

The Neural Substrates of Visual Perceptual Learning of Words: Implications for the Visual Word Form Area Hypothesis

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Abstract

■ It remains under debate whether the fusiform visual word form area (VWFA) is specific to visual word form and whether visual expertise increases its sensitivity (Xue et al., 2006; Cohen et al., 2002). The present study examined three related issues: (1) whether the VWFA is also involved in processing foreign writing that significantly differs from the native one, (2) the effect of visual word form training on VWFA activation after controlling the task difficulty, and (3) the transfer of visual word form learning. Eleven native English speakers were trained, during five sessions, to judge whether two subsequently flashed (100-msec duration with 200-msec interval) foreign characters (i.e., Korean Hangul) were identical or not. Visual noise was added to the stimuli to manipulate task difficulty. In functional magnetic resonance imaging scans before and after training, subjects performed the task once with the same noise level (i.e.,

parameter-matched scan) and once with noise level changed to match performance from pretraining to posttraining (i.e., performance-matched scan). Results indicated that training increased the accuracy in parameter-matched condition but remained constant in performance-matched condition (because of increasing task difficulty). Pretraining scans revealed stronger activation for English words than for Korean characters in the left inferior temporal gyrus and the left inferior frontal cortex, but not in the VWFA. Visual word form training significantly decreased the activation in the bilateral middle and left posterior fusiform when either parameters or performance were matched and for both trained and new items. These results confirm our conjecture that the VWFA is not dedicated to words, and visual expertise acquired with training reduces rather than increases its activity. ■

INTRODUCTION

The role of the visual word form area (VWFA) located in the left midfusiform cortex is a matter of continuing debate (Xue, Chen, Jin, & Dong, 2006; Cohen & Dehaene, 2004; Price & Devlin, 2003). Although the VWFA is consistently involved in visual word processing and shows cross-culture consistency (Bolger, Perfetti, & Schneider, 2005; Xue et al., 2005; McCandliss, Cohen, & Dehaene, 2003), researchers do not agree on whether the VWFA is specific to visual word form. It has been argued that VWFA is specified for prelexical visual word form processing (Cohen & Dehaene, 2004; McCandliss et al., 2003; Cohen et al., 2002), whereas others hold that the VWFA is also involved in lexical processing (Hillis et al., 2005; Kronbichler et al., 2004) and in processing other visual objects such as faces, houses, and tools (see Price & Devlin, 2003, for a review) and foreign writing¹ (Xue et al., 2006). The VWFA has also been proposed to play a role in integrating visual, phonological, and semantic information (Devlin, Jamison, Gonnerman, & Matthews, 2006; McCrory, Mechelli, Frith, & Price, 2005; Price & Friston, 2005).

Neuropsychological studies could help to resolve this issue, but the results are not consistent (Henry et al., 2005; Hillis et al., 2005; Cohen, Henry, et al., 2004; Leff et al., 2001; Cohen et al., 2000, 2003). One major reason is that lesions in this region due to tumors or strokes are usually not restricted to the VWFA but, rather, extend to a large part of the cortex. More recently, Gaillard et al. (2006) have been able to test a rare patient who underwent surgical resection of a small patch of cortex near the VWFA. The patient developed a specific reading deficit after surgery, whereas his general language ability (e.g., phonological and semantic processing) and ability to recognize and name other visual category (i.e., houses, faces, and tools) remained intact. This result provides support for some degree of regional specificity for visual word processing in the VWFA.

Recent advances in this area have led to finer functional division in the region. Particularly, researchers have proposed several models suggesting a posterior-versus-anterior distinction on VWFA function, including visuo-perceptual versus lexical/semantic (Simons, Koutstaal, Prince, Wagner, & Schacter, 2003), unimodal versus multimodal (Cohen, Jobert, Le Bihan, & Dehaene, 2004), and local combination versus larger fragments of words (Dehaene, Cohen, Sigman, & Vinckier, 2005; Cohen &

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Dehaene, 2004). These results suggest that different strategies should be used to examine the specificity hypothesis in the subregions of the VWFA. For example, object–word comparisons are ideal to examine the specificity in the anterior VWFA because both objects and words are associated with both phonological and semantic information (Price & Devlin, 2003). On the other side, because of the great differences in visual features between words and other categories of visual objects, the comparison between word and visually matched nonwords (e.g., consonant strings, false fonts, foreign writings) may be better able to address the specificity in the middle and posterior VWFA (Xue et al., 2006). However, neuroimaging studies along the latter line have obtained mixed results (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2007; Xue et al., 2006; James, James, Jobard, Wong, & Gauthier, 2005; Wong, Gauthier, Woroch, DeBuse, & Curran, 2005; Cohen et al., 2002; Polk & Farah, 2002; Tagamets, Novick, Chalmers, & Friedman, 2000; Indefrey et al., 1997; Petersen, Fox, Snyder, & Raichle, 1990). For example, several studies have not found word sensitivity in this region (Gaillard et al., 2006; Xue et al., 2006; Cohen et al., 2003; Tagamets et al., 2000; Indefrey et al., 1997). Some studies have revealed stronger fusiform activation for words/letters than for visual-matched nonwords/symbols, but the exact location varied significantly across studies (James et al., 2005; Cohen et al., 2002; Polk & Farah, 2002; Petersen et al., 1990).

It has been argued that word sensitivity/specificity in the VWFA is associated with the visual expertise that developed through years of reading experience (Cohen & Dehaene, 2004; McCandliss et al., 2003; Cohen et al., 2002). To the contrary, we have argued that differences in activity in the word-nonword comparison might reflect combined effects of several aspects of language experience (i.e., visual familiarity, phonology, and semantics) (Xue et al., 2006). We adopted an artificial language training paradigm to disentangle the roles of visual familiarity, phonology, and semantics in modulating VWFA activation. Results indicated that visual form training significantly decreased the activation in the VWFA, whereas phonology and semantic training increased VWFA activation, along with the increase in the left inferior frontal cortex (IFC) activation. This study shows that artificial language training paradigm is a useful tool to examine the developmental mechanisms of the VWFA. Moreover, it emphasizes that during word-nonword comparison, instead of merely focusing on the VWFA, it is also critical to examine the neural differences in the frontal lobe that support phonological and semantic processing (Poldrack, Wagner, et al., 1999), which could provide us with better understanding of mechanisms of VWFA activation.

The present study was aimed at extending previous studies to examine the mechanisms of the neural changes associated with visual word form training without the contamination of phonology and semantic information. Specifically, we aimed to address three questions. First,

we asked whether the VWFA is also involved in the processing of foreign writings that are significantly different from the native words, such as Korean Hangul versus English. The use of significant different systems minimizes the transfer of native language experience to the new system.

Second, we aimed to separate the effects of neural plasticity and task difficulty. Research on neural plasticity with training is often confounded by overall performance level and/or task difficulty (Poldrack, 2000). In the previous study, we used a passive viewing task to reduce the effect of task requirement. To further address this issue, the present study added visual noise to the characters to manipulate task difficulty. Subjects were scanned under two conditions in each scanning session, once before and once after training. In one condition, the amount of visual noise used in the pretraining and posttraining scan remained the same (i.e., parameter-matched scan). In the other condition, a parameter estimation procedure was used to determine the task parameters that would equate subjects' performance between the pretraining and posttraining scans (i.e., performance-matched scan).

