The Role of the Left Fusiform Gyrus in Reading:
An Examination of Chinese Character Recognition
by
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ABSTRACT

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The left fusiform gyrus is hypothesized to be selectively involved in visual word processing. Nevertheless, the particular components of reading to which this area responds is the subject of much controversy. In Experiment 1, activity in the left fusiform gyrus was measured using functional magnetic resonance imaging (fMRI) while subjects performed a phonological task with regular and irregular Chinese characters. Results exhibited greater activity for irregular than regular characters in the left fusiform gyrus, suggesting that this region is involved in the direct route of the dual-route model. In Experiment 2, activity was measured using fMRI while subjects performed phonological, semantic, and orthographic tasks with irregular Chinese characters. The left fusiform gyrus exhibited greater activity during the orthographic task than during the phonological and semantic tasks, which did not differ, suggesting that this region is involved in orthographic processing to a greater extent than phonological or semantic access.
Chinese Character Recognition

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Visual word reading can be independent from other modality language processes, such as oral comprehension and production. In addition, the visual word form processing in word recognition is not a simple perceptual process, but rather involves accessing an abstract representation, which allows one to recognize words quickly regardless of their size, font, or location (Mayall, Humphreys, & Olson, 1997; Paap, Newsome, & Noel, 1984). Thus, some cognitive models of reading have proposed a “visual word form system” for the visual form representation of words (Coltheart, 1987; Marshall & Newcombe, 1973; Patterson & Shewell, 1987).

One of the strongest pieces of evidence for the existence of a unique visual word form system comes from neuropsychology, in the form of a deficit known as pure alexia. Pure alexia is characterized by severe reading impairments following left occipito-temporal lesions in literate adults. Patients with pure alexia typically show intact production and comprehension of oral speech, as well as preserved writing skills, but they show a dramatic impairment in visual word reading (Benson & Geshwind, 1969; Beversdorf, Ratcliffe, Rhodes, & Reeves, 1997). Moreover, pure alexia affects word processing but not processing of other types of visual stimuli. For example, patients with pure alexia do not have difficulties with letter naming or color and picture processing (Warrington & Shallice, 1980). Based on findings such as this, Cohen et al. (2002) and Warrington and Shallice (1980) have suggested that the reading impairment in pure alexia results from damage to a visual word form system, rather than from a general perceptual disability. Moreover, they located this visual word area in the left fusiform gyrus, centered on
posterior occipito-temporal sulcus, which is the area most often damaged in pure alexia (Cohen et al., 2002; Cohen & Dehaene, 2004).

More recently, neuroimaging studies with healthy subjects have produced effects that are consistent with this hypothesis. For one, neuroimaging evidence suggests that the left fusiform is involved in visual word reading but not in auditory word perception (Dehaene, Le Clec'H, Poline, & Cohen, 2002; Booth et al., 2002). In addition, neuroimaging evidence suggests that this area is insensitive to changes in perceptual features, such as font, size, or case (Cohen et al., 2000; Dehaene et al., 2001). Finally, this area exhibits greater activity for words and pronounceable pseudowords than for random letter strings, even when the visual complexity for these types of stimuli is matched (Cohen et al., 2002; Price et al., 1994; Price, Wise, & Frackowiak, 1996), indicating that this area is involved in word-specific processing rather than individual letter processing. Thus, converging evidence supports a “visual word form system” in reading and suggests that the left fusiform gyrus plays an important role in this system. Nevertheless, the specific component of reading in which this area is involved is still a controversial issue.

According to a dual-route model of reading\(^1\), two routes may be used to access the pronunciation of printed words (Marshall & Newcombe, 1973; see Figure 1). Which route is used depends on the phonological regularity of the words (i.e., whether the pronunciations of the words are completely consistent with grapheme-phoneme conversion rules [e.g., cat] or not [e.g., yacht]). The first route is a direct lexical address phonological route for reading of real words. In this route, visual input will be recognized as a whole or as morpheme-sized units in a visual input lexicon that is composed of all abstract representations of real words or morpheme-sized units (regardless of regularity) in long-term memory, and then matched to a phonological representation in a phonological lexicon, either directly or after being matched to a semantic
representation in a semantic system. The second route is an indirect sublexical assembly route for phonologically regular words and pronounceable non-words. In this route, pronunciation is accessed based on sublexical grapheme-to-phoneme correspondence, whereby letters or letter combinations correspond to specific phonemes that help to assemble the pronunciation of the whole word (Marshall & Newcombe, 1973).

Patient data suggests that the left fusiform gyrus is involved in the direct lexical address phonological route. For example, patients with damage to the left fusiform read phonologically regular words correctly but make regularization errors when reading phonologically irregular words (i.e., mispronounce irregular words by pronouncing the sounds of their elements; Luo, Zhao, Wang, Xu, & Weng, 2007; Marshall & Newcombe, 1973). Since phonologically irregular words can be read only by the direct lexical route, the poor performance on irregular words by the patients indicates that the direct route is impaired. In this case, the indirect sublexical route must be applied to irregular words, and therefore, regularity-based but incorrect pronunciations are produced. Similar to the contrast between phonologically irregular and regular words, the Japanese writing system consists of two types of characters—kanji (Japanese morphograms) and kana (Japanese phonetic writing)—that involve the direct address phonological route and the indirect assemble phonological route, respectively. In line with the association between the fusiform gyrus and the direct address phonological route, patients with fusiform lesions read kanji characters more poorly than corresponding kana characters (Sakurai et al., 2006).

