Seeing Chinese characters in action: An fMRI study of the perception of writing sequences

Hongbo Yu [a], Lanyun Gong [a], Yinchen Qiu [b,c], Xiaolin Zhou [a,b,d,]*

[a] Center for Brain and Cognitive Sciences and Department of Psychology, Peking University, Beijing 100871, China
[b] Research Center for Learning Science and Key Laboratory of Child Development and Learning Science (Ministry of Education), Southeast University, Nanjing 210096, China
[c] Department of French and Italian, Beijing International Studies University, Beijing 100024, China
[d] Key Laboratory of Machine Perception and Key Laboratory of Computational Linguistics (Ministry of Education), Peking University, Beijing 100871, China

ARTICLE INFO

ABSTRACT

The Chinese character is composed of a finite set of strokes whose order in writing follows consensual principles and is learnt through school education. Using functional magnetic resonance imaging (fMRI), this study investigates the neural activity associated with the perception of writing sequences by asking participants to observe stroke-by-stroke display of characters. Violations were introduced by reversing the writing order of two or three successive strokes. Compared with the correct sequences, both types of violation engendered more activation in the left dorsolateral prefrontal cortex (DLPFC) while the two-stroke reversal elicited additional activation in the supplementary motor area and the three-stroke reversal elicited additional activation in the left fusiform area and the right inferior temporal gyrus. Compared with either type of incorrect sequences, the correct sequences elicited activation in the bilateral dorsal premotor areas and left superior parietal lobule. These findings suggest that a domain-general sequence processing network is implicated in the perception of Chinese character writing and that the left fusiform encodes not only the visual configuration but also the dynamic aspect of the writing script.

© 2010 Elsevier Inc. All rights reserved.

1. Introduction

Different languages use different visual configurations in writing to convey lexical information. While the basic writing units in alphabetic systems (i.e., letters) are usually arranged in linear strings, the basic writing units in Chinese (i.e., strokes) are organized in a 2D configuration, in which a finite set of basic strokes (e.g., horizontal, vertical, left-falling, dot, and turning strokes) are structured to form characters according to recognized principles (e.g., left before right, horizontal before vertical, center vertical before bilateral wings). The writing order is explicitly taught in primary schools according to a national standard (State Language Commission, 2000) when children learn and memorize the characters. This may provide clues to the tight coupling between the perception of characters and the action sequence producing them.

Although character writing is an indispensable part of language competence, studies focusing on its neural mechanism are relatively rare, as compared with studies focusing on other aspects of language processing. The few previous neuroimaging studies used either an explicit writing task, in which hand movements were engaged, or imagined writing, in which participants were visually

presented with the configuration or phonogram (e.g., *kana* in Japanese) of a character and were asked to imagine the writing process of the character. For example, Katanoda, Yoshikawa, and Sugishita (2001) conducted an fMRI study in which pictures of common objects, such as animals, plants and buildings were presented to their participants. In the writing condition, the participants were asked to write with their finger the phonograms (*kana*) of the object names; in the naming condition, the participants were asked to silently name the objects. In the motor control condition, the participants tapped their finger according to a visual cue. They found that the anterior part of the left superior parietal lobule, superior frontal gyrus, and the posterior part of the left middle frontal gyrus (or premotor area) were engaged in the process of writing as compared to naming and finger tapping. The authors concluded that the activation of parietal lobule reflects the recruitment of a graphic image of character and activation of the premotor area reflects the recruitment of a motor scheme, which guides hand movement in writing. As the authors acknowledged, however, the writing task required more complex temporal and spatial control of finger movements than tapping. The residual activation of the premotor area in the writing condition after subtraction might be due to specific motoric components of writing, rather than due to sequence processing in writing in general.

Using a different paradigm, Nakamura et al. (2002; see also Nakamural et al., 2000) revealed another aspect of neural

* Corresponding author. Address: Department of Psychology, Peking University, Beijing 100871, China. Fax: +86 10 6276 1081.
   E-mail address: xz104@pku.edu.cn (X. Zhou).

processing of character writing. They presented their participants with phonograms (*kana*) of Japanese *kanji* (i.e., characters similar to the Chinese ones) and asked them to perform four tasks in the MRI scanner. In the transcription task, the participants were required to write with their finger the corresponding *kanji* of the displayed *kana*; in the orthographic judgment task, they were instructed to decide whether or not the corresponding *kanji* contained two horizontally juxtaposed parts. The other two conditions involved phonological and semantic aspects of character processing, respectively. The authors found common activation in left posterior inferior temporal cortex in the first two tasks in which the retrieval of orthographic configuration was necessary, but such activation was absent in the last two tasks in which orthographic information was task-irrelevant. In the transcription task, in which not only the static configuration of the character but also the motoric sequence of writing was involved, additional activation was found in the left premotor area.

These studies suggest that character writing may involve two crucial cognitive components, i.e., a graphic or static representation corresponding to the structure of character and a motoric or dynamic representation corresponding to the motor sequence by which the character is normally written (Katanoda et al., 2001). By "dynamic" we mean that the representation of stroke sequence unfolds in time. This sequence information concerning how strokes are scheduled over time could be represented in specific brain regions and recruited during both writing and perceiving characters. These two types of representation may have separate neural substrates, as suggested by the studies on Japanese *kana* or *kanji* writing: the left posterior inferior temporal cortex or fusiform is recruited when the static configuration of character is needed; the left premotor–parietal network is activated when the dynamic writing sequence is additionally required.