Finally, visual word form learning could reflect either item-specific learning (i.e., repetition priming) or some general visual skills that can be transferred to new items (i.e., skill learning) (Poldrack & Gabrieli, 2001; Poldrack, Selco, Field, & Cohen, 1999; Poldrack, Desmond, Glover, & Gabrieli, 1998). To further examine the nature of visual word form learning, the present study included both old and new items in the training and functional magnetic resonance imaging (fMRI) scans. We also examined short-term repetition priming (STRP) by presenting sets of old or new items and then repeating the same items soon after (within five trials).

METHODS

Subjects

Eleven normal young adult subjects participated in this study (mean age = 26 years; 5 women and 6 men). All subjects had normal or corrected-to-normal vision and judged as right-handed using the Edinburgh Handedness Inventory (Oldfield, 1971). They were all native English speakers, and none had experience with any major logographic language (e.g., Chinese, Korean, Japanese). They provided informed consent according to a procedure approved by the University of California, Los Angeles Human Subject Committee. Three additional subjects were excluded because of substantial motion artifacts in pretraining and/or posttraining session.

Material

Figure 1 provides an example of stimulus used in this study. We used 1200 three-letter Korean Hangul characters.² There were two types of spatial layout: left–right–

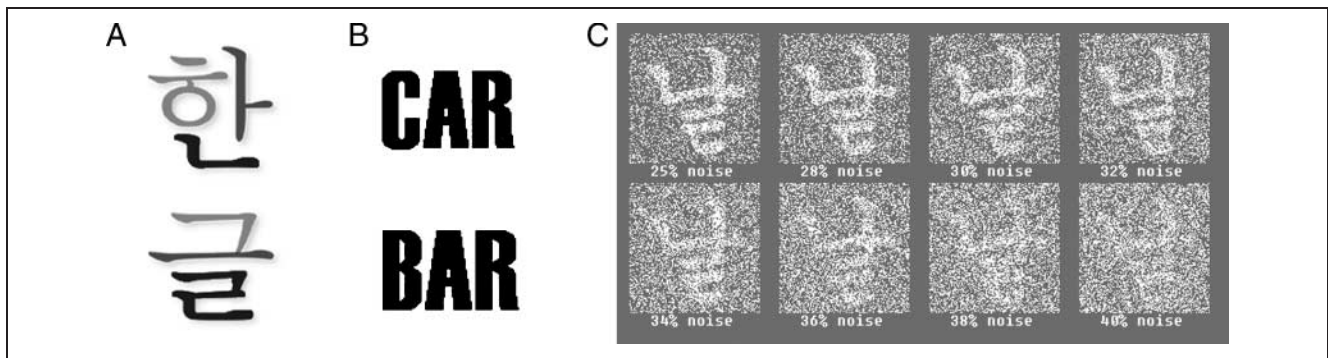


Figure 1. Example of the stimuli. (A) Korean characters. The top and bottom show an example character with left–right–bottom, and top–middle–bottom structure, respectively. The letters of the character are marked with different colors. (B) English words. All English words consisted of three letters. Capital letters and bold font were chosen to increase the difficulty of recognition. (C) Korean characters presented in varying amounts of visual noise; labels on each character indicate the percentage of noise.

bottom and top–middle–bottom (see Figure 1A, for an example). To control task difficulty in the visual discrimination task to be detailed later, special attention was paid in constructing the word pairs. First, these characters were organized into 600 pairs in which the two characters shared the same spatial layout and visual complexity but differed from each other by only one letter. Second, those 600 pairs were then divided into 20 matched groups that were assigned to each training and test condition and counterbalanced across subjects. Finally, to create equal number of “same” trial and “different” trial, we randomly chose one third of the pairs, broke them up to form the “same” trials. As a result, each group of stimuli (60 characters, 30 pair) produced 40 test pairs (i.e., 20 “same” and 20 “different”). Another 240 three-letter English words were used as control in fMRI scan (Figure 1B). Following a similar procedure, they were divided into four matched groups of 30 pairs, in which the two words only differed by one letter. We used the uppercase letters and a bold font for the English words. Pilot data indicated that this resulted in comparable performance on Korean and English.

The experiment was created in Matlab (Mathworks, Sherborn, MA) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Each stimulus was framed in a 113×113 -pixel window, drawn in white against a gray background. Random visual noise was added to the picture to manipulate the task difficulty (Figure 1C). The percentage of noise for English words was 28% for all the tasks, whereas that for Korean characters varied from 28% to 38% across conditions. To create the noise, we randomly chose a given percentage of pixels in the picture and reversed their color (white to gray or vice versa). The pattern of the visual noise was different for each presentation of each stimulus.

Behavioral Training and Test

Subjects participated in five training sessions. The basic paradigm throughout the training was a same–different

judgment task. At the beginning of each trial, there was a 400-msec fixation point followed by 200-msec blank screen. Two characters then flashed subsequently (100-msec duration with 200-msec interval). Subjects were asked to judge whether the two characters were identical or not with a key press. The next trial started 1 sec after the subjects making a response. Two groups of stimuli (120 characters in total) were trained every session (i.e., old items). One group of new stimuli (i.e., new items) was added in each training session to allow separation of repetition priming and skill learning (Poldrack, Selco, et al., 1999).

At the beginning of each training session, subjects took a parameter setup test to find the desirable task difficulty level. New items with four different noise levels (40 trials each) were mixed. Based on subject’s performance, a noise level that corresponded to accuracy closest to 70% was chosen. Subjects then finished 4 blocks of 280 trials (80 old trials repeated 3 times, plus 40 new trials) with the chosen noise level. There was a 2-min break between each block.

Upon finishing all the training, a recognition task was administered to examine subjects’ explicit memory of these old items. Sixty old items and 60 new items were randomly mixed, and subjects were to decide whether the character on the screen was new or old by pressing the button. Each trial began with a fixation of 400 msec, followed by 200-msec blank screen. The character then appeared and remained on the screen until subject indicated a key press. If no responses were made in 1900 msec, the character also disappeared. In either case, the next trial would start after a 1-sec interval.

fMRI Task

Each subject participated two fMRI scan sessions, one before training and one after training, separated by 6 to 8 days. Two scanning runs were included in both pre-training and posttraining sessions: one with matched parameters and one with parameters adjusted to match

performance. The noise level for the parameter-matched scan was 28% for pretraining and posttraining scans, as well as for the pretraining performance-matched scan. For the posttraining performance-matched scan, the noise level was set to match subjects' performance in pretraining scan, using a parameter setup procedure similar to that used in the training sessions. This task was administered in the scanner during an anatomical scan.