Although neuropsychological evidence suggests that the left fusiform gyrus is involved in the direct lexical route of reading, results from neuroimaging studies of this region are less clear. According to dual-route model, only pronunciations of real words can be accessed through the direct route, while pseudowords must be read by the indirect sublexical assembly route.
Supporting the role of the left fusiform gyrus in the direct lexical route, some studies have observed greater activity for words than pseudowords in this region (Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Price et al., 1996; Herbster, Mintun, Nebes, & Becker, 1997). Inconsistent with this perspective however, other studies have observed greater activity for pseudowords than for words (Fiez, Balota, Raichle, & Petersen, 1999; Hagoort et al., 1999) or no difference between words and pseudowords (Cohen et al., 2002; Simos et al., 2002; for discussion, see Mechelli, Gorno-Tempini, & Price, 2003). Thus, neuroimaging studies comparing words and pseudowords do not clarify the role of the left fusiform in the dual-route model of reading.

The role of the left fusiform in the dual-route model of reading has also been examined in neuroimaging studies comparing neural responses to phonologically regular and irregular words. According to the dual-route model, phonologically regular words can be pronounced through either the direct lexical address route or the indirect sublexical assemble route, while phonologically irregular words can only be pronounced through direct lexical address route. Therefore, if the left fusiform gyrus is involved in the indirect sublexical route, phonologically regular words should elicit greater activity in this region than phonologically irregular words. In contrast, if the left fusiform gyrus is involved in the direct lexical address route, there should not be any difference of activation in this area between phonologically irregular and regular words. Consistent with the direct lexical address perspective, some studies have found no difference between phonologically regular and irregular words in the left fusiform (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Herbster et al., 1997), even though this region responds specifically to words compared to control stimuli (Herbster et al., 1997). However, this lack of difference could be due to the use of alphabetic languages in these studies. In particular, alphabetic
languages can be read by relying on grapheme-phoneme conversion rules. Indeed, even phonologically irregular words such as 'yacht' contain parts ('y' 'a' and 't') that can help with the pronunciation of the whole word using grapheme-phoneme conversion rules. Thus, when alphabetic languages are tested, the indirect sublexical assemble route may be automatically involved in the reading of phonologically irregular words. If so, the left fusiform gyrus should not show a difference between phonologically regular and irregular words, even if it is involved in the indirect sublexical assembly route, because both types can rely on the indirect sublexical assemble route. Therefore, alphabetic languages do not provide the strongest test of the left fusiform’s involvement in the direct lexical address route. Indeed, a character-based language without grapheme-phoneme conversion rules, such as Chinese, may provide a better test.

In Chinese the basic writing unit, a character, represents a syllable as a whole. Therefore, there is no grapheme-phoneme conversion rule in Chinese. Indeed, some Chinese characters are entirely phonologically irregular, because none of their elements are phonologically related to their pronunciation, unlike “irregular” words in alphabetic languages. For example, the whole character shown in Figure 2A is pronounced “BAN”, while the left element is pronounced “ZHOU”, and the right element cannot be pronounced on its own. In contrast, other characters are phonologically regular in that their phonetic elements can provide information about the pronunciation of the whole. For example, the character shown in Figure 2B is pronounced “CHENG”, and the right element is also pronounced “CHENG”. Accordingly, Chinese surface dyslexia patients show a disability in reading phonologically irregular characters but are relatively intact when reading regular characters, and the dominant error type they make for irregular characters is regularization (Butterworth & Yin, 1991; Lou et al., 2007; Shu, Meng, Chen, Luan, & Cao, 2005). This suggests that the direct address route is impaired in these
patients and that reading relied on the indirect sublexical route. On the other hand, Chinese deep dyslexia patients exhibit severe impairment in reading both phonologically irregular and regular characters, indicating damage to the direct lexical route is also possible (Butterworth & Yin, 1991; Shu et al., 2005). Thus, Chinese may be a particularly useful language for examining the role of the left fusiform gyrus in direct lexical address route reading.

The goal of Experiment 1 is to investigate the role of the left fusiform gyrus in reading, in the context of a dual-route model. Accordingly, subjects performed a phonological task with phonologically regular and phonologically irregular Chinese characters while being scanned using functional magnetic resonance imaging (fMRI). If the left fusiform gyrus is involved in direct lexical address route reading, activity in this region should not vary according to the regularity of characters; if the left fusiform gyrus is involved in indirect sublexical route reading, activity in this region should be greater for phonologically regular characters than phonologically irregular characters.

Experiment 1

Method

Subjects. Twelve subjects were recruited. All subjects were native Chinese Mandarin readers who had completed high-school study (at least) in mainland China. Subjects were screened using a detailed questionnaire to ensure that they had no history of neurological or psychiatric problems. In addition, all subjects were right-handed and had normal or corrected-to-normal vision. Informed consent was obtained from each subject in accordance with the guidelines and approval of the Rice University Institutional Review Board.
**Materials.** Stimuli were left-right structural, simplified Chinese characters. Two types of experimental stimuli with differing degrees of regularity were used. Regular characters had a phonetic element with the identical pronunciation and tone to that of the whole character (e.g., the character displayed in Figure 2B). Irregular characters did not have a phonetic element (e.g., the character displayed in Figure 2A). None of the characters had a semantic element or any homophones. Ten characters of each type were used (see Appendix A). The types did not differ in terms of frequency or number of strokes, \( t(18) = -0.15, p = 0.88; \ t(18) = 0.56, p = 0.59 \), respectively (see Table 1). All characters were presented centrally, in white against a black background, and subtended approximately 2° x 2° of visual angle. Presentations and response-time measurement were controlled by the PsyScope software package (Cohen, MacWhinney, Flatt, & Provost, 1993).

**Procedure.** The characters were presented for 500 ms at intervals of 2.5 s, 5 s or 7.5 s (average rate of 1 character per 5 s). A fixation cross (+) preceded each presentation and remained on the screen between stimulus trials. In the phonological task, subjects were asked to determine whether the tone of the character is the first/second or third/fourth tone. Subjects were asked to respond as quickly and accurately as possible by pushing a button with their left (or right) hand to indicate the “first or second tone” and a button with their right (or left) hand to indicate the “third or fourth tone” response. The response hand was counterbalanced across subjects.