However, the question remains as to what exactly is represented in the two systems. One possibility is that the posterior inferior temporal cortex stores the static configuration of the character. This notion is supported by neuroimaging studies on orthographic processing, which found consistent activation around the middle portion of the left fusiform, the so called VWFA (visual word form area; Cohen et al., 2000, 2002), when character or word form is being retrieved. The peak of this region lies at about Talairach coordinates [−42 −57 −12], but it extends in the anteroposterior direction across at least 2 cm (Vinckier et al., 2007). VWFA is activated for different writing systems, including Chinese (Chan et al., 2009; Fu, Chen, Smith, Iversen, & Matthews, 2002; Kuo et al., 2004; Liu et al., 2008; but see Xue, Chen, Jin, & Dong, 2006; Xue & Poldrack, 2007 which found that different aspects of the language experience, such as visual familiarity, phonology and semantics, actually all have important but different impacts on the neural activation in VWFA during language learning). It is not clear from these studies, however, whether the dynamic information associated with Chinese characters, such as the writing sequence, is encoded in VWFA, as the stimuli used were all static configurations of characters. Positive but indirect evidence comes from an ERP study (Qiu & Zhou, 2010) which, using a design similar to the present experiment, showed that the stroke reversal could elicit an N170 effect, peaking around 170 ms post-onset of the reversal, over the left posterior scalp regions. As the N170 has been shown to be sensitive to orthographic processing and has been linked to activity in left fusiform (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Maurer, Zevin, & McCandliss, 2008), it is possible that the left fusiform encodes dynamic sequence information in Chinese character writing.

As for the role of premotor–parietal network in character writing, previous studies could not provide a conclusive answer due to their lack of proper motor control conditions. The activation of premotor area may simply reflect motor preparation in writing.

Alternatively, it may correspond to a domain-general computational process, in which information concerning the writing sequence of character is encoded. By domain-general we mean that such neural structure is not specific to any particular cognitive task, but to certain cognitive components or computations shared by various tasks. This latter hypothesis is in line with theories derived from studies on perceptual sequence processing. Based on a large number of neuroimaging studies (e.g., Bubic, von Cramon, Jacobsen, Schröger, & Schubotz, 2008; Schubotz & von Cramon, 2002a, 2002b, 2002c, 2003, 2004; Wolfensteller, Schubotz, & von Cramon, 2007) using the serial prediction task (SPT) or motor learning tasks, Shubotz proposed the Habitual Pragmatic Event Map (HAPEM) framework (Schubotz & von Cramon, 2003; Schubotz, 2007), which states that the human cognitive system adopts a sequential program mechanism, which utilizes information extracted from external stimuli or retrieved from long-term memory to form prediction about future events, which, in turn, will facilitate both perception and motor planning. Anatomically, predictions of abstract events engage the motor system, particularly the premotor area and its parietal projection area (Fiebach & Schubotz, 2006; Schubotz, 2007). Detection of sequential deviance activates pre-supplementary motor area (pre-SMA) and middle frontal gyrus (MFG) as compared with detection of non-sequential deviance, such as color deviance (Bubic et al., 2008). It is conceivable that this domain-general mechanism may also be recruited in perceiving Chinese character writing, which involves sequence representation.

However, studies have also demonstrated that the static and dynamic systems may interact with each other and are integrated into a network in response to the complex sensorimotor tasks in real life, such as writing and learning novel scripts (James & Atwood, 2009; Longcamp et al., 2008; also see Longcamp, Anton, Roth, & Velay, 2003, 2005). For example, James and Atwood (2009) investigated how motor and visual trainings shape the neural circuit underlying sensorimotor representation of pseudo letters. Three groups of participants were scanned while they were presented with Roman letters, pseudo letters and geometric shapes. They were then trained over a subset of the pseudo-letters. One group underwent a motor training task, in which they were required to copy the pseudo letters by writing them down; the second group was required to type the pseudo letters with a keyboard; the third group was required to passively view the pseudo letters on a computer screen. After two training sessions, these participants underwent a post-training fMRI scan. Results showed that only in the writing group did the left posterior fusiform gyrus and the left dorsal precentral gyrus respond differentially to the trained and untrained pseudo letters, suggesting that experience in writing may shape the functional specialization for letter perception.

Then how might the neural structures implicated in perceptual sequence processing interact? Parkinson and colleagues (2010) visually presented computer-generated letters against a blank screen as a temporally unfolding additive sequence of letter strokes. The last stroke could be presented at its appropriate position, resulting in a real letter, or could be presented somewhere else, resulting in a non-letter. Participants' task was to judge whether the presented stimulus is a letter or not. In one condition, the stroke presentation order was consistent with the order by which people normally write that letter; in another condition, the presentation was inconsistent with the correct writing order. It was found that the "yes" response was speeded up when the letter was written in correct order. This facilitatory effect corresponded to a latency shift of the N1 component in event-related potentials. As N1 has been implicated in early visual recognition of letters (Di Russo, Martınez, Sereno, Pitzalis, & Hillyard, 2002), the authors argued that the facilitatory effect was due to

perceptual prediction of the upcoming stroke, based on information derived from the previous action-consistent stroke sequence. The authors speculated that such prediction is generated in motor and premotor areas and it modulates activation in posterior part of brain in a top-down manner (see also Wilson & Knoblich, 2005).

In this study, we aim to investigate firstly whether the premotor–parietal network is activated when participants view the writing of Chinese characters, rather than write the characters themselves. Bubic et al. (2008) observed that the activation of the left dorsal premotor area (PMd) and superior parietal lobule (SPL) was greater when participants were presented with ordered perceptual sequences as compared with non-sequential stimulus trains. Similarly, Schubotz and von Cramon (2002a) found that premotor activation increases with the sequential complexity of the attended stimulus sequence. The authors suggested that PMd and SPL are responsible for maintaining dynamic prediction of future events according to certain rules. Once the violation of these rules is detected, the activity of these areas would reduce. Accordingly, if the perception of Chinese character writing sequences involves a domain-general sequence processing, then we should observe stronger activation of this network for correct sequences as compared with sequences with stroke reversals.