In each scan, there were 40 trials of old characters and 40 trials of new characters (they were all new at the pretraining scan). To examine the STRP effect, they were repeated once within five trials after its first presentation. In addition, there were 40 trials of English words. The same-different task described above was used in the fMRI scans. To improve the design efficiency, null events of random duration were imposed between every trial. The duration of null time was sampled from an exponential distribution with mean of 1 sec (range = 0.2-6 sec). A large number of sequences were generated within these constraints, and the sequences with the highest efficiency to detect the desired differences were selected (Dale, 1999). In total, each scan included 200 trials and lasted 9 min 36 sec.

MRI Data Acquisition

Imaging data collection was performed using a 3-T Siemens (Iselin, NJ) Allegra MRI scanner at the UCLA Ahmanson-Lovelace Brain Mapping Center. Blood oxygenation level-dependent-sensitive functional images were collected using a T2*-weighted echo-planar plus sequence (repetition time [TR] = 2 sec, echo time [TE] = 30 msec, flip angle = 90°, matrix = 64 × 64, field of view = 200, 33 slices, 4-mm slice thickness). Additionally, a T2-weighted matched-bandwidth high-resolution anatomical scan (same slice prescription as echo-planar imaging) and Magnetization Prepared Rapid Gradient Echo (MP-RAGE) were acquired for each subject to aid registration. The parameters for MP-RAGE were the following: TR = 2.3, TE = 2.1, matrix = 192 × 192, field of view = 256, sagittal plane, 160 slices, 1-mm thickness.

Data Analysis

Image preprocessing and statistical analyses were performed with Statistical Parametric Mapping (SPM2; Wellcome Department of Cognitive Neurology, London, UK), which is implemented in Matlab. The first two images in each time series were excluded from analysis to allow T1 equilibration. Functional images were realigned, unwarped (Andersson, Hutton, Ashburner, Turner, & Friston, 2001), normalized using a combination of linear and nonlinear basis functions to the Montreal Neurological Institute 305 (MNI305) template (Friston et al., 1995), and smoothed with an 8-mm full width half maximum Gaussian filter. A two-level statistical analysis approach was used. The general linear model was first

used to estimate condition effects in each individual participant (Friston et al., 1994) after convolving the reference functions with a canonical hemodynamic response. Statistical parametric maps were computed for each contrast of interest, and the contrast effect maps from these analyses were entered into a second-level model, which treats subjects as a random effect. Unless otherwise noted, clusters of at least 10 contiguous voxels that exceeded an uncorrected threshold of $p < .001$ were considered significant for the exploratory analysis. Further analyses focused on regions of interest (ROIs) in the fusiform/inferior temporal region and IFC, based on previous results.

ROI Selection and Quantification

Based on a previous study (Xue et al., 2006), the center of the fusiform ROI was defined as -39 , -60 , and -18 (x , y , and z , respectively, in MNI coordinates). This is near the VWFA region defined by Cohen et al. (2002): -42 , -57 , and -15 . Following James et al. (2005), we split the fusiform region into three smaller equal sized regions, namely, the anterior fusiform region (MNI center: -39 , -48 , and -18), middle fusiform region (MNI center: -39 , -60 , and -18), and posterior fusiform region (MNI center: -39 , -72 , and -18). A lateral region in the inferior temporal gyrus (ITG) (MNI center: -51 , -48 , and -18) was also selected based on the result of the pretraining Korean versus English comparison. The right homologue of these regions was also defined.

In the left IFC, analysis using small volume correction (SVC) with a search volume based on the automated anatomical labeling atlas (Tzourio-Mazoyer et al., 2002) identified two foci, one in the pars opercularis (MNI center: -45 , 15 , and 36), and one in pars triangularis (MNI center: -45 , 33 , and 18). All voxels within 6-mm radius of the above coordinates were defined as ROI using Marsbar (Brett, Anton, Valabregue, & Poline, 2002). The mean effect size for each subject and each condition was calculated and entered into SPSS (Chicago, IL) for further statistical analysis.

For both the behavioral and ROI results, unless otherwise noted, we used within-subject repeated measure analysis of variance (ANOVA), and within-subject standard error (*SE*) was reported (Loftus & Masson, 1994).

RESULTS

Behavioral Results

Behavioral data indicated that training significantly increased subjects' performance. First, in the parameter setup test, subjects' performance with the same noise level improved across session. For the two noise levels (i.e., 32% and 34%) that were tested in each of the five sessions, accuracy improved from 65.9% to 80% [$F(4,40) = 3.57$, $p = .014$] and from 54.5% to 74.1% [$F(4,40) = 5.77$,

$p = .001$], respectively (Figure 2A). As a result, the averaged noise level used for training increased from 29.8% to 36% [$F(4,40) = 96.39, p < .001$] (Figure 2B). Second, in the parameter-matched fMRI scan, there was significant training effect [$F(1,10) = 27.77, p < .001$] (Figure 3A). Because there was no effect of material (old vs. new) or STRP ($F < 1$ in both case), we merged these conditions and performed a stimuli (Korean vs. English) by training ANOVA. This analysis revealed significant Stimuli \times Training interaction [$F(1,10) = 5.95, p = .035$]. Further analysis indicated that there was no significant difference between Korean and English at the pretraining scan [$t(10) = .21, p = .835$], but the difference emerged after training [$t(10) = 2.87, p = .017$], suggesting the training effect is specific to the Korean characters (Figure 3B). Finally, in the performance-matched scans, the noise level was significantly higher in the posttraining scan than in the pretraining scan (34.4% vs. 28%), although the performance was constant [i.e., no training effect, $F(1,10) = 2.86, p = .122$] (Figure 3C). The behavioral data in performance-match scan indicated that our manipulation of task difficulty was effective, allowing examination of the neural changes associated with training without the confound of task difficulty.

Subjects had no explicit memory of the trained characters. The overall correct discrimination was 47.5% ($SD = 0.06$), which is not significantly greater from chance ($p = .326$, one-tailed test).

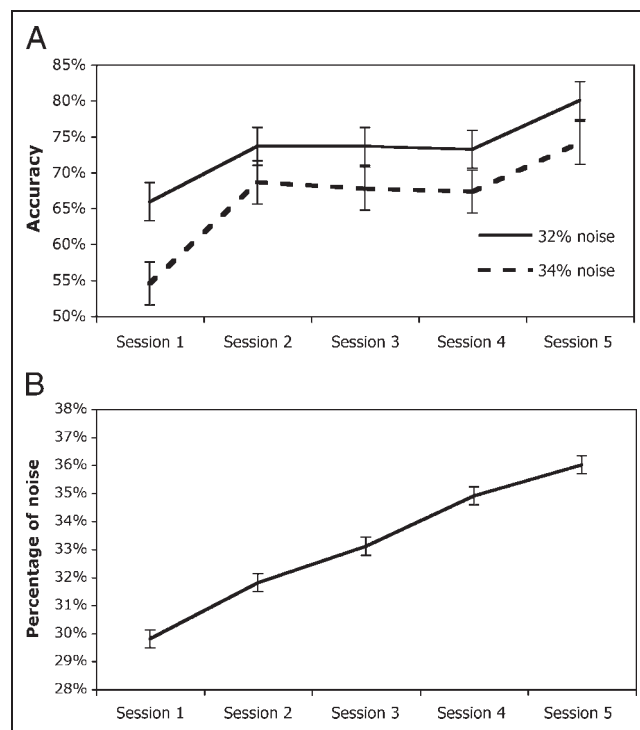


Figure 2. Behavioral performance during training. (A) Accuracy in the parameter setup test is plotted as a function of training session, separated by noise level. (B) Averaged percentage noise used in each training session. Error bar reflects within-subject *SE*.

