, J. T. (2004). The pro and cons of labelling a left occipitotemporal region: “The visual word form area.” *Neuroimage*, *22*, 477–479.
- Price, C. J., Gorno-Tempini, M. L., Graham, K. S., Biggio, N., Mechelli, A., Patterson, K., et al. (2003). Normal and pathological reading: Converging data from lesion and imaging studies. *Neuroimage*, *20*(Suppl. 1), S30–S41.
- Price, C. J., Wise, R. J., & Frackowiak, R. S. (1996). Demonstrating the implicit processing of visually presented words and pseudowords. *Cerebral Cortex*, *6*, 62–70.
- Puce, A., Allison, T., Asgari, M., Gore, J., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance study. *Journal of Neuroscience*, *16*, 5205–5215.

- Reinke, K., Fernandes, M., Schwindt, G., O'Craven, K., & Grady, C. L. (2008). Functional specificity of the visual word form area: General activation for words and symbols but specific network activation for words. *Brain and Language, 104*, 180–189.
- Rentschler, I., Treutwein, B., & Landis, T. (1994). Dissociation of local and global processing in visual agnosia. *Vision Research, 34*, 963–971.
- Saxe, R., Brett, M., & Kanwisher, N. (2006). Divide and conquer: A defense of functional localizers. *Neuroimage, 30*, 1088–1096; discussion 1097–1089.
- Simons, J. S., Koutstaal, W., Prince, S., Wagner, A. D., & Schacter, D. L. (2003). Neural mechanisms of visual object priming: Evidence for perceptual and semantic distinctions in fusiform cortex. *Neuroimage, 19*, 613–626.
- Tagamets, M. A., Novick, J. M., Chalmers, M. L., & Friedman, R. B. (2000). A parametric approach to orthographic processing in the brain: An fMRI study. *Journal of Cognitive Neuroscience, 12*, 281–297.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Vigneau, M., Jobard, G., Mazoyer, B., & Tzourio-Mazoyer, N. (2005). Word and non-word reading: What role for the visual word form area? *Neuroimage, 27*, 694–705.
- Vincent, F., Sadowsky, C., Saunders, R., & Reeves, A. (1977). Alexia without agraphia, hemianopia, or color-naming defect: A disconnection syndrome. *Neurology, 27*, 689–691.
- Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. *Neuron, 55*, 143–156.
- Warrington, E., & Shallice, T. (1980). Word-form dyslexia. *Brain, 103*, 99–112.
- Xu, B., Grafman, J., Gaillard, W. D., Ishii, K., Vega-Bermudez, F., Pietrini, P., et al. (2001). Conjoint and extended neural networks for the computation of speech codes: The neural basis of selective impairment in reading words and pseudowords. *Cerebral Cortex, 11*, 267–277.