Subjects completed 3 runs of the phonological task. The stimulus sets of both types were repeated 3 times in each run. In addition, in each run, no more than three trials of the same type (regular vs. irregular) or same response (first/second vs. third/fourth tone) appeared consecutively. Each run lasted approximately 5 minutes.
Image acquisition and analysis. fMRI scans were conducted at the Human Neuroimaging Laboratory at Baylor College of Medicine. At the beginning of each scanning run, there was a 10 s fixation to allow for stability in magnetization. At the end of each scanning run, there was a 15 s fixation to compensate for the delay of the hemodynamic response. MRI data were acquired on a Siemens 3T Allegra scanner (Erlangen, Germany). Anatomical images were acquired first, using a transverse MP-RAGE T1-weighted sequence (Siemens) with a voxel size of .5 x .5 x 1 mm (TR = 1200 ms; TE = 2.93 ms; flip angle = 12°). Functional images were acquired using an echo-planar sequence (TR = 2500 ms; TE = 40 ms; flip angle = 90°; voxel size = 3.5 x 3.5 in-plane resolution). During each functional run, 140 sets of 26 contiguous 4-mm thick axial images were acquired parallel to the anterior-posterior commissure plane.

Data from each subject were preprocessed to remove noise and artifacts, including correction for movement within and across runs using a rigid-body rotation and translation algorithm (Friston, Jezzard, & Turner, 1994; Snyder, 1996). Image slices were temporally realigned (using sinc interpolation) to the midpoint of the first slice, accounting for differences in the acquisition time for each individual slice. Data were then resampled into 2-mm isotropic voxels and warped into a standardized atlas space (Talairach & Tournoux, 1988).

Preprocessed data were analyzed based on the General Linear Model (GLM; Friston et al., 1994; Josephs, Turner, & Friston, 1997; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000; Worsley & Friston, 1995; Zarahn, Aguirre, & D'Esposito, 1997). Neural signals during the two character-type conditions (regular vs. irregular) were modeled in the GLM at the 7 time points (i.e., image acquisitions) immediately following each stimulus onset. In addition, a factor was coded to account for the within-run linear trend (linear drift and a constant term). All effects were modeled simultaneously in the GLM for each subject.
Regions of interest were defined based on a voxel-wise analyses. Regions exhibiting an effect of Type were identified via ANOVA comparing activity across 7 time points for regular and irregular character. Z statistical images produced by each analysis were smoothed with a 3-mm radius hard sphere kernel. A peak (local extremum) search algorithm was used to identify the coordinates (Talairach & Tournoux, 1988) of activation peaks ($p < .01$, uncorrected) in the smoothed images. Peaks separated by less than 10 mm in each image were consolidated by coordinate averaging, and spheres (10-mm radius) were centered on each peak. Spherical regions were then masked to exclude voxels that did not meet a statistical threshold of $p < .05$ (uncorrected). Voxels in each region were averaged for further analysis. Finally, the hemodynamic response was extracted from each region and the main effect of time (at the 7 estimated time points) was assessed in each. Only regions exhibiting a main effect of time ($p < .05$) and with the BOLD signal peak (including time points 2nd, 3rd, and 4th) exceeding .1 or -.1 are reported.

Results

Behavioral. The accuracy of participants in the phonological task was 97%. A dependent sample t-test comparing regular and irregular characters was conducted. No difference between character types was observed in either the response times, $t(11) = 1.33$, $p = .21$ (regular 844 ms vs. irregular 830 ms), or accuracy, $t(11) = 1.30$, $p = .22$ (regular 97% vs. irregular 98%).

Neuroimaging. One region in the left fusiform gyrus (centered at $x = -43$, $y = -58$, $z = -12$ in stereotactic space [Talairach & Tournoux, 1988], $Z=2.81$) was identified via an analysis of variance (ANOVA) assessing the main effect of type. As shown in Figure 3, activity was greater for irregular characters than for regular characters, $F(1, 11) = 19.48$, $p = .001$. All the regions exhibiting effect of type, $p < .05$, are shown in Table 2.
Discussion

The main finding of the present experiment is that one region in the left fusiform gyrus exhibited greater activity for irregular characters than regular characters. This finding clearly suggests that the left fusiform gyrus is not involved in the indirect route of the dual-route model, since this route should produce greater activity for regular words than irregular words. Nevertheless, this finding is not completely in line with the direct-route predictions either, as that route should produce similar activity for regular and irregular words. Therefore, to understand this result, a difference between Chinese characters and alphabetic languages must be considered.

Although for regular Chinese characters, the pronunciation of its part provides information for the phonology of the whole character as happens for regular English words, the process in the indirect route of Chinese regular character reading is a little different from that of English regular word reading. In the indirect route of English word reading, each phoneme converted from each grapheme is just a part of the whole pronunciation; hence to read the whole word, assembling of all phonemes is needed. On the contrary, the pronunciation of the whole character in Chinese is either identical to the smallest pronounceable part (eg. “清” sounds “QING”, and its part “清” sounds the same - “QING”) or very similar to the part (eg. “精” sounds “JING", and its part “精” sounds “QING”), so no assembling is required in indirect route of Chinese reading. Because of less effort required on assembling in indirect route and the fact that only processing part of the regular character that provides phonological information is adequate for Chinese regular character reading in indirect route, indirect route seems easier than direct route that needs to process the whole character, although both direct and indirect route could read regular character correctly. In normal reading, since only direct route can ensure correct output, direct route is
necessary for regular character reading. Nevertheless, in the present experiment, all characters were repeated 9 times in total. It was likely for subjects to establish the memory about which character could be read correctly by just the easier way, indirect route. Afterwards, indirect route might be activated faster or be more dominant for regular character reading. If this happened, direct route is not equally activated by regular and irregular characters anymore. Irregular character reading always required direct route, whereas regular character reading activated more indirect route and relatively less direct route. Therefore, if the left fusiform is involved in direct route, it could exhibit greater activity for irregular characters than regular characters.