Imaging Results

Pretraining Korean–English Comparison

To examine the neural differences between Korean and English processing, we compared the activation for the first presentation of Korean characters (old and new) and that for English in the pretraining parameter-matched scan. As shown in Table 1, this whole-brain comparison indicated that processing of Korean elicited stronger activation in the left lingual gyrus, right calcarine, and right postcentral gyrus. On the contrary, English elicited stronger activation than Korean in the left ITG area (Brodmann's area 37: $-51, -48, -18$), which is more anterior and lateral to the VWFA identified by Cohen et al. (2002). Significant more activation for English was also found in the left inferior parietal lobule and left middle temporal gyrus.

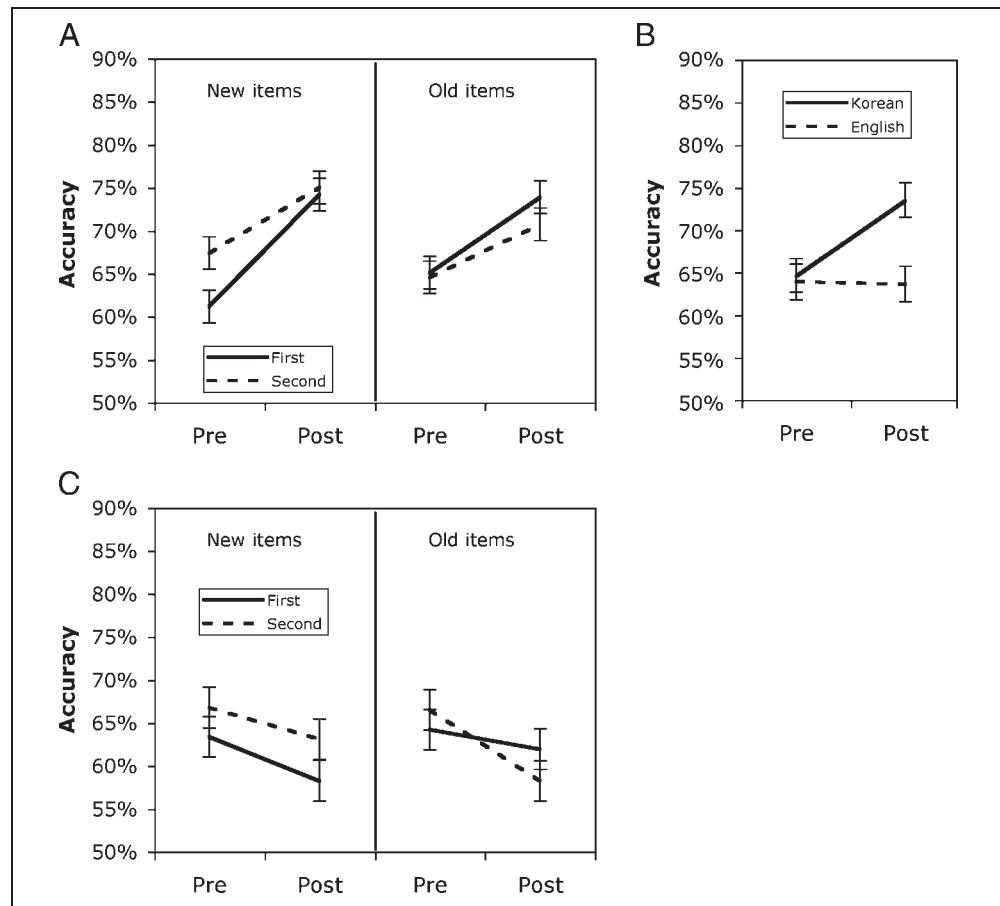
We quantified and compared the activation in the fusiform and adjacent ITG ROIs, and the results are shown in Figure 4. It is clear that the strongest activation was in the bilateral middle fusiform regions for both Korean and English, consistent with our previous study (Xue et al., 2006). One-way ANOVA revealed that the difference was statistically significant in the left ITG [$F(1,10) = 20.09, p < .001$] and marginally significant in the left anterior fusiform region [$F(1,10) = 4.20, p = .065$]. But it was not significant in the left middle [$F(1,10) = 2.84, p = .123$] and posterior fusiform area [$F(1,10) = .69, p = .426$]. The dissociation in the lateral/anterior ROIs and middle/posterior ROIs were confirmed with significant ROI \times Task interaction [$F(3,8) = 8.34, p = .008$]. In the right hemisphere, English elicited stronger activation in the ITG cortex [$F(1,10) = 4.98, p = .05$]. The differences in other regions were not significant ($p > .28$). However, no Task \times ROI interaction was found in right hemisphere ($F < 1$).

In the frontal lobe, SVC revealed that English elicited stronger activation in the left pars opercularis and pars triangularis regions. Further ROI analysis confirmed this result [pars opercularis: $F(1,10) = 8.00, p = .018$; pars triangularis: $F(1,10) = 6.88, p = .026$] (Figure 5).

Training Effect: Whole-brain Analysis

Neural changes with training under parameter- and performance-matched condition are shown on Figure 6 and the foci are listed in Tables 2 and 3, respectively. These data were obtained by merging across old and new items as well as first and second presentations. At the standard threshold, significant decreases were found for parameter-matched condition in the fronto-parietal network, possibly because of the decreased task difficulty as indicated by the behavioral improvement. The left insula showed significant increase. For performance-matched condition, significant increases were found in the calcarine, cuneus, and lingual gyrus, whereas the left putamen and cingulate cortex showed significant

Figure 3. Behavioral performance during fMRI scans. (A) Accuracy for Korean characters in the parameter-matched scans. (B) Mean accuracy for English and Korean characters (merged across old and new as well as first and second presentation). (C) Accuracy for Korean characters in performance-matched scans. Pre = pretraining; Post = posttraining; First = first presentation; Second = second presentation. Error bar reflects within-subject *SE*.



decreased activation. At a slightly reduced threshold (i.e., $p < .005$, cluster size > 10), the superior frontal lobe and left anterior inferior temporal lobe extending to temporal pole showed significant increased for both conditions, and the left lingual also showed increase in the parameter-matched condition. Based on our previ-

ous study (Xue et al., 2006), SVC over the anatomical region of the occipital and fusiform gyrus were applied. This revealed significant decrease for both conditions in the bilateral fusiform cortex and left inferior occipital gyrus. The left frontal lobe showed no increase using SVC, suggesting the pretraining difference is not because of visual expertise but might more likely reflect phonology and/or semantic processing.