The second aim of this study is to investigate whether left fusiform, more specifically, the VWFA represents the dynamic aspect of character writing. As we reviewed above, part of the left fusiform (VWFA) is sensitive to the processing of orthographic structure. The ERP study on the perception of stroke reversal (Qiu & Zhou, 2010) suggested that this area may encode dynamic sequence information in Chinese character writing as well. The training studies by James and Atwood (2009) and by Longcamp et al. (2008) also suggested that the functional specialization of the left posterior fusiform gyrus is sensitive to writing experience. If the left posterior fusiform encodes the sequence information concerning how the strokes are scheduled over time, we may observe differential activity of this area for the correct sequences and sequences with stroke reversals.

To achieve these aims, we adopted a perceptual task in which participants were asked to observe the stroke-by-stroke display of Chinese characters and to judge the correctness of the writing sequences. Violations were introduced by reversing the writing order of two or three successive strokes. Given the explicit sequence correctness judgment task, the occurrence of stroke sequence reversal may have two consequences: (1) it triggers processes related to stroke deviance detection and sequence restructuring, in which case we expect to see higher activation of VWFA in the reversal conditions as compared with the correct condition, for cortical foci falling within the relevant processing stream respond more robustly when there is a mismatch between the observed sensory signal and the expected perceptual template (Summerfield & Koechlin, 2008; see also Friston, 2005); (2) it may terminate the normal sequential anticipation processes in such trials and consequently brain structures subserving these processes, i.e., the premotor–parietal network as we hypothesized, may exhibit a decrease in activity, as compared with the correct condition. Since the participants need not perform the writing themselves, any activation of the premotor–parietal network cannot be attributed to motor preparation for writing but to a domain-general mechanism underlying sequence processing. Moreover, by introducing different levels of reversal (two-stroke reversal, 2R and three-stroke reversal, 3R; see Fig. 1), we are able to test whether the activity

Table 1

MNI coordinates of the activation foci revealed by four contrasts. DLPFC = dorsolateral prefrontal cortex, VLPFC = ventrolateral prefrontal cortex, SMA = supplementary motor area, SPL = superior parietal lobule, ITG = inferior temporal gyrus, FG = fusiform gyrus, CU = cuneus, PCU = precuneus, MOG = middle occipital gyrus, PMd = dorsal premotor area, BG = basal ganglia.

Brain region (BA)	Hemisphere	MNI coordinates			Max z-value	Voxel size
		x	y	z		
2R > C						
DLPFC (46)	L	−28	58	22	4.21	86
VLPFC (47)	L	−36	46	−4	3.68	101
pre-SMA (6/32)	L	−2	28	40	4.39	281
3R > C						
SFG (46)	L	−28	58	22	3.88	88
Postcentral (5)	R	10	−36	72	4.18	210
ITG (20)	R	60	−46	−10	4.09	66
FG (37)	L	−34	−62	−10	4.74	216
PCU	R	4	−74	54	3.50	54
CU	L/R	0	−94	28	3.64	79
MOG (17)	L	−18	−100	4	3.97	99
C > 2R						
Superior Medial (10)	R	10	58	4	3.66	405
PMd (6)	L	−50	−8	46	5.75	4391
PMd (6)	R	40	−12	60	5.02	1996
BG	R	30	−12	−2	4.44	345
Thalamus	R	14	−18	2	4.08	166
Supramarginal (48)	R	58	−20	26	4.39	318
SPL (7)	L	−22	−46	60	4.73	1496
C > 3R						
Thalamus	L	−8	−6	8	4.06	406
PMd (6)	L	−42	−8	58	4.83	1993
PMd (6)	R	42	−10	62	4.43	528
Postcentral (48)	L	−58	−18	30	4.66	495
SPL	L	−14	−58	60	4.33	581

Fig. 1. Experimental design and sample stimuli. The first frames of the boxed sequences were the critical stroke displays.

of brain areas which we hypothesized to house the representation of stroke sequence covaries with the degree of sequence violation.

2. Methods

2.1. Participants

Nineteen undergraduate and graduate students (11 male, mean age 22.6) at Peking University participated in the experiment. They were native speakers of Chinese and were right-handed as assessed by the Chinese Handedness Questionnaire (Li, 1983). They had normal or corrected-to-normal vision, and none of them reported to have a history of neurological or psychiatric disorder. Informed written consents were obtained from all participants prior to scanning and the study was approved by the Institutional Review Board of Beijing Normal University for Brain Research.

2.2. Stimuli and procedures

A total 147 left–right structured Chinese characters were used for the correct, baseline condition. Each character consisted of a semantic radical on the left and a phonetic radical on the right (Zhou & Marslen-Wilson, 1999a, 1999b). The number of strokes per character varied from 8 to 10, with a mean of 9.13 (SD = 0.78). Sequences with 2-stroke reversal (2R) or 3-stroke reversal (3R) were constructed on the basis of these characters (Fig. 1). If we refer to the critical stroke as 1, the subsequent stroke in correct sequence order as 2 and the next as 3, then in the correct condition (C) the stroke presentation order is naturally 1–2–3; in

2R condition, the order is 2–1–3; in 3R condition, the order is 3–2–1. Thus the violation in 2R condition is more subtle and perhaps calls for more effortful sequence monitoring than the violation in 3R condition. The critical stroke was located anywhere from the second to the antepenultimate position in the sequence. All the reversals took place within either the left semantic radical or the right phonetic radical (i.e., no cross-boundary reversal).

These stimuli were assigned into three test versions, using a Latin square design, with each version having 49 sequences from each condition. Each participant received one version, in which characters from different conditions were presented in a pseudo-random order, with the restriction that no more than four consecutive trials were from the same condition. The participant was required to observe the stroke-by-stroke display carefully and judge, by pressing a response button, the correctness of the presented writing order after the sequence. He was not required to distinguish between 2-stroke reversal and 3-stroke reversal.