Experiment 2

Based on the dual-route model, the direct lexical route consists of three levels of representations—namely orthographic, phonological, and semantic (see Figure 1). From printed words, the orthographic lexicon is accessed first, and then phonological lexicon and semantic system are accessed. Whether the left fusiform gyrus is involved in orthographic lexical representation, phonological lexicon access, or semantic system access is still a controversial issue.

The most popular idea is that the left fusiform gyrus is sensitive to orthographic representation. This idea was first supported by pure alexia cases that patients with lesions in this region showed preserved ability in production and comprehension of oral speech, while they exhibited severe impairment in visual word reading (Benson & Geshwind, 1969; Beversdorf, Ratcliffe, Rhodes, & Reeves, 1997). Intact comprehension ability of auditory words indicated that the dysfunction of this region did not affect phonological and semantic processing, and therefore some researchers associated the damage to orthographic representation (Cohen et al.,
2004; Warrington & Shallice, 1980). However, this association is not necessarily the case, because the damage could also happen during the mapping from orthographic representation to phonological, or to semantics. More evidence for the orthographic idea came from functional imaging studies that the left fusiform responded more to visual words than to auditory words (Dehaene, Le Clec'h, Poline, & Cohen, 2002; Booth et al., 2002), comparable to previous neuropsychological findings. This still does not rule out the hypothesis that this region is involved in the mapping between orthography and the other two components. Other pieces of evidence from functional imaging studies are also controversial. For example, Cohen et al. (2002) found that the left fusiform was equally activated by words and pseudowords and argued that this result demonstrated the tuning of this region to orthographic regularity. Firstly, this equal activation of left fusiform evoked by words and pseudowords was not always observed in previous studies (Fiez, Balota, Raichle, & Petersen, 1999; Hagoort et al., 1999). Moreover, both words and pseudowords are pronounceable, so this result could also suggest that this region is involved in sublexical reading route or phonological access in direct route.

Indeed, findings from existing patient studies suggest that the left fusiform gyrus is not necessary for orthographic representation. Some pure dyslexia patients with damage in the left fusiform gyrus exhibit better performance during lexical decision, semantic categorization, and written word/picture verification tasks than during naming tasks (Bub & Aruguin, 1995; Coslett & Saffran, 1989; Hillis et al., 2005; Sakurai et al., 2006). Since orthographic access is the first step in direct lexical route, successful lexical decision and semantic access indicates that the orthographic lexicon is intact. Thus, impairment of the direct route due to lesions in the left fusiform gyrus is not necessarily associated with impaired orthographic lexicon. On the contrary,
these patient data suggested that this region was involved in phonological access that is required in naming task.

This hypothesis was also supported by a training study (Xue et al., 2006). In this study, Chinese subjects were trained to recognize the visual forms, the phonologies, and the meanings of words in an artificial language. The artificial language was created by arbitrarily pairing Korean characters with phonologies and meanings, such that there was no phonological or semantic regularity in any of the pairings. The training procedure was divided into three parts—visual training, phonological training, and semantic training. In the first two weeks of the study, subjects were trained on the visual forms; in the following two weeks, they learned to link the visual forms to their (arbitrary) phonologies; in the last two weeks, they learned to link the visual forms and phonologies to their (arbitrary) meanings. Importantly, activity in the left fusiform gyrus was significantly greater after phonological training than before (immediately after visual training), although it is possible that greater visual familiarity lead to this increase, since phonological training included additional visual exposure. Nonetheless, results from this study provide support for the role of the left fusiform in phonological access.

Interestingly, results from the study by Xue et al. (2006) also indicate a role for semantic lexicon access in the left fusiform gyrus. In particular, activity in the left fusiform was greater after semantic training than before (immediately after phonological training), suggesting that learning the meanings of visual forms may also be important for left fusiform involvement. Further support for this idea comes from studies observing priming modulation that depends on the semantic relationship between prime and target words (Devlin, Jamison, Gonnerman, & Matthews, 2006; Klaver et al., 2007; Raposo, Mossa, Stamatakis, & Tyler, 2006; Wheatley, Weisberg, Beauchamp, & Martin, 2005). Therefore, in addition to evidence that the left fusiform
is involved in phonological access, evidence also suggests a role for the left fusiform in accessing the meanings associated with visual forms.

Experiment 2 was designed to discriminate between these three hypothesized roles for the left fusiform. Accordingly, activity in the left fusiform was measured using fMRI and compared during three tasks that varied in their orthographic, phonological and semantic demands. If the left fusiform plays a role in orthographic representation, activity in this region should be greater during the orthographic task than the others. If the left fusiform plays a role in phonological access, activity in this region should be greater during the phonological task than the others. Alternatively, if the left fusiform plays a role in semantic access, activity in this region should be greater during the semantic task than the other two tasks. Critically, it should be noted that some evidence suggests that phonological access is involved in comprehension (Folk, 1999; Van Orden, 1987; Van Orden, Johnston, & Hale, 1988), and semantic access occurs during phonological tasks (Wheatley, Weisberg, Beauchamp, & Martin, 2006). If so, it may be difficult to observe a difference between the phonological and semantic tasks in the proposed experiment. To address this possibility, the orthographic task plays an important role. Accordingly, even if there is no activity difference in the left fusiform gyrus between semantic and phonological tasks, if both of these two tasks evoke greater activity in this region than the orthographic control task, at least, it suggest this region is involved in semantic or phonological access instead of orthographic processing.

Method

Subjects. Seventeen subjects adhering to the same criteria used in Experiment 1 were recruited, except that not all the subjects completed high school in mainland China. Data from five subjects were excluded because their accuracy during one of the three tasks was below 80%.
Materials. Sixteen irregular Chinese characters were used in this experiment. Irregular characters were used in order to increase reliance on the direct reading route (see Appendix B). Mirror images of real characters were used in the orthographic task as orthographically illegal stimuli. Half of the stimuli (including both real characters and mirror images) in the orthographic task were rotated by 180 degrees.