Table 1. Foci of Difference between English and Korean at the Pretraining Scan

Regions	<i>x</i>	<i>y</i>	<i>z</i>	Z Value
<i>English > Korean</i>				
Left inferior frontal pars triangularis ^a	-45	33	18	2.75
Left inferior frontal pars opercularis ^a	-45	15	36	2.92
Left inferior parietal lobule	-45	-48	39	3.59
Left middle temporal gyrus	-57	-33	0	3.84
Left ITG	-51	-48	-18	3.49
<i>Korean > English</i>				
Right postcentral gyrus	45	-12	60	4.23
Right calcarine	6	-84	18	3.83
Left lingual gyrus	-18	-69	3	4.90

^aSVC over the search volume of left inferior frontal cortex.

Training Effect: ROI Results

Focusing on each ROI in the fusiform and adjacent ITG area, we performed a four-way repeated measures ANOVA, including training (pretraining vs. posttraining), material (old vs. new), matching condition (parameter vs. performance), and STRP (first vs. second presentation) as within-subject factors. The result is shown in Figure 7.

We found three regions that showed significant training effects: left middle fusiform region [$F(1,10) = 5.18$, $p = .046$], left posterior fusiform region [$F(1,10) = 7.30$, $p = .022$], and right middle fusiform region [$F(1,10) = 7.62$, $p = .02$]. Training effects in the right anterior fusiform region [$F(1,10) = 3.36$, $p = .097$] and right posterior fusiform region [$F(1,10) = 3.20$, $p = .104$] were marginally significant.

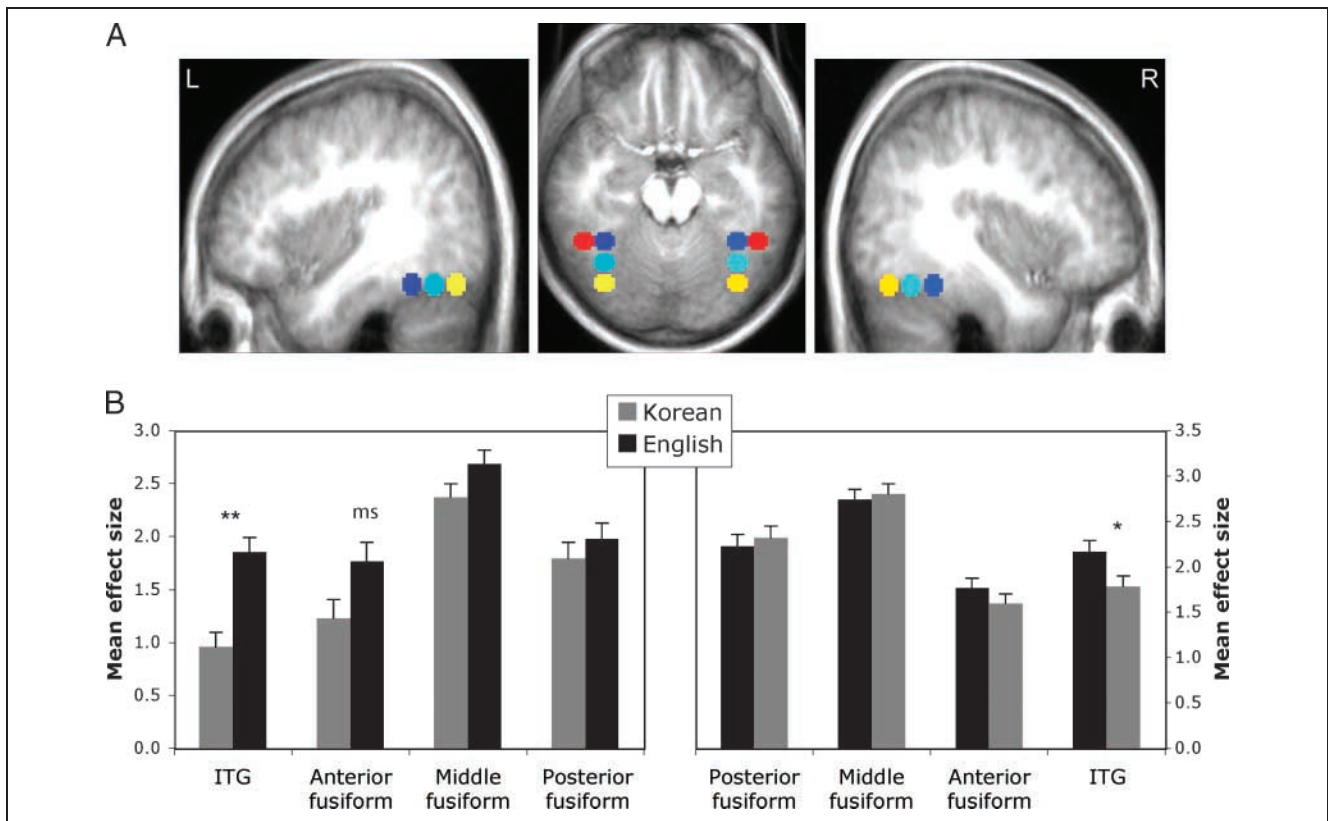


Figure 4. Pretraining Korean–English comparison in the occipito-temporal region. (A) Location and shape of the ROIs. The ROIs were overlaid on the structural anatomy averaged across all 11 subjects. (Middle) Axial view of the ROIs. (Left and Right) sagittal view of the fusiform ROIs in left and right hemispheres, respectively. (B) Mean effect size in each ROI as a function of language. (Left and right) Results in the left and right ROIs, respectively. Error bar reflects within-subject SE. * $p < .05$, ** $p < .01$; ms = marginally significant.

The effect of task difficulty in training was examined via the interaction between training and matching condition (parameter vs. performance match). That is, if task difficulty contributed to the training effect, we should expect no differences between parameter- and performance-matched conditions during the pretraining scan (because the noise levels were identical) and significant differences during the posttraining scan. It turned out that no region showed this interaction, suggesting that the observed decreases in bilateral middle fusiform and left posterior fusiform were not because of decreased task difficulty.

Similarly, the differences between old and new items were examined via the interaction between training and material, because both new and old items were new to subjects at the pretraining stage. We found no region with a significant Training \times Material interaction, suggesting that the training effect on old items transferred completely to new items.

We also examined the STRP effect. Two regions that showed significant or marginally significant STRP effect were the right middle fusiform region [$F(1,10) = 12.62$, $p = .005$] and the right posterior fusiform region [$F(1,10) = 4.57$, $p = .058$]. The right anterior fusiform region showed marginally significant Training \times STRP interaction [$F(1,10) = 4.82$, $p = .052$]. Further analysis

indicated that STRP only appeared in the posttraining scans [$F(1,10) = 10.90$, $p = .008$]. These results indicated that the neural change in these regions could occur as fast as one repetition, although the absolute neural change was not as strong as that of long-term training (averaged activation in the first/second presentation were 2.24/2.10 in the right middle fusiform region, 1.99/1.84 in the right posterior fusiform region, and 1.28/1.17 in the right anterior fusiform region during the posttraining scans). The STRP effect is not shown in Figure 6, because we merged the activation for the first and second presentations to make the figure less complex and more readable.