For a trial, a fixation cross was displayed first for 600 ms, followed by a 600 ms blank screen. Then the entire character in blue, subtending a visual angle of about 2° horizontally and 2° vertically, was displayed against a black background, allowing the participant to recognize the character before the display of strokes. After 400 ms, the strokes of the displayed character began to turn into white incrementally, stroke-by-stroke, until the character was completely filled with white strokes. The interval between strokes was 300 ms (see Fig. 1). This procedure allowed the system to activate semantic and phonological information associated with the character and its components throughout the trial. The stroke reversal introduced later on thus should not influence or be
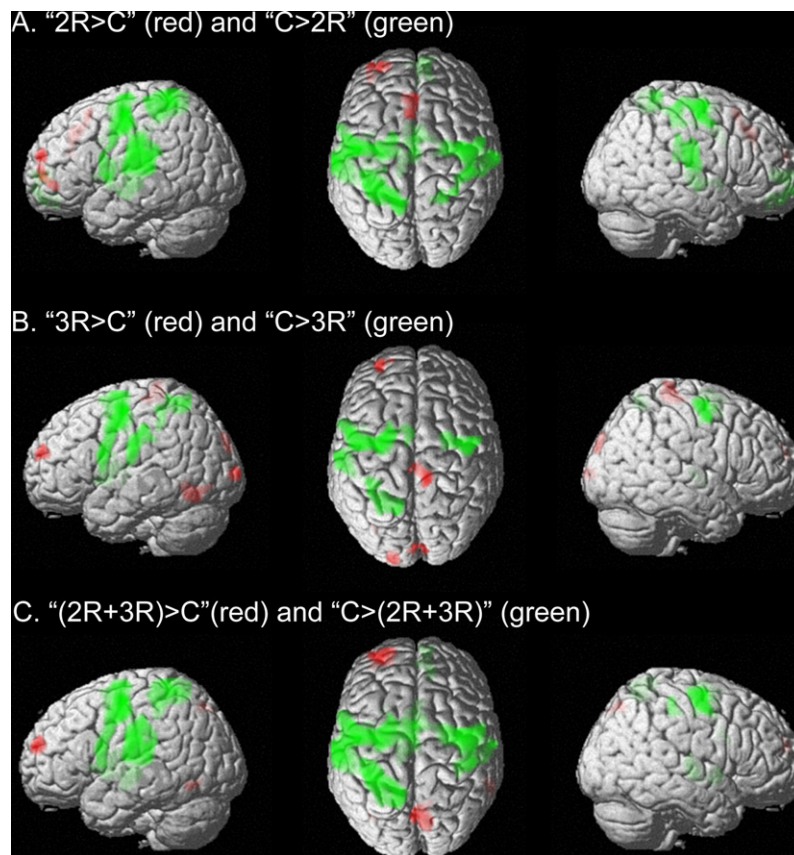

Fig. 2. The activated brain areas in different contrasts. (A) Significant clusters as revealed by "2R > C" (red) and "C > 2R" (green); (B) Significant clusters as revealed by "3R > C" (red) and "C > 3R" (green); (C) Significant clusters as revealed by "(2R + 3R) > C" (red) and "C > (2R + 3R)" (green). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

influenced by the neural activity associated with semantic and phonological processing. The character disappeared after the last stroke and participants were to judge the correctness of the sequence during a 1500 ms period. Note that, since the static configuration of the character was present throughout a trial, phonological, semantic and orthographical information associated with the character had been activated before the stroke reversal was introduced and the stroke reversal should have no impact upon the activation state of this information. For half the participants, the "yes" button was pressed by the right index finger and the "no" button by the right middle finger; for the other half, the mappings between fingers and buttons were reversed. The intertrial interval was jittered between 2000 and 6000 ms (step size: 500 ms), during which a fixation cross was displayed (but with a 200 ms blank screen at the end of the interval).

There were two functional scanning sessions, the first of which consisted of 74 trials and the second 73. Each session lasted about 13 min. A fixation was displayed at the beginning of each session for 10 s (5 volumes) to allow the scanner to reach stability. Before entering the scanner, all the participants completed a practice session consisting of 21 characters.

2.3. fMRI data acquisition and analysis

Functional images were acquired on a 3T Siemens Trio system at the Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, using a T2*-weighted echo planar imaging (EPI) sequence, with 2 s repetition time, 30 ms echo time, and 90° flip angle. Each image consisted of 28 axial slices covering the whole brain. Slice thickness was 4 mm and inter-slice distance was 1 mm, with a 20 mm field of view, 64 ∗ 64 matrix, and 3 ∗ 3 ∗ 4 mm voxel size.