Procedure. The procedure was the same as in Experiment 1, except that subjects performed three different tasks. The phonological task was the same as the one in Experiment 1. In the semantic task, subjects were asked to determine whether the meaning of the character is imageable (e.g., “clock”) or not (e.g., “skill”). In the orthographic task, subjects were asked to determine whether each stimulus is a real character or not regardless whether the stimuli were rotated by 180 degrees. Each run included all three tasks, and subjects were cued for particular task by a red underlined Chinese character indicating the next task. In addition, in each run, for both semantic and phonological tasks, all characters were presented; for orthographic task, half of the characters were presented as their mirror images, while the other half were not; half of the mirror images and real characters were rotated by 180 degrees, while the other half were not. All the characters presented as the mirror images in one run were presented as real characters in another run. Similarly, all the characters presented rotated in one run were presented as not rotated characters or mirror images in another run. 6 runs were used in total. The order of tasks was counterbalanced across runs.

Image acquisition and analysis. Image acquisition and preprocessing procedure were identical to those in Experiment 1. Preprocessed data were analyzed based on the General Linear Model (GLM; Friston et al., 1994; Josephs, Turner, & Friston, 1997; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000; Worsley & Friston, 1995; Zarahn, Aguirre, & D’Esposito, 1997).
Neural signals during the three task conditions (orthographic vs. phonological vs. semantic) were modeled in the GLM at the 7 time points (i.e., image acquisitions) immediately following each stimulus onset. In addition, a factor was coded to account for the within-run linear trend (linear drift and a constant term). All effects were modeled simultaneously in the GLM for each subject.

Regions exhibiting an effect of Task were identified via an ANOVA comparing activity across 7 time points among all three tasks. Z statistical images produced by each analysis were smoothed with a 3-mm radius hard sphere kernel. A peak (local extremum) search algorithm was used to identify the coordinates (Talairach & Tournoux, 1988) of activation peaks ($p < .000001$, uncorrected) in the smoothed images. Peaks separated by less than 10 mm in each image were consolidated by coordinate averaging, and spheres (10-mm radius) were centered on each peak. Spherical regions were then masked to exclude voxels that did not meet a statistical threshold of $p < .01$ (uncorrected). Voxels in each region were averaged for further analysis. Finally, the hemodynamic response was extracted from each region and the main effect of time (at the 7 estimated time points) was assessed in each. Only regions exhibiting a main effect of time ($p < .05$) and with the BOLD signal peak (including time points $2^{nd}$, $3^{rd}$, and $4^{th}$) exceeding .1 or -.1 are reported.

Results

Behavioral. No main effect of Task among three tasks was observed in either the response times, $F(2,33) = .88; p = .42$, or accuracy, $F(2,33) = .99; p = .38$. (see Table 3). In addition, none of the individual comparisons between two tasks were significant, in either response times, $t(11) = .12; p = .93$ (orthographic vs. phonological), $t(11) = 1.19; p = .30$ (phonological vs. semantic), $t(11) = 1.74; p = .11$ (orthographic vs. semantic), or accuracy,
Neuroimaging. One region in the left fusiform gyrus (centered at $x = -41, y = -66, z = -10$ in stereotactic space [Talairach & Tournoux, 1988], $Z=5.10$) was identified via a analysis of variance (ANOVA) assessing the main effect of task, $F(2,22) = 45.53; p < .001$. Additionally, another region in the right fusiform gyrus (centered at $x = 49, y = -57, z = -10$ ($Z=5.12$), in stereotactic space [Talairach & Tournoux, 1988]) were identified via the same analysis, $F(2,22) = 34.29; p < .001$. For both regions, when comparing the peaks (the average of time points 2\textsuperscript{nd}, 3\textsuperscript{rd}, and 4\textsuperscript{th}), the simple effect of Task showed no difference between phonological task and semantic task, but greater activity for orthographic task than other two tasks [$x = -41, y = -66, z = -10$: $t(11)= 6.80, p = .000$ (orthographic vs. phonological); $t(11)= 9.43, p = .000$ (phonological vs. semantic); $t(11)= .20, p = .84$ (phonological vs. semantic). $x = 49, y = -56, z = -10$: $t(11)= 7.43, p = .000$ (orthographic vs. phonological); $t(11)= 8.78, p = .000$ (phonological vs. semantic); $t(11)= 1.66, p = .13$ (phonological vs. semantic)]. The hemodynamic response from the left fusiform region is shown in Figure 4A, and that from the right fusiform region is shown in Figure 4B. All the regions exhibiting effect of Task, $p < .05$, are shown in Table 4.

Discussion

The ANOVA assessing the effect of Task demonstrated that regions in fusiform gyrus exhibited greater activity during orthographic task than phonological and semantic task, and no difference between phonological and semantic task was observed, indicating that the fusiform gyrus is involved in orthographic processing.

As reviewed earlier, previous studies revealed controversial findings in terms of the role of the left fusiform gyrus in orthographic, phonological and semantic processing. Especially,
neuropsychological evidence suggests that the left fusiform gyrus is required for phonological processing (Bub & Arguin, 1995; Coslett & Saffran, 1989; Hillis et al., 2005; Sakurai et al., 2006), whereas findings from priming effect in some neuroimaging studies suggested that this region responded to semantic information of words (Devlin, Jamison, Gonnerman, & Matthews, 2006; Klaver et al., 2007; Raposo, Mossa, Stamatakis, & Tyler, 2006; Wheatley, Weisberg, Beauchamp, & Martin, 2005; Xue et al., 2006), neither of which is consistent with the results of the present experiment. How to explain this inconsistency?