DISCUSSION

We examined the neural substrates for processing (English) words and foreign writings (i.e., Korean Hangul) and how neural processing of these stimuli changed with psychophysical training. At the pretraining scan, both words and foreign characters strongly activated the VWFA, and their difference was not significant, although stronger activation for words than for foreign writings was revealed in the left ITG and left IFC. Visual word form training with foreign writings caused significant

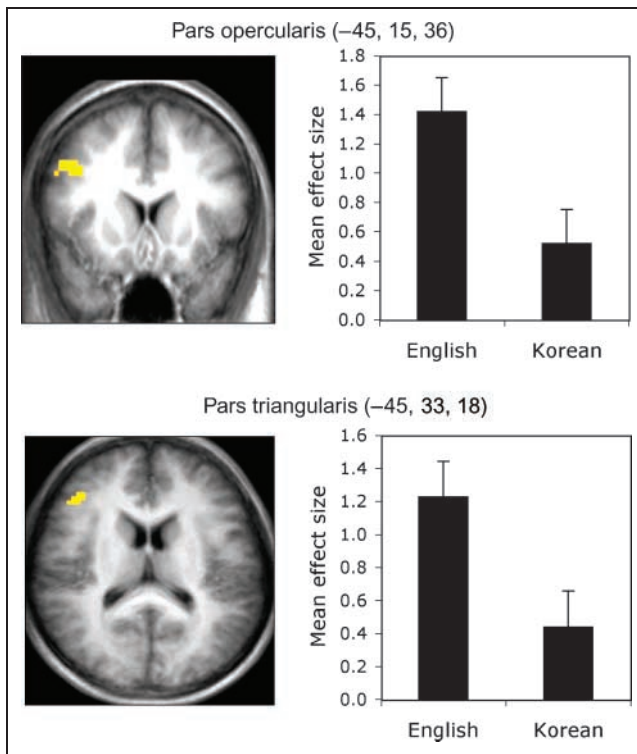


Figure 5. Pretraining Korean–English difference in the left inferior frontal lobe. Activation was overlaid on the structural anatomy averaged across all 11 subjects. Error bar reflects within-subject *SE*.

decreases in the fusiform cortex. These results provide convergent evidence to our previous study (Xue et al., 2006) but do not support the VWFA hypothesis (Cohen & Dehaene, 2004; McCandliss et al., 2003; Cohen et al., 2002).

Neural Specificity/Sensitivity of the VWFA

The results of the present study seem difficult to reconcile with the VWFA hypothesis. First, in the middle fusiform area (the VWFA), both Korean and English showed very strong activation, and the difference between two languages was not significant. This result corroborates existing studies comparing native words with foreign writing (Xue et al., 2006; Callan, Callan, & Masaki, 2005; Kuo et al., 2004; Tagamets et al., 2000), suggesting that the VWFA is not specific to the processing of words. Rather, this region might be involved in shape processing of all sorts of visual stimuli (words, objects, and false fonts) (Ben-Shachar et al., 2007). Still, although some studies have reveal stronger activation for words in this region, this might reflect a modulation of phonology and semantic (Xue et al., 2006). This will be further discussed below.

Second, the left ITG and anterior fusiform cortex, which showed stronger activation for word, might be related to lexical processing and not specific to visual word processing. These regions are more anterior and lateral than the VWFA identified by Cohen et al. (2002) and are closer to the multimodal area than to the unimodal area (Cohen, Jobert, et al., 2004). It is been proposed there is a posterior-to-anterior progression between regions involved in processing visuo-perceptual and lexical/semantic information (Simons et al., 2003). The lateral ITG region has recently been suggested to be involved in connecting orthography and phonology (Hashimoto & Sakai, 2004), and several studies have argued that the (anterior) fusiform is involved in lexical processing (Hillis et al., 2005; Kronbichler et al., 2004) or in integrating visual form, phonology, and semantic information (Devlin et al., 2006; McCrory et al., 2005; Price &

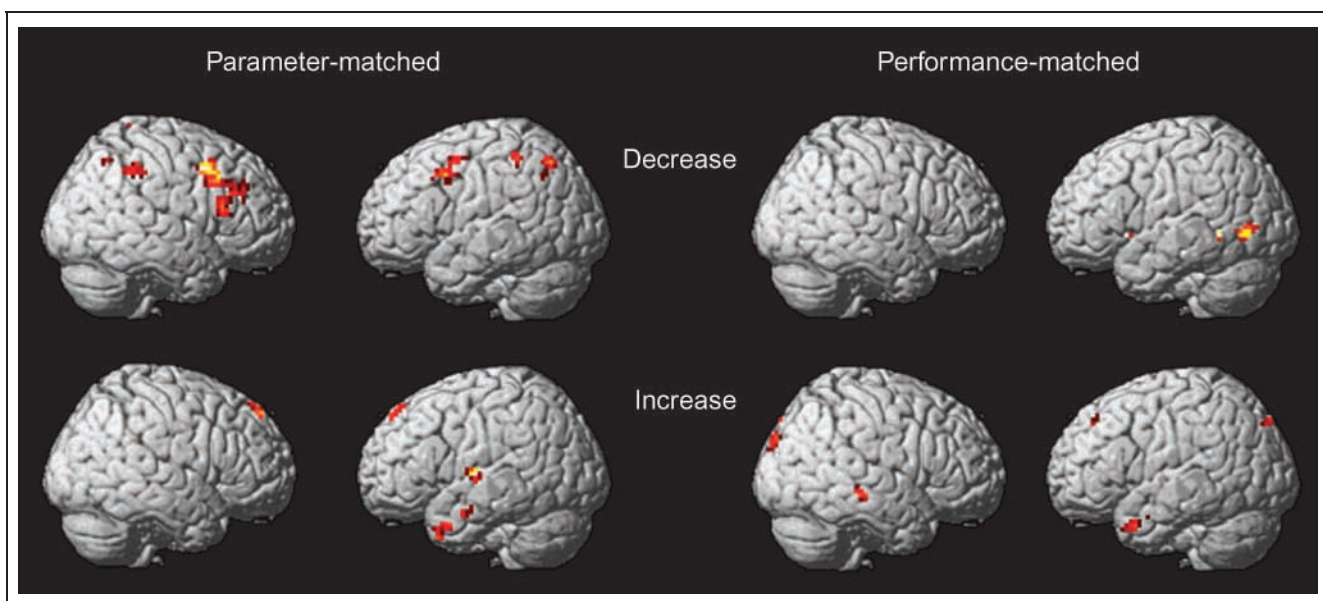


Figure 6. Whole-brain result of the training effects. Training-induced changes thresholded at $p < .005$ and cluster size > 10 were merged across the old and new items as well as first and second presentations. They were rendered on the 3-D brain template from SPM.