Data were pre-processed with Statistical Parametric Mapping software SPM5 (Wellcome Department of Imaging Neuroscience, London, http://www.fil.ion.ucl.ac.uk). The first five volumes of each session were discarded to allow stabilization of magnetization. Images were realigned to the sixth volume of the first session for head movement. For each participant, the extent of head movements did not exceed one voxel size (2 mm ∗ 2 mm ∗ 2 mm). A temporal high-pass filter with a cutoff frequency of 1/128 Hz was used to remove low-frequency drifts in an fMRI time series. Images were segmented into different tissue classes and normalized to the MNI space (resampled to $2 * 2 * 2 \text{ mm}^3$ voxel) by matching grey
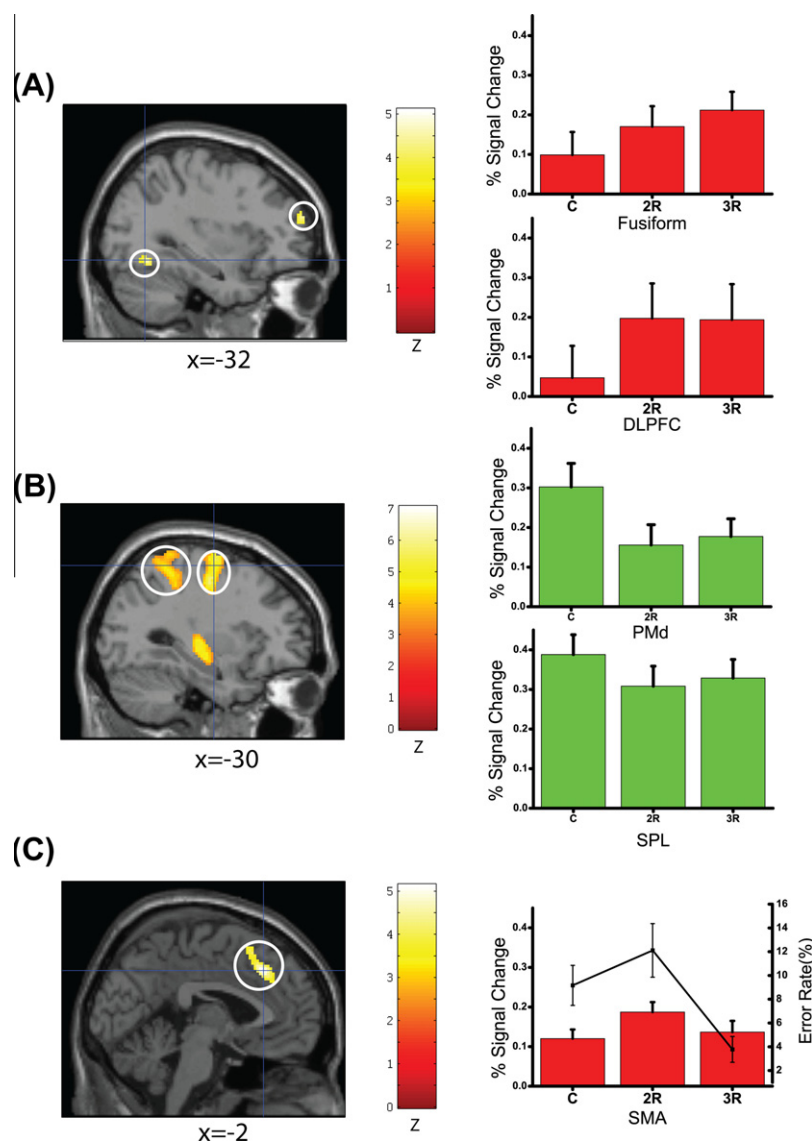

Fig. 3. Five regions of interest (left column) and their percentage signal changes (right column). (A) DLPFC and left fusiform gyrus as revealed by the contrast "(2R + 3R) > C"; (B) PMd and SPL as revealed by "C > (2R + 3R)"; (C) SMA as revealed by "2R > C". Also plotted in the last chart is the averaged error rate of three conditions (right axis). Error bar indicates standard error. DLPFC = dorsal lateral premotor cortex, PMd = dorsal premotor area, SPL = superior parietal lobule, SMA = supplementary motor area.

matter (Ashburner & Friston, 2005), and smoothed with a Gaussian kernel of 8 mm full-width half-maximum (FWHM).

Statistical analysis was based on the general linear model (GLM). The hemodynamic response to each event was modeled with a canonical hemodynamic response function (HRF) with its temporal derivative. We defined five regressors for each session: three corresponded to the correctly judged trials in the three conditions (interested regressors), one corresponded to button press and one corresponded to the incorrectly judged trials (nuisance regressors). The six rigid body parameters were also included to correct for the head motion artifact. The onset of the critical regressors was set to the appearance of the critical stroke.

To pinpoint regions significantly activated in the reversal conditions as compared with the correct condition, we first calculated the simple main effects for each of the three conditions for each participant. The three first-level individual contrast images were then fed to a flexible factorial test across participants in the second-level design matrix. We defined altogether eight contrasts: four for contrasts between conditions: "2R > C", "3R > C", "C > 2R" and "C > 3R"; four for the combined effects: "2R > C"∩"3R > C", "C > 2R"∩"C > 3R", "(2R + 3R)>C", and "C>(2R + 3R)".

3. Result

3.1. Behavioral results

One participant was excluded due to her chance-level accuracy in judging the sequence correctness. For the remaining 18 participants, the mean accuracy of judgment was 90.7% ($SD = 7.1\%$) for the correct condition, 87.8% ($SD = 9.5\%$) for the 2R condition, and 96.1% ($SD = 4.7\%$) for the 3R condition. A repeated-measures ANOVA revealed a significant main effect of condition, $F(2, 34) = 5.98$, $p < 0.01$, with the accuracy rate in the 3R condition significantly higher than those in the other two conditions ($p < 0.05$ or $p < 0.005$). Thus the 2-stroke reversal condition is the most difficult one (see Fig. 3C).

3.2. fMRI results

Table 1 and Fig. 2A and B present the significant activation foci revealed by "2R > C" and "3R > C", and the two reversed contrasts. These activation foci survived the threshold of $p < 0.001$ uncorrected at voxel level and contained more than 50 contiguous voxels. The contrast "2R > C" revealed activation in left dorsal lateral prefrontal cortex (DLPFC, or anterior superior frontal gyrus), ventrolateral prefrontal cortex (VLPFC) and pre-SMA. The contrast "3R > C" revealed activation in left DLPFC as well as in posterior areas, including left fusiform, postcentral gyrus and middle occipital gyrus (MOG). The two reversed contrasts showed very similar patterns to each other, with the most significant activations in bilateral dorsal premotor areas and left superior parietal lobule (SPL).

Since we were interested in the differential activations across experimental conditions, we adopted two independent approaches to explore the detailed activation patterns. One approach was to conduct two conjunction analyses, i.e., "2R > C"∩"3R > C" and "C > 2R"∩"C > 3R". The other approach was to collapse the two reversal conditions and to contrast it with the correct condition. We first adopted the statistical standard we described above. Under this relatively strict standard, the conjunction analysis "2R > C"∩"3R > C" yielded only one activation focus, which is in the DLPFC. Other commonalities between "2R > C" and "3R > C", such as the left fusiform activation we find in both contrasts, is lost. However, the collapsed analysis (2R + 3R) > C retained more information concerning common activation under the same standard. Therefore, we report the activation information from the collapsed approach in Table 2 and Fig. 2C.