Firstly, patient data showed that for patients with lesion or dysfunction in the left fusiform gyrus, their abilities in lexical decision, semantic categorization, and written word/picture verification tasks were relatively preserved, while they exhibited poor performance during naming tasks (Bub & Arguin, 1995; Coslett & Saffran, 1989; Hillis et al., 2005; Sakurai et al., 2006). This finding indicates that the left fusiform gyrus is involved in phonological processing, but not necessarily in orthographic or semantic processing. Why activation of this region is a reliable finding during orthographic tasks in neuroimaging studies then? Hillis et al. (2005) postulated a role of this left fusiform gyrus in orthography-phonology mapping in reading. More specifically, in this proposal, this region is involved in both orthographic processing and the access to phonology from the orthographic processing outcomes. Additionally, the role of this region in orthographic processing could be taken charge of by the region in the right hemisphere symmetrical to the left fusiform gyrus when the left region is dysfunctional. This hypothesis is consistent with both functional imaging data with normal participants and neuropsychological findings. Moreover, the activation of the right fusiform gyrus in visual word reading was observed in this experiment and some previous studies (Chen, Xue, Dong, Jin, Li, Xue, Zhao, & Guo, 2007; Cohen, Jobert, Bihan, & Dehaene, 2004; Nelson, Liu, Fiez, & Perfetti, 2008).
With regard to the evidence that the left fusiform gyrus is involved in semantic processing, most is from functional imaging studies using priming paradigm (Devlin, Jamison, Gonnerman, & Matthews, 2006; Klaver et al., 2007; Raposo, Mossa, Stamatakis, & Tyler, 2006; Wheatley, Weisberg, Beauchamp, & Martin, 2005) that is different from the tasks used in the present experiment. Since it is observed that phonologies and semantics were often automatically activated by written words regardless of tasks (Lukatela & Turvey, 1994a, 1994b; Folk, 1999), no difference between phonological and semantic tasks in terms of the activation of the left fusiform gyrus in this experiment may be due to the automatic activation between phonological and semantic information. Semantic priming paradigm used in previous studies with semantically related words that are neither orthographic nor phonological similar seems a better way to tease apart phonological and semantic processing.

In sum, it was observed in this experiment that the left fusiform gyrus exhibited greater activity during the orthographic task than during the phonological and semantic tasks of Chinese character reading, suggesting that this region is involved in orthographic processing.

**General Discussion**

Two experiments were conducted to investigate the role of the left fusiform gyrus in Chinese character reading. In Experiment 1, one region in the left fusiform gyrus was identified exhibiting greater activity for irregular characters than regular characters; in Experiment 2, two regions in both the left and right fusiform gyrus were found exhibiting greater activity during orthographic task than phonological and semantic tasks.
**Functional lateralization in the fusiform gyrus**

The functional lateralization of the fusiform gyrus in visual form recognition has been supported by many studies, that the left fusiform is specifically involved in word recognition (VWFA), whereas the right fusiform is specifically involved in face recognition (fusiform face area, FFA) Gauthier, Skudlarski, Gore, & Anderson, 2000). However, as in the results of the present study, some researches also observed the activation of right fusiform gyrus responding to visual words, especially for Chinese reading (Chen, Xue, Dong, Jin, Li, Xue, Zhao, & Guo, 2007; Cohen, Jobert, Bihan, & Dehaene, 2004; Nelson, Liu, Fiez, & Perfetti, 2008; Tan, Liu, Perfetti, Spinks, Fox, & Gao, 2001).

In terms of the lateralization of the fusiform gyrus in object recognition, Dien (2008) postulated that the left and right fusiform gyrus are not distinct because of their sensitivity to different domains of stimuli (e.g., words vs. faces), rather they processes different feature representations of visual objects. For example, a neural subsystems model argues (Marsolek & Burgund, 1997; Marsolek, Kosslyn, & Squire, 1992; Marsolek et al., 1996; Marsolek, 2004; Marsolek & Andresen, 2005) that visual form recognition relies on two subsystems, specific-exemplar subsystem and abstract-category subsystem. The holistic processing is more important to recognize specific exemplars of visual objects, since exemplars from one category usually share parts but have different whole shapes. Conversely, feature processing of parts is more useful to recognize abstract categories, because objects from different categories may have similar whole shape, but definitely do not share the same parts. In addition, in this model, although each hemisphere process both subsystems, right hemisphere is stronger in specific-exemplar subsystem (holistic processing), while left hemisphere is stronger in abstract-category subsystem (feature processing). Apparently, feature processing is more
important for word recognition than holistic processing, since all words have very similar string-like holistic shapes but different letter components. Hence left fusiform gyrus is activated greater than the right fusiform gyrus in reading. This idea is supported by the evidence that the left fusiform gyrus is case-insensitive in repetition priming of words (Dehaene et al., 2001; Dehaene et al., 2004), whereas in the homologous right hemisphere region case-dependent priming was observed (Dehaene et al., 2001).

Why was the right fusiform activated in Chinese reading tasks then? Because Chinese characters are logographic and contain more spatial information, the holistic processing of the whole character shapes is more useful to discriminate Chinese characters than English words, which explains that more involvement of the right fusiform gyrus was observed in Chinese reading.

*Functional distinction between two clusters in the fusiform gyrus*

It is noticeable from our results that two regions found in the left fusiform gyrus in Experiment 1 (TC: $x = -43, y = -58, z = -12$) and Experiment 2 (TC: $x = -41, y = -66, z = -10$) are slightly apart from each other. The region from Experiment 2 is more posterior to the region from Experiment 1.

Consistent with the detection of two regions in the fusiform gyrus in this study, Cohen et al. (2004) identified two bordered but distinct regions during orthographic task. Nevertheless, the lateral temporal cluster (TC: -48, -60, -16; probably corresponding to the anterior region identified in Experiment 1) responded to orthographic processing to both visual words and auditory words, while the posterior occipital-temporal cluster (TC: -44, -68, -4; probably corresponding to the posterior region identified in Experiment 2) was exclusively activated by visual words. The authors proposed that the lateral temporal region played integration and lexical
role in supramodel language processing, and contrarily the posterior occipital-temporal region is involved in unimodel pre-lexical orthographic processing (VWFA as proposed by Cohen & Dehaene, 2004).