Table 2. Training-induced Neural Changes in Parameter-matched Scan

<i>Regions</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z Value</i>
<i>Parameter-matched: increase</i>				
Left insula	-27	30	9	3.91
Superior medial frontal gyrus*	3	45	48	3.42
Left anterior ITG*	-39	6	-33	3.62
Left lingual gyrus*	-24	-51	0	3.28
<i>Parameter-matched: decrease</i>				
Left precentral gyrus	-48	12	45	4.05
Left middle frontal gyrus	-30	0	51	3.89
Right inferior frontal gyrus	51	21	15	4.15
Right middle frontal gyrus	42	18	39	3.74
Precuneus	-12	-60	51	4.18
	0	-45	54	3.75
Left fusiform ^a	-39	-66	-15	2.82
Right fusiform ^a	36	-57	-18	3.02
Left inferior occipital gyrus ^a	-51	-72	-3	3.34

*Significant at $p < .005$ and cluster size > 10 .

^aSVC.

Friston, 2005). Existing studies show that both objects naming/recognition and words processing activate this region (Moore & Price, 1999; Price et al., 2006; also see Price & Devlin, 2003, for a review). This idea is not inconsistent with the patient study mentioned above, which showed the posterior fusiform may not be involved in semantic and phonological processing (Gaillard et al., 2006).

Furthermore, along with the difference in the inferior temporal cortex and anterior fusiform region, there were differences in the left IFC. A tight coupling of frontal and fusiform activation has been identified by numerous studies. For example, many studies have revealed stronger activation in the left inferior frontal lobe and midfusiform area for pseudowords than for words (see Mechelli, Gorno-Tempini, & Price, 2003, for a review). Repetition priming usually elicits significant neural decrease in both frontal lobe and fusiform cortex (Buckner, Koutstaal, Schacter, & Rosen, 2000; Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000; Buckner et al., 1998). Neural suppression in the fusiform cortex and frontal lobe has also been found when the priming stimuli and target share no visual similarity, such as priming cross letter case (Dehaene et al., 2001), script (Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2005), and language (Chee, Soon, & Lee, 2003). Our previous study found that phonological training elicited increased activation in both regions (Xue et al., 2006). These studies are consistent

with the view that semantic and/or phonological processing may involve top-down modulation of occipital and temporal cortices. As a direct evidence of this top-down modulation, it has been shown that repetition-induced neural suppression in the fusiform cortex is eliminated by transcranial magnetic stimulation that disrupted the activity in the left frontal cortex during repeated classification of objects (Wig, Grafton, Demos, & Kelley, 2005).

Finally, whereas comparisons between visual word and other object categories argue against the specificity hypothesis, results from visual word form training provide evidence against the visual expertise hypothesis. The present study replicates and extends previous results on Chinese readers (Xue et al., 2006). We found that training significantly decreased the activation in the bilateral middle fusiform cortex and left posterior fusiform cortex. Similar to the long-term training effect, STRP also caused significant decrease in the right middle and posterior fusiform cortex and in the right anterior fusiform cortex during the posttraining scan. We have argued that because of the tight connection among visual form, phonology and semantic, visual word form training provides the most direct evidence to test the visual expertise hypothesis (Xue et al., 2006). The two studies using this paradigm obtained convergent evidence to against this hypothesis. Consistent with our findings, decreased activation in the fusiform has also been found in perceptual

Table 3. Training-induced Neural Changes in Performance-matched Scan

<i>Regions</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z Value</i>
<i>Performance-matched: increase</i>				
Left superior medial frontal gyrus*	-12	36	42	2.94
Left middle temporal pole*	-39	9	-30	4.03
Right lingual gyrus	15	-36	-6	4.22
Calcarine	0	-75	15	4.86
Cuneus	3	-90	21	4.77
<i>Performance-matched: decrease</i>				
Anterior cingulate	-6	27	27	4.11
Left posterior middle temporal gyrus*	-36	-60	12	3.68
Left inferior occipital gyrus ^a	-51	-69	-3	3.23
Left fusiform ^a	-39	-66	-15	2.73
Right fusiform ^a	36	-66	-15	2.55
Left putamen	-27	15	0	4.57
Left pallidum/thalamus*	-24	-12	6	3.65
Left cerebellum*	-21	-63	-33	3.35

*Significant at $p < .005$ and cluster size > 10 .

^aSVC.

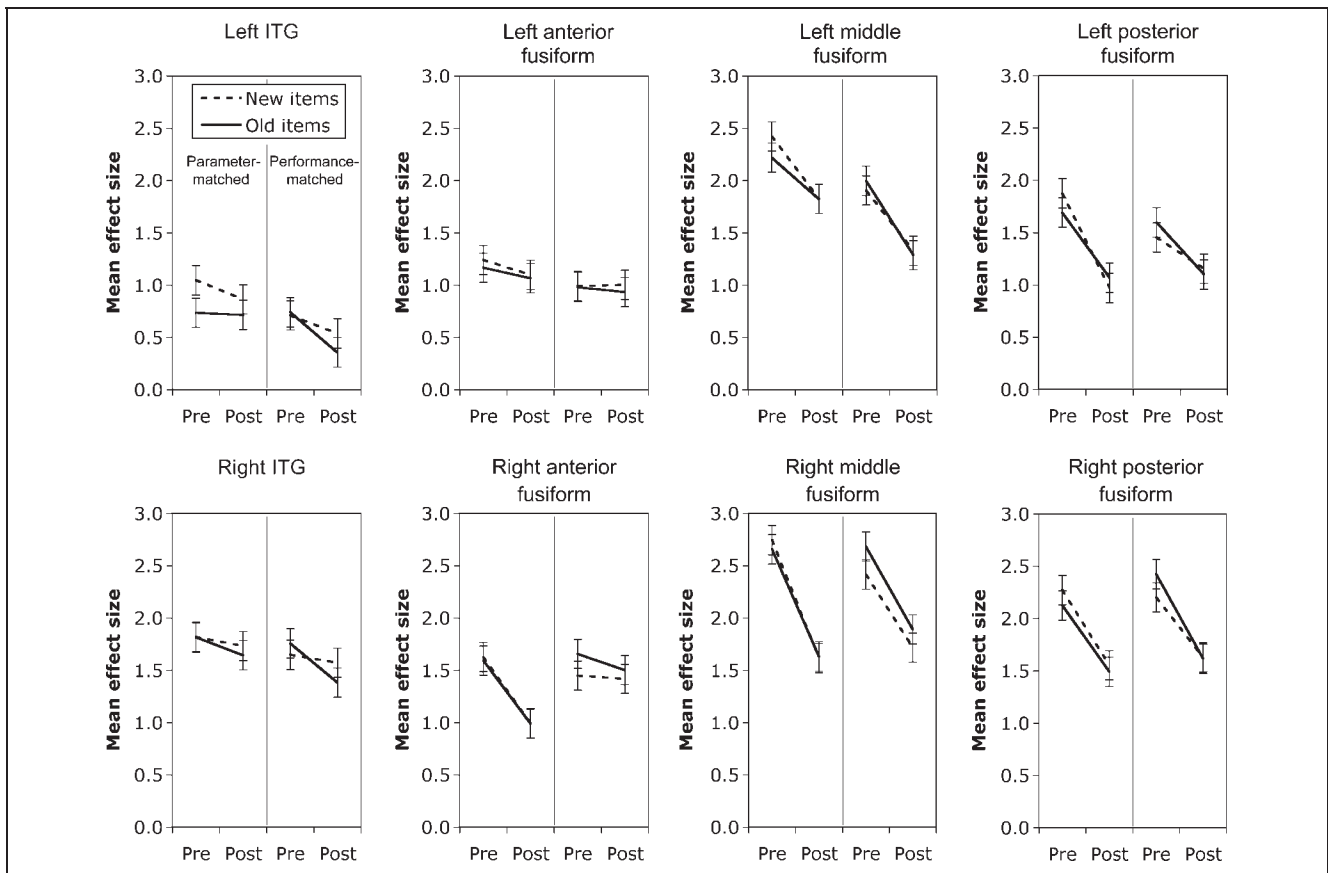


Figure 7. Training effects in the fusiform region. The mean effect size in each ROI is merged across the first and second presentations and plotted as function of training (pretraining vs. posttraining), matching condition (parameter-matched vs. performance-matched), and material (old vs. new). Error bar reflects within-subject *SE*.