To show more detailed information concerning the activity in regions of interest (ROIs), we computed percentage signal changes of the peak voxels in five regions and conducted ANOVA for each of them. The ROI is defined as a sphere with a radius of 3 mm, centered at the maximum coordinates of a cluster we are interested in. Fig. 3 plots the percent signal changes in these ROIs. Note that it is a common fallacy in neuroimaging study that the selection criterion (e.g., ROI selection) and the selective analysis (e.g., ROI analysis) are based on non-independent data set. This so-called "double dipping" strategy is prone to be a circular analysis and result in misleading conclusions (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009; Vul, Harris, Winkielman, & Pashler, 2009). However, we do not intend to make more inferences based on ROI analysis than what we have found in the whole brain analysis. What the ROI analysis shows here is what has already been found in the whole brain analysis, but in a clearer manner. This avoids the circularity fallacy.

All the statistical tests showed significant main effects for the different ROIs: the smallest F value was in the test for SPL, with $F(2, 34) = 4.51$, $p < 0.05$. Pairwise comparisons showed two patterns for different ROIs. On the one hand, activation in left dorsal premotor (PMd), left SPL and left DLPFC distinguished only between the reversal and the correct conditions, not between the two reversal conditions ($ps > 0.1$). On the other hand, activation in left fusiform showed a significant difference between the three conditions, $F(2, 34) = 5.44$, $p < 0.01$. Further tests showed that the percentage signal change in the 2R condition was larger than that in the correct condition ($p < 0.07$) and smaller than that in the 3R condition ($p < 0.08$). This pattern was confirmed when we used beta values for statistical purposes: the differences between the

Table 2
MNI coordinates of activation foci revealed by the contrasts between the collapsed reversal conditions and the correct condition. PMd = dorsal premotor area, SPL = superior parietal lobule, DLPFC = dorsal lateral prefrontal cortex, FG = fusiform gyrus, PCU = precuneus.

Brain region (BA)	Hemisphere	MNI coordinates			Max z-value	Voxel size
		x	y	z		
C > (2R + 3R)						
PMd (6)	L	−50	−8	46	5.50	2274
Postcentral (48)	L	−58	−18	28	5.12	1375
SPL	L	−12	−58	62	4.67	1206
PMd (6)	R	42	−10	62	4.94	783
Thalamus	R	12	−14	2	4.06	199
Postcentral (3)	R	40	−30	52	3.72	124
(2R + 3R) > C						
DLPFC (6)	L	−28	58	22	4.36	143
FG (37)	L	−32	−62	−12	3.92	50
PCU (7)	L	2	−70	50	4.36	57

2R condition and the other two conditions became even more significant ($ps < 0.05$).

4. Discussion

Compared with the correct sequence, both two types of sequence reversal activated left DLPFC, left fusiform gyrus and precuneus. Compared with either type of the reversal sequences, the correct sequences activated bilateral premotor areas and left DLPFC. Moreover, left fusiform showed a linear increase in signal over the correct, 2R and 3R conditions. In the following paragraphs, we explore the roles of these brain regions in the perception of sequence information in Chinese character writing in relation to the two questions we raised in Section 1.

We asked whether activation of the premotor–parietal network in previous studies on character or kanji writing (Katanoda et al., 2001) is specifically related to motoric components of writing or to a domain-general system for sequence processing. Given that the task used in this study was perceptual in nature, the activation of the premotor–parietal network must be related to motor control at a more abstract level. In fact we would like to suggest that the premotor–parietal network recruited in the perception of character writing is the same one recruited in general perceptual sequence processing and motor learning (Bubic et al., 2008; Schubotz & von Cramon, 2002a, 2002b, 2002c, 2003, 2004). Note that, sequential predictability of stimuli is not a necessary condition of the recruitment of the aforementioned neural circuitry underlying sequential processing. Rather, it is the subjective attempt to make serial prediction induced by task demand that drives the activity of the premotor area (Schubotz, 2004; Schubotz & von Cramon, 2002b). Nonetheless, the nature of our stimuli and the task requirement should induce the cognitive processes of serial prediction and the associated neural activity. Therefore, the findings of this study extend the generality of the "HAPEM framework" of sequence processing (Schubotz, 2007; Schubotz & von Cramon, 2003) to such situations in which the serial prediction is based on well-learned rules and sensorimotor skills, rather than newly-acquired perceptual regularity, as in the classic SPT paradigm (Bubic et al., 2008; Schubotz & von Cramon, 2002a, 2002b, 2002c, 2003, 2004). Information concerning various aspects of the external visual stimuli, including the configuration of the character and the identity of the current stroke, converges in the parietal cortex (Bubic et al., 2008).

As hypothesized, the left fusiform VWFA responded differentially to different levels of sequence reversal, indicating that it encodes dynamic information associated with Chinese character writing. The present study provided supporting evidence, perhaps for the first time, for this dynamic encoding in VWFA. In addition to orthographic processing in character recognition (Chan et al., 2009; Fu et al., 2002; Kuo et al., 2004; Liu et al., 2008), activation of VWFA has been observed in kanji writing (Nakamural et al., 2000; Nakamura et al., 2002). The latter finding was interpreted as indicating the retrieval of the representation of orthographic information stored in VWFA during writing. The current study went further to suggest that VWFA itself encodes the dynamic, sequence information associated with character writing. Here the participants saw the whole characters beforehand and needed not to write characters, but simply observed the sequential display of strokes. It is possible that a stroke reversal would negate the sequential information stored in VWFA, leading directly to the higher activation of VWFA in the reversal conditions; the more severe the reversal, the higher the activation. The finding of the early N170 effect (Qiu & Zhou, 2010) for stroke reversal can be taken to support this argument.