This hypothesis is supported by the results in Experiment 1 that only the anterior temporal region exhibited the effect of type. Since irregular characters involve more lexical processing than regular characters, greater activity in the anterior region for irregular characters than regular characters suggests that this region is involved in lexical processing in direct route of reading. On the other hand, the posterior area did not exhibit any effect of Type.

Since these two clusters of regions in fusiform gyrus are so close together, it is very possible that the might be confused in patient studies, and even in functional imaging studies, which may contribute to the contradictory of findings from previous studies. The functional distinction between these two regions in the fusiform gyrus needs to be considered more carefully in future studies.

To summarize, a posterior occipital-temporal region in left fusiform and a region in right fusiform were identified exhibiting greater activity during orthographic task than phonological and semantic tasks, suggesting that they are involved in orthographic processing. Additionally, the result that an anterior temporal region exhibited greater activity for regular characters than irregular characters indicates that this region plays a role in the orthographic lexicon.
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In addition to the dual-route model, connectionist models are another line of theories proposed to explain the mechanisms underlying reading (Harm & Seidenberg, 1999, 2004; Plaut, McClelland, Seidenberg, & Patterson, 1996; Seidenberg and McClelland, 1989). According to these models, orthography and phonology of words are represented in a network as distributed neuron-like units. For example, orthographic representations are composed of letters, while phonological representations are composed of phonemes. The infinite set of units in the network is used to represent a large set of patterns (like an alphabet represented many words) based on the statistical knowledge that is also represented in the network. There is no difference between the representations of regular and irregular words in these models, because both kinds of words are represented by the same units. The regular words and irregular words are represented in a continuum of spelling and pronunciation consistency. The orthographic representations are able to successfully correspond to the phonological representations because of the statistical knowledge of the "correct" mapping acquired during the learning.

Chinese characters have several different kinds of orthographic structure. For example, "听" is left-right structure; "青" is up-down structure; "国" is encompassed structure. In order to exclude the effect of structure, only left-right structure is used in present study.

Chinese characters have four tones for each pronunciation, and each character has a specific pronunciation and tone. For example, the four characters, "一", "直", "椅", and "易"
have the same pronunciation “YI”, but have different tones, referred to as 1\textsuperscript{st} tone, 2\textsuperscript{nd} tone, 3\textsuperscript{rd} tone, and 4\textsuperscript{th} tone.

4 Except for phonological elements, some Chinese characters have semantic elements that can provide semantic information for the whole characters. For example, the character shown in Figure 1B is semantically regular because its element provides information about its meaning. That is, the whole character means “city”, and the right element means “land”, a concept that is semantically related to the meaning of the whole character. In contrast, the character shown in Figure 1A is semantically irregular because its different elements do not provide any information about its meaning. That is, the whole character means “sort”, while the left element means “boat”, and the right element does not have meaning on its own. As such, the meanings of the elements in this character are related to or meaning of the whole character. Since any issue about the semantic elements in Chinese will not be addressed in the present research, characters vary in phonological regularity but not having semantic elements are needed. In addition, a questionnaire was used to examine whether there are semantic elements\textsuperscript{6} in the characters respectively from the perspective of subjects. Subjects were asked to rate the characters by score 0 – 5 based on how much they believe that there is a part of this character providing semantic information for the whole character. The average score the subjects rated for all characters was .73, which indicated that subjects did not detect obvious semantic elements in the stimuli.

5 Since there is no clear criterion of correct responses during the semantic task, the accurate answers in the semantic task were determined individually for each participant by the most often response for each character across runs.
Table 1

Mean frequency, number of strokes each character type in Experiment 1.

<table>
<thead>
<tr>
<th>Character type</th>
<th>Frequency (value/million)</th>
<th>Number of strokes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regular</td>
<td>432.4</td>
<td>10.8</td>
</tr>
<tr>
<td>Irregular</td>
<td>482.4</td>
<td>10.2</td>
</tr>
</tbody>
</table>
Table 2

Regions exhibiting an effect of type (regular vs. irregular).

<table>
<thead>
<tr>
<th>Coordinates (x, y, z)</th>
<th>BA</th>
<th>Name</th>
<th>Peak Z</th>
<th>Voxel size</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>irregular &gt;</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-9, -4, 51</td>
<td>24</td>
<td>left cingulate gyrus</td>
<td>3.15</td>
<td>64</td>
</tr>
<tr>
<td><strong>regular</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-44, -58, -12</td>
<td>37</td>
<td>left fusiform gyrus</td>
<td>2.81</td>
<td>38</td>
</tr>
<tr>
<td>-31, -12, 58</td>
<td>6</td>
<td>left precentral gyrus</td>
<td>2.66</td>
<td>63</td>
</tr>
<tr>
<td>-44, -54, 40</td>
<td>40</td>
<td>left inferior parietal lobule</td>
<td>2.60</td>
<td>80</td>
</tr>
<tr>
<td><strong>regular &gt;</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8, -47, 0</td>
<td></td>
<td>right culmen</td>
<td>3.03</td>
<td>85</td>
</tr>
<tr>
<td><strong>irregular</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-3, -72, 10</td>
<td>23</td>
<td>left cuneus</td>
<td>2.93</td>
<td>210</td>
</tr>
<tr>
<td>-14, -32, 34</td>
<td>31</td>
<td>left cingulate gyrus</td>
<td>2.83</td>
<td>176</td>
</tr>
<tr>
<td>2, -94, 3</td>
<td>18</td>
<td>right cuneus</td>
<td>2.79</td>
<td>90</td>
</tr>
<tr>
<td>21, -55, -12</td>
<td></td>
<td>right declive</td>
<td>2.78</td>
<td>146</td>
</tr>
<tr>
<td>45, -77, 10</td>
<td>19</td>
<td>right middle occipital gyrus</td>
<td>2.70</td>
<td>87</td>
</tr>
<tr>
<td>45, 21, 11</td>
<td>45</td>
<td>right inferior frontal gyrus</td>
<td>2.68</td>
<td>74</td>
</tr>
<tr>
<td>-32, 35, -5</td>
<td>47</td>
<td>left middle frontal gyrus</td>
<td>2.64</td>
<td>95</td>
</tr>
<tr>
<td>-44, -23, 7</td>
<td>13</td>
<td>left superior temporal gyrus</td>
<td>2.59</td>
<td>50</td>
</tr>
</tbody>
</table>

*Note.* Coordinates are given in standardized space (Talairach & Tournoux, 1988); BA refers to the approximate Brodmann’s area.
Table 3

Reaction times and accuracy during the orthographic task, phonological task, and semantic task for the irregular characters in Experiment 2.