learning of visual discrimination (Schiltz, Bodart, Michel, & Crommelinck, 2001; Schiltz et al., 1999).

In the present study, we carefully matched the performance between foreign and native task to reduce its effect on neural activity, which has been a major confounding factor in many previous studies. This was accomplished by making the English letters more compact and similar and thus harder to discriminate, whereas it is relatively easier to discriminate the letters in the Korean characters. The absence of performance difference, however, does not imply that this task did not tap into visual expertise. Theoretically, to correctly perform this task, subjects need to first recognize visual words/characters under noisy display conditions, which relies more on the internal template, one important aspect of visual expertise, than recognition under clear display conditions. Second, training significantly improved subjects' visual expertise and performance in the task. Imaging data indicate that this task significantly activated the fusiform cortex, and training with this task elicited significant decrease in this region.

Still, our training results cannot be attributed to change of task difficulty or performance. To overcome the confounds by overall performance level, previous studies either chose stimulus intensity that yield performance levels close to chance (e.g., 53-58% correct) (Schwartz,

Maquet, & Frith, 2002) or close to ceiling (e.g., 93-98% correct) (Schiltz et al., 1999; also see Petrov, Doshier, & Lu, 2005, for a review). In the present study, by manipulating the noise level, we were able to match the task difficulty across scans while still keeping performance in a range away from either floor or ceiling (60-76% correct). We found that the neural decreases were evident when both parameter and performance were matched and there was no interaction between training and matching condition.

Mechanisms of Visual Word Form Training

In the present study, we found that for both old and new items, training significantly improved performance and decreased neural activity in the fusiform region. More interestingly, the present study did not reveal any behavioral or neural differences between old and new items, suggesting there was no long-term item-specific learning. In other words, training on old items was readily transferred to new items. This could provide some hints on the underlying mechanisms of visual word form training.

Because the old and new items share the same letters, our result suggests that visual word form learning might occur at the subcharacter (e.g., letter) level. That is, subjects may have changed their perceptual template by

learning specific components of the Korean characters. This pattern might reflect the distinct nature of visual word form learning. As we all know, the countless words in one language are usually composed of many fewer basic writing units (e.g., letters). To learn to recognize the visual form words, the more efficient way is first to learn the basic letters. Moreover, because similar words (e.g., only differing by one letter) are abundant in a given language, subjects have to identify every letter to correctly recognize each word. This could prevent the visual system from forming higher perceptual units. As a result, there is cumulative evidence indicating that whole-word recognition might not be possible under certain situation. In alphabetic scripts, it has been shown that even very fluent readers cannot recognize words beyond the level of individual letters (i.e., holistic recognition) (Pelli, Farell, & Moore, 2003). Comparable to letters in alphabetic scripts, the basic functioning unit for Chinese characters is strokes pattern, which is defined as the group of strokes functioning dependently as the basic orthographic component in different characters (Chen, Allport, & Marshall, 1996). Studies have suggested that the basic perceptual unit of Chinese is strokes pattern, rather than whole character or single stroke (Chen et al., 1996; Xue, unpublished dissertation).

The absence of item-specific learning may also reflect the nature of our specific training paradigm. First, we trained subjects with character pairs that only differed by one letter. In the Korean Hangul language, it is very common to generate a number of different characters by changing just one letter. Moreover, in the present study, the old items only had been trained 12 times in each session (60 times in total). Third, during training, all stimuli were present very briefly and under very noisy conditions. Finally, to perform the same-different judgment task, subjects had to direct their attention to the consisting letters to point out the subtle differences between two characters. All these factors would make it extremely difficult, if not impossible, to form perceptual template beyond single letters. These differences in experimental tasks and training methods might account for the discrepancies with previous studies, which show that supraletter orthographic information is acquired in normal reading development (Cunningham, Perry, Stanovich, & Share, 2002) and plays important role in normal reading (Coltheart, 2004). Further studies need to examine how the design principles of the particular language and specific training method affect the formation of item-specific learning.

Existing studies suggest different perceptual learning mechanisms under clear and noisy display (Doshier & Lu, 2005). For noisy displays, practice improves performance by learned external noise filtering, that is, the retuning of the perceptual template (Lu & Doshier, 2004), whereas for clear displays, performance can be improved by improved amplification or enhancement of the stimulus through the reduction of internal noise. In high-noise

displays, amplification of stimulus would amplify signal and external noise as well, and the reduction of internal noise would similarly be of no benefit. This model could well explain the results in the present study and our previous study. In a previous study (Xue et al., 2006), subjects were trained in clear displays, and performance is improved by reduction of internal noise. Thus, training is partially transferred to Chinese task. Under the noisy display in the present study, however, internal noise or efficiency cannot be trained, resulting in an absence of transfer to English task. On the contrary, performance for Korean character is improved by retuning of perceptual template, in our case, the Korean Hangul letters. Consistent with our result, a previous study of perceptual learning of Roman letter identification under noisy conditions also found improvement in perceptual template but not in internal noise (Chung, Levi, & Tjan, 2005).

Conclusion

We have shown that foreign writing and words equally engage the VWFA, and visual word form training reduced VWFA activation. These results replicate our previous findings and suggest that the VWFA is neither specific to words nor sensitized by visual expertise with specific writing systems. Ample evidence has suggested that reading is supported by a distributed and interconnected neural network (Fiez & Petersen, 1998). Given these facts, our results hint that a better understanding of the nature of the VWFA could be achieved both by interpreting the findings in the whole language network and by breaking down these connections in artificial language learning situation.

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Notes

1. "Foreign writing" in this article is used to refer to an actual writing system (e.g., Korean Hangul) that subjects are not able to read. Thus, "Korean" here means a foreign writing but not a second language. It may be functionally similar to "false fonts," but the latter does not share the same degree of systematicity in their visual features as an actual writing system.
2. Hangul script consists of 24 letters (10 vowels and 14 consonants), which represent the phonemes of the language. These letters are combined into a compact square-framed syllable blocks, visually similar to Chinese. The blocks are, thus, called "characters."

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