However, before we accept the above argument, we need to rule out an alternative interpretation suggesting that the activation pattern in VWFA is due to top-down modulation from motor and premotor areas (Kherif, Josse, & Price, 2011). Although it is not clear how the activity in PMd would modulate the activity in VWFA, we nevertheless conducted dynamic causality modeling (Friston, Harrison, & Penny, 2003) to examine the direction of the effective connectivity between VWFA and left PMd. Specifically, we tested whether the normal perceptual sequence processing could be better explained by a feedforward or a feedback model. In the feedforward model, the correct condition was assigned to enhance the effective connectivity from VWFA to PMd; in the feedback model, the correct condition was assigned to enhance the effective connectivity from PMd to VWFA. Bayesian model selection (Penny, Stephan, Mechelli, & Friston, 2004; Stephan, Penny, Daunizeau, Moran, & Friston, 2009) favored the feedforward model, with the exceedance probability for feedforward model being 85.1%, and $\alpha = 12.27$. The parameter for modulation of the connection from VWFA to PMd by correct writing order was positive and significant ($p < 0.05$, Bonferoni-corrected for multiple comparisons), indicating that it was more likely that the activity in VWFA affected the activity in PMd, rather than the other way around. Thus the differential activity in VWFA in response to different levels of reversal cannot be due to the top-down modulation from the activity in PMd.

We propose a scheme for the perception of Chinese character writing: the premotor area extracts the correct sequence information from VWFA and the current state of writing from parietal cortex to form anticipation concerning future stimulus input, i.e., the next stroke. When the next stroke is actually presented, it is compared with the anticipated one: if they match, the anticipation process continues; if they do not, anticipation is temporarily interrupted and executive control process intervenes. The DLPFC, a structure central to executive control, may act to reconstruct the correct sequence.

As can be seen from Fig. 2A, apart from the common activation of DLPFC and VWFA (Fig. 2C), the contrast "2R > C" additionally activated pre-SMA while the contrast "3R > C" additionally activated cuneus and middle occipital gyrus (MOG). The pre-SMA activation was in line with Bubic et al. (2008), which also observed this activation for sequential violations involving two adjacent items. The stroke reversal in the 2R condition was more subtle and difficult to detect than the stroke reversal in the 3R condition, as indicated by the lower accuracy in behavioral judgment. It is possible that the early visual processing system in the posterior part of the brain has to pass information concerning stroke reversal to the anterior part of the brain, where the violation is finally checked by pre-SMA (and possibly other frontal regions, see Bubic et al. (2008)). It has been found that pre-SMA is tuned to complex aspects of hierarchical processing, including sequence updating and switching (Bapi, Miyapuram, Graydon, & Doya, 2006). The activation of pre-SMA in the 2R condition may reflect the more effort devoted to detect the stroke reversal (Fig. 3C). In contrast, the 3-stroke reversal was more brutal and could be easily detected and determined by the posterior visual processing system. Attempt to construct correct representation could be carried out together with DLPFC and VWFA.

To conclude, by asking participants to observe stroke-by-stroke display of Chinese characters and by introducing different levels of stroke reversal, we found graded activation of left fusiform (VWFA), suggesting that it encodes dynamic sequence information associated with Chinese character writing. We also found activation of the premotor–parietal network when correct sequences were compared to stroke reversals, indicating a domain-general role of this network in sequence processing. These findings should be able to deepen our understanding of the mechanisms underlying Chinese character processing specifically and sequence processing in general.

Acknowledgements

References

Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *NeuroImage, 26*, 839–851.

Bapi, R. S., Miyapuram, K. P., Graydon, F. X., & Doya, K. (2006). fMRI investigation of cortical and subcortical networks in the learning of abstract and effector-specific representations of motor sequences. *NeuroImage, 32*, 714–727.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience, 11*, 235–260.

Bubic, A., von Cramon, D. Y., Jacobsen, T., Schröger, E., & Schubotz, R. I. (2008). Violation of expectation: Neural correlates reflect bases of prediction. *Journal of Cognitive Neuroscience, 21*, 155–168.

Chan, S. T., Tang, S. W., Tang, K. W., Lee, W. K., Lo, S. S., & Kwong, K. K. (2009). Hierarchical coding of characters in the ventral and dorsal visual streams of Chinese language processing. *NeuroImage, 48*, 423–435.

Cohen, L., Dehaene, S., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M. A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123*, 291–307.

Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain, 125*, 1054–1069.

Di Russo, F., Martínez, A., Sereno, M., Pitzalis, S., & Hillyard, S. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*, 95–111.

Fiebach, C. J., & Schubotz, R. I. (2006). Dynamic anticipatory processing of hierarchical sequential events: A common role for broca's area and ventral premotor cortex across domains? *Cortex, 42*, 499–502.

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society: B Biological Science, 360*, 815–836.

Friston, K., Harrison, L., & Penny, W. (2003). Dynamic causal modelling. *NeuroImage, 19*, 1273–1302.

Fu, S., Chen, Y., Smith, S., Iversen, S., & Matthews, P. M. (2002). Effects of word form on brain processing of written Chinese. *NeuroImage, 17*, 1538–1548.

James, K. H., & Atwood, T. P. (2009). The role of sensorimotor learning in the perception of letter-like forms: Tracking the causes of neural specialization for letters. *Cognitive Neuropsychology, 26*, 91–110.

Katanoda, K., Yoshikawa, K., & Sugishita, M. (2001). A functional MRI study on the neural substrates for writing. *Human Brain Mapping, 13*, 34–42.

Kherif, F., Josse, G., & Price, C. (2011). Automatic top-down processing explains common left occipito-temporal responses to visual words and objects. *Cerebral Cortex, 21*, 103–114.

Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S. F., & Baker, Chris (2009). Circular analysis in systems neuroscience: The dangers of double dipping. *Nature Neuroscience, 12*, 535–540.

Kuo, W. J., Yeh, T. C., Lee, J. R., Chen, L. F., Lee, P. L., & Chen, S. S. (2004). Orthographic and phonological processing of Chinese characters: An fMRI study. *NeuroImage, 21*, 1721–1731.

Liu, C., Zhang, W. T., Tang, Y. Y., Mai, X. Q., Chen, H. C., Tardif, T., et al. (2008). The visual word form area: Evidence from an fMRI study of implicit processing of Chinese characters. *NeuroImage, 40*, 1350–1361.

Longcamp, M., Anton, J. L., Roth, M., & Velay, J. L. (2003). Visual presentation of single letters activates a premotor area involved in writing. *Neuroimage, 19*, 1492–1500.

Longcamp, M., Anton, J. L., Roth, M., & Velay, J. L. (2005). Premotor activations in response to visually presented single letters depend on the hand used to write: A study on left-handers. *Neuropsychologia, 43*, 1801–1809.

Longcamp, M., Boucard, C., Gilhodes, J. C., Anton, J. L., Roth, M., Nazarian, B., et al. (2008). Learning through hand-or typewriting influences visual recognition of new graphic shapes: Behavioral and functional imaging evidence. *Journal of Cognitive Neuroscience, 20*, 802–815.

Maurer, U., Zevin, J. D., & McCandliss, B. D. (2008). Left-lateralized N170 effects of visual expertise in reading: Evidence from Japanese syllabic and logographic scripts. *Journal of Cognitive Neuroscience, 20*, 1878–1891.

Nakamural, K., Honda, M., Okada, T., Hanakawa, T., Toma, K., Fukuyama, H., et al. (2000). Participation of the left posterior inferior temporal cortex in writing and mental recall of kanji orthography: An functional MRI study. *Brain, 123*, 954–967.

Nakamura, K., Hongda, M., Hirano, S., Oga, T., Sawamoto, N., Hanakawa, T., et al. (2002). Modulation of the visual word retrieval system in writing: A functional MRI study on the Japanese orthographies. *Journal of Cognitive Neuroscience, 14*, 104–115.

Parkinson, J., Dyson, B. J., & Khurana, B. (2010). Line by line: The ERP correlates of stroke order priming in letters. *Experimental Brain Research, 201*, 575–586.

Penny, W. D., Stephan, K. E., Mechelli, A., & Friston, K. (2004). Comparing dynamic causal models. *NeuroImage, 22*, 1157–1172.

Qiu, Y., & Zhou, X. (2010). Perceiving the writing sequence of Chinese characters: An ERP investigation. *NeuroImage, 50*, 782–795.

Schubotz, R. I., & von Cramon, D. Y. (2002a). Predicting Perceptual Events Activates Corresponding Motor Schemes in Lateral Premotor Cortex: An fMRI Study. *NeuroImage, 15*, 787–796.

Schubotz, R. I., & von Cramon, D. Y. (2002b). A blueprint for target motion: fMRI reveals perceived sequential complexity to modulate premotor cortex. *NeuroImage, 16*, 920–935.

Schubotz, R. I., & von Cramon, D. Y. (2002c). Dynamic patterns make the premotor cortex interested in objects: Influence of stimulus and task revealed by fMRI. *Cognitive Brain Research, 14*, 357–369.

Schubotz, R. I., & von Cramon, D. Y. (2003). Functional–anatomical concepts of human premotor cortex: Evidence from fMRI and PET studies. *NeuroImage, 20*, S120–S131.

Schubotz, R. I. (2004) Human premotor cortex: Beyond motor performance. *MPI Series in Human Cognitive and Brain Sciences, vol. 50*. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences. ISBN:3-936816-23-9.

Schubotz, R. I., & von Cramon, D. Y. (2004). Sequences of abstract nonbiological stimuli share ventral premotor cortex with action observation and imagery. *The Journal of Neuroscience, 24*, 5467–5474.

Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new framework. *Trends in Cognitive Sciences, 11*, 211–218.

State Language Commission, (2000). *Standardized stroke order of modern Chinese characters (Xiandai Hanyu Tongyongzi Bishun Guifan)*. Beijing: Language Press (Yuwen Chubanshe).

Stephan, K. E., Penny, W. D., Daunizeau, J., Moran, R. J., & Friston, K. J. (2009). Bayesian model selection for group studies. *NeuroImage, 46*, 1004–1017.

Summerfield, C., & Koechlin, E. (2008). A neural representation of prior information during perceptual inference. *Neuron, 59*, 336–347.

Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. *Neuron, 55*, 143–156.

Vul, E., Harris, C., Winkielman, P., & Pashler, H. (2009). Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. *Perspectives on Psychological Science, 4*, 274–290.

Wilson, W., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin, 131*(3), 460–473.

Wolfensteller, U., Schubotz, R. I., & von Cramon, D. Y. (2007). Understanding non-biological dynamics with your own premotor system. *NeuroImage, 36*, T33–T43.

Xue, G., Chen, C., Jin, Z., & Dong, Q. (2006). Language experience shapes fusiform activation when processing a logographic artificial language: An fMRI training study. *NeuroImage, 31*, 1315–1326.

Xue, G., & Poldrack, R. A. (2007). The neural substrates of visual perceptual learning of words: Implications for the visual word form area hypothesis. *Journal of Cognitive Neuroscience, 19*, 1643–1655.

Zhou, X. L., & Marslen-Wilson, W. (1999a). The nature of sublexical processing in reading Chinese characters. *Journal of Experimental Psychology: Learning Memory and Cognition, 25*, 819–837.

Zhou, X. L., & Marslen-Wilson, W. (1999b). Phonology, orthography, and semantic activation in reading Chinese. *Journal of Memory and Language, 41*, 579–606.