<table>
<thead>
<tr>
<th>Tasks</th>
<th>Reaction times (ms)</th>
<th>Accuracy (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orthographic task</td>
<td>1083</td>
<td>.92</td>
</tr>
<tr>
<td>Phonological task</td>
<td>1077</td>
<td>.95</td>
</tr>
<tr>
<td>Semantic task</td>
<td>1016</td>
<td>.93</td>
</tr>
</tbody>
</table>
Table 4

Regions exhibiting an effect of task (orthographic vs. phonological vs. semantic).

<table>
<thead>
<tr>
<th>Coordinates (x, y, z)</th>
<th>BA</th>
<th>Name</th>
<th>Peak Z</th>
<th>Voxel size</th>
</tr>
</thead>
<tbody>
<tr>
<td>orthographic &gt;</td>
<td>28, -65, 40</td>
<td>7</td>
<td>Superior parietal lobule</td>
<td>5.50</td>
</tr>
<tr>
<td>phonological = semantic</td>
<td>34, -55, 40</td>
<td>40</td>
<td>Inferior parietal lobule</td>
<td>5.34</td>
</tr>
<tr>
<td></td>
<td>-23, -66, 40</td>
<td>7</td>
<td>Precuneus</td>
<td>5.22</td>
</tr>
<tr>
<td></td>
<td>31, -75, 30</td>
<td>19</td>
<td>Precuneus</td>
<td>5.19</td>
</tr>
<tr>
<td></td>
<td>49, -57, -10</td>
<td>37</td>
<td>Fusiform gyrus</td>
<td>5.13</td>
</tr>
<tr>
<td></td>
<td>-41, -66, -10</td>
<td>19</td>
<td>Fusiform gyrus</td>
<td>5.10</td>
</tr>
<tr>
<td></td>
<td>-49, -44, 39</td>
<td>40</td>
<td>Inferior parietal lobule</td>
<td>5.05</td>
</tr>
<tr>
<td>orthographic &gt; semantic</td>
<td>23, -3, 55</td>
<td>6</td>
<td>Sub-gyral</td>
<td>5.51</td>
</tr>
<tr>
<td>&gt; phonological</td>
<td>-28, -3, 51</td>
<td>6</td>
<td>Middle frontal gyrus</td>
<td>5.04</td>
</tr>
<tr>
<td></td>
<td>-29, -76, 24</td>
<td>19</td>
<td>Middle occipital gyrus</td>
<td>5.02</td>
</tr>
<tr>
<td></td>
<td>-11, -74, 47</td>
<td>7</td>
<td>Precuneus</td>
<td>4.98</td>
</tr>
</tbody>
</table>

Note. Coordinates are given in standardized space (Talairach & Tournoux, 1988); BA refers to the approximate Brodmann's area.
Figure 1

Direct route

Print

Visual feature units

Letter units

Orthographic lexicon

Semantic system

Phonological lexicon

Sublexical Grapheme-phoneme conversion

Speech

Indirect route
Figure 2

A

ZHOU "boat"

BAN "sort"

B

CHENG "city"

TU "land"

CHENG "complete"
Figure 3

Change of BOLD signal (%)

-0.1

0

0.05

0.1

0.15

0.2

-0.05

-0.1

-0.05

0

0.05

0.1

0.15

Time (seconds)

2.5 5 7.5 10 12.5 15

-43, -58, -12

regular

irregular
Figure 4

A

B

-41, -66, -10

49, -57, -10

Change of BOLD signal (%)

Time (seconds)
### Appendix A

Stimuli used in Experiment 1:

<table>
<thead>
<tr>
<th>Stimulus type</th>
<th>character</th>
<th>meaning</th>
<th>tone</th>
</tr>
</thead>
<tbody>
<tr>
<td>regular</td>
<td>致</td>
<td>cause</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>稀</td>
<td>rare</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>猥</td>
<td>like</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>郵</td>
<td>mail</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>營</td>
<td>busy</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>豫</td>
<td>comfort</td>
<td>4</td>
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<td></td>
<td>郊</td>
<td>suburb</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>歌</td>
<td>song</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>球</td>
<td>ball</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>理</td>
<td>reason</td>
<td>3</td>
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<tr>
<td></td>
<td>法</td>
<td>law</td>
<td>3</td>
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<tr>
<td></td>
<td>粗</td>
<td>thick</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>猜</td>
<td>guess</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>欲</td>
<td>desire</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>略</td>
<td>brief</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>酷</td>
<td>cruel</td>
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</tr>
<tr>
<td></td>
<td>移</td>
<td>move</td>
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<td>胁</td>
<td>force</td>
<td>2</td>
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<td>独</td>
<td>single</td>
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<td></td>
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Stimuli used in Experiment 2:

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<td></td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>阻</td>
<td>block</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>隐</td>
<td>hind</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>猜</td>
<td>guess</td>
<td>1</td>
</tr>
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<td></td>
<td>欲</td>
<td>desire</td>
<td>4</td>
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<td></td>
<td>权</td>
<td>power</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>祖</td>
<td>ancestor</td>
<td>3</td>
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